



Description of the male of *Darditilla araxa* (Cresson, 1902) (Hymenoptera, Mutillidae) with geographical distribution, biological notes and key to males of Brazil

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Abstract

The previously unknown male of *Darditilla araxa* is here described based on association with females *in copula*. We also present a map with its geographical distribution, additional biological notes and a key for known Brazilian males of *Darditilla*.

Key words: velvet ants, sexual association, Savannah, Cerrado, wasp

Introduction

Mutillidae is a monophyletic group with 8 subfamilies (Brothers & Lelej 2017). Only Mutillinae and Sphaeropthalminae occur in the Neotropical region, accounting for more than 1,500 described species (Brothers & Lelej 2017; Nonveiller 1990). These are solitary aculeate wasps whose larvae act as parasitoids of encapsulated insects (Brothers 2006). This family, with a few exceptions, is characterized by extreme sexual dimorphism, where males are alate, rarely brachypterous or wingless, and females are always apterous.

Remarkable sexual dimorphism has been historically considered one of the greatest impediments to taxonomic studies on Mutillidae. Traditionally, male-female associations are described based on observations of mating couples (Bergamaschi *et al.* 2010; Luz *et al.* 2016). However, since males and females exhibit striking differences in behavior and habitat use, such observations are rarely reported (Brothers 1975). This difficulty may lead to erroneous descriptions, like males and females of different genera being associated as a single species (Pilgrim & Pitts 2006). Molecular methods, morphological similarities and overlapping distribution ranges have recently been used as alternative methods for associating sexes, resulting in synonymies in many cases (Pilgrim & Pitts 2006; Pitts *et al.* 2007; Pilgrim *et al.* 2008; Luz & Williams 2014; Cambra *et al.* 2018).

The genus *Darditilla* Casal has thirty-five species described from Brazil, Bolivia, and Argentina and was originally established based only on males of a single species, *D. botija* Casal (Brothers 2006; Nonveiller 1990). Taxonomic studies after Casal were based only on females (e.g. Fritz & Martinez 1974; Nonveiller 1990; Quintero & Cambra 2001), until Luz & Williams (2014) recently provided the first sexual associations within the genus, describing the males of four species. Herein we add to the literature by describing and illustrating the male of *D. araxa* (Cresson, 1902), providing additional photographs, a distribution map, a key to the Brazilian males, and biological notes for the studied species.

Material and methods

Specimens were collected *in copula* by BMT in an artificial sand field close to a riparian forest in a Cerrado fragment near Jardim, Mato Grosso do Sul State, Brazil (21°25'14"S; 56°23'23"W) in 31.x.2014. Jardim is located in the Prata River microbasin, which is inserted in the hydrological basin of the Paraguay River. This site is characterized by savannah, flat fields, deciduous and semideciduous Dry Forests (Ribeiro & Walter 2008; Baptista-Maria *et al.* 2009). The area is threatened by ecotourism, agriculture and cattle herding.

Morphological terminology follows Luz & Williams (2014) for consistency sake. For sculpture of the integument, we follow the glossary of Harris (1979). Voucher specimens are deposited at the Biodiversity Museum (MuBio) of the Federal University of Grande Dourados, (male: Hym-00475-M and female: Hym-00476-M).

The distribution map was built using the software DIVA-GIS. We adopted the biogeographical classification of Morrone (2014) and the shapefiles published by Löwenberg-Neto (2014). Most of the distribution data was acquired as a courtesy of Dr. Kevin A. Williams. Additional data were obtained from literature and specimens from the following museums: MZSP, UFES, DZUP, MPEG, MNRJ, MuBio, EMUS and CASC.

MZSP	Brazil, São Paulo, São Paulo, Museu de Zoologia da Universidade de São Paulo;
UFES	Brazil, Universidade Federal do Espírito Santo, Departamento de Biologia, Coleção Entomológica
DZUP	Brazil, Paraná, Curitiba, Universidade Federal do Paraná, Museu de Entomologia Pe. Jesus Santiago Moure;
MPEG	Brazil, Pará, Belem, Museu Paraense Emilio Goeldi;
MNRJ	Brazil, Rio de Janeiro, São Cristóvão, Universidade do Rio Janeiro, Museu Nacional;
MuBio	Brazil, Dourados, Mato Grosso do Sul, Universidade Federal da Grande Dourados, Museu da Biodiversidade;
EMUS	USA, Utah, Logan, Utah State University;
CASC	USA, California, San Francisco, California Academy of Sciences;

Results

Darditilla araxa (Cresson, 1902)

Mutilla araxa Cresson, 1902, Trans. Amer. Ent. Soc. 28:34, female.

Darditilla araxa: Nonveiller, 1990; 28.

Diagnosis. Male. (Figs. 1–10). Males of *D. araxa* can be recognized by the slightly triangular clypeus, with the ventral margin slightly oblique with protruded lamella (Fig. 4) and tegula convex and obovoid in dorsal view (Fig. 1). Penis valve similar to *D. amabilis*, but in *D. araxa* the preapical process is more acute and the apical tooth is shorter in relation to the process (Fig 8).

Female. (Figs. 11–15). Body length 9.8 mm. Mesosoma with a pair of silvery or yellow pubescent longitudinal stripes along the entire length of its lateral margins (Fig. 11). Metasoma with two yellow/reddish spots, segments 2–5 have lateral and medial patches of dense silvery setae that together appear to form uninterrupted stripes of silvery setae (Fig. 12, 14).

Material examined. 1♂, 1♀ *in copula*, Brazil: Mato Grosso do Sul, Jardim, Rio da Prata, 27-31/X/2014, Trad, B.M. et. al. col. (MuBio); 1♀, Brazil: Mato Grosso do Sul, Itahum, 31/X/2014, Lopez, V.M. col. (MuBio); 1♀, Brazil: Mato Grosso do Sul, Três Lagoas, (MZSP); 1♀, Brazil: Mato Grosso, Barra do Tapirapé, 28/XII/1962, Malkin, B. col. (CASC); 1♀, same locality, (MZSP); 2♀, Brazil: Mato Grosso, Chapada dos Parecis, 1-15/XII/2001, Foucart, A. col. (EMUS); 1♀, same locality, 1-15/XII/2000, same col. (EMUS); 1♀, Brazil: Mato Grosso, Diamantino, Alto Rio Arinos, X/1983, Silva, B. col. (MNRJ); 1♀, Brazil: Mato Grosso, Barra dos Bugres, XI/1983, Roppa col. (MNRJ); 1♀, Brazil: Mato Grosso, Chapada dos Guimarães, Fazenda Buriti, 16/XI/1982, Zanute, M. & Overal, W. col. (MPEG); 1♀, Brazil: Mato Grosso, Utiariti (MZSP); 1♀, Brazil: Mato Grosso, Rosario Oeste, (MZSP); 4♀, Brazil: São Paulo, Luís Antônio, Estação Ecológica de Jataí, 10/X/1999, Melo, G.A.R. col. (DZUP); 1♀, Brazil: São Paulo, Itirapira, 16/XII/1992, Azevedo, C.O. col. (UFES); 1♀, Brazil: Rondônia, Vilhena, 27/XII/1986, Elias, C. col. (DZUP); 1♀, Brazil: Minas Gerais, Uberlândia, CCPI-Cerrado, 23/X/2004, Augusto, S.C. col. (DZUP); 2♀,

Brazil: Maranhão, Mirador, Parq. Mirador, Volta do Rio, 9/XII/2009, Borges, R.C. col. (DZUP); 2♀, Brazil: Maranhão, Rt. 316, 30 km W of Caxias, 24/I/2001, Pitts, J.P. col. (EMUS); 1♀, Brazil: Maranhão, Carolina, 20/V/1956, Alvarenga, M. col. (MNRJ); 2♀, Brazil: Goiás, Campinas, XII/1936, Borgmeier & Lopes, col. (MNRJ); 2♀, Brazil: Goiás, Jataí, Faz. Aceiro, Exp. Dep. Zool., X/1962, Silva, Becker & Roppa, col. (MNRJ); 1♀, Paraguay: Cororo, Rio Ypane, XI/1979, Fritz, M.A. col. (CASC); 1♀, Paraguay: Caaguazu, XII/1979, same col. (CASC); 10♀, Paraguay: San Pedro, Rio Ypane, Cororo, Fritz, col. (EMUS); 1♀, Paraguay: Concepcion, Cororo, 25/II-1/III/1997, Garcete, B. col. (EMUS).



FIGURES 1–6. *Darditilla araxa*, male: 1. Habitus, dorsal view; 2. Habitus, lateral view; 3. Head, dorsal view; 4. Head, anterior view; 5. Metasoma, dorsal view; 6. Pygidium, T5 and T6 in dorsal view. Scale bars: 1 mm.

Description. Male. Body length 10.14 mm. *Coloration.* Body and appendages black, except tarsal segments brown apically, mandible and palps brown. Tibial spurs translucent white. Strigilis brown. Forewing and hindwing membrane infuscated at tip, wing cells less infuscated with less setae than wing tip, venation brown. Body covered with whitish setae, mesoscutum black with black setae, T6 and T7 with thick dark brown setae, bristles of tergal fringes white in T1–4 and dark brown in T5–7. *Head.* Head (except appendices) densely covered with white setae except for ventral anterior region with scattered bristles. Posterior margin transverse in dorsal view (Fig. 3). Ocellular distance $7.1 \times$ length of lateral ocellus. Occipital carina obscure. Front and gena densely micropunctate and vertex moderately punctate, when comparing to pronotum. Gena ecarinate. Antennal scrobe broadly concave to eye margin, with transverse tubercle dorsally. Clypeus densely punctate, ventral margin with protruded lamella, slightly oblique (Fig. 4). Mandibles with bidentate apex, dorsal carina gradually becoming obsolete towards apical part; edentate ventrally. *Mesosoma.* Epaulets smoothly rounded in dorsal view. Pronotum punctate and densely covered

with white setae; smooth anteriorly; lateral surface punctate. Tegula convex and obovoid in dorsal view, glabrous except for long recumbent setae anterolaterally and posteromedially (Fig. 1–2). Mesoscutum densely covered with black setae and with deep punctures when comparing to punctures in pronotum; lateral margins forming irregular pattern of reentrances undulated in lateral view; posterolateral margin forming a small angulate lobe in dorsal view. Scutellum densely covered with white setae, slightly convex dorsally, with punctures. Axilla flat and punctate, covered with white setae. Metanotum surface covered with white setae. Propodeum convex, Areolate-Rugose, with fine and sparse white setae, except smooth and shining in region adjacent to metapleuron. Lateral face of propodeum punctate, with fine minute white setae. Mesopleuron densely covered with white setae. Metapleuron mostly smooth and shiny, except for small ventral portion near metacoxa, the posterior margin and small patch on dorsal surface with fine white setae (Fig. 2). *Wings*. Forewing with elongate sclerotized pterostigma; marginal cell rounded and slightly expanded after pterostigma in dorsal view, rounded apically; three submarginal cells. *Legs*. Mid- and hind tibiae lacking strong spines, and with finely serrate spurs apically. *Metasoma*. T1 gradually broadened from base, not constricted apically, sessile with T2, $0.6 \times$ width of T2, punctate; apex with fringe of thickened white bristles. T2 punctuated and sparsely covered with setae; apex with thick fringes, parallel and recumbent; felt line $0.5 \times$ lateral length of T2. T3–7 finely pointed, with erect bristles interspersed with short bristles, except fringes with rows of bristles as in T2 (Fig. 5). T7 posterior half with oval pygidium margined laterally and posteriorly by strong sharp carina, apical margin rounded and up-curved, granulate with numerous large irregular transverse rugae (Fig. 6). In S1, punctation and setae scattered, with medial longitudinal carina extending from base to apex. S2 moderately punctate with white setae. S3–6 moderately and finely punctate, with fairly sparse erect and recumbent setae. Hypopygium transversely rectangular and coarsely punctate, posterior margin with a medial process with a small apical tooth and two lateral processes. *Genitalia* (Figs. 7–10) Paramere rounded and with long setae apically, in lateral view upcurved apically and curved medially, scattered smaller setae along inner and lateral margins. Cuspis short and pad-like, extending $\sim 0.4 \times$ free length of paramere, densely setose. Digitus truncate with convex process apically, $\sim 0.2 \times$ free length of paramere, asetose. Penis valve asetose, with apical tooth and preapical process, with basal prolongation and slight medial expansion on basoventral margin.

Distribution: *D. araxa* occurs in Brazil (São Paulo, Mato Grosso, Mato Grosso do Sul, Goiás, Maranhão, Rondônia, Minas Gerais) and Paraguay (Fig. 16).

Host: Unknown.

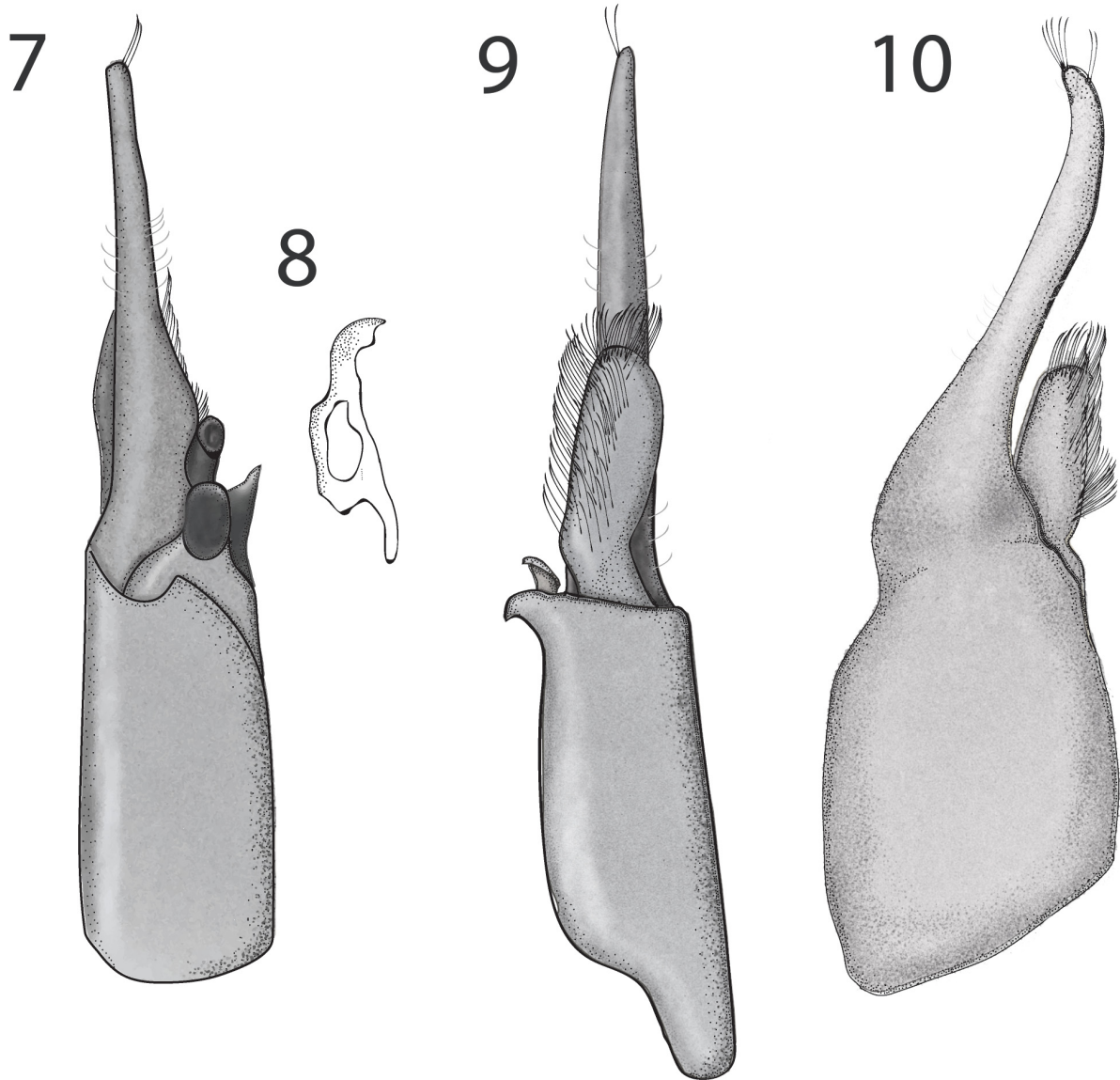
Biological notes. One female from Itahum, Mato Grosso do Sul State, Brazil ($21^{\circ}59'S$ $55^{\circ}19'W$) was observed entering a nest of the crabronid *Bicyrtes variegatus* (Oliver). The nest was excavated, but no oviposition was observed. Another female was seen digging a sandy patch, with its head down and antennating the upturned sand, but apparently it gave up searching for the host on the sand and walked towards the savannah where it was lost. Most females were observed from 8:00h to 11:00h and from 15:00h to 18:00h (hourly observations, *unpublished data*). An observable increase in female density occurs after males arrive at the sand patch where females commonly forage. Males were seen flying around the patch and approaching females to mate, which often escaped from male mating attempts. We observed mites on several body parts, and on other mutillids collected at the same site (both males and females).

Etymology. The etymology of the species name is not mentioned by Cresson (1902). However, Araxa is a Tupi-Guarani word (indigenous languages) which means “a place where you can see the world or vast horizons; highlands; plateau”, from the root “ara” (world) and “eca” (to see) (Chiradia 2018). Cresson mentions *D. araxa* was collected in Chapada, Mato Grosso State in Brazil, which is a plateau. Probably, Cresson referred to this region by using the indigenous language of the people inhabiting the site at that time. Additionally, Araxá is also a small town in Minas Gerais State in Brazil and, since “a few *Mutilla* from Minas Geraes were given to [Cresson] by [a] friend Sr. Carvalho...” (Cresson, 1902), there could be a possible relationship with this town, although Cresson recorded this species from Chapada and Corumba only.

Key to *Darditilla* males known from Brazil

- 1 Medial clypeal lobe narrower than space between antennal tubercles, entire, often obscured by punctures or setae; T2–5 fringes usually with bristle rows. 2
- Medial clypeal lobe broader than space between antennal tubercles, medially depressed, laterally smooth and shelf-like; T2–4 fringes with bristle rows, T5 setae usually simple, dark (see figure 1E in Luz & Williams, 2014) 4

- 2 Clypeus mostly punctate with short transverse carina 3
 - Clypeus with broadly lamellar ventral margin, mostly smooth and hyaline (see fig. 7D in Luz & Williams, 2014) - **Atlantic Rainforest in Brazil and Paraguay** - *D. felina* (Burmeister)
 3 Tegula truncated in lateral view, with flat posterior face (see figure 3B in Luz & Williams, 2014); penis valve with widely separated teeth (see figure 15 in Luz & Williams, 2014) - **Atlantic Rainforest in Brazil and Argentina**-
 *D. bejaronoi* Casal
 - Tegula convex and not truncated (see figure 5B in Luz & Williams, 2014); penis valve with coalescent teeth (see figure 19 in Luz & Williams, 2014) - **Forests and grasslands in Brazil, Argentina, Paraguay and Uruguay** -
 *D. debilis* (Gerstaecker)
 4 Transverse clypeus and with subapical brush of golden setae (see fig. 1D in Luz & Williams, 2014) - **Argentina, Uruguay and Rio Grande do Sul, mainly in grasslands** - *D. amabilis* (Gerstaecker)
 - Clypeus slightly triangular, with scopa densely covered by white bristles (Fig.4) (CAUTION: bristles may be broken) - **Brazil and Paraguay, mainly in Cerrado** *D. araxa* (Cresson)



FIGURES 7–10. *Darditilla araxa*, male genitalia: 7. Dorsal view; 8. Penis valve, lateral view; 9. Ventral view; 10. Lateral view with penis valve removed.

Discussion

Of the 35 recognized *Darditilla*, nine species and one more morphotype are known from Brazil. They are: *D. amabilis* (Gerstaecker), *D. araxa*, *D. bejaronoi* Casal, *D. debilis* (Gerstaecker), *D. felina* (Burmeister), *D. juazeira* Casal,

D. mita Casal, *D. tornela* Casal, and *D. vianai* Casal (Luz & Williams 2014; Luz *et al.* 2017; Luz & Bartholomay 2018); now, five of these have both sexes associated. It is interesting to note that morphologically the males seem to form apparent groups. For example, (*D. araxa* + *D. amabilis*) and (*D. debilis* + *D. bejaronoi*) are similar within pairs that are easily differentiated by the clypeus (Luz & Williams 2014).



FIGURES 11–15. *Darditilla araxa*, female: 11. Habitus, dorsal view; 12. Habitus, lateral view; 13. Head, frontal view; 14. Metasoma, dorsal view; 15. Pygidium and T5, posterodorsal view. Scale bars: 1 mm.

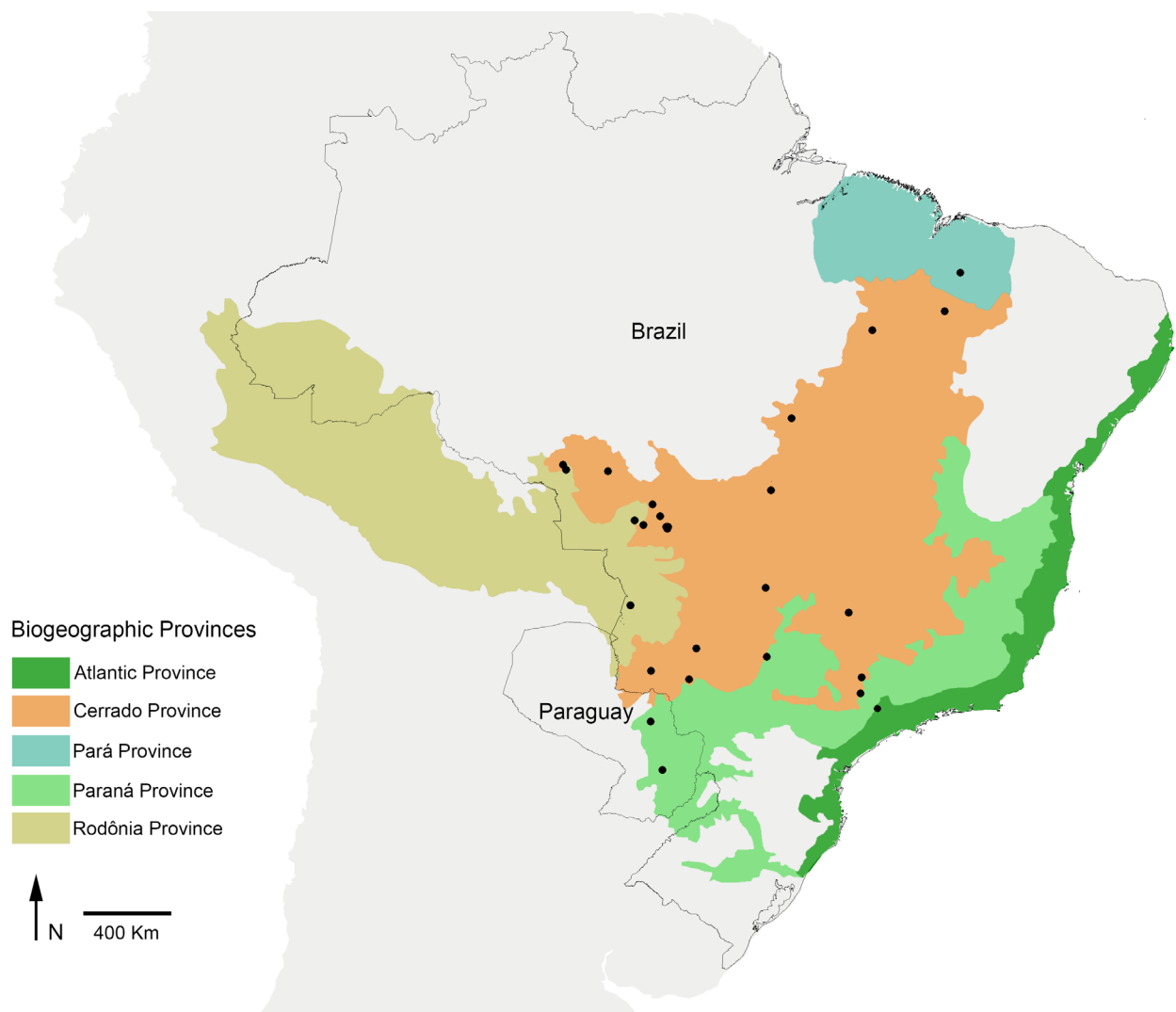


FIGURE 16. Map of South America, with emphasis on the biogeographical provinces where *Darditilla araxa* occurs.

Investigating the morphology of the species known from both sexes, we can see a correlation between clypeal characteristics of the male and T2 pattern of the female (Kevin Williams, personal communication). When the female shows setal spots on T2, the male has a weak and simple clypeus (e.g., *D. debilis*). When the female has cuticular spots on T2, then the male has an expanded shelf on the clypeus (e.g., *D. felina*). Based on the premise that this pattern will be repeated in other species of the group, the male of *D. juazeira* will probably be similar to the males of *D. debilis* / *D. bejaronoi* and the male of *D. vianai* will be similar to the males of *D. amabilis* / *D. felina* / *D. araxa*, since the females of *D. juazeira* present setal markings on T2 and females of *D. vianai* spots on T2.

Darditilla araxa was not included in the only functional key for *Darditilla* females (see Casal, 1968). However, *D. tornela* and *D. usta* are present in the key and are morphologically similar to *D. araxa*, apparently differing only in coloration, specifically in the T2 spot shape and whitish setal bands of the vertex and front. Taking into account the key proposed by Casal (1968), *D. araxa* would key out to couplet nine. It can be separated from *D. tornela* because the spots of T2 are subcircular in *D. araxa*, but transversely subovate in *D. tornela*. It can be separated from *D. usta* because it has yellow integumental circular spots on T2, compared to the reddish spots of *D. usta*. In addition, *D. usta* has the vertex with totally black setae, while *D. araxa* has white setal bands (Fig. 11).

Studies on the relationship and the delimitation between these three species would be useful, since males of *D. usta* and *D. tornela* are likely similar to the males of *D. araxa*. There is also a good chance that *D. tornela* and *D. usta* could be synonymous with *D. araxa*, given the subjective nature of the diagnostic traits to separate these species (Kevin Williams, personal communication). Finding the males of *D. tornela* and *D. usta* would permit a more robust taxonomic hypothesis.

Darditilla araxa occurs mainly in the Neotropical Savannah and its distribution coincides with the open/dry biomes of South America, or “dry diagonal” (Figure 16). The “dry diagonal” is characterized by regions with seasonal climates that present water restrictions for part of the year and includes the provinces of Caatinga, Cerrado and Chaco (Zanella, 2011). If the hypothesis that *D. tornela* and *D. usta* are synonymous with *D. araxa* is correct, this species may be a good model to study the biogeographic evolutionary history of “dry diagonal” taxa, as *D. tornela* occurs in Caatinga, *D. araxa* is common in Cerrado, and *D. usta* belongs to the biogeographic province of Chaco. This is an interesting scenario, since groups of Mutillidae have been suggested as good model organisms for biogeographic research (Pitts *et al.* 2010; Wilson & Pitts 2010, 2011, 2012; Wilson *et al.* 2012).

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References

- Baptista-Maria, V.R., Rodrigues, R.R., Damasceno Junior, G., Maria, F.D.S. & Souza, V.C. (2009) Floristic composition of seasonal riparian forests in Mato Grosso do Sul state, Brazil. *Acta Botanica Brasilica*, 23 (2), 535–548.
<https://doi.org/10.1590/S0102-33062009000200025>
- Bergamaschi, A.C., Cambra, R. & Melo, G.A. (2010) Male description and host record for *Lophomutilla corupa* Casal, 1968 (Hymenoptera: Mutillidae), with behavioural notes on mating behaviour and host nest attacks. *Journal of Natural History*, 44 (43–44), 2597–2607.
<https://doi.org/10.1080/00222933.2010.499574>
- Brothers, D.J. (1975) Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *University of Kansas Sciences Bulletin*, 50, 483–648.
- Brothers, D.J. (2006) Familia Mutillidae. In: Fernandez, F. & Sharkey, M.J. (Eds.), *Introducción a los Hymenoptera de la Región Neotropical*. Sociedad Colombiana de Entomología & Universidad Nacional de Colombia, Bogotá D.C., pp. 577–594.
- Brothers, D.J. & Lelej, A.S. (2017) Phylogeny and higher classification of Mutillidae (Hymenoptera) based on morphological reanalyses. *Journal of Hymenoptera Research*, 60, 1–97.
<https://doi.org/10.3897/jhr.60.20091>
- Cambra, T., Roberto, A., Williams, K.A., Quintero, D., Windsor, D.M., Pickering, J. & Saavedra, D. (2018) *Dasymutilla* Ashmead (Hymenoptera, Mutillidae) from Panama: new species, sex associations and seasonal flight activity. *Insecta Mundi*, 0608, 1–17.
- Casal, O.H. (1968) Aportaciones para el conocimiento de las Mutillidae de la Republica Argentina. I. – Las hembras del genero *Darditilla* (Hymenoptera). *Revista de la Sociedad Entomológica Argentina*, 30 (1–4), 83–96.
- Chiradia, C. Dicionário Tupi Guarani. Available from: <https://www.dicionariotupiguarani.com.br/dicionario/araxa> (accessed 13 January 2018)
- Cresson, E.T. (1902) Descriptions of some *Mutilla* from Brazil. *Transactions of the American Entomological Society*, 28 (1), 1–82.
- Fritz, M.A. & Martínez, A. (1974) Notas sobre Mutillidae, II. (Hymenoptera). *Studia Entomologica*, 17 (1–4), 313–316.
- Harris, R.A. (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology Sacramento*, (28), 1–31.
- Luz, D., Waldren, G.C. & Melo, G.A. (2016) Bees as hosts of mutillid wasps in the Neotropical region (Hymenoptera, Apidae, Mutillidae). *Revista Brasileira de Entomologia*, 60 (4), 302–307.
<https://doi.org/10.1016/j.rbe.2016.06.001>
- Luz, D.R. & Bartholomay, P.R. (2018) Mutillidae in Catálogo Taxonômico da Fauna do Brasil. PNUD. Available from: <http://fauna.jbrj.gov.br/fauna/faunadobrasil/13429> (accessed 12 Set 2018)
- Luz, D.R. & Williams, K.A. (2014) The first sexual associations in the genus *Darditilla* Casal, 1965 (Hymenoptera, Mutillidae). *ZooKeys*, 454, 41–68.
<https://doi.org/10.3897/zookeys.454.8558>
- Löwenberg-Neto, P. (2014) Neotropical region: a shapefile of Morrone’s (2014) biogeographical regionalisation. *Zootaxa*, 3802 (2), 300.

- <https://doi.org/10.11646/zootaxa.3802.2.12>
- Morrone, J.J. (2014) Biogeographical regionalisation of the Neotropical region. *Zootaxa*, 3782 (1), 1–110.
<https://doi.org/10.11646/zootaxa.4239.1.1>
- Nonveiller, G. (1990) *Catalogue of the Mutillidae, Myrmosidae and Bradynobaenidae of the Neotropical Region including Mexico (Insecta, Hymenoptera). Hymenopterorum Catalogus. Nova Editio. Vol. 18.* SPB Academic Publishing, Den Haag, 150 pp.
- Pilgrim, E.M. & Pitts, J.P. (2006) A molecular method for associating the dimorphic sexes of velvet ants (Hymenoptera: Mutillidae). *Journal of Kansas Entomology*, 79 (3), 222–230.
<https://doi.org/10.2317/0511.09.1>
- Pilgrim, E.M., Williams, K.A. & Pitts, J.P. (2008) Sex association and synonymy in Southwestern U.S. species of *Dasymutilla* (Hymenoptera: Mutillidae). *The Pan-Pacific Entomologist*, 84 (1), 57–68.
<https://doi.org/10.3956/2007-13.1>
- Pitts, J.P., Boud, T.J. & Pilgrim, E.M. (2007) Molecular sex associations of three species of nocturnal velvet ant (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society*, 80 (2), 136–145.
[https://doi.org/10.2317/0022-8567\(2007\)80\[136:MSAOTS\]2.0.CO;2](https://doi.org/10.2317/0022-8567(2007)80[136:MSAOTS]2.0.CO;2)
- Pitts, J.P., Wilson, J.S. & Von Dohlen, C.D. (2010) Evolution of the nocturnal Nearctic Sphaerophthalminae velvet ants (Hymenoptera: Mutillidae) driven by Neogene Orogeny and Pleistocene Glaciation. *Molecular Phylogenetics and Evolution*, 56 (1), 134–145.
<https://doi.org/10.1016/j.ympev.2010.03.033>
- Quintero, D. & Cambra, R.A. (2001) On the identity of *Scaptopoda* F. Lynch Arribálzaga, new taxonomic changes and new distribution records for Neotropical Mutillidae (Hymenoptera), with notes on their biology. *Transactions of the American Entomological Society*, 127 (3), 291–304.
- Ribeiro, J.F. & Walter, B.M.T. (2008) As principais fitofisionomias do bioma cerrado In: Sano, S.M., Almeida, S.P. & Ribeiro, J.F. (Eds.), *Cerrado: Ecologia e flora*. Embrapa Informação Tecnológica, Brasília, pp. 421–1279.
- Wilson, J.S. & Pitts, J.P. (2010) Pleistocene diversification of the *Odontophotopsis unicornis* species-group (Hymenoptera: Mutillidae). *Annals of the Entomological Society of America*, 103 (4), 555–565.
<https://doi.org/10.1603/AN09177>
- Wilson, J.S. & Pitts, J.P. (2011) Pleistocene connection between the Nearctic Mediterranean and desert regions in the *Sphaerophthalma unicolor* species-complex (Hymenoptera: Mutillidae). *Insect Conservation and Diversity*, 4 (3), 222–234.
<https://doi.org/10.1111/j.1752-4598.2010.00124.x>
- Wilson, J.S. & Pitts, J.P. (2012) Identifying Pleistocene refugia in North American cold deserts using phylogeographic analyses and ecological niche modeling. *Diversity and Distributions*, 18 (11), 1139–1152.
<https://doi.org/10.1111/j.1472-4642.2012.00902.x>
- Wilson, J.S., Clark, S.L., Williams, K.A. & Pitts, J.P. (2012) Historical biogeography of the arid-adapted velvet ant *Sphaerophthalma arota* (Hymenoptera: Mutillidae) reveals cryptic species. *Journal of Biogeography*, 39 (2), 336–352.
<https://doi.org/10.1111/j.1365-2699.2011.02580.x>
- Zanella, F.C.V. (2011) Evolução da biota da diagonal de formações abertas secas da América do Sul. In: Carvalho, C.J. & Almeida, E.B. (Eds.), *Biogeografia da América do Sul: padrões e processos*. Editora Roca, São Paulo, pp. 198–220.