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New data on the systematics and biogeography of the Neotropical ant genus *Thaumatomyrmex* Mayr, 1887 (Insecta, Hymenoptera, Formicidae) with description of a new species from the inland paleo-dunes of the middle São Francisco River, northeastern Brazil

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Abstract. The Neotropical ant genus *Thaumatomyrmex* Mayr, 1887 (Ponerinae, Ponerini) is currently represented by 13 valid species divided into three taxonomic groups, distributed between southern Mexico and northern Argentina, with a presence in the Caribbean islands. We propose the first morphological phylogeny and biogeographical hypotheses for the genus. Based on this morphological phylogeny, we redescribe the genus. The phylogeny revealed the "*ferox* species group" to be paraphyletic, while the *mutilatus* species-group forms a clade defined by 12 synapomorphies, which we used to give a new diagnosis. We give the definition of the two species already described of this *mutilatus*-group and compare them with the description of a new species, *Thaumatomyrmex carranca* Celante & Jahyny sp. nov. from the São Francisco Dunes district in the Caatinga Dominion, in northeastern Brazil. We present data on the natural history and conservation status of the new species. We provide an identification key for the three taxonomic groups and for the worker morphotype of all described *Thaumatomyrmex* species of the "*ferox*" and *mutilatus* species groups.

Keywords. Morphology based phylogenetics, biogeography, Caatinga Dominion, species group, identification key.

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Introduction

Thaumatomyrmex Mayr, 1887 is a genus of Neotropical ants (Insecta, Hymenoptera, Formicidae) with a geographic distribution ranging from northern Argentina/southern Brazil to Mexico and the Caribbean (Jahyny *et al.* 2015). *Thaumatomyrmex* species can live in many different environments, from tropical rainforests or periodically flooded areas to savannas in semiarid regions (Jahyny *et al.* 2015).

With the last described species, *Thaumatomyrmex fraxini* D'Esquivel & Jahyny, 2017, the genus currently contains 13 valid species (Bolton 2026). Whitin the subfamily Ponerinae Lepeletier de Saint-Fargeau, 1835, the *Thaumatomyrmex* species are characterized by a peculiar head morphology: the torular lobes are widely spaced, and the mandibles are elongated, thin, and curved with three long spiniform teeth. It was undoubtedly this unique head shape that led Emery (1901) to create the tribe Thaumatomyrmecini (as Thaumatomyrmii). Although widely accepted by subsequent authors, Kempf (1954, 1975) departed from this view. Based on newly discovered males and larvae—stages unknown to Emery (1911)—Kempf (1954) argued that *Thaumatomyrmex* should either be nested within Ponerini or retain a distinct tribe, though he notably omitted the term "Thaumatomyrmecini" without explanation. The genus was eventually integrated into the *Pachycondyla* Smith, 1858 genus group within Ponerini by Schmidt & Shattuck (2014), a placement lately validated by Doré *et al.* (2025). The gyne of *Thaumatomyrmex ferox* Mann, 1922 was described by Vazquez *et al.* (2010), but Jahyny *et al.* (2015) believe it is likely *Thaumatomyrmex zeteki* Smith, 1944.

The first study assessing the taxonomy of the genus is the one of Kempf (1975), which provided an identification key to eight species, organized in three groups mainly based on differences of the sculpture of the cuticle. The *mutilatus*-group includes *Thaumatomyrmex mutilatus* Mayr, 1887, and *Thaumatomyrmex contumax* Kempf, 1975, both characterized by a sharply shagreened cuticle with a silky sheen. The *cochlearis*-group includes *Thaumatomyrmex bariay* Baroni Urbani & De Andrade, 2003, *Thaumatomyrmex cochlearis* Creighton, 1928, *Thaumatomyrmex mandibularis* Baroni Urbani & De Andrade, 2003, and *Thaumatomyrmex nageli* Baroni Urbani & De Andrade, 2003, all with a cuticle partly sculptured. The *ferox*-group comprises *Thaumatomyrmex atrox* Weber, 1939, *Thaumatomyrmex ferox* Mann, 1922, *Thaumatomyrmex manni* Weber, 1939, *Thaumatomyrmex paludis* Weber, 1942, and *Thaumatomyrmex zeteki* Smith, 1944. *Thaumatomyrmex fraxini* D'Esquivel & Jahyny, 2017, was subsequently added to the group (D'Esquivel *et al.* 2017), while *Thaumatomyrmex soesilae* Makhan, 2007, also fits Kempf's (1975) definition. All species in this group are characterized by a completely smooth and highly polished cuticle.

Longino (1988) conducted a less extensive taxonomic revision based on comparative morphology and geographic distribution. Given the lack of known sympatry at the time, he suggested that the genus *Thaumatomyrmex* represents either a single species with continuous variation, a complex of allopatric populations with arbitrary boundaries, or a patchwork of parapatric or sympatric species (Longino 1988). Following the discovery of several cases of sympatry (Jahyny *et al.* 2008, 2015), certain hypotheses put forward by Longino (1988) had to be reexamined.

Here, we describe a new species of *Thaumatomyrmex* collected within the unique inland paleodunes of the São Francisco River, in the Caatinga Dominion (CAAD sensu Moro *et al.* 2024) a semiarid climate region of xeric shrubland and thorn forest in northeastern Brazil. This discovery provides a timely opportunity to restart the systematic study of the genus, fifty years after the revision by Kempf (1975). To this end, we: (1) present the first morphological phylogeny and biogeographical study of the genus based on nine species; (2) broaden the generic definition; (3) redescribe the *mutilatus* species-group; (4) redescribe *T. mutilatus* and *T. contumax*, describe the new species, and discuss its conservation; and (5) update the identification key for all taxonomic groups and worker morphotypes of the "*ferox*" and *mutilatus* species-groups.

Material and methods

Institutional abbreviations

The material used on this study is deposited in the following institutions (most of the information comes from Evenhuis (2026)):

CPDC = Centro de Pesquisas do Cacau, Itabuna, Bahia, Brazil
DZUP = Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
MFCE = Coleção Entomológica do Museu de Fauna, Centro de Conservação e Manejo de Fauna da Caatinga, Universidade Federal do Vale do São Francisco, Petrolina, Pernambuco, Brazil
MPEG = Museu Paraense Emilio Goeldi, Belém, Pará, Brazil
MZSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil.
NHMW = Naturhistorisches Museum Wien, Vienna, Austria

Origin of the material

The new species was collected in 2016 during a field exploration of some dunes of Casa Nova, State of Bahia, northeastern Brazil. We searched visually for foraging ants at night with lanterns, collected them with a brush and put them in tubes filled with 70% ethanol. During the following expeditions aimed at cataloguing the ant fauna in the dunes, we collected more specimens of the new species. The dead specimens were point-mounted on insect pins and observed under the stereomicroscope and microscope. In some specimens the abdominal segments A3 and A4 were dissected to provide better access to specific characters. Ant collection was authorized by license n° 72721 (Chico Mendes Institute for the Conservation of Biodiversity (ICMBio), Biodiversity Authorization and Information System (SISBIO)).

Specimens deposited in the MFCE were assigned a unique specimen identifier, consisting of the collection acronym followed by a six-digit Arabic numeral (e.g., MFCE014593).

The new species was assigned to Kempf's (1975) *mutilatus* species-group and was compared with the two species already described for this group. We directly examined the holotype of *Thaumatomyrmex contumax* during a visit to the Hymenoptera collection of the MZSP, and the holotype of *T. mutilatus* has been loaned from NHMW.

Stacked colour imaging

Light micrographs were produced through a multi-focused montage processing from a series of images taken by focusing the sharpness on different levels of the specimens. For the type of *Thaumatomyrmex mutilatus* we use the camera (64 MP) of a Samsung Galaxy A52s smartphone mounted on the eyepiece of a microscope Nikon Microphot-FXA which was used at × 40 and × 100 magnifications. For focus bracketing, the Android application ProCam X HD Camera Pro was used to take series of images with

focus distance intervals of 5 µm. For the type of *T. contumax* a Leica digital camera attached to a Leica microscope were used (equipment of the MZSP). For the new species, we used a DSLR camera Nikon D5600 with extension tubes of different length screwed directly with an adapter to the nosepiece of a modified microscope using a 10 magnification objective lens (10×/0.25 -∞/0.17) and two flashes for illumination. The photographs were stacked using Helicon Focus software ver. 8.2.2 and then images were edited and organized into plates using the software Adobe Photoshop ver. 24.7.2 or Adobe Photoshop Elements 21.

Terms for the external morphology

Terminology of external morphology follows Bolton (1994) and Tozetto *et al.* (2022). For the cuticle sculpturing, we follow or adapt the terms proposed by Harris (1979). For the setae stature we follow Wilson (1955).

Measurements and indices

Most of the measures and indices used in this study follow Kempf (1975) and D'Esquivel *et al.* (2017), but some have been modified (*) and others are being used for the first time for the genus (#). The measurements are presented in a drawing in Supp. file 1. Measurements were taken with a micrometer coupled to an eyepiece on a stereo microscope. They are presented in millimetres with two decimal places. For each measurement and index, the first number corresponds to the holotype, and the minimum and maximum values among the specimens measured are indicated in parentheses.

BLCM# = Body length comparative measurement (HL + WL +PL + TASL#)
CI = Cephalic index (HW* × 100 / HL)
FTI# = First tooth index: (FTM × 100 / HW*)
FTM = First long tooth measurement (head in full-face view, length between the most lateral margin of the mandibular articulation and the tip of the first long tooth)
GL = Gaster length (gaster in lateral view, maximum length the gaster from the anterior most point of the third abdominal segment (first segment of the gaster) to the posterior most point excluding the sting)
HL = Head length (head in full-face view, distance from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin of vertex)
HW* = Head width (head in full-face view, the maximum distance between outer margin of the mandibular articulations)
IfI = Interfrontal index (IfW × 100 / HW*)
IfW = Interfrontal width (head in full-face view, the maximum distance between outer margin of the torular lobes)
MFL = Metafemur length in dorsal view (maximum length of the metafemur from its margin with the articulation with the trochanter to its margin with the articulation with the metatibia)
PL = Petiole tergite length (in lateral view, maximum length of the petiole tergite)
PrW = Pronotum width (in dorsal view, the maximum width of the pronotum)
PW = Petiole tergite width (in dorsal view, the maximum width of the petiole tergite)
SL = Scape length (the maximum length of the scape, excluding the basal bulbus and its neck)
TASL# = Third abdominal segment length (gaster in lateral view, length of the tergosternal fusion of the third abdominal segment (first segment of the gaster))
TBL = Total body length (HL + WL + PL + GL)
TLTI# = Third Long Tooth Index (TTM# × 100 / HW*)
TTM# = Third long tooth measurement (head in full-face view, length between the most lateral margin of the mandibular articulation and the tip of the third long tooth)
WL = Weber's length (in lateral view, length from the anterior margin of the pronotum, excluding the projecting collar, to the posterior extremity of the metapleural lobe)

Since the gaster can be more or less distended, we created the BLCM index, which accounts for the measurements of body parts of fixed size in an individual, to compare sizes across specimens and species.

Species concept used

Species delimitation follows the Unified Species Concept (de Queiroz 2017), treating species as separately evolving metapopulation lineages. Under this framework, we used two primary operational criteria to diagnose independent lineages: the presence of autapomorphies recovered in the morphological phylogeny and/or a unique combination of character states that distinguishes the taxon from all known related species. This approach ensures that the proposed species represents a distinct evolutionary entity based on diagnosable morphological evidence.

Cladistic and biogeographic analysis

The ingroup comprised nine taxa: the new species and eight other *Thaumatomyrmex* species from three taxonomic subgroups (*mutilatus*, *cochlearis*, and *ferox*). *Belonopelta deletrix* Mann, 1922 was used as the outgroup, based on the molecular phylogeny proposed by Borowiec *et al.* (2019) and Doré *et al.* (2025) (Supp. file 2). We described 48 discrete unordered morphological characters following Sereno (2007). These included seven characters from Keller (2011) and 41 based on our examination of specimens deposited at MFCE (Supp. file 3). The character matrix (Supp. file 4) was prepared in Mesquite ver. 3.81 software, with missing or inapplicable data denoted by "?" and "-" respectively. Cladistic analysis was performed in TNT ver. 1.6 (Goloboff & Morales 2023) using the "implicit enumeration" function, with tree collapse after the search. Analysis and treatment of results were conducted in Mesquite ver. 3.81 (Maddison & Maddison 2023) and WinClade ver. 1.00.08 (Nixon 1999) for observation of synapomorphies / character tracing using parsimony.

An additional analysis was performed in MrBayes ver. 3.2.7 software, employing a morphological evolution model (datatype = standard; rates = gamma with four categories; state frequencies fixed as equal) and a relaxed clock model (independent gamma rates–IGR: brlenspr = clock:uniform and clockvarpr = igr), constrained by the topology derived from the TNT cladistic analysis. The root was calibrated using a uniform prior between 35.21–66.78 Ma, based on the divergence of the *Belonopelta* and *Thaumatomyrmex* genera (Doré *et al.* 2025). This analysis consisted of two independent runs, each with four chains (three heated, one cold; temperature = 0.1), 5 000 000 generations (sampling every 500 generations, diagnostic every 5000 generations), and the first 25% of samples were discarded as burnin. Convergence was assessed by checking that the Potential Scale Reduction Factor (PSRF) approached 1.0 and that effective sample sizes (ESS) exceeded 200 for all parameters (in addition to an average standard deviation of split frequencies < 0.01).

Ancestral range reconstruction and the assessment of biogeographical processes were conducted in the BioGeoBEARS package in R, based on a dated phylogeny (lenght obtained from relaxed clock model) of the study group (*Thaumatomyrmex*) and distribution data across four subregions (Morrone 2001): Neotropical North (Caribeña), Amazonian (Amazónica), Atlantic Forest (Paranaense), and Chacoan/ Caatinga (Chaqueña). The list of localities and corresponding biogeographic zones according to Morrone *et al.* (2022) and Morrone (2001) for specimens of the ten species used in this study is available in Supp. File 5. The analysis followed Matzke (2018), testing six biogeographical models, with max range = 4: DEC, DIVALIKE, BAYAREALIKE, and their respective versions incorporating the founder-event speciation parameter ("+J"). Model comparison and selection were performed using Likelihood Ratio Tests (LRT) for nested models and the Akaike Information Criterion (AIC) for all models."

Maps

The maps were produced using QGIS 3.8.0-Zanzibar. The vectors used for the area of Caatinga Dominion were provided by Moro *et al.* (2024).

Results

Cladistic analysis and biogeographic analysis

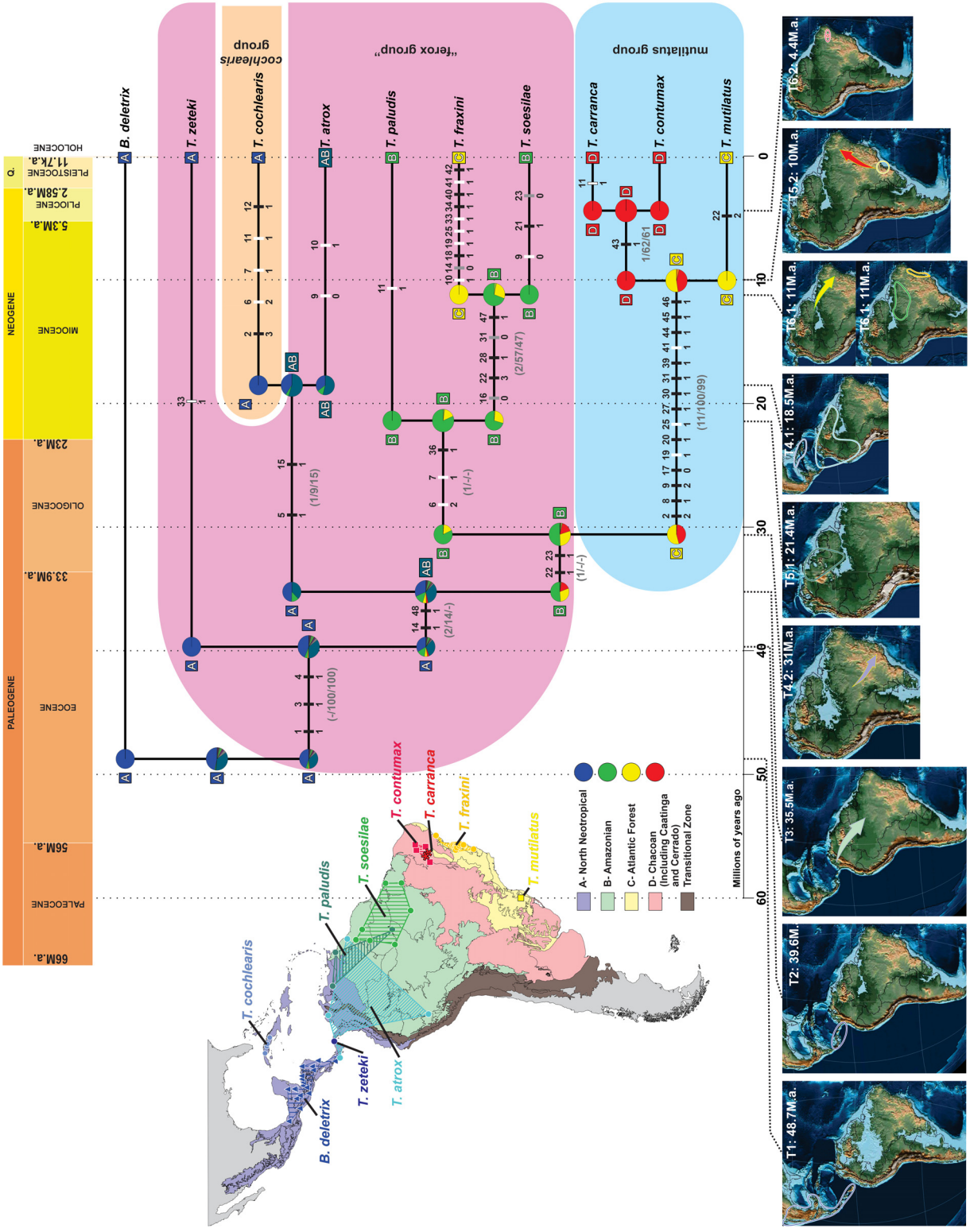
Cladistic analysis yielded one most parsimonious tree (Fig. 1; Supp. file 6), with a length (L) = 68 steps, consistency index (CI) = 0.794, and retention index (RI) = 0.781. The *mutilatus* species-group (*Thaumatomyrmex mutilatus* + *T. contumax* + *T. carranca* sp. nov.) and the *cochlearis* species-group were recovered as separate monophyletic groups embedded within a paraphyletic "*ferox* species-group" (Fig. 1). In the *mutilatus* clade, the new species *Thaumatomyrmex carranca* sp. nov., is more closely related to *T. contumax* than to *T. mutilatus* (Fig. 1).

The biogeographic analysis strongly favors models that include a founder-event parameter (J) over those that excluded it. This is evidenced by the consistently higher log-likehoods and lower AIC values for the DEC+J, DIVALIKE+J, and BAYAREALIKE+J models. For instance, the DEC model, with an AIC of 44.48, performs substantially worse than DEC+J (AIC = 35.54). Among the models that incorporate a J parameter, DEC+J emerges as the best-supported model, with the highest AIC weight of 0.534, followed by DIVALIKE+J (AIC weight = 0.285). This indicates that within this dataset, the DEC+J model provides the most plausible explanation for the observed range evolution patterns. Additionaly, the dispersion (d values) are low in all models.

For the *mutilatus* clade, *Thaumatomyrmex carranca* sp. nov. is distributed in the Caatinga province, belonging to the Chacoan dominion, as is *T. contumax*, its sister species, while the holotype of *T. mutilatus* was encountered much further south in the Araucaria Forest province in the Paraná dominion (Fig. 1). The outgroup *Belonopelta deletrix* is present in the Mexican transition zone, the Brazilian subregion of the Mesoamerican dominion and the Pacific dominion. *Thaumatomyrmex zeteki*, the sister species of all other *Thaumatomyrmex* studied here, is found in the Pacific dominion. *Thaumatomyrmex cochlearis* Creighton, 1928 has a distribution restricted to the Cuban province in the Antillean subregion, while *T. atrox*, its sister species can be found in three dominions in the American continent, the Pacific dominion, the Boreal Brazilian dominion and the South Brazilian dominion. *Thaumatomyrmex paludis* occupies the Pacific dominion, the Boreal Brazilian dominion and the South Brazilian dominion. *Thaumatomyrmex soesilae* is found in the Boreal Brazilian dominion, the South Brazilian dominion and the Chacoan subregion of the Southeastern Amazonian dominion, while *T. fraxini*, its sister species, is found only in the northern half of the Atlantic province in the Paraná dominion.

Based on our morphological study and phylogeny of nine species of the genus, including three of the *mutilatus* species-group, we broaden and revise the descriptions of the genus given by Kempf (1975) and Schmidt & Shattuck (2014). We also revise Kempf's (1975) definition of the *mutilatus* species-group for the female worker morphotype, and we give possible unique derived features for the genus and for this group.

Fig. 1 (Figure next page). Single most-parsimonious tree obtained in a cladistic analysis of morphological data of nine taxa of *Thaumatomyrmex* Mayr, 1887 with *Belonopelta deletrix* Mann, 1922 as outgroup with Bremer, Boostrap and Jacknife supports. The biogeographic results are shown in the cladogram, with DEC+J biogeographic analysis (d~0; e=0; j=1.444; LnL=-14.48). The current distribution of the *Thaumatomyrmex* species studied is shown in the biogeographic dominions from Morrone *et al.* (2022) and subregions (Morrone 2001). Paleogeographic maps are based on Scotese (2014).


B. deletrix
T. zeteki
T. cochlearis
T. atrox
T. paludis
T. fraxini
T. soesilae
T. carranca
T. contumax
T. mutilatus
"cochlearis group"
"ferox group"
mutilatus group
(1/9/15)
(-/100/100)
(2/14/-)
(1/-/-)
(2/57/47)
(11/100/99)
1/62/61
Millions of years ago
A- North Neotropical
B- Amazonian
C- Atlantic Forest
D- Chacoan (Including Caatinga and Cerrado)
Transitional Zone
T1: 48.7M.a.
T2: 39.6M.a.
T3: 35.5M.a.
T4.2: 31M.a.
T5.1: 21.4M.a.
T4.1: 18.5M.a.
T6.1: 11M.a.
T6.2: 10M.a.
T6.2: 4.4M.a.
PALEOGENE
NEOGENE
Q.
HOLOCENE
PLEISTOCENE
PLIOCENE
MIOCENE
OLIGOCENE
EOCENE
PALEOCENE
11.7K.a.
2.58M.a.
5.3M.a.
23M.a.
33.9M.a.
56M.a.
66M.a.

Taxonomy

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Formicidae Latreille, 1809
Subfamily Ponerinae Lepeletier de Saint-Fargeau, 1835
Tribe Ponerini Lepeletier de Saint-Fargeau, 1835

Genus ***Thaumatomyrmex*** Mayr, 1887

Thaumatomyrmex Mayr, 1887: 530. Type species: *Thaumatomyrmex mutilatus,* by monotypy.

Diagnosis

The genus *Thaumatomyrmex* cannot be confused with any other by the following characteristics which represent its autapomorphies within the Ponerini: mandibles elongate, thin and curved inward, with three longer or shorter spiniform teeth of which the 1st (apical) tooth is the longest and the other ones are gradually smaller; a smaller, pointed tooth may also be present at the base of the mandibles; torular lobes widely separated and protruding anteriorly over the clypeus, directed outward overhanging the lateral area of the clypeus and reaching, or surpassing its anterior margin; almost all the body with long, subdecumbent to erected, and widely spaced setae, arranged according to a standard pattern.

Description

Worker

Size range, TL 2.57–5.0 mm, respectively: *Thaumatomyrmex fraxini* D'Esquivel & Jahyny, 2017, and *Thaumatomyrmex manni* Weber, 1939 (Kempf 1975; D'Esquivel *et al.* 2017). Ants with the standard characters of Ponerini sensu Schmidt & Shattuck (2014). Mandibles elongate, thin and curved inward, with three long spiniform and horizontally pointed teeth of which the 1st (apical) tooth is the longest and the other ones are gradually smaller; a denticle may be present on the inner mandibular margin, located within the basal third of the first tooth, it is counted as the second tooth; 5th tooth, if we count the denticle, smaller than the 1st, 3rd and 4th ones, spiniform or reduced to a small pointed protuberance, present or absent at the base of the mandibles. Mandibular articulations forming weakly to strongly protruding anterolateral projections.

The clypeus features a broad median area extending posteriorly between the torular lobes; the frontoclypeal sulcus varies in form and shape when viewed posterodorsally; sculpture may be present or absent; when present, it typically consists of regular longitudinal costulae extending from the anterior margin to the frontoclypeal sulcus. Torular lobes widely separated and protruding anteriorly over the clypeus, directed outward overhanging the lateral area of the clypeus and reaching, or surpassing its anterior margin. Eyes large and convex, situated immediately posterior to the mandibular articulations anterior of head midline. Pronotum with or without a transversal carina on its anterior region; in profile, ranging from a uniformly convex shape giving a 'humpbacked' appearance to a convex but flatter shape. Mesonotum differentiated or not from the propodeum. Metapleuron with a protuberance at its anterior base near the mesometapleural suture, at the base of a hollow, almost overhanging it. Metathoracic spiracle concealed by a spiracular lobe or exposed, with opening round to oval. Propodeal angle between its dorsal face and declivity in lateral view rounded or forming an almost right angle. Posteropropodeum forming a regular declivity with a posterior almost horizontal platform in its two thirds. Tibial spurs formula (protibia; mesotibia; metatibia - s, simple; p, pectinate): (1p; 1s; 1p) or (1p; 0; 1p). Posterior surface of the probasitarsal notch without stout setae or with only two/three aligned setae. Petiole, cuboid or scalelike. Slight constriction between the abdominal segments III and IV. Abdominal segment IV with or without suture or groove between pretergite and posttergite and between presternite and postternite. Stridulitrum on A4 pretergite distinct, vestigial, or absent.

Body colour black except for mandibles, antennae and legs, generally lighter. Head and body with variable sculptures, ranging from smooth and shining to substriolate with a silky sheen, or appearing distinctly rough. Almost all the body with long, subdecumbent to erect, and widely spaced setae, arranged according to a standard pattern; setae that are similarly spaced but shorter may also be present in addition to the long ones; setae appressed and much shorter on scape and on legs; fine pubescence confined to antennal funiculus and tarsomeres.

Diagnosis of the *Thaumatomyrmex mutilatus* species-group (Supp. file 7)

Most of the diagnostic characters are accompanied by their corresponding cladistic character indicated between brackets with their character state and put in bold when it is an autapomorphy.

Almost all the integument of the body, from the head to abdominal segment IV, including gular surface of head, substriolate with a silky sheen (**2/2**); Interfrontal Index (IfI): $67 < \times < 79$ (5/1); on the median area of the clypeus between the widely separated torular lobes, the position of the four long erect setae is as follows: one seta on each lateral margin of the clypeus and two setae in the middle of the clypeus (some specimens have one or more additional setae) (**8/1**); clypeus median area biconcave in posterodorsal view (**9/2**); the 2nd tooth on the mandible is a simple denticle, located on the inner margin of the mandible in the first third from the base of the 1st tooth (12/0 and 13/1); scape with one long, appressed, externally directed and stand out seta inserted on the dorsal distal region (**17/0**); in lateral view, curvature of the imaginary line of the vertex with the occipital region very convex (19/1); a transversal groove cutting the pronotal neck (**20/1**); mesonotum, metanotum and propodeum form a continuous dorsal surface with no suture (23/1); metathoracic spiracle exposed, opening round to oval (25/1); one seta present beside the propodeal spiracle, in anterior position (**27/1**); posterior platform of the posteropropodeum without transversal groove well marked in dorsal position (29/1 and **30/1**); posterior base of the petiole with a broad superficial dorsolateral trench interrupted by an inverted Y carina (**31/1**); petiole scalelike, its anterior and posterior surfaces meeting dorsally and laterally forming a subacute margin, showing in dorsal view as a distinct transverse carina; stridulitrum absent on the pretergite of abdominal segment IV (**39/1**); pretergite of abdominal segment IV forming an even, uninterrupted surface with the posttergite, without transverse constriction in the form of a depressed line or deep groove (41/1); spiracle of abdominal segment IV situated on posttergite at the edge of the pretergite (**44/1**) and with the shape of a water drop directed backwards (**45/1**); foveae present on the posterior margin of the tergite of abdominal segment IV (**46/1**).

Identification key for the three taxonomic groups and for the worker morphotype of all described *Thaumatomyrmex* species of the "*ferox*" and *mutilatus* species-groups

We present an identification key for the three taxonomic groups and for the worker morphotype of all described *Thaumatomyrmex* species of the "*ferox*" and *mutilatus* species-groups, including *T. carranca* sp. nov., the last described species *Thaumatomyrmex soesilae* and *Thaumatomyrmex fraxini*. For the four species of the *cochlearis* species-group see the key in Baroni-Urbani & De Andrade (2003).

1. Mandibles without a denticle on the inner margin and at the base of the first (apical) long tooth (Fig. 2A); main sculpture pattern: frontal area of the head covered with rough sculptures as minute, dense punctures, thin, longitudinal rugosities, sparse or superficial piligerous foveae or punctures (Fig. 2A), part of the mesosoma covered with rough sculptures too as punctures, reticulations, and piligerous foveae..... ***cochlearis*** species-group
– Mandibles with a denticle on the internal margin and at the base of the first (apical) long tooth (Fig. 2B–C); main sculpture pattern on the body different from above 2

2. Clypeus with two median setae (rarely more) closely approximated (Fig. 2C); almost all the integument of the body, from the head to the abdominal segment IV, including gular surface of head, substriolate that give a silky sheen (Fig. 2C) .....3 ***mutilatus*** species-group
– Clypeus without median setae (Fig. 2B); almost all the integument of the body smooth and shining, but the head and parts of the body can be covered with some discrete and superficial marks aciculate and/or areolate-polygonal (Fig. 2B) .....5 "***ferox*** species-group"

3. Head only slightly broader than long (CI: 105.81); mandibles with three long teeth and with a smaller basal tooth; in posterior view, the margins of the pronotum form subtriangular shape with rounded tip ..... ***Thaumatomyrmex mutilatus*** Mayr, 1887
– Head distinctly wider than long (CI > 115); mandibles with three long teeth and a smaller basal tooth can be present; in posterior view, the lateral and dorsal margins of the pronotum form a rounded shape, not triangular..... 4

4. Mandibles with three long teeth and with a smaller basal tooth, when the mandibles are closed, the third long teeth cross each other distinctly in front of the clypeus (TLTI: 55)..... ..... ***Thaumatomyrmex contumax*** Kempf, 1975
– Mandibles: with three long teeth (some specimens have a fourth small tooth which is attached to the base of the third long tooth and is similar in size to the denticle located at the base of the first long tooth), when the mandibles are closed, the third long teeth are far apart and never touch or cross each other (TLTI < 42)..... ***Thaumatomyrmex carranca*** sp. nov.

5. In posterior view, lateral margins of the pronotum form parallel straight lines marking an offset with the rather flat dorsal margin (Fig. 3A); three or more short setae are present on the torular lobes besides the long and basal setae (one to three) (Figs 2B, 4A)..... 6
– In posterior view, lateral margins of the pronotum are convex and form a continuous rounded surface with the convex dorsal margin (Fig. 3B); only one to three long setae at the base of the torular lobes, no short setae (Figs 6A–B, 7A–B)..... 7

6. Occipital carina present (Fig. 4A); anterior transverse carina of pronotum present (Fig. 4B); presclerites on fourth abdominal segment delineated from postsclerites by a transverse groove..... ..... ***Thaumatomyrmex soesilae*** Makhan, 2007
– Occipital carina absent; anterior portion of the pronotum without a transverse carina; presclerites on fourth abdominal segment forming an even surface with postsclerites..... ..... ***Thaumatomyrmex fraxini*** D'Esquivel & Jahyny, 2017

7. Pronotum in profile strongly convex giving a 'humpbacked' appearance; mesonotum and propodeum in profile form a continuous structure, without metanotal groove (Fig. 5A); mandibles with only three long teeth, without a basal smaller tooth ..... ***Thaumatomyrmex paludis*** Weber, 1942
– Pronotum in profile convex, not vaulted; mesonotum longitudinally narrow and flat, separated from propodeum by a shallow metanotal groove (Fig. 5B) 8

8. Head slightly wider than long (CI: 101–105); when mandibles closed, the first (apical) long tooth only slightly exceeds the opposite genae (FTI: 102–105) (Fig. 6A); TL < 4.00 mm..... ..... ***Thaumatomyrmex zeteki*** Smith, 1944
– Head wider than long (CI > 120) with lateral margins wider at its anterior portion and narrowing posteriorly; when mandibles closed, the first (apical) long tooth notably exceeds the opposite genae FTI: 110–114 (Figs 6B, 7A–B); TL > 4.00 mm..... 9

9. Mandibles with only three long teeth, without a basal smaller tooth; dorsal surface of the pretergite of the fourth abdominal segment forming an even surface with posttergite, the side of this tergite can have a beginning of a groove, but which does not extend dorsally ..... ***Thaumatomyrmex ferox*** Mann, 1922
– Mandibles with three long teeth and with a basal smaller tooth; pretergite of the fourth abdominal segment separated from the posttergite by a complete transverse constriction or groove, that crosses the tergite from one side to the other 10

10. Semicircular rugulae present between the posterior end of frontal carinae and inner border of eyes (Fig. 7A); IfW subequal to PrW ..... ***Thaumatomyrmex atrox*** Weber, 1939
– Semicircular rugulae absent between the posterior end of frontal carinae and inner border of eyes (Fig. 7B); IfW much greater than PrW ..... ***Thaumatomyrmex manni*** Weber, 1939



Fig. 2. Head, full-face view. **A**. *Thaumatomyrmex mandibularis* Baroni Urbani & De Andrade, 2003, holotype (MCZ:Ent:35267), Cuba. **B**. *T. fraxini* D'Esquivel & Jahyny, 2017 (MFCE015114), Brazil. **C**. *T. contumax* Kempf, 1975 (MFCE014546), Brazil. The red circles indicate the denticle on the internal margin between the first (apical) long tooth and the second long tooth. The red arrow indicates the two setae in the centre of the clypeus. Scale bars: 0.5 mm.

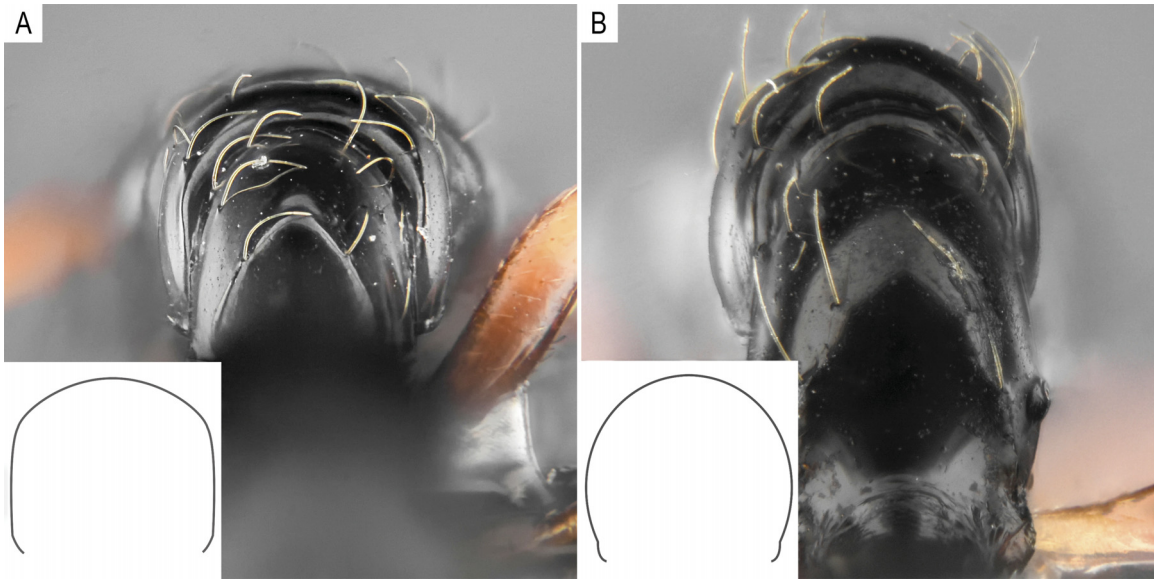


Fig. 3. Thorax in posterior view. **A**. *Thaumatomyrmex fraxini* D'Esquivel & Jahyny, 2017 (MFCE015114), Brazil. **B**. *T. zeteki* Smith, 1944 (CPDC W12338), Panama.

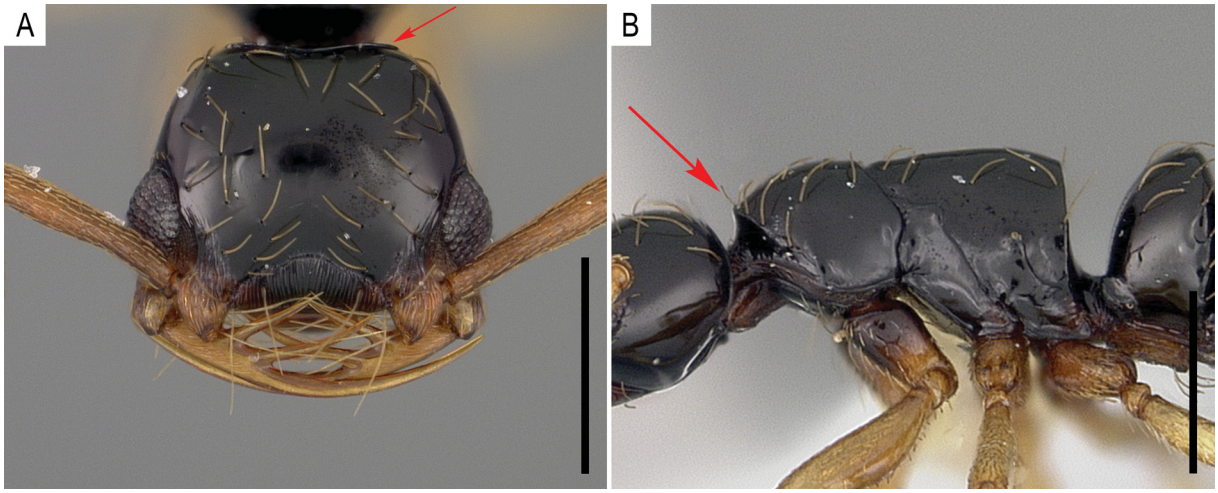


Fig. 4. *Thaumatomyrmex soesilae* Makhan, 2007 (USNMENT00412378), Guyana. **A**. Head, full-face view, the red arrow indicates the occipital carina. **B**. Thorax, profile, the red arrow indicates the transverse carina on the pronotum. Micrographs by Emma Hanisch available from www.antweb.org. Scale bars = 0.5 mm.

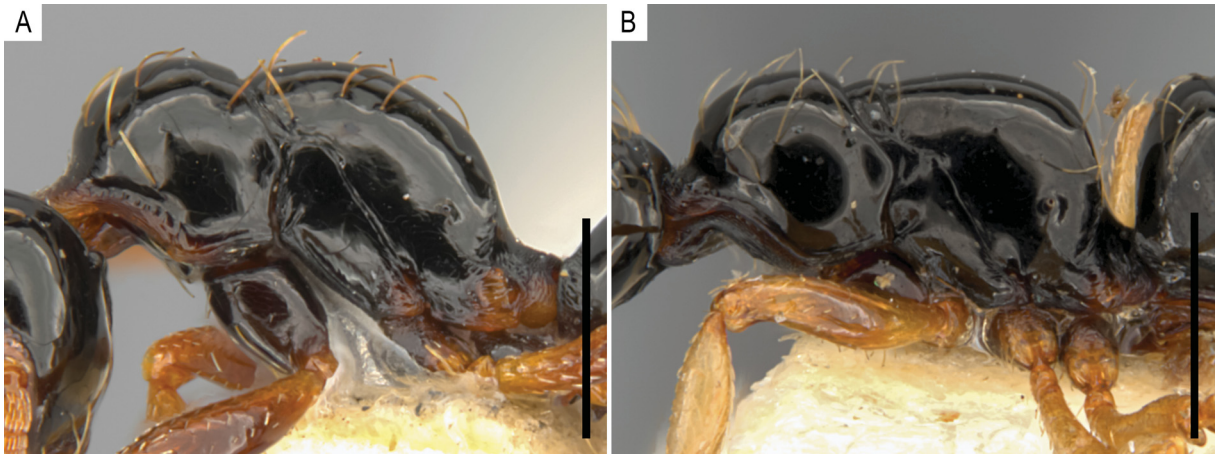


Fig. 5. Thorax in profile view. **A**. *Thaumatomyrmex paludis* Weber, 1942, holotype (MCZ:Ent:32204), Venezuela. **B**. *T. zeteki* Smith, 1944, paratype (USNM56483), Panama. Scale bars = 0.5 mm.

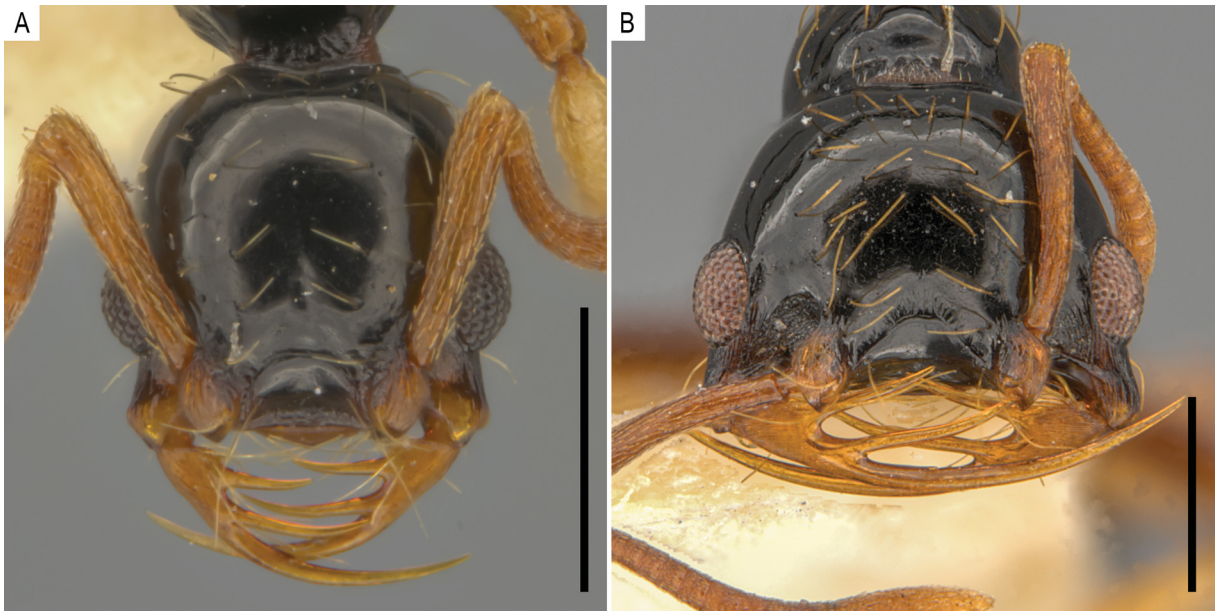


Fig. 6. Head, full-face view. **A**. *Thaumatomyrmex zeteki* Smith, 1944, paratype (USNM56483), Panama. **B**. *T. ferox* Mann, 1922, lectotype (USNMENT00921837), Honduras. Scale bars = 0.5 mm.

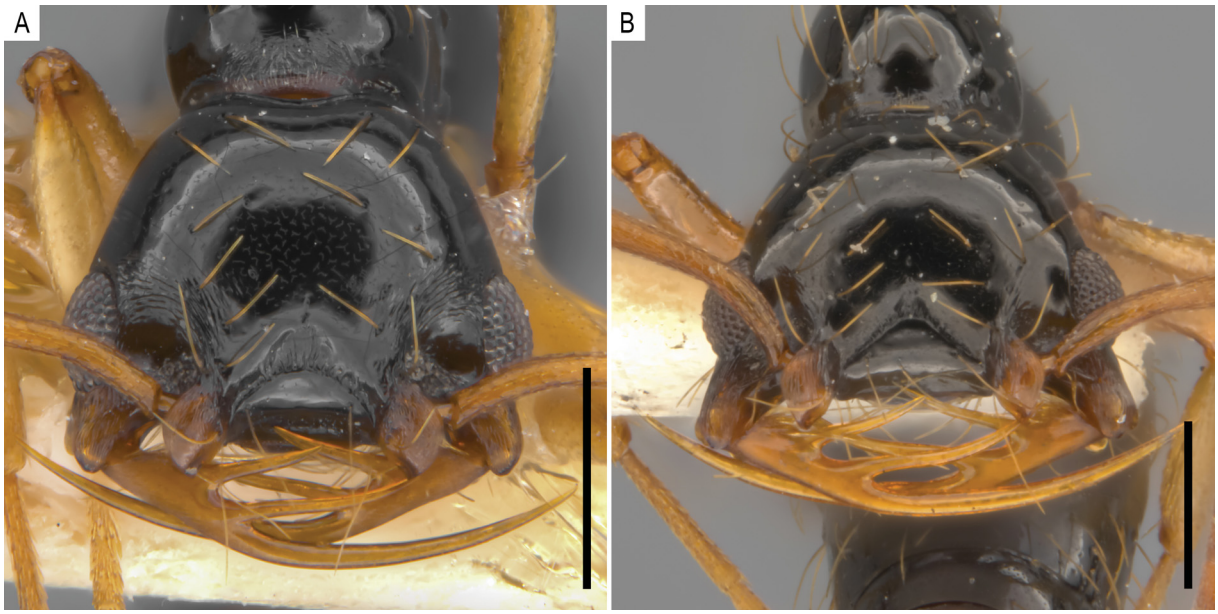


Fig. 7. Head, full-face view. **A**. *Thaumatomyrmex atrox* Weber, 1939, holotype (M.C.Z.TYPE.32205), Guyana. **B**. *T. manni* Weber, 1939, holotype (USNMENT00922340), Bolivia. Scale bars = 0.5 mm

Thaumatomyrmex carranca Celante & Jahyny sp. nov.
lsid:zoobank.org:act:B7AEA212-7AC2-443E-9B39-BB09ACA2C760
Figs 8, 11–13

Diagnosis

TBL = 4.75 mm; head wider than long (CI: 121); three teeth in addition to the denticle at the base of the first (apical) tooth (some specimens have a 4th smaller tooth bonded to the base of the 3rd long tooth); when the mandibles are closed, the 3rd long teeth are widely separated and never cross each other (TLTI: 39), and the 1st (apical) tooth surpasses the opposite gena (FTI: 107).

Etymology

The specific name "*carranca*" is treated as a noun in the nominative singular standing in apposition to the generic name in accordance with Article 11.9.1.2 of the International Code of Zoological Nomenclature (1999). It refers to the "*carranca*", a cultural object typically related to the São Francisco River, which, among other mystical meanings, served as protection for the boats sailing on the São Francisco River,



Fig. 8. *Thaumatomyrmex carranca* sp. nov., holotype (MFCE014593). **A**. Head in full-face view. **B**. Body in dorsal view. **C**. Body in profile view. Scale bars = 0.5 mm.

keeping away evil spirits and monsters that tried to sink the boats. The choice of this popular and regional name comes from the proposal to facilitate communication with the communities that use the dunes.

Type material

Holotype

BRAZIL – **Bahia State** • ♀; Casa Nova, dunas; 9.3948° S, 41.3587° W; 25 Nov. 2016; G.L. Celante leg.; hand collection at night; MFCE014593.

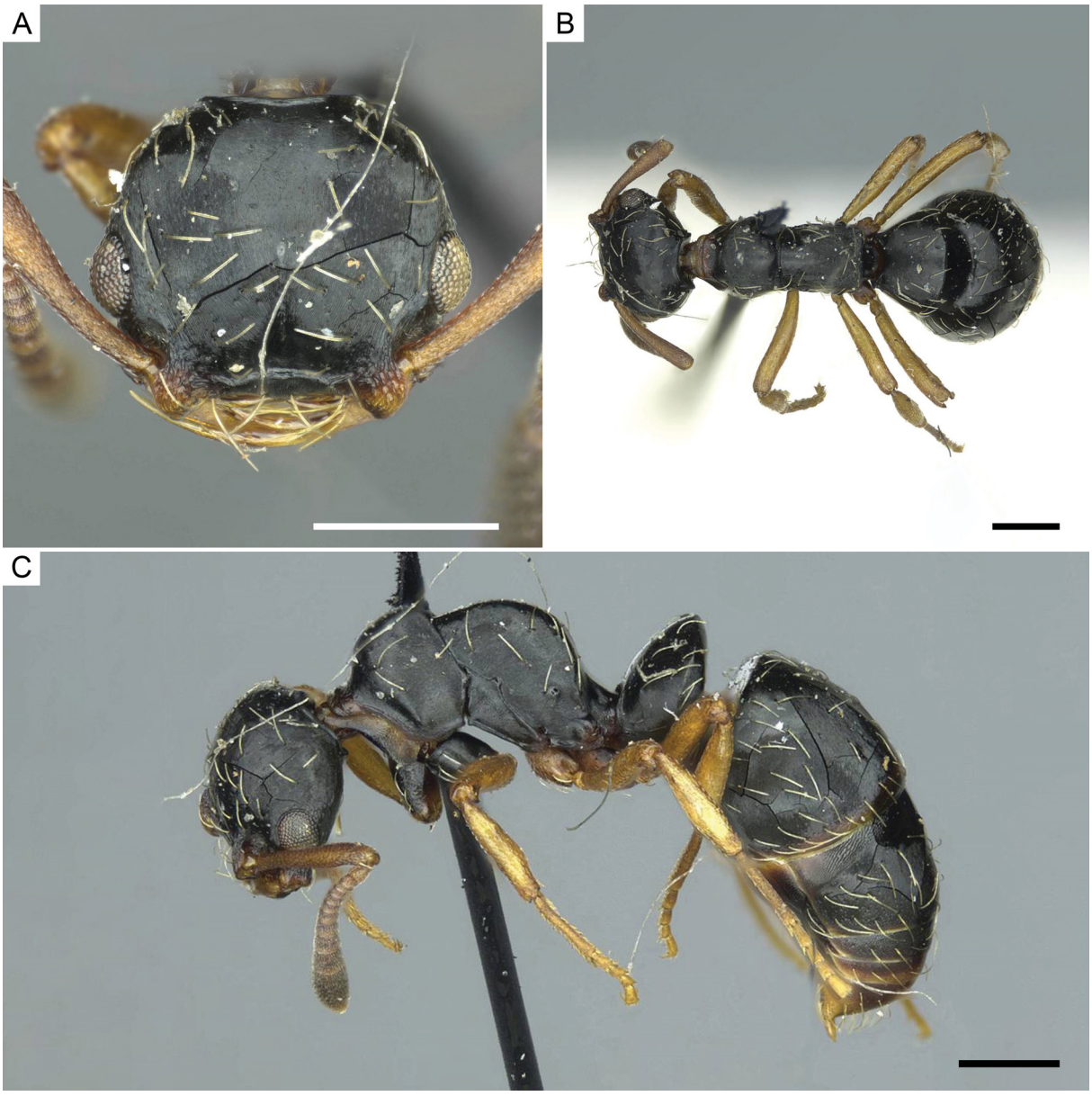


Fig. 9. *Thaumatomyrmex mutilatus* Mayr, 1887, holotype (CASENT0915903). **A**. Head, full-face view. **B**. Body, dorsal view. **C**. Body, profile view. Micrographs by Anna Pal, available in www.antweb.org. Scale bars = 0.5 mm.

Paratypes

BRAZIL – **Bahia State** • 1 ♀; same data as for holotype; MFCE014588 • 1 ♀; same data as for holotype; DZUP, MFCE01587 • 1 ♀; Casa Nova, Sítio Varginha; 9.3988° S, 41.8202° W; 8 Dec. 2016; G.L. Celante leg.; hand collection at night; DZUP, MFCE014584 • 2 ♀♀; Casa Nova, dunas da Fazenda Santarém; 9.6081° S, 41.3780° W; 11–13 Apr. 2025; G.L. Celante leg.; hand collection at night; MPEG, MFCE015115–116 • 2 ♀♀; same data as for preceding; MZSP, MFCE015117–118 • 2 ♀♀; same data as for preceding; CPDC, MFCE015119–120.

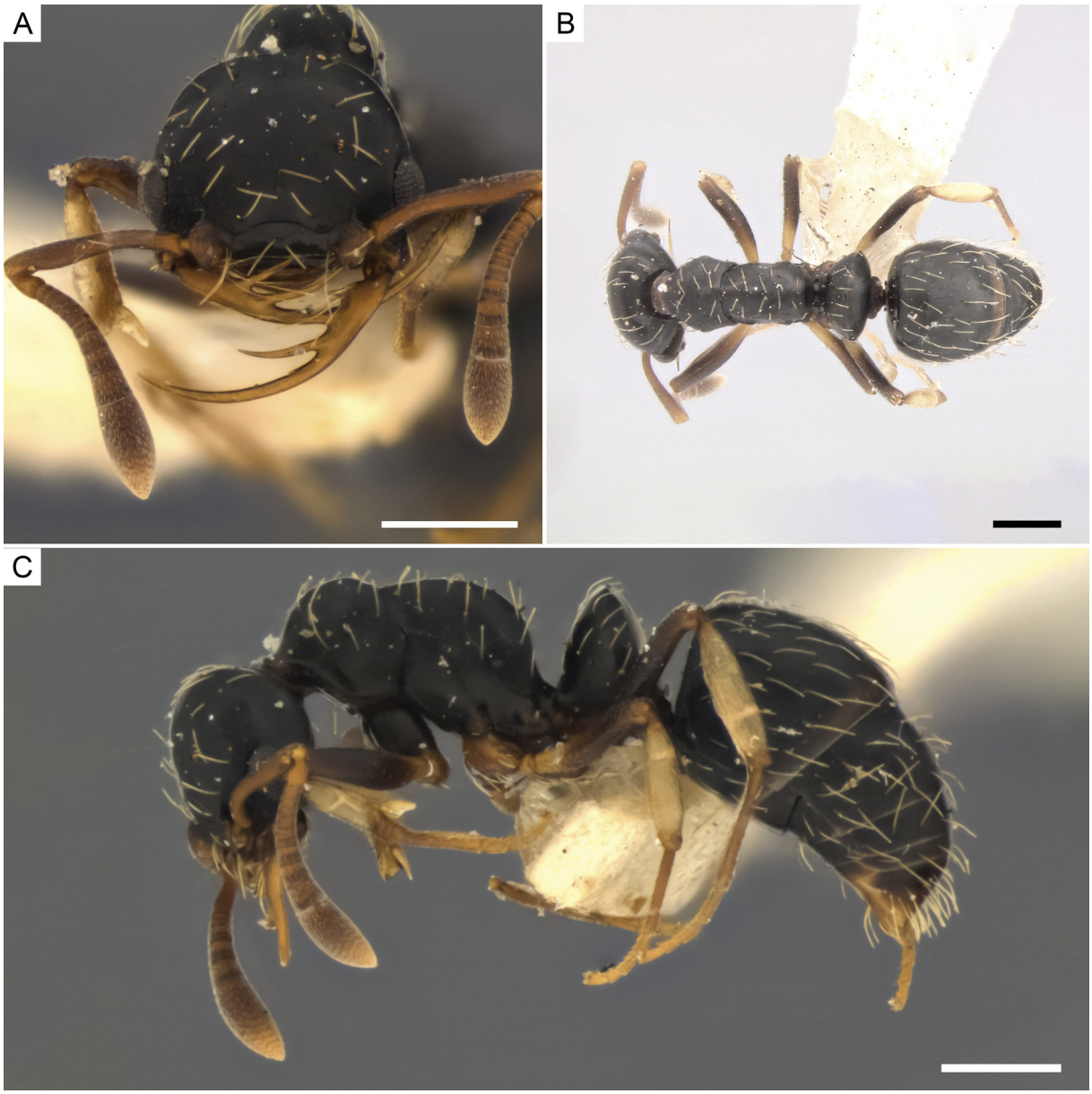


Fig. 10. *Thaumatomyrmex contumax* Kempf, 1975, holotype (MZSP0089779). **A**. Head in full-face view. **B**. Body in dorsal view. **C**. Body in profile view. Micrographs A and C by MZSP Hymenoptera collection staff. Scale bars = 0.5 mm.

Definition

As the *mutilatus* species-group has only three species, the definition of the new species can be presented in the form of a comparative table with our own definition of the two other ones, *T. mutilatus* (Fig. 9) and *T. contumax* (Fig. 10), based on Mayr (1887), Kempf (1975) and on our direct analysis of each holotype (Table 1). The holotype of *T. mutilatus* is in a deplorable state because of its mounting conditions: it has an oxidized minuten pin that crosses the thorax from bottom to top. However, we were able to observe most of the characters we were looking for. The definition of each species is supplemented by a table of measurements and indices (Supp. file 8) and with high-quality images (Figs 8 A–C, 9 A–C, 10 A–C) available for consultation on AntWeb (http://www.antweb.org) for *T. mutilatus* (CASENT0915903) and *T. carranca* sp. nov. (MFCE014593).

Morphometric data (Supp. file 8)

HL = 0.90 (0.88–0.97), HW = 1.09 (1.06–1.16), IfW = 0.75 (0.74–0.81), FTM = 1.17 (1.10–1.23), TTM = 0.43 (0.40–0.46), SL = 0.73 (0.72–0.77), PrW = 0.69 (0.68–0.79), WL = 1.45 (1.36–1.58), MFL = 0.97 (0.95–1.06), PW = 0.86 (0.84–0.97), PL = 0.55 (0.53–0.64), TASL = 0.57 (0.57–0.68), GL = 1.85 (1.69–2.24), BLCM = 3.48 (3.36–3.87), TBL = 4.75 (4.52–5.43), CI = 120.73 (118.52–122.50), FTI = 107.07 (103.09–108.33), TLTI = 39.39 (37.11–41.18), IfI = 68.69 (68.00–71.84).

Biology

Two colonies were collected inside an abandoned carton termite nest on the ground, cavities commonly used by *Thaumatomyrmex* species for nesting (Santos *et al.* 2010; Jahyny *et al.* 2015). Other nests we have discovered were located at the base of shrubs and some had the entrance ornated with exuviae of Dermestidae larvae (Insecta, Coleoptera), Penicillata trichomes (Myriapoda, Diplopoda) and some other arthropod body parts (Fig. 11A). We only saw the foragers coming back to the nest carrying Zygentoma (Insecta) (Fig. 11B), a curculionid weevil (Coleptera, Curculionidae) and other unidentifiable material. The foraging was solitary and nocturnal, initiating after sunset and all foragers returning to the nest shortly after sunrise (Andrade *et al.* unpublished data). The predation of Zygentoma (Muniz *et al.* unpublished data) is a surprising new dietary item for ants and for the genus *Thaumatomyrmex*, most

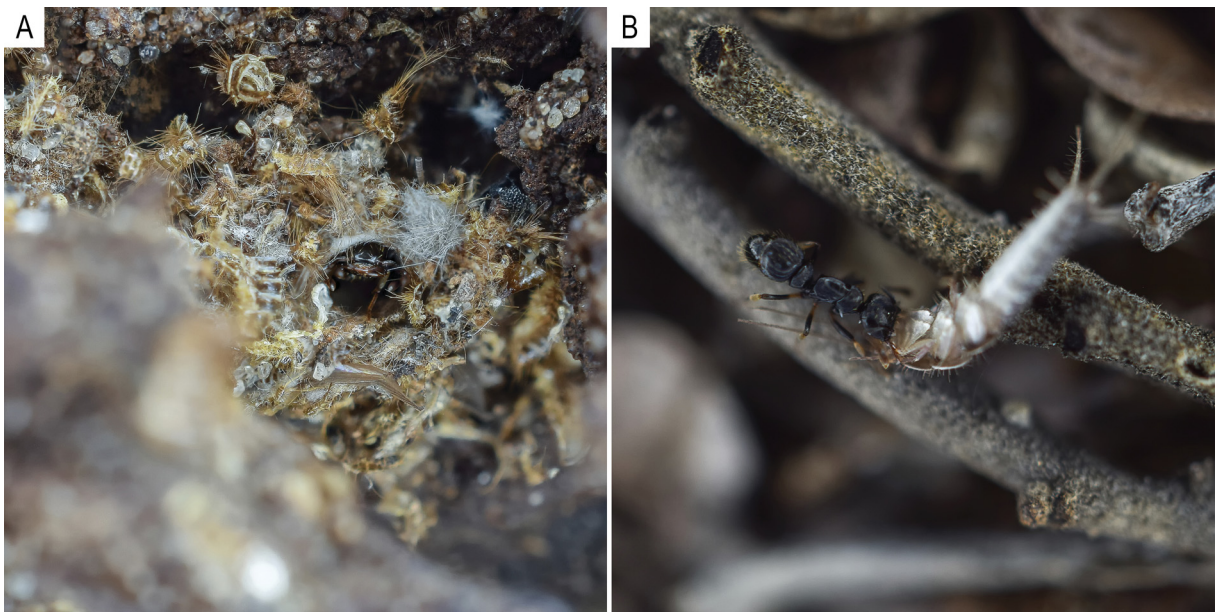


Fig. 11. Field images of *Thaumatomyrmex carranca* sp. nov. **A**. A worker sticks her head out at the ornate nest entrance. **B**. Forager carrying a Zygentoma.

Table 1. Definition based on the holotype of *Thaumatomyrmex carranca* sp. nov. compared to our definition of the holotype of *T. mutilatus* Mayr, 1887 and *T. contumax* Kempf, 1975. The autapomorphies of *T. carranca* sp. nov. are indicated in bold.

Body part	Character	***T. carranca* sp. nov. - TBL = 4.75 mm**	***T. mutilatus* - TBL = 4.61 mm**	***T. contumax* - TBL = 4.08 mm**
Head	General format in full face-view (without considering the eyes and mandibles)	Head wider than long (CI: 121), can be inserted into a rectangle	Head subquadrate, slightly broader than longer (CI: 106)	Head wider than long (CI: 119), can be inserted into a rectangle
Mandibles	Teeth number in addition to the denticle at the base of the first tooth	**3** (some specimens have a 4th smaller tooth bonded to the base of the 3rd one)	4	4
	Size and position of 3rd long tooth	**Mandibles, when closed, the 3rd long teeth are far apart and never touch or cross each other (TLTI: 39)**	Mandibles, when closed, the 3rd long teeth are very close together, touching or crossing each other moderately in front of the clypeus (TLTI: 50)	Mandibles, when closed, the 3rd long teeth cross each other distinctly in front of the clypeus (TLTI: 55)
	Size and position of 2nd long tooth	**Mandibles, when closed, the 2nd long tooth does not overpass the opposite 3rd long tooth but almost reaches its tip and does not reach the opposite torular lobe**	Mandibles, when closed, the 2nd long tooth reaches (exceeds a little bit) the middle of the opposite 3rd long tooth and does not reach the opposite torular lobe	Mandibles, when closed, the 2nd long tooth overpass the base of the opposite 3rd long tooth and reaches the opposite torular lobe
Mandibles and head	Relation FTM (First Tooth Measurement) and HW (Head Width)	Mandibles, when closed, the 1st tooth of the mandible exceeds the opposite genae (FTI: 107)	Mandibles, when closed, the 1st tooth of the mandible does not exceed the opposite genae (FTI: 95)	Mandibles, when closed, the 1st tooth of the mandible exceeds the opposite genae (FTI: 114)
Pronotum	Shape in posterior view	In posterior view, the lateral and dorsal margins of the pronotum form a rounded shape, not triangular	In posterior view, the lateral and dorsal margins of the pronotum form a subtriangular shape with rounded tip	In posterior view, the lateral and dorsal margins of the pronotum form a rounded shape, not triangular
Legs	Coloration (general pattern for the femurs, tibiae, and tarsi)	All coxae and femurs darker than the trochanters, tibiae, and the tarsi, the tibiae are the lightest segments	Procoxae and metacoxae darker than the mesocoxae and the other segments	Procoxae, metacoxae and femurs darker than mesocoxae, the trochanters, tibiae, and the tarsi, the tibiae are the lightest segments

of whose studied species are specialized predators of Penicillata (Myriapoda, Diplopoda) (Brandão *et al.* 1991; Jahyny *et al.* 2008; Rabeling *et al.* 2012). But the presence of trichomes of Penicillata at the nest entrance indicates that *T. carranca* sp. nov. may very likely also feed on them. It is possible that the different head shape and mandibular morphology of *T. carranca* compared to the other *Thaumatomyrmex* species allow for another prey spectrum in the special environment of the dunes. More field observations are essential to better understand the trophic ecology of *Thaumatomyrmex* spp. The two collected colonies were composed respectively of nine and 12 workers and some immatures. It is another species of *Thaumatomyrmex* without a gyne female morphotype, and which forms very small colonies (Jahyny *et al.* 2008).

Geographic distribution and habitat

All the specimens of *Thaumatomyrmex carranca* sp. nov. were collected in the dune fields of the municipality of Casa Nova, State of Bahia, northeastern Brazil, within the São Francisco Dunes District (SFD), Sandy Caatinga subprovince, Caatinga province, Caatinga dominion (CAAD; sensu Moro *et al.* 2024) (Fig. 12). The regional climate is hot and semi-arid, type "BSh" in the Köppen-Geiger-Pohl system (Alvares *et al.* 2013). Conditions vary sharply from day to night, from up to 44°C and 22% relative humidity at the hottest hour to about 15°C and 100% before dawn. Dune vegetation comprises deciduous thorn scrub, herbaceous plants, bromeliads, and cacti forming islands of litter (Fig. 13A–B).

Discussion

Molecular studies have confirmed the monophyly of the genus *Thaumatomyrmex* (Schmidt 2013; Doré *et al.* 2025), and based on our morphological study, we can provide information on probable synapomorphies for the genus. According to the study by Schmidt & Shattuck (2014) on the subfamily Ponerinae, the characters 1/1, 3/1 and 4/1 are not convergent with any genus of Ponerini. Some species of the genus *Platythyrea* Roger, 1863 of the tribe Platythyreini Emery, 1901, have torular lobes widely separated (which corresponds to our character 4/1), but they do not protrude anteriorly over the clypeus as in *Thaumatomyrmex* (character 3/1). So, the characters 1/1, 3/1 and 4/1 are probably synapomorphies of the genus studied here. The general form of the mandibles of *Thaumatomyrmex* could be considered as a synapomorphy too. They are different from those of all other ponerine species, they are elongated, thin, and curved inward with three long spiniform teeth and a denticle as the 2nd tooth (absent in *T. cochlearis*), some species have one additional small basal tooth. This mandible with five teeth, the 2nd one a simple denticle, is plesiomorphic in *Thaumatomyrmex*. The losses of the 2nd and/or the 5th tooth are apomorphic (characters 11/1 and 12/1 respectively). In *T. carranca* sp. nov., some specimens have a very small 5th tooth, the size of a denticle, very close to the base of the 4th tooth, which confirms the transformational series of this character. In this population the two character states are still present, but there are more individuals that lost the 5th tooth. The loss of the 5th in *T. carranca* sp. nov. is an autapomorphy of the species within the *mutilatus* clade, but other *Thaumatomyrmex* species have convergently lost this 5th tooth. It is a character which deserves to be better studied, especially the form of the base of the mandibles.

Thaumatomyrmex zeteki and *T. fraxini*, two of the smallest species of the genus, have, convergently, no more stout setae on the posterior apex of the protibia (character 33/1). The absence of stout setae on the posterior surface of the probasitarsal notch is an autopomorphy of *T. fraxini* (character 34/1) while these stout setae are present in the other species of *Thaumatomyrmex* and in *Belonopelta deletrix* (character 34/0). However, these species of *Thaumatomyrmex* have only two/three aligned setae parallel to the strigil comb (character 35/1) while *B. deletrix* has a row of many (more than 10) stout setae (character 35/0). The characters 34 and 35 correspond to the character 72 of Keller (2011) that considered the states: (0) absent, (1) single and (2) row parallel to strigil comb. This character 72 must be refined, especially indicating the number of stout setae and it is why we could not define our character 35/1 as a synapomorphy of the genus *Thaumatomyrmex*.

If the lack of a mesotibial spur is a synapomorphy of the clade (*Thaumatomyrmex paludis* + (*T. soesilae* + *T. fraxini*)) (character 36/1), it is not possible to determine that the simple form (not pectinate) of the mesotibial spur (character 37/1), is a synapomorphy of the genus *Thaumatomyrmex*. Further study of these diagnostic characters in the Ponerinae is needed.

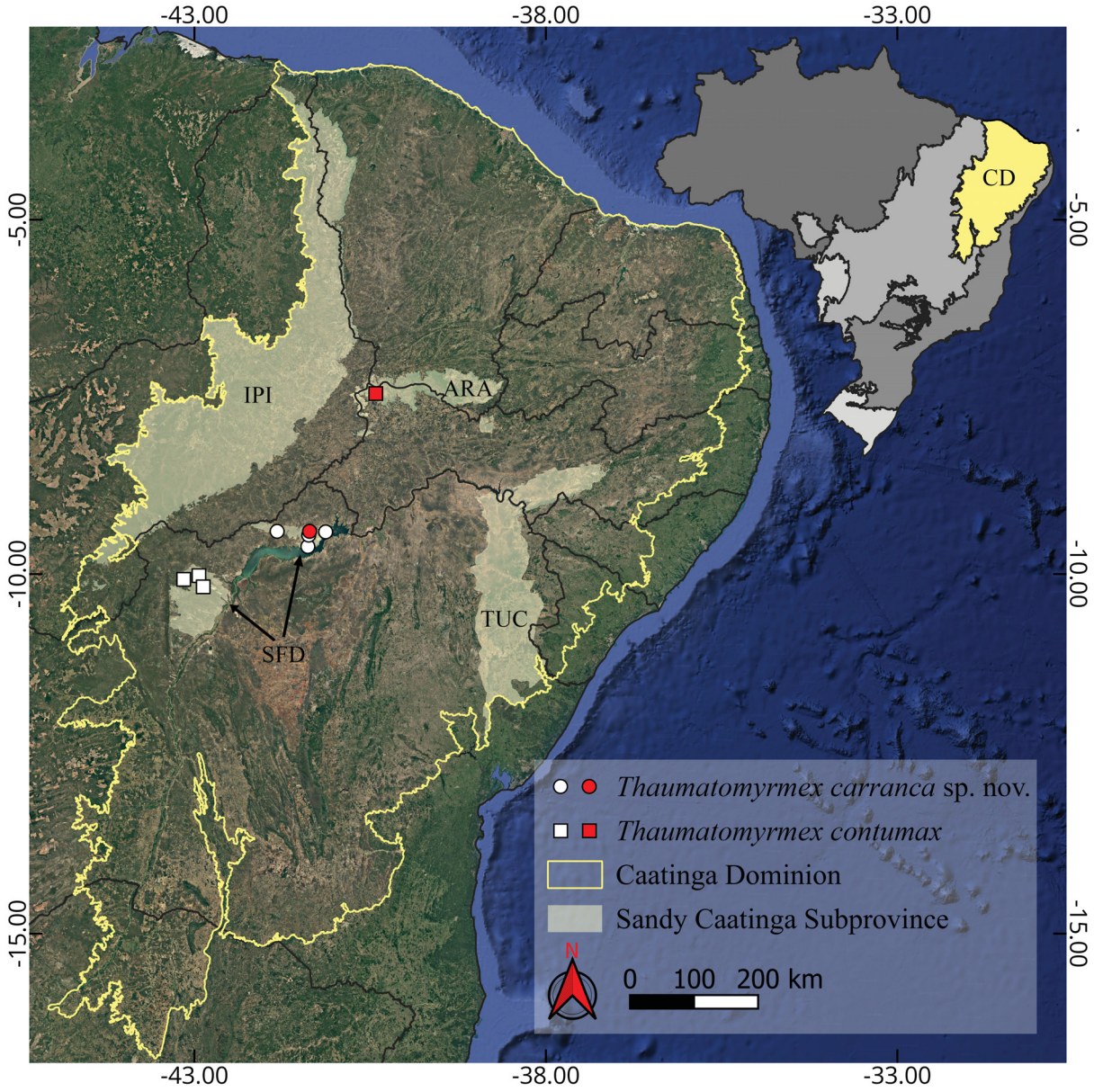


Fig. 12. Distribution map of *Thaumatomyrmex carranca* sp. nov. and *Thaumatomyrmex contumax* Kempf, 1975, for specimens that we have formally identified as belonging to these species. The small map shows Brazil and the different Dominions that comprise it, with Dominion Caatinga (CD) highlighted. The large map shows part of northeastern Brazil with the boundaries of the Caatinga Dominion (CD) and the districts of the Sandy Caatinga Subprovince highlighted. ARA = Araripe District; CD = Caatinga Dominion; IPI = Ibiapara-Piauí District; SFD = São Francisco Dunes District; TUC = Tucano-Jatobá District. Red marks: holotype localities. White marks: other specimens' locality.

The cladistic analyses show that *Thaumatomyrmex zeteki* is the sister taxon to all the other eight species analysed. The sister clade (*T. atrox* to *T. carranca* sp. nov.) is supported by the synapomorphies presence of costulae perpendicular to the hypostomal carina on the head ventral face (14/1) and the absence of the gyne female morphotype (48/1). For character 48/1, we have no data for *T. cochlearis* or *T. mutilatus*. For species that we assigned to *T. soesilae* or *T. paludis*, only females of the worker morphotype were present in the colonies collected (Celante unpublished data), and it is very likely that these species reproduce via *gamergates*, mated, egg-laying workers (sensu Peeters & Crewe, 1985), rather than via females of the gyne morphotype. In the genus, at least one other species, which can be attributed to the "*ferox* taxonomic group", has gynes in addition to *T. zeteki* (Jahyny *et al.* 2015). While *T. atrox*, *T. carranca*, *T. contumax* and *T. fraxini* have no gynes, and they must reproduce through gamergates (Jahyny *et al.* 2008, 2015; Jahyny & Celante unpublished data), which must be the case for most of the species of the genus. To have gynes is plesiomorphic in Ponerinae and Ponerini. This character (48/0) must be plesiomorphic in *Thaumatomyrmex,* and raises the question on how many times the gynes were lost in this genus.

The clade (*Thaumatomyrmex paludis* to *T. carranca* sp. nov.) is supported by the synapomorphies 22/1, with transformation in *T. mutilatus* (22/2) and in the clade (*T. soeasilae* + *T. fraxini*) (22/3), and 23/1, however with a reversal in *T. soesilae* (23/0) which mesonotum is differentiated from the propodeum but in a much more subtle form.

The cladistic analysis reveals that the *mutilatus* species group forms a clade defined by the following 12 synapomorphies: 2/2, 8/1, 9/2, 17/0, 20/1, 27/1, 30/1, 31/1, 39/1, 44/1, 45/1 and 46/1.

Within the *mutilatus* clade, the character 43/1, groups the new species *Thaumatomyrmex carranca* sp. nov. with *T. contumax*, which are found in the same region and biome, while *T. mutilatus* occurs much further south in another region and biome.

The *cochlearis* species group has four valid species *Thaumatomyrmex bariay* Fontenla Rizo, 1995, *Thaumatomyrmex cochlearis* Creighton, 1928, *Thaumatomyrmex mandibularis* Baroni Urbani & De

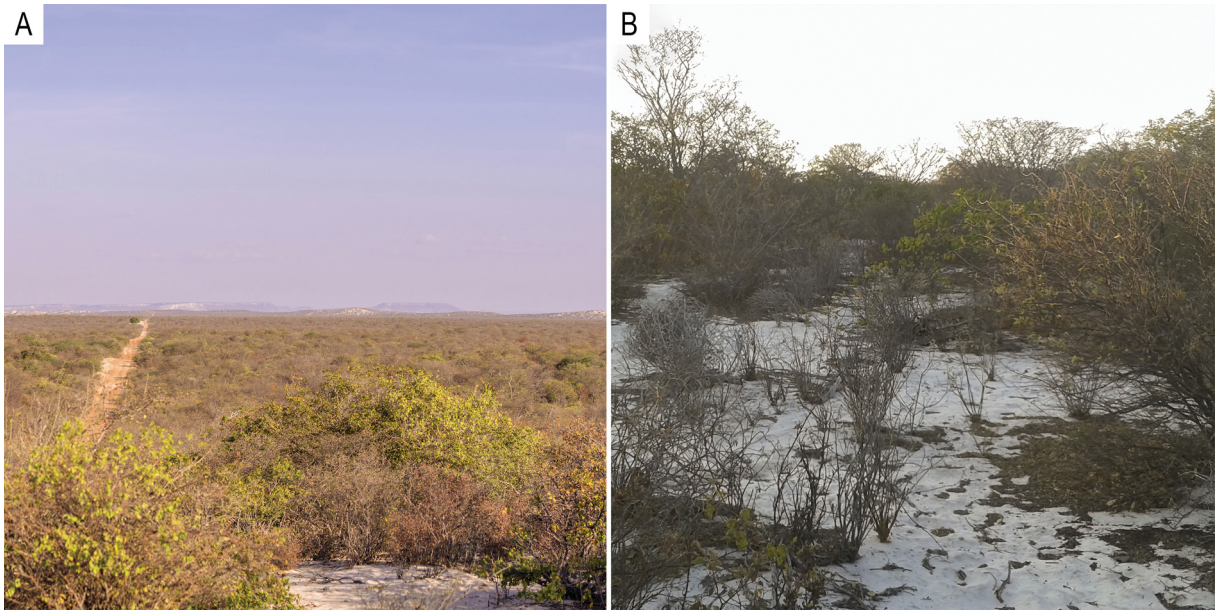


Fig. 13. The Casa Nova dune fields. **A**. Some dunes with their vegetation. **B**. Vegetation and plant litter. Photographies by Benoit J.B. Jahyny.

Andrade, 2003 and *Thaumatomyrmex nageli* Baroni Urbani & De Andrade, 2003, but this group was represented by the sole species *T. cochlearis* in our analysis, which has the following autapomorphies: 2/3 and 12/1. These autapomorphies, the sculpture of the cuticle (2/3) and the lack of the 2nd tooth (12/1), which is a simple denticle in the other species examined, must be the synapomorphies of the *cochlearis*-group thus forming a clade.

The *mutilatus* species-group (*mutilatus* clade) and *Thaumatomyrmex cochlearis* clade were nested among species or groups of species of the "*ferox* species-group", which makes the taxonomic "*ferox* species group" defined by Kempf (1975) a non-natural group as suspected by Jahyny *et al.* (2015). The sculpture of the cuticle (character 2) was one of the characters used by Kempf (1975) to separate the species in the three groups. The smooth and shining cuticle with discreet marks, is plesiomorphic in the genus and the marked sculptures are apomorphic and are the synapomorphies of the *mutilatus* clade (character 2/2) and certainly of the *cochlearis* species-group too (character 2/3). Kempf (1975) divided the "*ferox* species-group" in two species subgroups (*T. zeteki* + *T. paludis*) and (*T. atrox* + *T. ferox* + *T. manni*), our cladistic analyse not support at least the first subgroup too.

The presence of a dorsal stridulatory organ on the pretergite of abdominal segment IV was considered as a character of the genus (Schmidt & Shattuck, 2014). However, our cladistic analysis shows that it is plesiomorphic (character 39/0), with its reduction in *T. fraxini* (character 40/1), while its absence is a synapomorphy of the *mutilatus* clade (character 39/1).

Biogeographic analysis

The newly described species, *Thaumatomyrmex carranca* sp. nov., and *T. contumax* both belong to the Caatinga Dominion, and can occupy the same district (São Francisco Dune District), but each in one of two dune complexes, separated by a 90 km wide strip of crystalline Caatinga. Our analysis revealed that the DEC+J model was the most consistent in explaining the geographical distribution of the genus, and the time-calibrated Bayesian analysis indicated the divergence times of its internal nodes. Although exploratory and requiring corroboration by more robust molecular analyses of species of *Thaumatomyrmex*, these data suggest that the initial divergence of the genus occurred approximately 48.7 Ma in the Eocene, within the North Neotropical area. During this period, South America was still disconnected from North America, and higher oceanic levels promoted isolated areas due to marine transgression in the Amazon basin (De La Parra *et al.* 2021). In this context, around 39 Ma, a divergence occurred between the common ancestor and *T. zeteki*, which occupies an isolated portion of areas within what would become the connection between South and North America, in the North Neotropical region. The common ancestor of *T. carranca* and *T. atrox* expanded its biogeographical distribution, likely through dispersal, occupying both the North Neotropical and Amazonian areas (Fig. 1). This broad distribution persisted in the ancestor of *T. atrox* and *T. cochlearis*, which diverged approximately 19 Ma in the Miocene, a period when marine regression in the Amazon basin allowed greater connectivity between areas. Part of this ancestor, which inhabited the continental regions of North America and Amazonia, likely dispersed to the Caribbean Plate, an event that gave rise to *T. cochlearis* about 19 Ma. Some biogeographic hypotheses (e.g., IturraldeVinent & MacPhee 2023) propose the existence of an emerged terrestrial connection (GAARlandia–Greater Antilles RiseAves Ridge) in the Caribbean Basin around 35–32 Ma. Although this land bridge predates the divergence between *T. atrox* and *T. cochlearis*, the presence of their common ancestor is estimated to date back to about 35 Ma, thus coinciding with the existence of such a possible continental connection.

The ancestor of *Thaumatomyrmex carranca* sp. nov. and *T. fraxini* diverged around 31 Ma in the Oligocene, restricting its distribution to the Amazonian area. In its ancestral Amazonian range, the *T. paludis* plus *T. soesilae* lineage persisted, with *T. paludis* diverging approximately 21 Ma in the Amazon, and *T. fraxini* and *T. soesilae* diverging around 11 Ma. The ancestor of *T. fraxini* dispersed to the Atlantic

Forest, likely via a northern route in Brazil, as this species currently occupies the northern Atlantic Forest region.

The *Thaumatomyrmex carranca* sp. nov. plus *T. mutilatus* lineage dispersed to the Atlantic Forest around 31 Ma, likely through a southern route in Brazil. Around 10 Ma, a divergence led to *T. mutilatus* in the Southern Atlantic Forest, and the ancestor of *T. carranca* + *T. contumax*. This ancestor dispersed to the Caatinga, possibly due to the formation of a dry diagonal of South America, suggesting the potential for undescribed species in the Cerrado Biome. Finally, this ancestor diverged into the two species approximately 4 Ma, consistent with the estimated period for the formation of the Caatinga Biome (Fernandes *et al.* 2022). Additionally, the genus occupation of the Atlantic Forest may have occurred at two distinct times.

New species recognition

Thaumatomyrmex carranca sp. nov. can be easily differentiated from any other species of the genus and can be clearly assigned to the *mutilatus* species-group as defined in this study. Within the *mutilatus*-group, *T. carranca* sp. nov. can be differentiated since it is the only known species of this group with a mandible composed of three long teeth (in addition to the denticle at the base of the first tooth) versus four seen in *T. mutilatus* and *T. contumax*. However, as noted above, some specimens possess a fourth very small tooth close to the base of the third tooth but due to its very small size it cannot be confused with the well-developed teeth seen in the other two species. *Thaumatomyrmex carranca* sp. nov. is also differentiated from the other two by the length of its third long tooth, which is relatively short (TLTI: 38.8 ± 1.45 [37.1–41.18]). In *T. carranca*, when the mandibles are closed, the third long teeth are far from each other, neither cross nor meet, while in *T. mutilatus* they meet each other at the middle of the clypeus (TLTI: 50.55) and in *T. contumax* they cross each other distinctly in front of the clypeus (TLTI: 55.1). It can be noted, that in addition to geographical proximity, the species *T. carranca* sp. nov. and *T. contumax* are morphologically closer to each other than to *T. mutilatus*.

Geographic distribution

The Casa Nova dune fields extend over about 70 km in a west-northwest direction from the left bank of the São Francisco River and are one of the two dune complexes of the São Francisco Dunes District (SFD), in the Sandy Caatinga Subprovince, a sandy sedimentary terrain of the Caatinga Dominion (CAAD - sensu Moro *et al.* 2024) (Fig. 12). The SFD is one of the nine inland paleo-dune systems of South America, East of the Andes (Tripaldi & Zarate 2016).

The SFD has two separate dune complexes, the Casa Nova dune complex at the northeast side and the Barra/Pilão Arcado dune complex at the southwest side (Fig. 12). The two dune complexes are separated by a less than 100 km wide strip of crystalline terrains in the Southern Depressão Sertaneja District of the Depressão Sertaneja Subprovince (Moro *et al.* 2024). *Thaumatomyrmex carranca* sp. nov. was only found in the Casa Nova dune fields and no other *Thaumatomyrmex* species was encountered there. While in the West, we found only *T. contumax* in the Barra/Pilão Arcado dune complex (Fig. 12), whose holotype was collected in the Araripe District which is also part of the Sandy Caatinga Subprovince (Moro *et al.* 2024) (Fig. 12). Moreover, we have not found *T. carranca* in the East of the dunes, in the Southern Depressão Sertaneja district, surrounding the SFD, nor on the other side of the São Francisco River in the Chapada Diamantina province (Fig. 12). Based on this data *T. carranca* could be, for now, considered endemic to the Casa Nova dune complex thus extending the list of endemic species of this region.

Thaumatomyrmex carranca sp. nov. does not live in sympatry with another *Thaumatomyrmex* species although there are some cases of sympatry in the genus (Jahyny *et al.* 2015). *Thaumatomyrmex carranca* and *T. contumax* each live in their own dune complex, and it is one more case of animal taxon pairs with

an allopatric distribution pattern between two separated dunes complexes (Recoder & Rodrigues, 2020), the first one described for a non-vertebrate. The evolutionary and natural history of these two taxa should contribute to the understanding of the origin and evolution of these dune complexes.

Conservation assessment and threats

Given that the range of *Thaumatomyrmex carranca* sp. nov. appears to be restricted to the Casa Nova dune complex, an area spanning only 1900 km², its conservation status is a pressing concern as its habitat is currently under threat. The São Francisco Dune District SFD, as the other districts of the Caatinga Dominion (CAAD; sensu Moro *et al.* 2024), harbours endemic flora and fauna (Rocha *et al.* 2004; Queiroz *et al.* 2017; Recoder & Rodrigues 2020). Eleven new arthropod species, including a new family of Strepsiptera (Insecta), have been described from this region (Xavier & Rocha 2001; Bravo 2007, 2008; Del Río & Lanteri 2007; Bravo *et al.* 2009; Galileo & Martins 2010; Vieira *et al.* 2012; Menezes & Bravo 2013; Celante *et al.* 2024a, 2024b, 2025). These findings designate the SFD as a priority area for biodiversity conservation (Ministério do Meio Ambiente 2002; Mesquita *et al.* 2017), demanding further taxonomic and ecological studies to understand and protect the biodiversity of this unique environment. Of the 15 endemic Squamata species occurring in the SFD (Recoder & Rodrigues 2020), ten are classified under the "Endangered (EN)" extinction risk category, meeting B1ab(iii) criteria, with declining range and habitat quality being the main risks (Instituto Chico Mendes de Conservação da Biodiversidade 2018). Despite being located within the boundaries of two Environmental Protection Areas (Área de Proteção Ambiental: APA)—the APA Lago de Sobradinho for the Casa Nova dune complex and the APA Dunas e Veredas do Baixo-Médio São Francisco for the Barra/Pilão Arcado dune complex (6800 km²)—these dune complexes are not immune to anthropogenic disturbance. Threats to the SFD can be categorized as acute disturbances (AD), which cause rapid and easily perceived environmental changes, and chronic anthropogenic disturbances (CAD), which act more subtly but continuously, becoming evident only after careful observation (Melo 2017).

Among ADs, habitat loss due to deforestation and fragmentation for solar panel and/or wind turbine installations (already observed near the dune fields) or by fires (more frequently observed in the Barra/Pilão Arcado dune complex) are prominent. The main CADs in this ecoregion include the extraction of wood for firewood (subsistence use) and/or fence construction, and extensive livestock grazing. Although the impacts of these CADs are not well studied in the region, their effects are likely less severe than those caused by the removal of vegetation cover from large areas for wind/solar farms or other activities requiring vegetation suppression. Evidence of past attempts to utilize these sandy soils is visible in both dune complexes. Parts of the dunes are owned by families and communities whose livelihoods depend on them, and whose interests align with preserving this environment. However, the intentions of large landowners and corporations acquiring land in the dunes remain uncertain and may represent the greatest potential threat. As observed with Squamates, it is expected that other organisms also depend on a relative environmental stability and, consequently, on the conservation of these paleodunes to maintain stable populations. Further investigations into the population status of *T. carranca* sp. nov. within the dunes, its geographic distribution, and threats to its habitat are necessary to determine its conservation status.

Conclusion

Thaumatomyrmex carranca sp. nov. represents the first described species of the *mutilatus*-group since 1975, following revision of Kempf for the genus, which included the description of *T. contumax* based on a unique worker (Kempf, 1975). Kempf, with only 18 specimens of *T. mutilatus*, noted variations among those collected in Agudos (São Paulo State, Brazil) compared to others, but opted against describing new species due to the limited number of individuals examined. Today, a larger number of *mutilatus*-group specimens are deposited in entomological collections, primarily in Brazil. This increased sampling provides a better understanding of character variability or stability, suggesting that

other new species are likely to be described soon. A clear link exists between the specialized mandibular morphology of *T. carranca* and its environment, particularly prey availability, when compared to other *Thaumatomyrmex*. Future studies on the biology of each species will further elucidate these morphological differences. Despite *T. carranca* being the first ant species described from the SFD, other new ant species have been identified from this region, and the identity of more species are currently under analysis. Collectively, these discoveries can contribute to the protection of this district of the Caatinga Dominion and enhance our understanding of South American biogeography. We have also proposed the first phylogeny of the genus, based on morphological data. The provided matrix will enable other researchers to incorporate data from newly described species, thus enriching future phylogenetic studies to better understand the evolution of characters and species groups. This morphological phylogeny can also be tested with molecular data to further understand the evolutionary history and biogeography of this genus. The genus *Thaumatomyrmex* appears to be a promising model for a better understanding of Neotropical Region biogeography.

Authors contribution

Conceptualization: BJBJ, GLC, MAGF. Data curation: BJBJ, GLC, RVDA. Formal analysis: BJBJ, GLC, MAGF. Funding acquisition: BJBJ, MAGF. Investigation: BJBJ, GLC, RVDA, SL. Methodology: BJBJ, GLC, MAGF. Project administration: BJBJ, MAGF. Resources: BJBJ. Supervision: BJBJ, MAGF. Validation: BJBJ, GLC, MAGF. Visualization: GLC, MAGF. Writing - original draft: BJBJ, GLC, MAGF. Writing - review and editing: BJBJ, FHG, GLC, MAGF, RVDA, SL.

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Supplementary file

Supp. file 1. Drawing of a worker of *Thaumatomyrmex carranca* sp. nov. with the double-headed arrows illustrating the measurements used in this study. https://doi.org/10.5852/ejt.2026.1119.3354.14682

Supp. file 2. List of the ten specimens, all of the worker caste, used for the phylogenetic analysis. https://doi.org/10.5852/ejt.2026.1119.3354.14683

Supp. file 3. List of the morphological character and their respective character states, for the cladistic analyses of the nine species of *Thaumatomyrmex* with the out-group *B. deletrix*. https://doi.org/10.5852/ejt.2026.1119.3354.14684

Supp. file 4. Character matrix in NEXUS format. https://doi.org/10.5852/ejt.2026.1119.3354.14685

Supp. file 5. Locality and and the corresponding biogeographic zone according to Morrone et al. (2022) and Morrone (2001) of specimens of the ten species used in this study. https://doi.org/10.5852/ejt.2026.1119.3354.14686

Supp. file 6. Analytical scripts, parameters, and outputs of the phylogenetic and biogeographic analyses. https://doi.org/10.5852/ejt.2026.1119.3354.14687

Supp. file 7. Revised Kempf 1975's diagnose of the *Thaumatomyrmex mutilatus* species-group for the female of the worker morphotype with the autapomorphies indicated in bold. https://doi.org/10.5852/ejt.2026.1119.3354.14688

Supp. file 8. Morphometric data of *Thaumatomyrmex carranca* sp. nov. and our own morphometric data of the holotype of *Thaumatomyrmex mutilatus* Mayr, 1887 and *Thaumatomyrmex contumax* Kempf, 1975. The measurements are expressed in millimetres to two decimal places. "n" represents the number of workers measured for T. carranca sp. nov. (the holotype and the nine paratypes) and we give the mean and standard deviation (SD). https://doi.org/10.5852/ejt.2026.1119.3354.14689