Deelemanian ant mimicry: on the natural history and new records of *Tapixaua callida* Bonaldo, 2000 (Araneae, Corinnidae, Corinninae)

Mimetismo deelemaniano de formigas: sobre a história natural e novos registros de *Tapixaua callida* Bonaldo, 2000 (Araneae, Corinnidae, Corinninae)

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Abstract: The genus *Tapixaua* Bonaldo, 2000 is known only by a single species, *Tapixaua callida* described by Bonaldo in 2000 from Brazil and Peru. The species can be easily recognized by having abundant modified hairs on the apex of the femora, patellae, and tibiae of leg I, a condition previously suggested as instrumental in simulating the cephalic tagma of ants. Herein, we expanded the knowledge on the geographical distribution of the taxon from Huánuco (Peru), and Amazonas and Mato Grosso (Brazil), to Loreto (Peru) and Caquetá (Colombia), to the north, and to the states of Pará and Maranhão, Brazil, to the east, and provided a distribution map with all the records of *T. callida* obtained so far. Additionally, data on its natural history based on observations, photographs, and videos are presented. The ant-mimiking solution presented by this species, by combining morphological and behavioral elements to trigger resemblance with ants 'as needed,' was previously reported only for the South Asian *Pranburia mahannopi* Deeleman-Reinhold, 1993 and is here named Deelemanian mimicry.

Keywords: Neotropical region. Ant-mimicry spiders. Dionycha. New records.

Resumo: *Tapixaua callida* é a única espécie conhecida do gênero, descrita por Bonaldo em 2000 no Brasil e Peru. Esta espécie é facilmente reconhecida pela presença de pelos modificados no ápice dos fêmures, patelas e tíbias das pernas I, uma condição previamente sugerida como instrumental para simular o tagma cefálico de formigas. Aqui, estendemos o conhecimento da distribuição geográfica do táxon ao norte de Huánuco (Peru), Amazonas e Mato Grosso (Brasil) para Loreto (Peru), Caquetá (Colômbia) e, ao leste, para os estados do Pará e Maranhão (Brasil). Fornecemos um mapa com todos os registros de *T. callida* obtidos até o momento. Além disso, apresentamos, pela primeira vez, dados sobre sua história natural com base em observações, fotografias e vídeos. A solução de mimetismo de formigas apresentada por essa espécie, combinando elementos morfológicos e comportamentais para desencadear a semelhança com as formigas 'quando necessário', foi relatada anteriormente apenas para *Pranburia mahannopi* Deeleman-Reinhold, 1993, do sul da Ásia, e é aqui denominada mimetismo deelemaniano.

Palavras-chave: Região Neotropical. Mirmecomorfia. Dionycha. Novos registros.

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INTRODUCTION

The morphological and behavioral resemblance to ants, known as myrmecomorphy, is common among spiders and is present in at least 15 families (Cushing, 1997, 2012; Pekár, 2014). Myrmecomorphic species can be classified into imprecise mimics, which often exhibit coloration similar to the model ant as a myrmecomorphic trait, and precise mimics, which resemble ants in aspects such as size, shape, and behavior (Cushing, 2012; Haddad, 2013; Pekár et al., 2022).

Several spiders' groups of the family Corinnidae Karsch, 1880 are known for their association with ants (Bonaldo, 2000; Deeleman-Reinhold, 2001; Candiani & Bonaldo, 2017; Bonaldo et al., 2018; García & Bonaldo, 2023). This phenomenon is more frequent in taxa of the subfamily Castianeirinae Reiskind, 1969, which exhibit mimicry in varying degrees of precision. For example, imprecise mimics include several Nearctic species of Castianeira Keyserling (Reiskind, 1969, 1974). In contrast, precise mimics include species presenting constrictions on the cephalothorax simulating an extra tagma such as in Sphecotypus niger (Perty, 1833) and Myrmecium ricetti Candiani & Bonaldo, 2017 (Reiskind, 1969; Candiani & Bonaldo, 2017), abdominal modifications such as constrictions, pedicel collars or spine-like hairs, as in Mazax O. Pickard-Cambridge, 1898 (Leister & Miller, 2014; Candiani & Bonaldo, 2017; Silva-Junior et al., 2024), and tufts of hairs on the femora I, simulating the cephalic tagma of ants, as in Pranburia mahannopi Deeleman-Reinhold, 1993 (Deeleman-Reinhold, 2001) (Figure 3B). In the subfamily Corinninae, which representatives present a more conservative body morphology, myrmecomorphic species are less common. There are more records of myrmecophilous and myrmecophagous behavior, such as species in the genera Falconina Brignoli, 1985, Attacobius Mello-Leitão, 1925 and Ecitocobius Bonaldo & Brescovit, 1998 (Bonaldo et al., 2018; Mendonça et al., 2019; García & Bonaldo, 2023; Ibarra-Núñez & Marín,

2024). However, *Tapixaua callida* Bonaldo, 2000 is the only known myrmecomorphic species in this subfamily (Figures 1, 2A-2B, 3A).

The genus Tapixaua was proposed by Bonaldo (2000) to include a single species, T. callida based on males and females from Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil (the type locality), Diamantino, Mato Grosso, Brazil and Estacion Biologica Panguana, Huanuco, Peru. T. callida is easily distinguished from other Corinninae genera by presenting a series of unique characteristics. The palpus of the male has the subtegulum divided into two independent parts: a proximal 'T'-shaped part (STp) and a distal part (STd), visible in the expanded bulb, which has a large curved conical process that accompanies the retrolateral margin of the tegulum in the unexpanded bulb (SPT) (Figures 4D-4E). Additional conspicuous features, likely related to myrmecophily, include an abruptly lowered carapace in the posterior region, a high clypeus, and the presence of spatulate hairs at the apex of the femora and on the patellae and tibiae of the first pair of legs (See figures 288-289 in Bonaldo, 2000; Figures 4A-4H). The name of the genus refers to these modified hairs and stands for 'broom' in the Tupi language (Bonaldo, 2000). Bonaldo (2000) suggested that these hairs may play a role in ant mimicry, similar to that described for Pranburia Deeleman-Reinhold (Corinnidae, Castianeirinae) by Deeleman-Reinhold (1993), where the simulation of the cephalic tagma is produced by the cluster of hairs formed by the junction of the femora in front of the cephalothorax (Figure 3A-3B).

To date, the only available information on *Tapixaua* is from its original description. In this paper, we provide new geographical records of *T. callida* from Brazil, Peru, and Colombia. Besides, we include new data on its natural history, supported by photographic and video records which corroborate Bonaldo's (2000) hypothesis on the role of the modified hairs in *Tapixaua*. Finally, we discuss the evolutionary convergence of its morphology with that of *Pranburia mahannopi*.



Figure 1. Tapixaua callida, juvenile from Paragominas, Pará state, Brazil. Photo: César Favacho (2019).

MATERIAL AND METHODS

The material examined of the new records is deposited in the following institutions (acronyms and curators in parentheses): Museu Paraense Emílio Goeldi, Belém (MPEG, A. Bonaldo, Brazil); Museo de Historia Natural, Universidad Nacional de San Marcos, Lima (MUSM, D. Silva, Peru); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP, R. Pinto da Rocha, Brazil) and Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN, E. Florez, Colombia).

Specimens were examined in 80% alcohol with a Leica MZ16 stereomicroscope. Morphological terms

follow Bonaldo (2000) and Ramírez (2014). The multifocal images were taken using a DFC420 camera attached to a Leica M205A stereomicroscope and compiled with Leica Application Suite. The resulting images and plates were edited and prepared using Adobe Photoshop 2020. Geographical coordinates were obtained from the vial labels, when available. If not, approximate coordinates, marked in [square brackets], were obtained from Google Maps. Antmimicry: for the analysis of ant similarity, we considered all available ants collected together with the individuals. The similarity was analyzed based on a qualitative assessment according to the criteria of Perger and Rubio (2020).

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Figure 2. *Tapixaua callida*, juvenile from Paragominas, Pará state, Brazil: A) specimen mimicking an ant's head with the scopulas of the leg I; B) live specimen, detail; C) specimen (yellow arrow) walking in the retreat (delimited by yellow pointed line); D) tree trunk where the specimen was collected, yellow circle indicates where the spider was found. Photos: César Favacho (2020).



Figure 3. A-B) Living specimens of *Tapixaua callida* Bonaldo, 2000 and *Pranburia mahannopi* Deeleman-Reinhold, 1993: A) *Tapixaua callida* (MPEG), from Paragominas, Brazil, juvenile, photo by C. Favacho (2019); B) *Pranburia mahannopi* (not collected), from Angkor Wat, Cambodia, female, photo by A. Anker (2013). C-D) Ant of the genus *Camponotus* aff. *fastigatus* (MZSP 44994) collected alongside a male of *T. callida* in Abunã Porto Velho, state of Rondônia, Brazil. Possible model of mimicry: C) dorsal view; D) lateral view. Scale bar = 1 mm.

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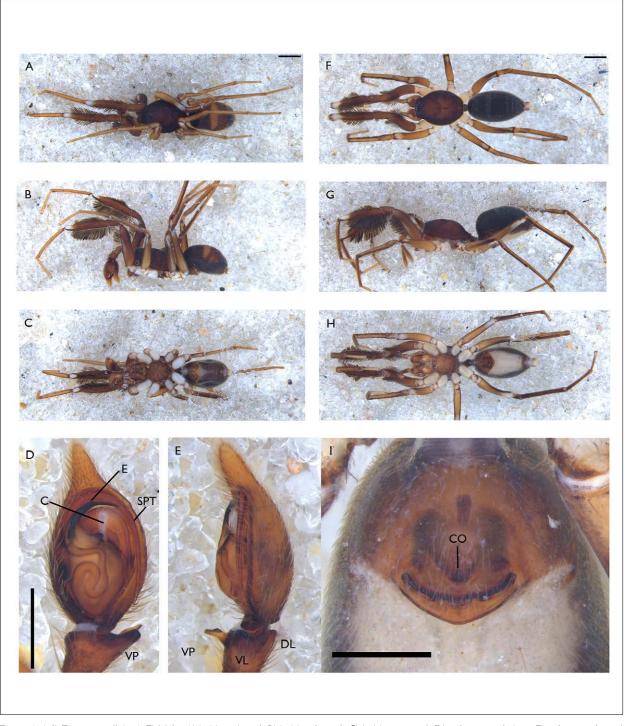


Figure 4. A-I) *Tapixaua callida*. A-E) Male: A) habitus dorsal; B) habitus lateral; C) habitus ventral; D) palp, ventral view; E) palp, retrolateral view; F-I. Female: F) habitus dorsal; G) habitus lateral; H) habitus ventral; I) epigynum, ventral view. Abbreviations: E = embolus; C = conductor; SPT = subtegular process of *Tapixaua*; VP = ventral process of the retrolateral tibial apophysis; DL = dorsal lobe of the retrolateral tibial apophysis; VL = ventral lobe of the retrolateral tibial apophysis; CO = copulatory opening. Scale bar = 1 mm.

RESULTS

So far, *T. callida* was only known from Central Amazonia (Reserva Florestal Adolpho Ducke, Manaus, state of Amazonas, Brazil; type locality), central west of Brazil (Alto Rio Arinos, Diamantino, state of Mato Grosso) and a single locality in Peru (Estación Biológica Panguana, Huánuco) (Bonaldo, 2000). With the new records presented in this paper, we expand the distribution range of the species to the west (Peru and Colombia) and to the east (states of Pará and Maranhão in Brazil). These records depict a pan-Amazon distribution for this species (Figure 5).

NEW RECORDS

The new records refer to three males, two females, and two juveniles collected in five different locations in Brazil. Peru, and Colombia (Figure 5), as follows: BRAZIL: Rondônia, Porto Velho, Abunã, 1 male, 1 ant of the genus *Camponotus,* 19.XI.2011, [9° 41' 52.6" S, 65° 21' 43.8" W], D.F. Candiani leg., sampled at night (MZSP 44994); Pará, Belém, Parque Estadual do Utinga, 1 female, 23.II.2011, 1° 25' 13.24" S, 48° 26' 21.67" W, E.L.S. Costa leg., beating tray (MPEG 39677); Paragominas, 1 juvenile, 20.III.2019, 3° 15' 02.3" S, 47° 45' 46.8" W, C. Favacho leg. (MPEG 39678); 1 juvenile, 21.I.2020, 3° 14' 22.6" S, 47° 47' 00.9" W, C. Favacho leg. (MPEG - lost); 1 male, 03-18.VI.2019, 03° 12' 56.3" S, 47° 43' 08.9" W, R. Silva e equipe, Malaise trap (MPEG 40146); Maranhão, Mirinzal, 1 female, 12. VIII. 2011, [2° 04' 06.6" S, 44° 48' 01.3" W], E.L.S. Costa leg. (MPEG 39676); COLOMBIA: Caquetá, Florencia, Centro de Investigaciones Macagual, 1 male, 23.IX.2016, 1° 30' 3.99" N, 75° 36' 22.86" W, beating tray, (ICN); PERU: Loreto, Río Samiria, Cocha Shinguito, 1 female, 1 subadult male, 1 ant of the genus Azteca, V-VI.1990, [5° 10' 00.0" S, 74° 39' 00.0" W], T. Erwin & D. Silva leg. (MUSM); BOLIVIA: Beni, Vaca Diez, 525ft: 2 km NW Tumichucua, 1 male, [1° 08' 45.6" S, 66° 09' 55.1" W] (FMNHINS 055001). The male specimen from Bolivia



Figure 5. Geographical distribution of *Tapixaua callida* Bonaldo, 2000. Records from published sources and museum collections; the yellow circle denotes the type locality. Area highlighted in darker green represents the Amazon region. Map: Fabián García (2024).

was recorded in GBIF (Grant et al., 2025) and after we received photos of the specimen, we could confirm that it is *Tapixaua callida*.

NATURAL HISTORY

On two separate occasions in 2019 and 2020, two juvenile spiders in a fragment of Terra Firme Forest were observed by C.F in the municipality of Paragominas, Pará, Brazil (Figures 1, 2, and 3A). These observations, which lasted between 20 and 30 minutes, are detailed below:

On March 20, 2019, around 2:30 PM, the first spider was found on the stem of a small tree near the entrance of a forest trail (Figure 2D). The spider was walking with short pauses, in a manner very similar to the movement of a similarly sized ant of the genus *Camponotus* Mayr, 1861 (see video in supplementary material)¹. When it stopped, it extended its front legs forward, moving its tarsi independently to mimic the antennae of an ant, while the modified hairs on its tibia remained static, resembling the ant's head (Figure 2A). The specimen was collected, but it did not survive to adulthood in captivity.

¹ Link for the video: https://www.youtube.com/watch?v=O4iSL7sWYRA

On January 21, 2020, at approximately 10:30 AM, the second spider was observed walking on one of the tabular roots of a large tree. It was circling a small retreat built into the root wall, about 60 cm above the ground. The retreat was elliptical, about 15 mm long and 10 mm wide, constructed with silk and covered in debris (Figure 2C). After entering the retreat, the spider turned to face the entrance, with the tips of its front tarsi visible. During the observation, the spider repeatedly entered and exited the retreat, briefly patrolling the surrounding area before retreating back inside. The same mimetic behavior as in the previous encounter was observed several times. The specimen was collected but, like the first, it did not survive in captivity until adulthood. It remains to be confirmed whether adult spiders exhibit the same retreat-building behavior.

SEX FORMS ASSOCIATION

Bonaldo (2000) when describing *T. callida* highlighted that the association between males and females of this species needed to be confirmed since they were collected in distant localities. In the original description, the males were found in a single locality in central Amazonia (Reserva Florestal Adolpho Ducke, Manaus, Brazil), while the only female in the type material was collected much further south, more than 1,200 km apart (Alto Rio Arinos, Diamantino, Mato Grosso, Brazil).

We also did not record males and females collected from the same locality in the examined material. However, in the material examined from Rondônia, Brazil (MZSP 44994), a sub-adult male was found alongside an adult female. The shortest distance between the locations of adult males and females was 489.27 km, as observed in the Peruvian specimens. Despite this, no morphological differences were observed in the specimens examined compared to the literature data, and the somatic characters matched flawlessly between males and females. To further validate our findings, it would be interesting to conduct barcoding in the future to confirm that the females are indeed of the same species as the males. This genetic analysis would provide additional evidence to support our hypothesis and address any remaining uncertainties regarding the species' distribution and identification.

Coincidentally, the Asian species *Pranburia mahannopi*, which has a similar morphology to *T. callida*, is also known from males and females collected in different locations. In this case, the males and females were collected more than 1,000 km apart. Cushing (2012) mentions that mimics must be rarer than models for Batesian mimicry to be favored. The presence of only a few individuals (or just one in this case) can be explained by the individual's behavior of mimicry, which involves avoiding other mimics of the same species as a protective strategy. This is a possible explanation for why so few individuals of both *T. callida* and *P. mahannopi* are found and why they are so distant located from each other.

DISCUSSION

ANT MIMICRY

In one of the new records (MZSP 44994), one specimen of *Camponotus* aff. *fastigatus*, Roger, 1863 (Hymenoptera, Formicidae) (Figures 3C-3D) was collected alongside a male of *T. callida*. Besides the similar coloration (brownishdark carapace and light brown legs), certain morphological characters such as a subglobose abdomen and truncated carapace suggest mimicry of ants from the Camponotini or Dolichoderini tribe (Perger & Rubio, 2020). The field of modified hairs on the first leg, from femur to tibia, may allude to the darker head of this ant, while the lighter metatarsi and tarsi could resemble the model's antennae.

Several Castianeirinae mimics use ants of the genus *Camponotus* as models, such as *Myrmecotypus* O. Pickard-Cambridge, 1894, and *Myrmecium* Latreille, 1824 (Oliveira, 1988; Rubio et al., 2013; Perger & Rubio, 2020). Although the mimic and model have not yet been observed together in situ, here we provide the first evidence of a likely model for *T. callida*.

EVOLUTIONARY CONVERGENCE

Convergent evolution can be understood as the independent evolution of some type of similarity between two taxa that did not arise from common ancestry (Arbuckle & Speed, 2016). Several myrmecomorphic species of spiders can be considered as good models of convergent evolution concerning their body modifications for mimicry.

Both *Tapixaua callida* and *Pranburia mahannopi* seem to have diurnal habits, that exhibit a strikingly similar solution for Batesian mimicry, which is unique by combining morphological and behavioral elements to trigger resemblance with ants 'as needed,' without the constraints of a fixed morphology. Bringing the first pair of legs together and so joining the tufts of tibial modified hairs, provides the necessary volume to produce, the resemblance of an ant head, while the more distal segments, with light colored bases, produces the resemblance with the ant antennae (Figures 3A-3B) (Deeleman-Reinhold, 1993, 2001; Bonaldo, 2000). If we consider both these behavioral and morphological traits as adaptations to ant mimicry, both species can be considered as precise mimics (Haddad, 2013; Pekár et al., 2022).

Despite these similarities, that these characteristics arose independently in these two species is undisputable, since they are phylogenetically distant one from another. Pranburia mahannopi shares with other castianeirines the pear-shaped tegulum, a contorted apical embolus and the absence of a conductor (Deeleman-Reinhold, 1993, 2001; Zhang & Jin, 2018). On the other hand, T. callida shares with other corinnines the presence of a conductor (Figure 4D) and a double spiral spermophore meander in the tegulum, with ventral folds oriented axially, resembling a double-branched Fermat's spiral (Bonaldo, 2000; Ramírez, 2014; García & Bonaldo, 2023). Furthermore, the modified hairs in Tapixaua and Pranburia are not homologous, as evidenced by both its fine morphology and distribution. While in Pranburia the tibial hairs are long, thin shafts, evenly distributed across the entire perimeter of the article (see Zhang & Jin, 2018, figures 3F-3G), in *Tapixaua* the hairs

are spatulated, with papillate surfaces and are unevenly distributed across the article, arranged mainly in lateroventral and lateral-dorsal rows (Bonaldo, 2000, figures 51-53, 288). These differences suggest that the disguise in *Pranburia*, being efficient from both lateral and dorsal points of view, is more effective than that in *Tapixaua*, which appears to be more efficient from lateral points of view.

This particular ant-mimic syndrome, which we single out here as Deelemanian ant mimicry (in honor of arachnologist Christa Deeleman-Reinhold, who first observed it), may prove to be a much more common phenomena than currently known, occurring in spiders other than Corinnidae. Some Phrurotimpus Chamberlin & Ivie, 1935 (Phrurolithidae) species show modifications on leg I (N.I. Platnick, personal communication to ABB, 2015) that could conceivably play such a role and even Salticidae with enlarged tibiae, such as some species of *Tutelina* Simon, 1901 and Harmochirus Simon, 1886 may have reached similar solutions (David Hill, personal communication, 2024). The habitus of males of the afrotropical genus Asceua Thorell, 1887 (Zodariidae) presents a great similarity to that of an ant with their enlarged palp resembling an ant's head, which might be related to their preference on preying on ants (Jocqué & Henrard, 2024).

On the other hand, the enlargement of Leg I in Salticidae may be related to sexual dimorphism or agonistic display between males. For example, some groups of the subtribe Dendryphantina, which is composed of genera where the males have enlarged Leg I, include ant-mimic species who use Leg II to mimic antennae (as in *Peckhamia* Simon, 1900) (see Cala-Riquelme et al., 2020). The main premise of Deleemanian mimicry proposed here is that it is essentially triggered by certain predator-stimuli. In a strict sense, it involves a mixture of morphology and behavior, making mimicry optional. Salticids with enlarged tibiae may not maintain their first pair of legs joined together due to an anatomical constraint imposed by the cephalothorax shape. In that regard, the antennae-mimic behavior referred to above is not triggered by external stimuli, being part of their walking behavior, as suggested by Shamble et al. (2017). In Asceua the ant-resembling morphology is restricted to males, and the body morphology apparently does not make the mimicry optional. Even the most myrmecomorphic spiders also use behavior as a complement to the disguise, but most of the time, the ant-like behavior is stereotyped (or constrained by morphology) and not truly optional. The question would be whether the behavior is variable or constrained by morphology, that is, whatever produces the impression of the ant head (enlarged palps or enlarged or tufted tibiae) should increase or decrease effectiveness depending on behavior. These hypotheses need to be tested by field observations since mimicry, as a dendrnatural phenomenon, is composed of a model-mimic-receptor triad, where understanding how the receptor interprets the message given by the mimic is critical.

CONCLUSION

The *Tapixaua callida* exhibits an interesting behavior of building retreats in tree trunks. Since nothing was known about its behavior until now, it is possible that traditional spider sampling methods failed to capture individuals of this species in arachnofaunistic surveys. The information presented in this manuscript may be useful for future collections of specimens of this genus, potentially revealing whether the behavior observed in juveniles persists in adult individuals (in one or both sexes).

We also confirm the hypothesis of Bonaldo (2000) that the modified hairs on leg I simulate the cephalic tagma of ants (Figure 2A, see Favacho, 2024), highlighting the need of further investigation on the occurrence of Deelemanian ant mimicry in other groups of spiders.

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AUTHOR'S CONTRIBUTION

C. Xavier contributed to conceptualization, data curation, writing (original draft, writing, review & editing), investigation, methodology; C. J. Silva-Júnior contributed to conceptualization, data curation, writing (review & editing), investigation; C. Favacho contributed to data curation, writing (review & editing); F. García contributed to data curation, writing (review & editing); A. A. Bustamante contributed to data curation, writing (review & editing) and A. B. Bonaldo contributed to data curation, writing (review & editing), investigation, writing (review & editing) and A. B.

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