



## Monograph

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# Large ants are not easy – the taxonomy of *Dinoponera* Roger (Hymenoptera: Formicidae: Ponerinae)

Amanda Martins DIAS<sup>1,\*</sup> & John Edwin LATTKE<sup>2</sup>

<sup>1,2</sup> Universidade Federal do Paraná, Departamento de Zoologia, Curitiba, Paraná, Brazil.

\* Corresponding author: [amandamdbio@gmail.com](mailto:amandamdbio@gmail.com)

<sup>2</sup> Email: [lattke@ufpr.br](mailto:lattke@ufpr.br)

<sup>1</sup> [urn:lsid:zoobank.org:author:D8E29645-E8DC-419D-ADFB-7ECA76541FCD](https://zoobank.org/author:D8E29645-E8DC-419D-ADFB-7ECA76541FCD)

<sup>2</sup> [urn:lsid:zoobank.org:author:7AE0D94C-619B-4E77-B16F-3F18731EE390](https://zoobank.org/author:7AE0D94C-619B-4E77-B16F-3F18731EE390)

**Abstract.** The taxonomy of the giant ants of the genus *Dinoponera* is revised based on female and male morphology. Eight species are recognized. *Dinoponera nicinha* sp. nov., from Amazonas and Rondônia, Brazil, is described and *D. grandis* (Guérin-Méneville, 1838) is revived. The species *D. australis* Emery, 1901 and *D. snellingi* Lenhart, Dash & Mackay, 2013, plus the subspecies *D. australis bucki* Borgmeier, 1937 and *D. australis nigricolor* Borgmeier, 1937 are synonymized under *D. grandis* sp. rev. An unnamed and unidentified male is reported. In general, male morphology has greater and more discrete variation than in females, but they are scarce in museum collections. Species distributions are updated and illustrated, the genus ranging from southern Colombia to northern Argentina, with no reliable records from the Guiana Shield and all nominal species occurring in Brazil. Intraspecific variation and natural history are discussed. New illustrated identification keys are provided for both sexes. Future studies should address the collection of fresh specimens for molecular work and to assess the conservation status of several species and populations.

**Keywords.** Cryptic species, gamergate, predatory ants, South America, threatened ants.

Dias A.M. & Lattke J.E. 2021. Large ants are not easy – the taxonomy of *Dinoponera* Roger (Hymenoptera: Formicidae: Ponerinae). *European Journal of Taxonomy* 784: 1–66. <https://doi.org/10.5852/ejt.2021.784.1603>

## Introduction

Ants of the ponerine ant genus *Dinoponera* Roger, 1861 may have a body length exceeding 3.5 cm, making them the genus with the largest known ant workers. They are exclusively South American, with their center of diversity in Brazil, the only country where all described species can be found. *Dinoponera* was described by J. Roger (1861) to include *Ponera gigantea* Perty, 1833 and *Ponera grandis* Guérin-Méneville, 1838, the latter being considered a junior synonym by Roger. According to the principle of taxonomic priority, *Dinoponera gigantea* was defined as the valid name of the species (Bequaert 1926). Since then, several authors have used variations in size, integument brightness, petiole shape and male color to name such forms as subspecies and varieties of *D. gigantea* (Emery 1901; Santschi 1921, 1928;

Borgmeier 1937). Borgmeier (1937) raised one variety to species, *D. australis* Emery, 1901, on account of male morphological differences.

The first taxonomic revision of *Dinoponera* was carried out by Kempf (1971). He elevated several subspecies and varieties previously described by Emery (1901) and Santschi (1921) to species, providing detailed descriptions and increasing the number of species from two to seven. One of the species he described, *D. opaca* Kempf, 1971, was later synonymized by Kempf (1975) himself. The taxonomy of the group remained untouched until Lenhart *et al.* (2013) revised the genus. These authors described two new species as well as the male of one known species. Schmidt (2013) found the genus to be the sister group to *Pachycondyla* Smith, 1858 using molecular data. Schmidt & Shattuck (2014) provided a morphological and natural history synopsis of the genus. Tozetto & Latke (2020) described, imaged and analyzed the genitals of several species of *Dinoponera* in a comparative study.

Despite these studies, significant problems still overshadow the taxonomy of *Dinoponera*. Despite their spectacular large size, a trait that would conceivably make them attractive to even general insect collectors, there are surprisingly few specimens of these ants in collections. This relative dearth of specimens negatively affects both our knowledge regarding their distribution and about the intra- and interspecific variability of the species. Another problem concerns the species only known by one sex, such as *D. hispidula* Lenhart, Dash & Mackay, 2013, *D. mutica* Emery, 1901 (only females) and *D. snellingi* Lenhart, Dash & Mackay, 2013 (only males). Here we revise the species of *Dinoponera*, using the largest amount yet studied of females and males, mostly from Brazilian institutional collections. We describe a new species, revive one name and synonymize two species and two subspecies. We also redescribe the known species, discuss their morphological variability and natural history, and provide distribution maps and images for all species. We also provide new identification keys for females and males that take intraspecific variability into account.

## Material and methods

### Repositories

We examined 1145 specimens of *Dinoponera* from the following institutions:

- CASC = California Academy of Sciences, San Francisco, California, USA
- CPDC = Centro de Pesquisas do Cacau, Comissão Executiva do Plano de Lavoura Cacaueira, Ilhéus, Bahia, Brazil
- DZUP = Departamento de Zoologia da Universidade Federal do Paraná, Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
- ICNC = Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá DC, Colombia
- INPA = Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil
- MCSN = Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy (one type examined by images available at [www.antweb.org](http://www.antweb.org))
- MCZC = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
- MNHNP = Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Asunción, Paraguay
- MPEG = Museu Paraense Emílio Goeldi, Belém, Pará, Brazil
- MZSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
- UEG = Laboratório de Pesquisa Ecológica e Educação Científica, Universidade Estadual de Goiás, Anápolis, Goiás, Brazil
- UEMS = Laboratório de Ecologia Comportamental, Universidade Estadual do Mato Grosso do Sul, Dourados, Mato Grosso do Sul, Brazil
- UFES = Laboratório de Biodiversidade de Insetos (LABI), Universidade Federal do Espírito Santo, Vitória, Espírito Santo, Brazil

UFGD	=	Museu da Biodiversidade, Universidade Federal da Grande Dourados, Dourados, Mato Grosso do Sul, Brazil
UFOPA	=	Centro de Formação Interdisciplinar (CFI), Universidade Federal do Oeste do Pará, Santarém, Pará, Brazil
UFRGS	=	Laboratório de Ecologia de Interações, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil
UFRN	=	Laboratório de Biologia Comportamental, Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte, Brazil
UFSC	=	Laboratório de Biologia de Formigas, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil
UFU	=	Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil
UFV	=	Laboratório de Ecologia de Comunidades, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil
ZSM	=	Zoologische Staatssammlung München, Munich, Bavaria, Germany
ZUFMS	=	Coleção Zoológica de Referência da Universidade Federal de Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul, Brazil

All legible label data was transcribed for the ‘Material examined’ section of each species account. Quotes of label text that could not easily be made to conform to the presentation format of the journal are provided within citation marks. In the case of two or more sequential series of specimens sharing some data, the term ‘same locality as for preceding’ was used when just locality data is shared, and the term ‘same collection data as for preceding’ was used when more information is shared. Different pieces of information were transcribed normally after these terms, if applicable. The symbol ♀ is used to indicate females (workers) and ♂ for males.

### Morphology

All female specimens, regardless of reproductive status, are referred to as females. Terms used for external morphology follow Bolton (1994), Keller (2011) and Boudinot (2015). Surface sculpturing follows Harris (1979) and hair position follows Wilson (1955). Male genitalia follow Boudinot (2013) and Tozetto & Lattke (2020). The male genital capsule was extracted from all possible specimens, except when it already lacked genitalia or gaster. Most of the dissections were done previously by Tozetto & Lattke (2020) and additional dissections followed their procedures.

Characters that are shared throughout the genus are not repeated in each species description. For the head the term “internal” is used for structures closest to the median longitudinal cephalic axis and “external” for structures closest to the lateral cephalic margin.

Cold light sources are recommended for examining these ants and optics with at least 32× magnification and an ocular micrometer. Dried specimens of *Dinoponera* frequently have layers and deposits of fat on their bodies that obscure the observation of finer sculptural features. The careful use of a fine brush moistened with alcohol may help to dislodge or partially dissolve some of these deposits.

### Measurements

Measurements were taken using a Zeiss Stemi DV4 stereoscope with a micrometer in a 10× ocular lens. All measurements are expressed in mm. Among the criteria used for selecting specimens for measuring we considered those representing the largest and smallest intraspecific variance. The number of measured specimens is placed between parentheses at the beginning of each ‘measurements’ section in the species accounts. The dimensions of type specimens, when measured, are given separately from those of other specimens. Most measurements, indices and their acronyms are based on Lattke (2011), Lenhart *et al.* (2013) and Escárraga *et al.* (2017), and are listed below (Figs 1–2). Each measurement is followed by

‘male’ and/or ‘female’, indicating the sex measured. A spreadsheet with all measurements and indices for each measured specimen is available at [www.zenodo.org](http://www.zenodo.org) (<https://doi.org/10.5281/zenodo.5168830>).

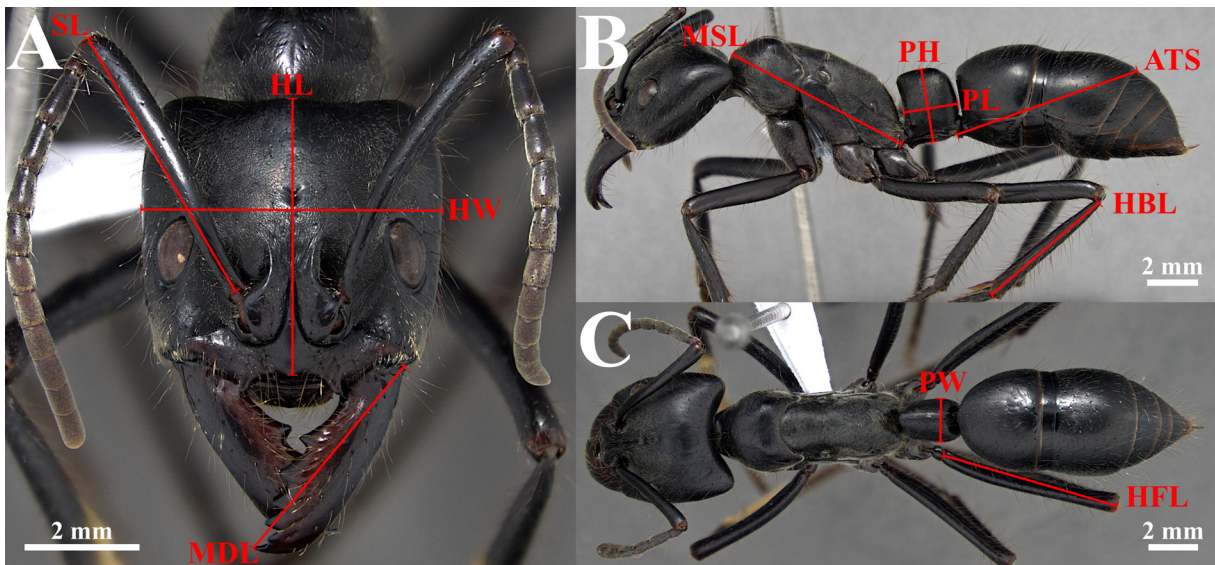
- ASL = Abdominal sternites III and IV, length. In lateral view, a longitudinal line from the anteriormost point of abdominal sternite III to the distal edge of abdominal sternum IV. Male.
- ATS = Abdominal tergites III and IV, size. In lateral view, a diagonal line from the anteriormost point of abdominal sternite III to the posteriormost point of abdominal tergite IV. Female.
- EL = Eye length. In full-face view, maximum length from anterior to posterior margin of compound eye. Male.
- HBL = Hind basitarsus length. Maximum length of hind basitarsus in lateral view. Female.
- HFL = Hind femur length. Maximum length of hind femur in lateral view, from the end articulation with the trochanter to the apex of the articulation with the tibiae. Female and male.
- HL = Head length. In full-face view, a median line traced on the head from the mid-point of the anterior clypeal margin to the posterior head margin. Female and male.
- HW = Head width. Maximum width of head in full-face view. Female.
- HW1 = Head width. Maximum width of the head in full-face view, including the compound eyes. Male.
- LOD = Lateral ocellus diameter. Maximum diameter of lateral ocellus with head positioned such that the anterior and posterior margins of the lateral ocellus are in the same focal plane. Male.
- MDL = Mandible length. In full-face view, a straight line distance from the mandibular apex to the external margin of the articulation with the clypeus. Female and male.
- MOD = Median ocellus diameter. Maximum diameter of median ocellus with head positioned such that the anterior and posterior margins of the median ocellus are in the same focal plane. Male.
- MSL = Mesosoma length. In profile, a diagonal line from the middle point between the anterior and dorsal faces of the pronotum to the posteroventral metapleural corner. Female and male.
- PH = Petiole height. Maximum height of petiole in profile, tracing a transverse line between the dorsal and ventral margins (with sternum). Female and male.
- PL = Petiole length. In profile, maximum longitudinal length between the anterior and posterior margins of the petiolar node. Female.
- PL1 = Petiole length. Length of petiole in profile from the inflection point of the petiolar presclerites to the most posterior point of the sclerite. Male.
- PW = Petiole width. Maximum width of petiole in dorsal view tracing a transverse line between the lateral margins. Female and male.
- SL = Scape length. Maximum length of first antennomere along its anterior surface without the bulbous and radicular constriction. Female and male.
- BL = Body length. Sum of MDL, HL, MSL, PL and ATS. Female.
- BL1 = Body length. Sum of MDL, HL, MSL, PL1 and ASL. Male.

Indices:

- CI = Cephalic index: HW/HL. Female.
- CI1 = Cephalic index: HW1/HL. Male.
- DPI = Dorsal petiole index: PW/PL. Female.
- SEI = Scape–eye index: EL/SL. Male.
- SI = Scape index: SL/HW. Female.
- SI1 = Scape index: SL/HW1. Male.

**Images and maps**

Ant images were obtained using a Zeiss Stereo Discovery V20 stereo microscope with a Zeiss Axiocam 305 color video camera. Due to the enormous size of these ants, separate pictures were taken of the anterior and posterior regions of the body for the lateral and dorsal views. Image stacks were combined

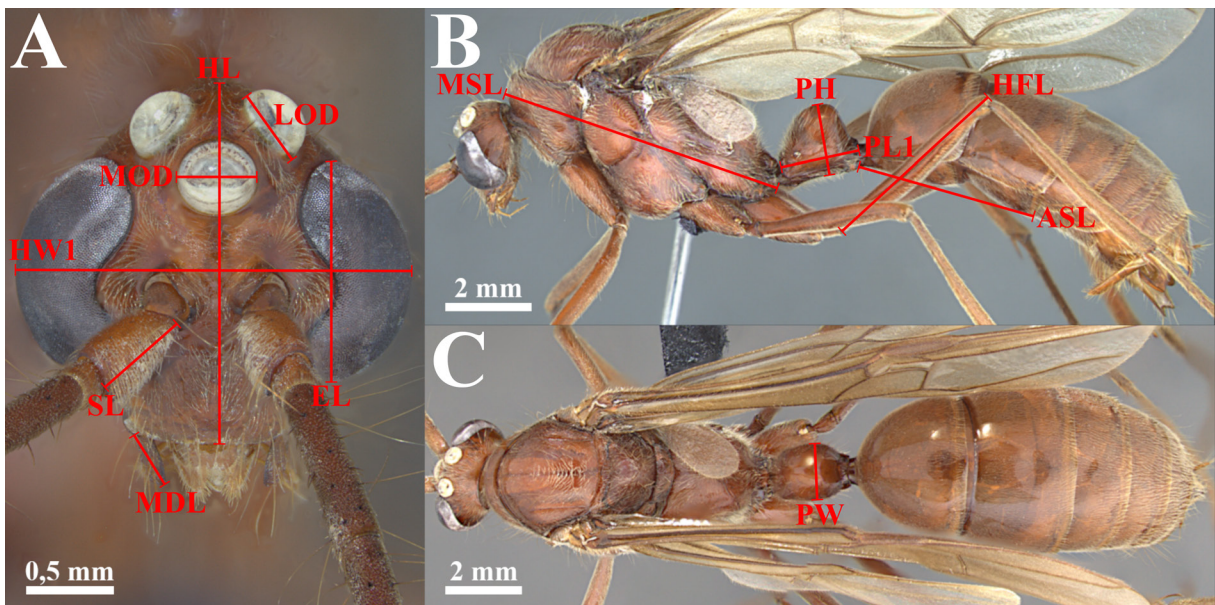


**Fig. 1.** Measurements of *Dinoponera quadriceps* Kempf, 1971, ♀ (DZUP 549811). A. Full-face view. B. Full body in lateral view. C. Full body in dorsal view.

with Zerene Stacker ver. 1.04. Images of the anterior and posterior body regions were stitched with Photoshop CC 14. All images were edited using GIMP ver. 2.10.8.

One specimen of each sex and species was photographed. Additionally, the lectotype and two paralectotypes of *Ponera gigantea*, and the lectotypes of *Dinoponera australis bucki* and *D. australis nigricolor* were also imaged and are available at [www.antweb.org](http://www.antweb.org) (ZSM HYM-25181, ZSM HYM-25182, ZSM HYM-25183, MZSP 65800, and MZSP 65801, respectively).

Distribution maps were created using QGIS ver. 3.16.0 and are based on the locality data for examined specimens only. In the case of specimens with no coordinates the specimen was georeferenced using the central point of the smallest locality on the label using Google Earth.



**Fig. 2.** Measurements of *Dinoponera quadriceps* Kempf, 1971, ♂ (DZUP 549804). A. Full-face view. B. Full body in lateral view. C. Full body in dorsal view.

## Results

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

Genus *Dinoponera* Roger, 1861

*Dinoponera* Roger, 1861: 37 (type species: *Ponera gigantea* Perty, 1833).

### Diagnosis

#### Female

Mandible subtriangular. Anterior clypeal margin with lateral tooth along same longitudinal axis as antennal insertion. Head width greater than 4 mm. Pygidium and hypopygium each with lateral row of stout setae. Body length (BL) longer than 22 mm.

#### Male

Head width, including compound eyes, greater than 2.1 mm. Abdominal pretergite IV with stridulatory file. Meso- and metatibiae each with two pectinate spurs at apex. Easily diagnosed among Ponerinae by the large size (BL1 > 12 mm).

### Redescription

#### Female

MEASUREMENTS. Body length greater than 22 mm. Head width greater than 4 mm.

HEAD. In full-face view sub-rectangular, posterior margin concave, lateral margins subparallel, broadly convex. Anterior clypeal margin in frontal view with lateral tooth along same longitudinal axis as antennal insertion; clypeal disc with longitudinal raised area that narrows posteriorly between frontal lobes. Clypeal disc generally microareolate, laterally smooth to striate; anterior margin with hairs as long as or longer than clypeal tooth; external side of tooth usually with row of short hairs. Anterior tentorial pit region with oblique striae. Frontal lobe covers most of antennal insertion, anteriorly distinctly elevated above surrounding cuticle, internal margin forms fine longitudinal strip below frontal lobe surface; anterior region usually areolate, posterior constriction longitudinally striate. Malar area with varying amounts of longitudinal to oblique striae; if present, striae may reach all of anterior ocular margin and extend to gena, rarely surpassing posterior ocular margin. Gena may be smooth and shining to microareolate and opaque; pilosity variable. Anterior gena with or without longitudinal striae and variable appressed pubescence. Eye elliptical to broadly convex, placed on anterior half of head, occupying less than one-fourth of lateral cephalic margin, not reaching lateral cephalic margin in full-face view; circumocular sulcus present. Appressed pubescence present between eye and frontal lobe, extending posteriorly to frons. Frons smooth and shining to microareolate and opaque; insertion of hairs scalloped, posteriorly fading (particularly noticeable in *D. hispida*); pilosity variable; pubescence usually very sparse on median portion and densest laterally. Longitudinal median sulcus extends from between frontal lobes to frons, ending in tiny depression. Occipital corner strongly microareolate and opaque to smooth and shining (with no visible microsculpture with up to 32× magnification). Antenna with 12 segments. Scape extends beyond posterior margin of head; length usually longer than head width; smooth or microareolate; pilosity variable. First six funicular segments usually widening towards apex; funiculus with sparse hairs longer than scape diameter usually on first segments, rarely on four to five most apical segments; funicular segments densely covered by appressed and very short pubescence. Ventral surface smooth and shining to weakly microareolate or strigulate and opaque; strigulae absent

to covering all surface or just anterior half; pilosity variable; hypostomal tooth usually longitudinally striate. Labrum smooth or weakly transversely striate-punctate; median longitudinal sulcus present or absent. Mandible subtriangular; usually with seven teeth; basal tooth separated from other teeth by diastema; dorsum weakly longitudinally striate only at inner base or along masticatory margin; long hairs present along masticatory margin; integument widely impressed at hair insertions. Mandible ventrally curved in lateral view. Mandible in ventral view with shallow longitudinal basal sulcus that gradually fades apicad; sulcus and row of long, flexuous hairs parallel masticatory margin. Discal area of stipes depressed, usually smooth, sometimes weakly rugulose; usually two long and flexible hairs visible at base. Submentum with weak sulcus at base; discal protuberance present; usually no microsculpturing visible. Palpal formula 4,4.

**MESOSOMA.** In lateral view, dorsal margin slightly divided by promesonotal junction; pronotum slightly higher than rest of mesosoma. Dorsal margin of pronotum in lateral view convex. Pronotum with lateral dorsoposterior swelling of variable convexity; smooth and shining to opaque and microareolate and/or rugulose; lateral surface densely covered by appressed to decumbent pubescence. Anteroventral corner of pronotum rounded, angled or toothed. Propleuron densely punctulate and pubescent. Prosternal process longer than wide. Mesonotal and propodeal dorsal margins in lateral view continuous and widely convex, metanotal groove slightly impressed. Mesopleuron and mesosternum separated by well-developed carina. Anepisternum usually with mesopleural pit next to mesometapleural suture and to metathoracic spiracle. Mesometapleural suture straight and well developed. Metanotal spiracular sclerite ovoid. Dorsal and declivitous propodeal margins in lateral view rounded and continuous; propodeal spiracle opening vertical to oblique and slit-shaped; spiracle at same level as surrounding propodeal surface; metapleural-propodeal suture well-marked and straight, or weak and sinuous. Mesometapleuron and lateral surface of propodeum punctulate; appressed pubescence variable in length and density. Mesonotum and propodeal dorsum usually densely covered with punctulae bearing medially converging pubescence. Mesosoma usually with numerous long hairs, distance between each hair usually less than half length. Coxae, femora and tibiae microareolate or smooth, with long hairs throughout each surface, separated from each other by distance less than half its length. Protibial apex with robust seta and well-developed pectinate spur, spur lamellate on inner base. Protibia with pubescence concentrated on opposing side of robust seta. Meso- and metatibia each with row of robust setae around entire apex, each apex with simple spur and pectinate spur; pubescence more concentrated on opposite surface of pectinate spur. Posterior surface of probasitarsus with basal concavity containing row of dark brown setae and parallel row of fine, light brown hairs; surface covered by thick yellow hairs. Tarsi with dark brown setae concentrated ventrally on apex of each tarsomere. Tarsal claws bidentate, arolium absent.

**METASOMA.** Petiolar node in lateral view usually robust and sub-rectangular; taller than long; lateral surface smooth and shining to microareolate and opaque; anterior margin with short, whitish decumbent hairs. Node longer than broad in dorsal view, narrower than either propodeum or abdominal tergite III; lateral margins subparallel to anterodorsally converging, always with rounded corners; integument shining or opaque. Hairs present in variable density. Posterior surface usually with shallow longitudinal sulcus. Petiolar sternite height in lateral view always higher anteriorly than posteriorly; subpetiolar process anteroventrally projecting; anterior apex rounded or longitudinally carinate. Anterior margin of abdominal tergite III in lateral view broadly convex and vertical; dorsal margin broadly convex; prora discrete and slightly concave ventrally. Gastral spiracles rounded. Abdominal tergite III in dorsal view smooth and shining to microareolate and opaque, with hairs of variable length and density; pubescence either present on entire surface or concentrated only laterally. Abdominal pretergite IV with fine transverse striae, stridulatory file of variable size (usually well-developed in *D. lucida* Emery, 1901 and *D. longipes* Emery, 1901). Pygidium and hypopygidium each with lateral row of stout setae. Apex of hypopygium ending in two robust triangular spines which are usually covered dorsally by pygidium.

**COLOR.** Integument black.

### Male

MEASUREMENTS. Body length (BL1) greater than 12 mm. Head width greater than 2.1 mm.

HEAD. In full-face view ovoid, wider than long. Anterior margin of clypeus with a transverse lamella, concave; surface of clypeal disc with slight swelling. Anterior tentorial pit large. Epistomal sulcus usually broadly convex. Supraclypeal area flat and triangular-shaped, located between antennal sockets. Distance between antennal sockets less than their maximum diameter. Torular arch simple, exposing antennal condyles. Frontal carina reduced to a short median longitudinal swelling between posterior margins of antennal sockets. Eye large and convex, occupying entire lateral cephalic margin; inner margin emarginate at height of antennal socket. Median and lateral ocellus present; lateral ocellus surpassing posterior head margin in full-face view, except in some specimens of *D. grandis*. Posterior margin of head convex. Head punctulate and slightly microareolate, varying from shining to silky sheen; with decumbent to suberect yellowish pubescence; variable density of hairs. Antenna with 13 segments; filiform. Scape wider than all other segments; at least two times as long as pedicel; length approximately half that of third antennal segment. Antenna with appressed pubescence; hairs, if present, only on funiculus. Ventral surface of head varies from microareolate and subopaque to smooth and shining. Mandible reduced, edentate, spoon-shaped in lateral view; weakly punctulate and shiny. Labrum reduced, narrower than labium; anterior margin concave, rarely rounded in *D. quadriceps* Kempf, 1971. Palpal formula 4,3, sometimes 5,3.

MESOSOMA. Pronotum in dorsal view narrow, with concave posterior margin; posterolateral corner acute and bulging. Mesoscutum in dorsal view rounded; with anteromedian longitudinal carina and lateral parapsidal line; notaulus present or absent; in lateral view with convex dorsal margin. Mesopleural sulcus oblique and well-developed; mesopleural pit easily distinguishable, opening anteroventrally. Spiracular sclerite approximately rounded, opening posterodorsally. Scutoscutellar sulcus easily distinguishable and usually scrobiculate. Mesoscutellum in dorsal view with concave anterior margin and straight to convex posterior margin, usually with lateral strigulae; dorsal margin in lateral view strongly convex. Metanotum usually with silky sheen, narrow and sub-rectangular in dorsal view, convex in lateral view; metanotal disc slightly rugulose, laterally strigulate. Metapleuron with oblique median depression at posterior metapleural pit; metapleural pit opening usually facing anteroventrally, except in some specimens of *D. grandis* and *D. lucida*. Metapleuron with anteroventral carina that extends briefly posterodorsally. Metapleural-propodeal suture forms carina that fades dorsally to propodeal spiracle, becoming broad, sometimes scrobiculate, sulcus. Anterior margin of propodeum in dorsal view with median notch; dorsal and declivitous margins of propodeum slightly discontinuous, sometimes separated by weak carina; propodeal spiracle slit-shaped. Mesosoma varies from microareolate and subopaque to smooth and shining, becoming coarsely punctate on declivitous surface of propodeum, except in *D. grandis*; usually with decumbent pubescence; long hairs present or absent. Legs very slightly microareolate and shining; densely pubescent; long hairs present or absent. Protibial apex sometimes with one stout seta; protibial spur well-developed and pectinate with lamellate inner base. Meso- and metatibiae each with two pectinate spurs at apex: one well-developed and the other less developed. Posterior surface of probasitarsus with basal concavity containing row of short setae. Tarsi with decumbent setae, usually more concentrated on apex of each tarsomere; claws bidentate; arolium well-developed. Wings covered by short pubescence. Forewing with pterostigma and following longitudinal veins: C, Sc+R, R, Rs+M, M, M+Cu, Cu and A; crossveins 2r-rs, 2rs-m, 1m-cu and cu-a present. Hindwing with following longitudinal veins: R+Rs, Rs, M+Cu, M, Cu and A; crossveins 1rs-m and cu-a present.

METASOMA. Petiolar node in lateral view with rounded dorsal margin, anterior and posterior margins forming a continuous curve, usually with posterior hump; spiracle oval to rounded. Petiolar sternum continuous, lacking well-developed subpetiolar process, usually longitudinally carinate. In dorsal view longer than wide with rounded corners. Sculpturing varies from microareolate and subopaque to smooth and shining; pubescence and pilosity of variable density. Anterior margin of abdominal tergite



III in lateral view broadly convex and curving posterad. Gastral spiracles oval to rounded. Abdominal pretergite IV with stridulatory file. Well-marked constriction between abdominal segments III and IV; abdominal tergite VIII (pygidium) triangular to spiniform. Cercus apically dilated, with long hairs; hypopygium elongate, posterior margin concave to straight. Sculpturing varies from microareolate and subopaque to smooth and shining; pubescence and pilosity of variable density.

**GENITALIA.** Basal ring in dorsal view trapezoid, with lateral margins converging anteriorly; dorso-anterior margin thicker, forming lateral loop and median invagination; each loop surrounds a fenestra. Basal ring in lateral view with dorsal margin varying from straight to very concave, some species having anterior lobe; anteroventral process varying from rounded to subquadrate to subtriangular. Parameres notably divided in two regions: gonocoxite anteriorly and gonostylus posteriorly; gonostylus varying from broad and rounded to narrow and sharp. Cuspis volsellaris in lateral view finger-like and ventrally torulose, size variable; digitus volsellaris widening posteriorly, ventral margin varying from broadly to strongly concave; posterior region torulose. Penisvalva highly variable among species, with ventral margin serrated.

**COLOR.** Integument in shades of brown, with legs usually lighter.

### Remarks

This genus is rarely mistaken with any other due to its enormous size. *Dinoponera* shares some synapomorphies with *Pachycondyla* Smith, 1858, the most notable being the presence of a row of stout setae on the hypopygium on each side of the sting (Schmidt & Shattuck 2014). However, females of *Pachycondyla* have no tooth on the anterior margin of the clypeus and rarely exceed 2 cm in body length. Neither females nor males of *Pachycondyla* have a stridulatory file on abdominal pretergite IV, a character present in both sexes of *Dinoponera*. A possible karyotypic apomorphy of *Dinoponera* is the presence of a pair of pseudo-acrocentric chromosomes, observed in *D. grandis*, *D. gigantea*, *D. lucida* and *D. quadriceps* (Santos *et al.* 2012).

### Biology

Nests are always constructed in the soil, usually close to the base of trees or in areas shaded by vegetation (Araujo *et al.* 1990; Morgan 1993; Paiva & Brandão 1995; Fourcassié *et al.* 1999; Fourcassié & Oliveira 2002; Peixoto *et al.* 2010). Each nest may have one to thirty entrances, and some may be polydomic (Morgan 1993; Paiva & Brandão 1995; Fourcassié & Oliveira 2002). The entrances may contain branches and loose soil, forming mounds in *D. longipes* (Morgan 1993; Fourcassié *et al.* 1999; Peixoto *et al.* 2010). Nest depth varies from 10 to 143 cm, with species from more arid environments, such as *D. quadriceps* and *D. grandis*, usually having deeper nests. Nests are distributed in patches, and the spatial arrangement within each patch may be random or influenced by intraspecific territorial competition (Araujo *et al.* 1990; Paiva & Brandão 1995; Fourcassié & Oliveira 2002; Vasconcellos *et al.* 2004). Local density of nests can vary from 15 to 180 per hectare (Vasconcellos *et al.* 2004; Tillberg *et al.* 2014). In *D. longipes*, Morgan (1993) estimated an average distance of 35 m between nests.

The average number of workers per colony varies from 13 to 78, and can reach more than 140 in *D. quadriceps* (Paiva & Brandão 1995; Monnin & Peeters 1998; Monnin *et al.* 2003). Division of labour occurs mainly because of age polyethism, with the oldest workers responsible for activities outside the nest (Peixoto *et al.* 2008). Foraging is always solitary, regardless of resource size (Araújo & Rodrigues 2006; Azevedo *et al.* 2014). Their diet is omnivorous, with a preference for angiosperm seeds and living or dead invertebrates (Fourcassié & Oliveira 2002; Araújo & Rodrigues 2006; Peixoto *et al.* 2010; Tillberg *et al.* 2014). Each worker maintains fidelity to a foraging route, with only slight deviations while searching for food (Fourcassié *et al.* 1999; Fourcassié & Oliveira 2002; Vasconcellos *et al.* 2004; Tillberg *et al.* 2014). Studies suggest that spatial orientation occurs mainly through large-scale visual cues (Fourcassié *et al.* 1999; Araújo & Rodrigues 2006; Tillberg *et al.* 2014).

In *Dinoponera* there has been loss of the queen; consequentially, reproduction is carried out by workers called gamergates (Haskins & Zahl 1971; Peeters & Crewe 1984; Araujo *et al.* 1990; Peeters 1991; Peixoto *et al.* 2008). All workers have reproductive potential, but a hierarchical system of dominance guarantees that the colonies are usually monogynous (Monnin & Peeters 1999; Monnin *et al.* 2003; Peixoto *et al.* 2008). Each colony has a cadre of workers of elevated hierarchical status that usually compete with each other for the reproductive role. These workers are often referred to as alpha, beta, gamma, and delta, being defined by the frequency and intensity of specific behaviours (Monnin & Peeters 1999; Peixoto *et al.* 2008). The gamergate is the alpha, the highest status in the colony (Monnin & Peeters 1999). Agonistic interactions performed by workers of higher status usually are blocking, gaster rubbing and gaster curling (Monnin & Peeters 1999; Peixoto *et al.* 2008). When beta, gamma or delta workers lay unfertilized eggs, the gamergate often recognizes them and destroys them by oophagy (Monnin & Peeters 1997). Dominance hierarchy is also determined by age (Araujo *et al.* 1990), as usually only young workers have high level positions (Monnin & Peeters 1999). As workers age their ovaries atrophy and they lose their reproductive capacity (Araujo *et al.* 1990). Thus, a newly emerged worker has a good chance to become a beta and possibly an alpha (Araujo *et al.* 1990; Monnin & Peeters 1999). Gamergates, however, may be relatively old, which suggests that fertilization is an important factor that prevents ovary atrophy (Araujo *et al.* 1990).

Reproduction occurs when a virgin alpha leaves the nest at night and waits for a male to fertilize it (Monnin & Peeters 1998). Male attraction probably occurs through pheromones produced only by alpha females (Monnin & Peeters 1998). After mating, the male genitalia remain attached to the gamergate, ensuring monandry (Monnin & Peeters 1998). A newly fertilized alpha can replace a dead gamergate or found a new colony by fission (Monnin & Peeters 1998). Fission can be gradual, as demonstrated for *D. quadriceps* and *D. lucida* (Peixoto *et al.* 2010; Medeiros & Araújo 2014). Initially the new gamergate and other workers can migrate to a nearby nest and remain in contact with the parental nest. After this polydomous stage, that may continue for months, the two colonies gradually become independent from each other (Peixoto *et al.* 2010; Medeiros & Araújo 2014).

Several invertebrates can inhabit *Dinoponera* nests. The most common taxa are Termitidae, Gastropoda, Corinnidae, Zygentoma, Tenebrionidae, Histeridae, Phoridae, and Isopoda (Paiva & Brandão 1995; Vasconcellos *et al.* 2004). Ants of the genus *Pheidole* Westwood, 1839 are often found in nests of several species of *Dinoponera* (Paiva & Brandão 1995; Vasconcellos *et al.* 2004; Peixoto *et al.* 2010).

### Distribution

*Dinoponera* has been recorded in most Brazilian states except Amapá, Roraima and Rio de Janeiro. The genus also occurs in other countries of South America, such as Colombia, Ecuador, Peru, Bolivia, Paraguay and Argentina (Kempf 1971; Lenhart *et al.* 2013). Lenhart *et al.* (2013) recorded the genus in Guiana, but this single record may be a labeling error, since no other records have been reported throughout the region between the Rio Negro in the Amazon and the Bartica district of Guiana.

### Taxonomic synopsis

*D. gigantea* (Perty, 1833)

*D. grandis* (Guérin-Ménéville, 1838) **revived species**

= *D. australis* Emery, 1901 **syn. nov.**

= *D. australis brevis* Borgmeier, 1937

= *D. australis bucki* Borgmeier, 1937 **syn. nov.**

= *D. australis nigricolor* Borgmeier, 1937 **syn. nov.**

= *D. snellingi* Lenhart, Dash & Mackay, 2013 **syn. nov.**

*D. hispida* Lenhart, Dash & Mackay, 2013

*D. longipes* Emery, 1901

*D. lucida* Emery, 1901

*D. mutica* Emery, 1901

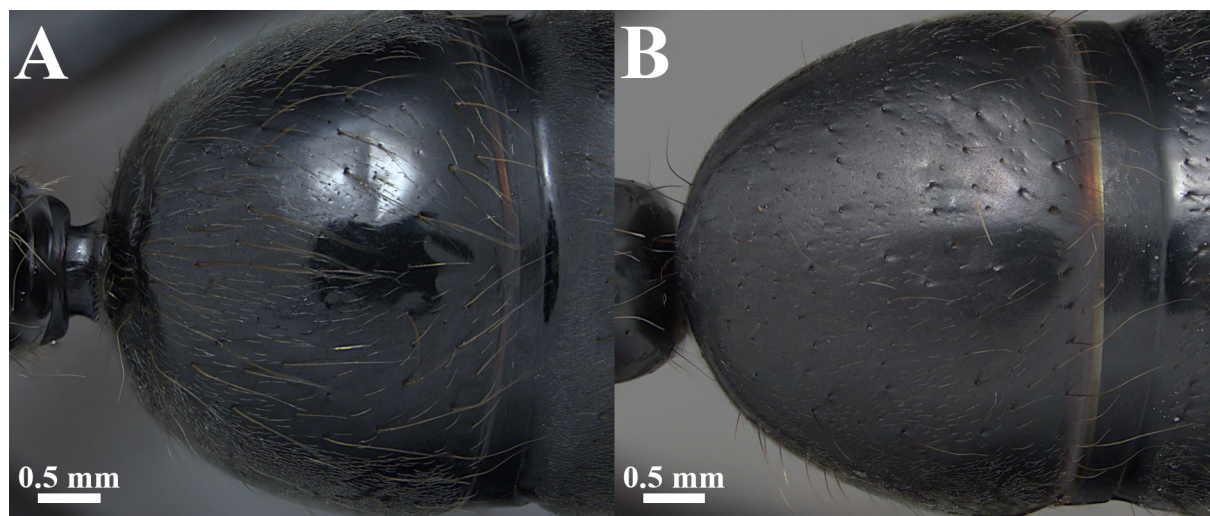
*D. nicinha* sp. nov.

*D. quadriceps* Kempf, 1971

= *D. opaca* Kempf, 1971

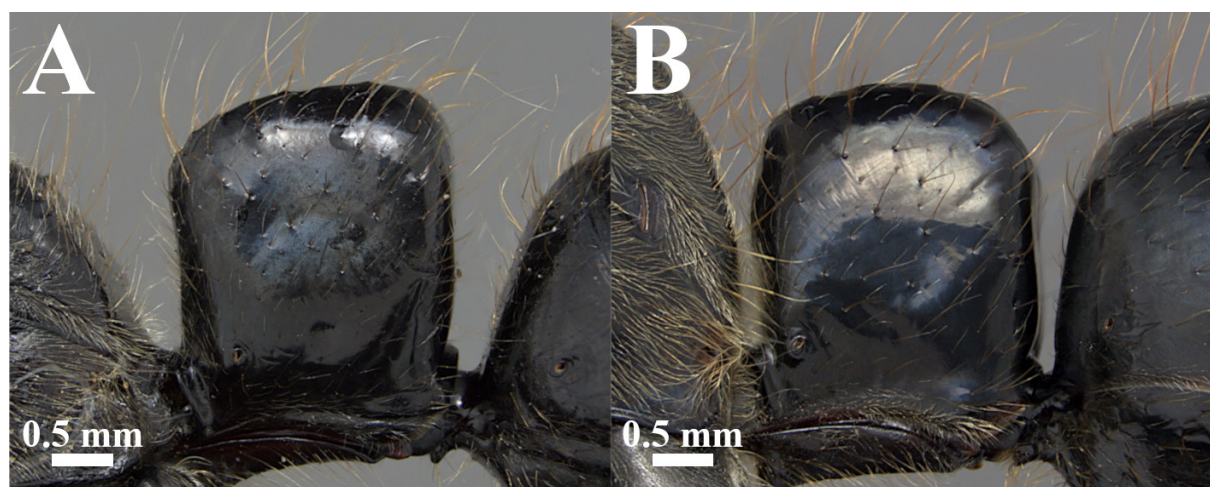
**Key to females of *Dinoponera* Roger, 1861**

1. Integument mostly smooth and shining; microsculpturing not visible on first gastric tergite (best seen at 32× magnification) (Fig. 3A) .....2
- Integument mostly microareolate and opaque; microsculpturing always visible on first gastric tergite (best seen at 32× magnification) (Fig. 3B) .....6



**Fig. 3.** Detail of first gastric tergite microsculpturing. **A.** *Dinoponera mutica* Emery, 1901. **B.** *D. quadriceps* Kempf, 1971.

2. Petiolar node in lateral view with the anterodorsal angle at a level clearly lower than the posterodorsal angle (Fig. 4A). Anteroventral corner of pronotum in lateral view with a tooth or forming an acute angle .....*D. lucida* Emery, 1901 (east of Brazil)
- Petiolar node in lateral view with the anterodorsal angle higher, at the same level as or slightly lower than the posterodorsal angle (Fig. 4B). Anteroventral corner of pronotum in lateral view without a tooth, forming obtuse angle at most .....3



**Fig. 4.** Petiolar node in lateral view. **A.** *Dinoponera lucida* Emery, 1901. **B.** *D. nicinha* sp. nov.

3. Body covered by thick and stiff hairs (Fig. 5A). Ventral surface of head posteriorly with well-marked transverse strigulae posteriorly .....*D. hispida* Lenhart, Dash & Mackay, 2013 (Brazil: Pará)  
 – Body covered by slender and flexuous hairs (Fig. 5B). Ventral surface of head posteriorly without strigulae; if strigulae present, only anterolaterally .....4

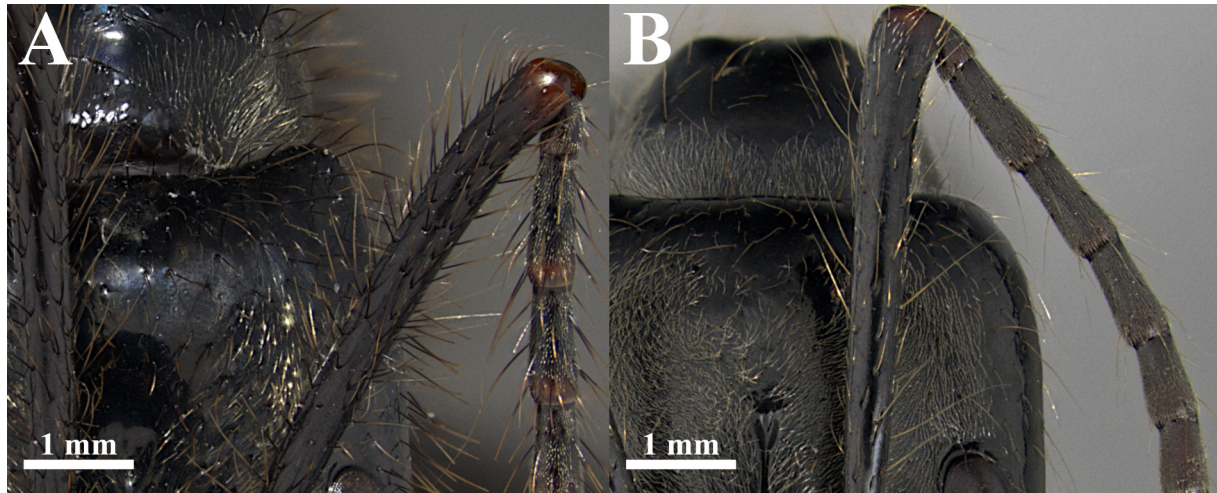


Fig. 5. Detail of pilosity types. A. *Dinoponera hispida* Lenhart, Dash & Mackay, 2013. B. *D. mutica* Emery, 1901.

4. Petiolar node in lateral view with its anterodorsal angle at a level clearly higher than the posterodorsal angle (Fig. 6A) .....*D. longipes* Emery, 1901 (northwest of Brazil, Colombia and Peru)  
 – Petiolar node in lateral view with its anterodorsal angle slightly lower or at approximately the same level as the posterodorsal angle (Fig. 6B) .....5

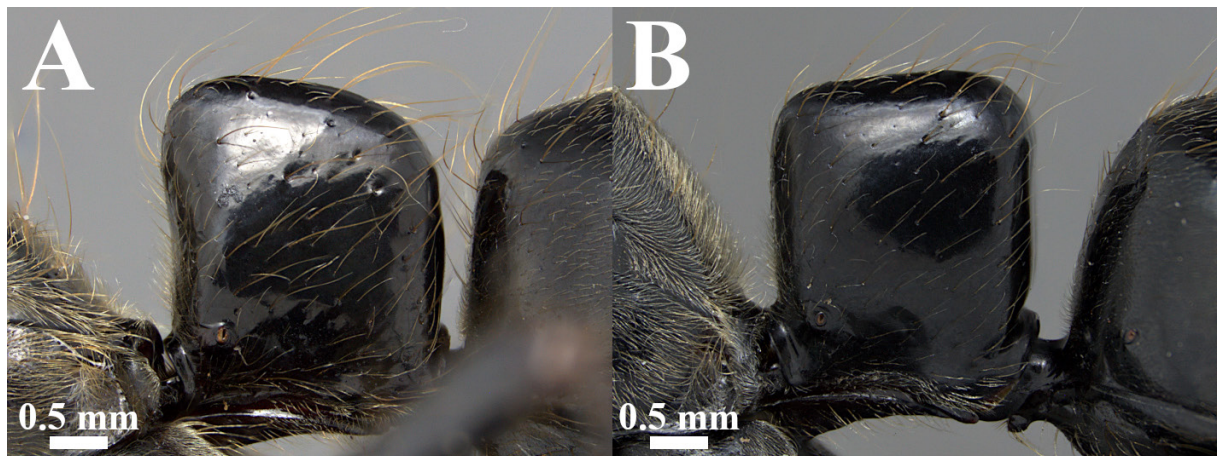


Fig. 6. Petiolar node in lateral view. A. *Dinoponera longipes* Emery, 1901. B. *D. mutica* Emery, 1901.

5. Dorsal margin of petiolar node in lateral view convex (Fig. 7A). Golden pilosity present on frons and first gastric tergite. First gastric tergite with sparse pubescence on entire surface .....  
 .....*D. nicinha* sp. nov. (northwest of Brazil)
- Dorsal margin of petiolar node in lateral view straight (Fig. 7B). Chestnut pilosity present on frons and first gastric tergite. First gastric tergite with dense pubescence laterally .....  
 .....*D. mutica* Emery, 1901 (northwest and midwest of Brazil, Bolivia and Paraguay)

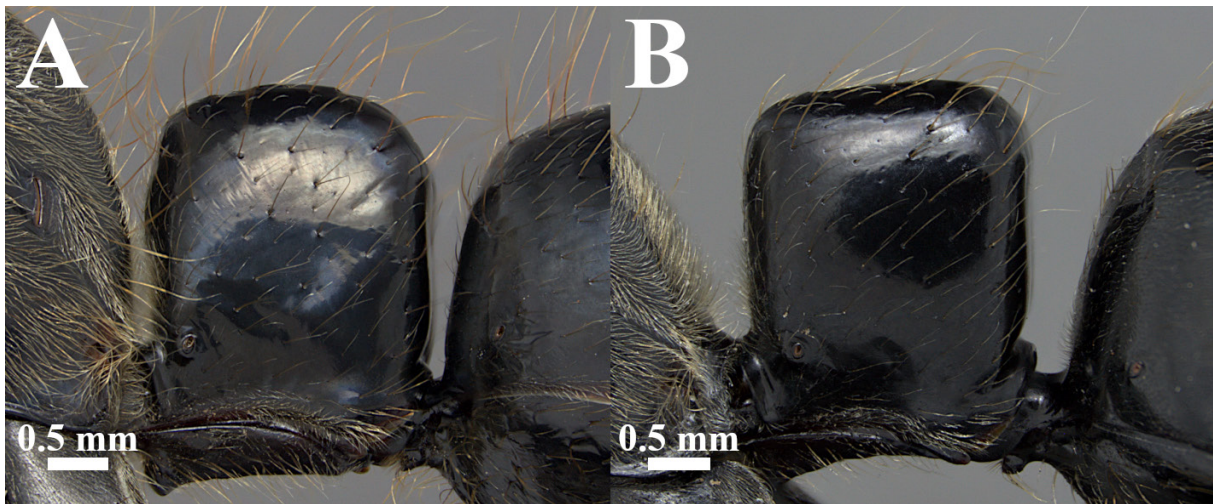


Fig. 7. Petiolar node in lateral view. A. *Dinoponera nicinha* sp. nov. B. *D. mutica* Emery, 1901.

6. Malar area with striae that reach entire anterior eye margin (Fig. 8A); hind basitarsus less than 6 mm long .....*D. grandis* (Guérin-Ménéville, 1838) (Argentina, Bolivia, Brazil and Paraguay)
- Malar area without striae or with weak striae that do not reach entire anterior eye margin (Fig. 8B); hind basitarsus usually more than 6 mm long .....7

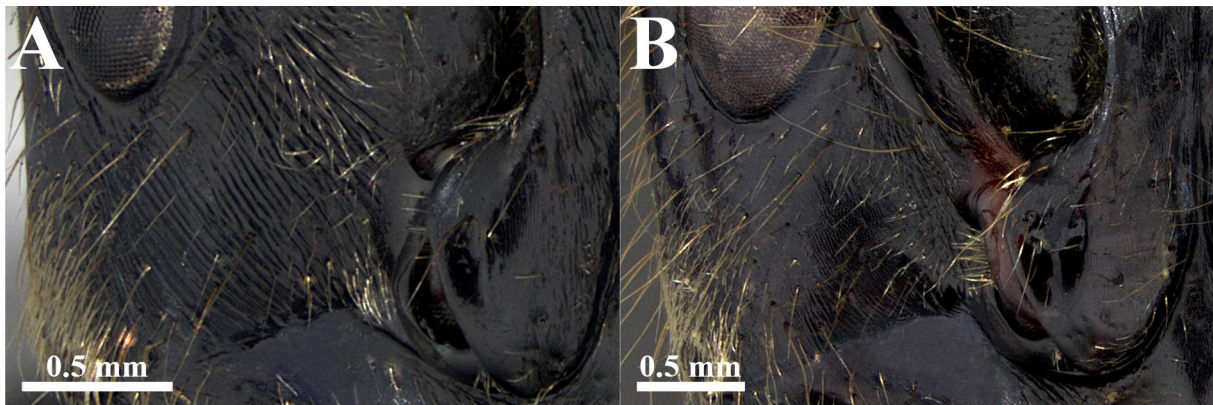
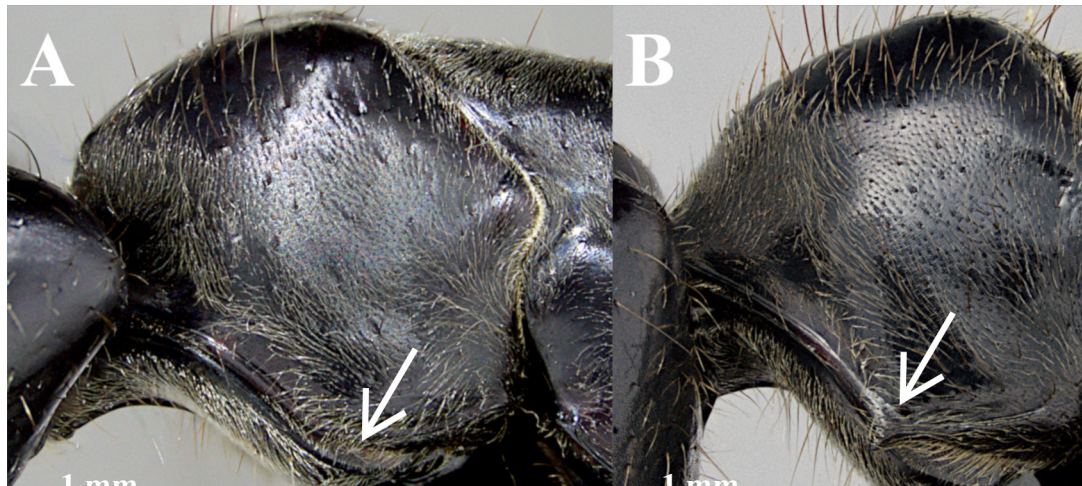


Fig. 8. Detail of malar area striae. A. *Dinoponera grandis* (Guérin-Ménéville, 1838). B. *D. gigantea* (Perty, 1833).

7. Anteroventral corner of pronotum in lateral view without tooth, at most forming an obtuse angle (Fig. 9A). Ventral surface of head without striae .....  
 .....*D. quadriceps* Kempf, 1971 (northeast of Brazil)
- Anteroventral corner of pronotum in lateral view with tooth or forming acute angle (Fig. 9B).  
 Ventral surface of head with striae at least on the anterior half .....  
 .....*D. gigantea* (Perty, 1833) (north of Brazil, Colombia and Peru)



**Fig. 9.** Anteroventral corner of pronotum in lateral view. **A.** *Dinoponera quadriceps* Kempf, 1971. **B.** *D. gigantea* (Perty, 1833).

**Key to males of *Dinoponera* Roger, 1861**

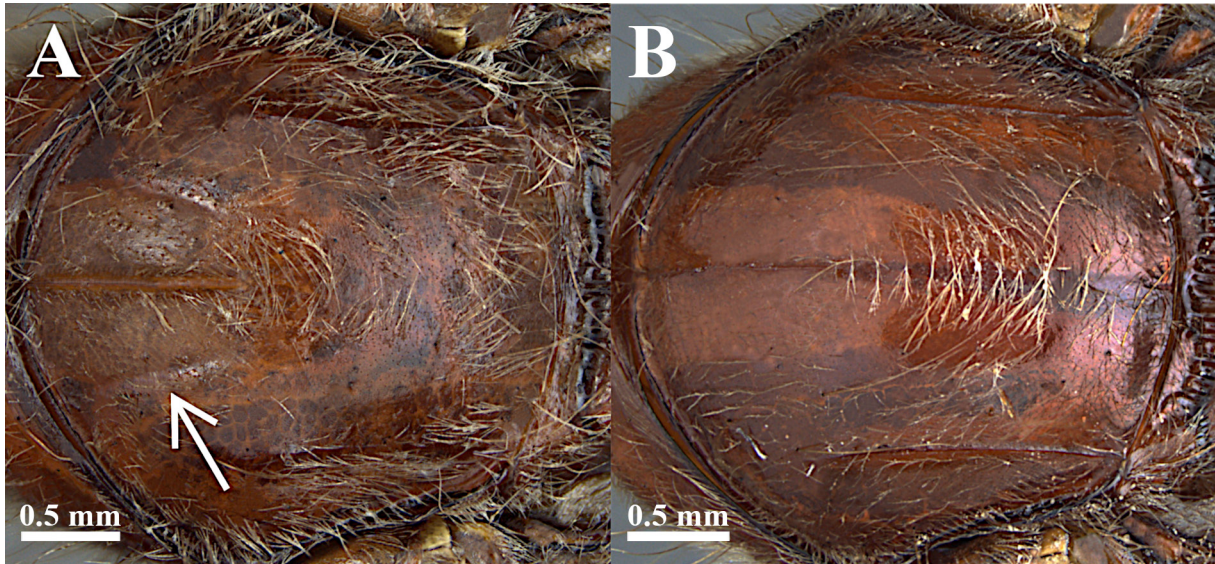
For detailed images of genitalia see Tozetto & Lattke (2020).

1. Antenna without long hairs (Fig. 10A). Anteroventral corner of volsella projecting ventrally .....  
 .....*D. grandis* (Guérin-Ménéville, 1838) (Argentina, Bolivia, Brazil and Paraguay)
- Antenna with long suberect to erect hairs, clearly longer than maximum scape diameter (Fig. 10B). Anteroventral corner of volsella bidentate .....2
- Antenna with thick and stiff decumbent hairs, usually shorter than maximum scape diameter (Fig. 10C). Anteroventral corner of volsella projecting anteriorly .....3



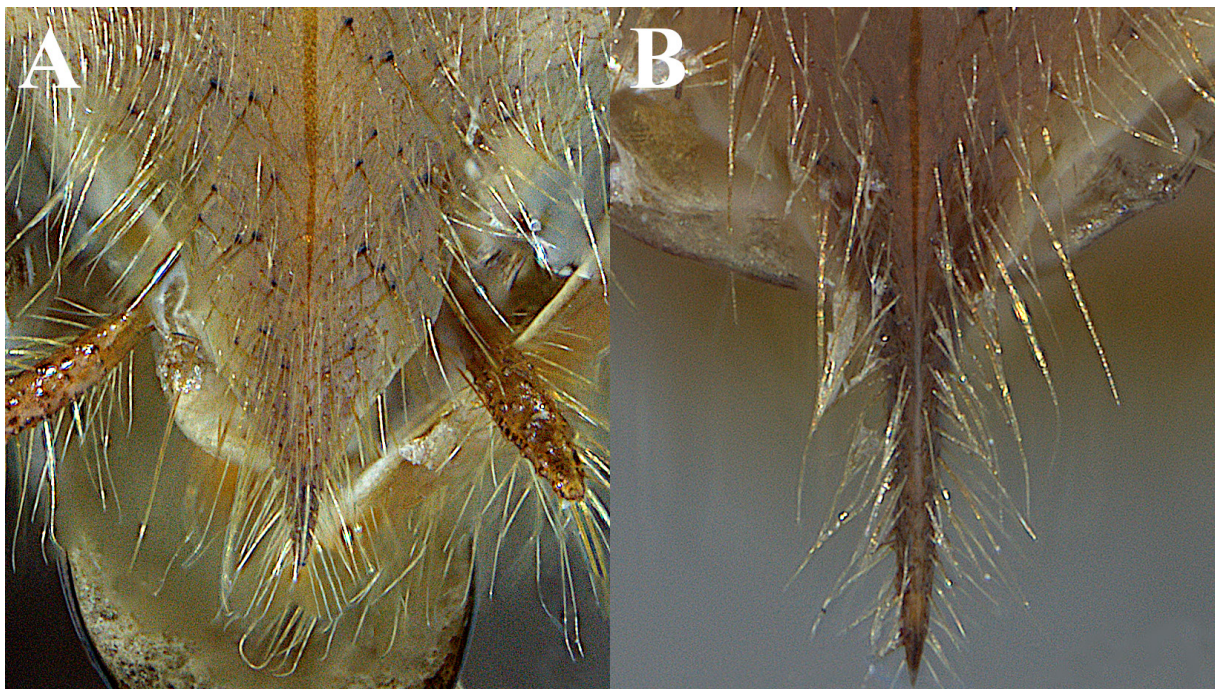
**Fig. 10.** Detail of antenna pilosity. **A.** *Dinoponera grandis* (Guérin-Ménéville, 1838). **B.** *D. quadriceps* Kempf, 1971. **C.** *Dinoponera* morphospecies 1.

2. Notaulus slightly impressed on mesoscutum (Fig. 11A). Penisvalva ending in rounded apex. Gaster with sparse suberect long hairs .....*D. gigantea* (Perty, 1833) (north of Brazil, Colombia and Peru)  
 – Notaulus absent (Fig. 11B). Penisvalva ending in a subacute apex. Gaster without long hairs ..  
 .....*D. quadriceps* Kempf, 1971 (northeast of Brazil)



**Fig. 11.** A. Detail of mesoscutum with notaulus (see arrow) in *Dinoponera gigantea* (Perty, 1833). B. Detail of mesoscutum without notaulus in *D. quadriceps* Kempf, 1971.

3. Abdominal tergite VIII triangular, with a very sharp apex (Fig. 12A). Penisvalva ending in a posteroventral lobe .....*D. lucida* Emery, 1901 (east of Brazil)  
 – Abdominal tergite VIII spiniform (Fig. 12B). Penisvalva without a posteroventral lobe .....4



**Fig. 12.** Detail of abdominal tergite VIII. A. *Dinoponera lucida* Emery, 1901. B. *Dinoponera* morphospecies 1. No scale.

4. Penisvalva in lateral view with a rounded apex; anteroventral corner with a long and very sharp spine .....*Dinoponera* morphospecies 1 (northwest of Brazil)  
– Penisvalva in lateral view with a wedge-shaped apex; anteroventral corner with a tooth .....  
.....*D. longipes* Emery, 1901 (northwest of Brazil, Colombia and Peru)

*Dinoponera gigantea* (Perty, 1833)

Figs 13–14, 28A

*Ponera gigantea* Perty, 1833: 135, pl. 27 fig. 3 (♀).

*Dinoponera gigantea* – Kempf 1971: 372, figs 8–12 (male description). — Lenhart, Dash & Mackay 2013: 139, figs 1d, 4a, f, k, 5c, 9c, 10c, 11c (redescription, male genitals, key). — Tozetto & Latke 2020: 5, figs 2–3, 6 (male genitals).

**Diagnosis**

**Female**

Malar area with weak longitudinal to oblique striae that do not reach anterior eye margin. Ventral head surface mostly strigulate. Anteroventral corner of pronotum in lateral view with tooth or acute angle. Dorsum of pronotum and abdominal tergite III strongly microareolate and opaque. Body length (BL) greater than 27 mm.

**Male**

Antenna with long suberect to erect hairs, clearly longer than maximum scape diameter. Mesoscutum with notaulus. Gastral tergites with long hairs. Dorsal margin of basal ring in lateral view broadly convex to straight.

**Material examined**

**Lectotype**

BRAZIL – **Amazonas** • ♀; Rio Negro; ZSM HYM-25181.

**Paralectotypes** (2 ♀♀)

BRAZIL – **Amazonas** • 1 ♀; ZSM HYM-25182 • 1 ♀; ZSM HYM-25183.

**Non-type specimens** (143 ♀♀, 4 ♂♂)

BRAZIL – **Amazonas** • 1 ♀; Manaus; D. Dias leg.; MZSP. – **Maranhão** • 2 ♀♀; Balsas, Gerais das Balsas; 9 Nov. 1999; Brandão, Yamamoto and Dietz leg.; lote 23; MZSP • 1 ♀; Carolina; 7.21533° S, 47.31867° W; 2 Oct. 2015; H. Vasconcelos and J. Maravalhas leg.; DZUP • 1 ♀; Carolina, PN Chapada das Mesas; 7°12'55" S, 47°19'7" W; 6 Oct. 2015; H. Vasconcelos, J. Maravalhas and F. Camarota leg.; DZUP • 2 ♀♀; Estreito, assentamento Vitória; 8 May 2004; Herpetologia MZSP, pitfall; MZSP • 1 ♀; Imperatriz; 1 Jul. 1974; Exc. Depto. Zool. exped.; DZUP • 1 ♀; same collection data as for preceding; 4 Jul. 1974; DZUP • 2 ♀♀; same collection data as for preceding; 20 Jul. 1974; DZUP • 1 ♀; Mirador, Reserva Mirador, Geraldina; 6°35' S, 45°49' W; 3 Dec. 2009; M.W.A. Mendonça leg.; DZUP • 1 ♀; Miranda do Norte, Babaçual; 30 Oct. 2012; Juliana Alves leg.; CPDC • 2 ♀♀; Nova Colinas; 7°1'10" S, 46°23'18" W; 23 Sep. 2009; D. Muniz leg.; DZUP • 1 ♀; Rio Santana, Grajaú; 15 Jun. 1966; H. Reichardt leg.; MZSP. – **Mato Grosso** • 1 ♀; Barra do Tapirapé; Dec. 1984; B. Malkin leg.; MZSP. – **Pará** • 1 ♀; Acará, Ilha do Combu; 16 Jul. 1988, J. Dias leg.; MPEG • 1 ♀; Água Azul, Paragominas; 22 Jul. 1974; Exc. Depto. Zool.



exped.; DZUP • 2 ♀♀; Alegre, 15 km NE of Marapanim; 10 Sep. 1965; Exp DZ-MG exped.; MZSP • 1 ♀; Ananindeua; Aug. 1964; Machado and Pereira leg.; MZSP • 1 ♀; Barcarena, Reserva Samaúma; 1.4963° S, 48.7088° W; 15–16 Nov. 2001; Iracenir and J. Dias leg.; MPEG • 1 ♀; Belém; 12 Jun. 2000; Delabie leg.; CPDC • 2 ♀♀; same locality as for preceding; 12–19 Aug. 1962; K. Lenko leg.; 2200; MZSP • 1 ♀; same locality as for preceding; 18 Dec. 1994; Gilberto leg.; MPEG • 1 ♀; same locality as for preceding; 22 Jul. 2007; M.A. Rodrigues leg.; DZUP • 1 ♀; same locality as for preceding; 26 Sep. 1934; Carvalho Neto leg.; MZSP • 1 ♀; same locality as for preceding; Jan. 1976; V.P. Daniel and Lucia Repp leg.; MZSP • 1 ♀; same locality as for preceding; Feb. 1956; P. Azevedo leg.; DZUP • 1 ♀; same locality as for preceding; Sep. 1955; Martinez leg.; MZSP • 1 ♀; Belém, Mocambo; 17 Apr. 1997; M.L. Macambira leg.; “coleta manual, floresta perturbada, área 10m<sup>2</sup>”; MPEG • 1 ♀; same locality as for preceding; 18 Apr. 1999; M. Barros leg.; “coleta manual, floresta perturbada, área 10m<sup>2</sup>”; MPEG • 1 ♀; same collection data as for preceding; M.L. Macambira leg.; MPEG • 1 ♀; Belém, MPEG C. pesquisa; 15–22 May 1997; C. Melo leg.; malaise; MPEG • 1 ♀; Belém, Reserva Guamá; 31 May 1966; Coll Kempf 5074; MZSP • 1 ♂; Benevides; 15 Mar. 1990; W.L. Overall leg.; MPEG HHY03045386 • 1 ♂; same collection data as for preceding; MPEG HHY03034653 • 1 ♀; Bragança, Tracuateua, Sta. Maria; 1 Sep. 1988; F.F. Ramos leg.; MPEG • 1 ♀; Bujaru; 3 Feb. 1979; A.F. Ramos leg.; INPA • 1 ♀; Canindé, Rio Gurupi; 1 May 1963; B. Malkin leg.; MZSP • 1 ♀; same collection data as for preceding; 1 Oct. 1964; MZSP • 1 ♀; same collection data as for preceding; 1 Dec. 1964; MZSP • 3 ♀♀; same collection data as for preceding; 7–9 Feb. 1966; MZSP • 7 ♀♀; same collection data as for preceding; Apr. 1963; MZSP • 1 ♀; Goianésia; 16–18 Jun. 2003; A.M. Elizabeth leg.; CPDC • 1 ♀; Igarapé Açu; 23–25 Jan. 2008; Santos J.A. leg.; pitfall 20 IASD0608; UFOPA • 1 ♀; same collection data as for preceding; pitfall 18; UFOPA • 1 ♀; same collection data as for preceding; pitfall 21; UFOPA • 1 ♀; same collection data as for preceding; 1.0443° S, 47.5944° W; pitfall 8; UFOPA • 2 ♀♀; same collection data as for preceding; pitfall 13; UFOPA • 1 ♀; same collection data as for preceding; pitfall 7 IASD1138; UFOPA • 1 ♀; same collection data as for preceding; pitfall 20 IASD0609; UFOPA • 1 ♀; “Igarapé Uruaim, 40 km Rio Gurupi”; 2 May 1963; J. Carvalho leg.; MZSP • 1 ♀; Marabá; 2017; DZUP • 1 ♀; Marituba; 1°22' S, 48°20' W; 21 Oct. 2004; J.R.M. Santos leg.; CPDC • 1 ♀; Óbidos; Dec. 1952; Pedro Telles leg.; MZSP • 2 ♀♀; Ourém, Patauateua; 1 May 1992; Delma leg.; arm. de luz; MPEG • 1 ♀; Outeiro, escola Bosque; 4 Apr. 1993; W. França leg.; MPEG • 25 ♀♀; Paragominas; 1 Mar. 2011; R. Solar leg.; DZUP • 27 ♀♀; same collection data as for preceding; 1 Jul. 2011; DZUP • 1 ♀; same collection data as for preceding; ANTWEB 1038257; UFV • 1 ♂; same locality as for preceding; 2°59'51" S, 47°21'13" W; alt. 85 m; Jan–Jul. 2011; R. Solar leg.; UFV LabEcol 449 • 1 ♀; same locality as for preceding; 5 Oct. 1993; Fowler leg.; 3231; CPDC • 1 ♀; Paragominas, Faz. Rio Capim, Empresa Cikel Brazil Verde; 3°33' S, 48°38' W; 1 Aug. 2002; DZUP • 1 ♀; Paragominas, Fazenda Sete; 18–23 Sep. 1997; S.M. Ketelhut leg.; “corte seletivo”; T3.3 pitfall 2; MPEG • 1 ♀; Paragominas, Fazenda Vitória; 21 Dec. 1991; Paulo Moutinho leg.; HB-CP T-8 PT4 A15-1 col2; MPEG • 3 ♀♀; same locality as for preceding; 1 Oct. 1999; P.S. Oliveira leg.; “mata seca”; MZSP • 1 ♀; Peixe-Boi, Fazenda Santoca, área de mata; 1.13991° S, 47.3006° W; 10 Mar. 2010; J. Dias leg.; “rede entomológica”; MPEG • 1 ♂; Primavera, Quadripaum Fal. Feitoria; 27 Nov. 1992; J. Dias leg.; “armadilha de luz”; MPEG 03006727 • 1 ♀; Rio Tocantins, base 4; 18 Jul. 1987; Wynes Barbosa leg.; Coleção Diniz; DZUP • 1 ♀; S.C. Odivelas; 19 Nov. 1982; P. Tadeu leg.; MPEG • 2 ♀♀; same locality as for preceding; 27 Feb. 1979; R.B. Neto leg.; INPA • 1 ♀; Serra Norte, Salobo; 17 Sep. 1985; Marcio Zanuto leg.; MPEG • 1 ♀; Tailândia; 30 Jun. 2005; M. Silva leg.; MZSP • 1 ♀; Tucuruí, Vila Brava; 22 Jun. 1980; Nunes de Melo leg.; INPA • 1 ♀; same collection data as for preceding; 27 Jun. 1980; INPA • 1 ♀; Tucuruí, Inajá; 20 Jun. 1980; B.M. Mascarenha leg.; INPA. – **Tocantins** • 1 ♀; Araguaína; 2 Oct. 2015; H.L. Vasconcelos and J.B. Maravalhas leg.; 251, T70-3S; DZUP • 1 ♀; Babaçulândia; 7°01'03" S, 47°52'14" W; 10–15 Dec. 1961; Albuquerque and Silva leg.; “isca solo”; MZSP.

PERU – Loreto • 2 ♂♂; Estirón, Río Ampiacú; 15 May 1966; B. Malkin leg.; 5881; MZSP • 1 ♂; same collection data as for preceding; DZUP.

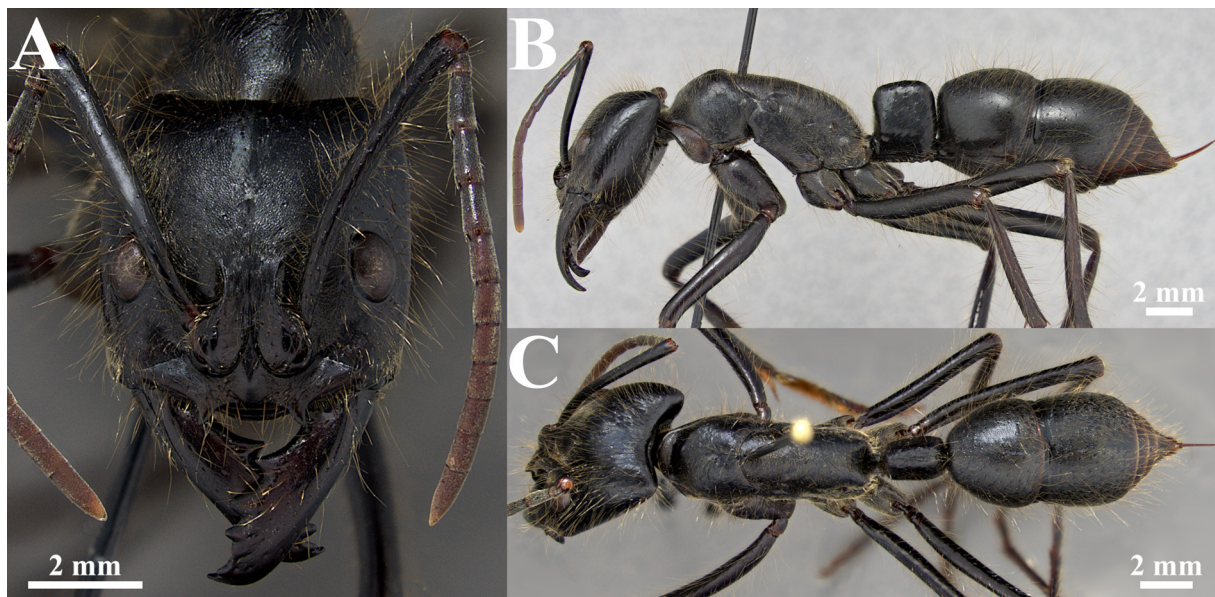
## Redescription

### Female

MEASUREMENTS. Lectotype: HL 5.85; HW 5.35; MDL 4.52; SL 5.98; MSL 8.8; HFL 8.2; HBL 6.64; PL 2.44; PH 3; PW 1.73; ATS 8; BL 29.63 (mm); CI 0.91; SI 1.11; DPI 0.7. Paralectotypes ZSM HYM-25183 and ZSM HYM-25182 (NA = not available): HL 5.35 and 5.95; HW 5 and 5.6; MDL 4.07 and 4.5; SL NA and 5.92; MSL 7.6 and 8.7; HFL 7 and 8.4; HBL 5.67 and 6.9; PL 2.24 and 2.57; PH 2.97 and 3.25; PW 1.78 and 1.89; ATS 6.96 and 8.4; BL 26.23 and 30.12 (mm); CI 0.93 and 0.94; SI NA and 1.05; DPI 0.79 and 0.73. Non-types (n = 26): HL 5.35–6.23; HW 5.29–6.11; MDL 4.09–4.97; SL 5.41–6.36; MSL 7.76–9.3; HFL 7.24–8.9; HBL 6.16–7.5; PL 2.32–2.69; PH 3.03–3.6; PW 1.67–2.07; ATS 7.52–9.6; BL 27.11–32.23 (mm); CI 0.94–1.03; SI 0.98–1.09; DPI 0.68–0.82.

HEAD. Malar area without striae or with weak longitudinal to oblique striae that do not reach anterior eye margin. Gena microareolate and opaque, usually without rugulae. Appressed brownish pubescence present between eye and frontal lobe, extending posteriorly to frons. Frons microareolate and opaque; with flexuous, brownish and suberect hairs, longer than scape diameter; pubescence densest laterally. Occipital corner strongly microareolate and opaque. Antennal scape microareolate and silky, suberect and long hairs usually present on antennal segments 1–3. Ventral surface of head microareolate with arched strigulae covering entire surface or at least anterior half; posterior to postgenal suture with well-marked transverse strigulae. Hypostomal tooth with longitudinal strigulae. Labrum with median longitudinal sulcus weakly marked or absent; transverse rugulae absent. Mandibular dorsum weakly longitudinally strigulate on inner base, sculpture gradually fading apicad.

MESOSOMA. Dorsal margin of pronotum in lateral view broadly convex, usually with no pronounced dorsoposterior swelling; anteroventral corner of pronotum toothed or forming acute angle. Pronotal dorsum strongly microareolate, rugulose and opaque. Metapleural-propodeal suture weak and sinuous, with at least one curve ventral to position of propodeal spiracle.



**Fig. 13.** *Dinoponera gigantea* (Perty, 1833), ♀ (specimen from Marituba, Pará, Brazil; CPDC). A. Full-face view. B. Full body in lateral view. C. Full body in dorsal view.

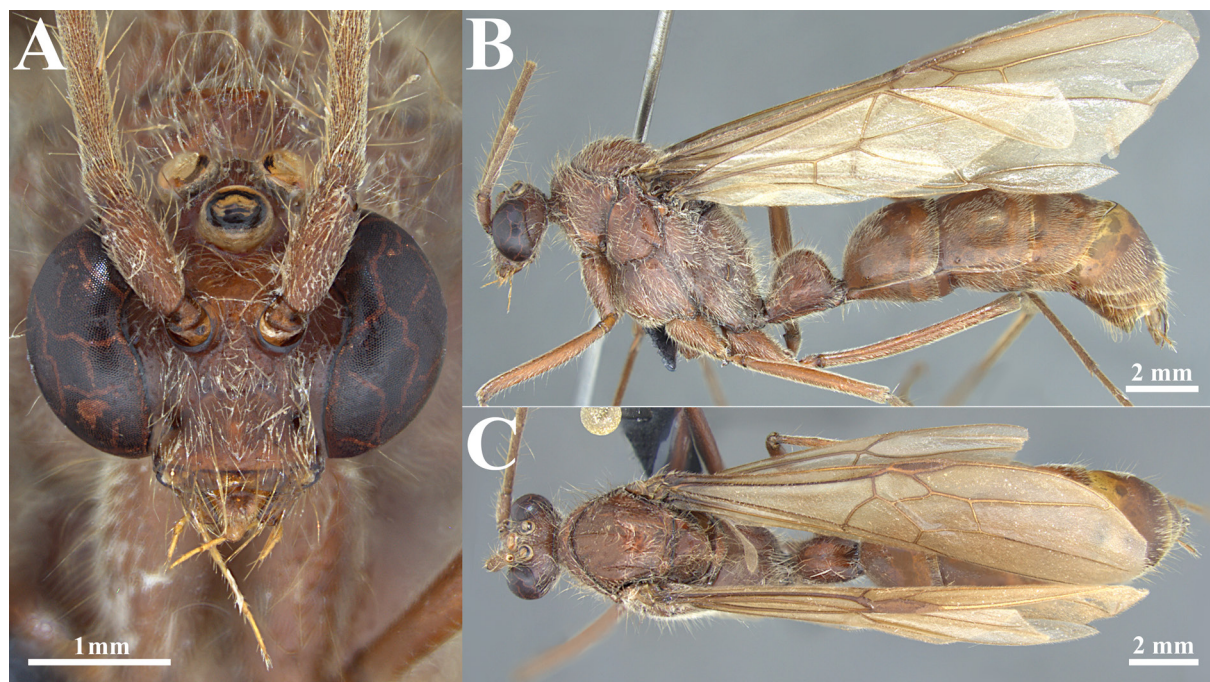
**METASOMA.** Petiolar node in lateral view elongate (usually  $DPI < 0.8$ ); anterodorsal corner at same level as posterodorsal corner, sometimes slightly higher; anterior margin straight or slightly concave, forming blunt angle with dorsal margin; dorsal and posterior margin each broadly convex and forming blunt to rounded angle. Node lateral face microareolate and opaque (rarely silky). Node anterior margin in dorsal view slightly convex; posterior margin straight to broadly convex; lateral faces broadly convex. Abdominal tergite III strongly microareolate and opaque; densely punctulate on dorsal and lateral surfaces; distance between each punctulae approximately equal to their diameter; densely covered with brownish, flexuous, erect hairs and appressed pubescence on all surfaces.

### Male

**MEASUREMENTS.** Non-types ( $n = 4$ ): HL 2.28–2.58; HW1 2.76–3.12; MDL 0.58–0.75; SL 0.9–0.92; EL 1.64–1.87; MOD 0.52–0.57; LOD 0.5–0.52; MSL 7–7.5; HFL 5.4–6.33; PL1 1.96–2.12; PH 1.68–2.01; PW 1.2–1.38; ASL 4.7–5.12; BL1 16.75–18.1 (mm); CII 1.1–1.21; SEI 1.82–2.02; SII 0.29–0.33.

**HEAD.** Frontal carina forming short longitudinal swelling. Lateral ocellus clearly surpassing posterior head margin in full-face view. Head punctulate, weakly microareolate and shining; with yellowish decumbent pubescence and long suberect to erect hairs longer than ocellus height in full-face view. Antenna with appressed pubescence and long suberect to erect hairs clearly longer than maximum scape diameter; third to fourth most apical antennomeres with few sparse hairs. Ventral surface of head punctulate and slightly microareolate with silky sheen.

**MESOSOMA.** Mesoscutum with notaulus slightly impressed. Mesopleural sulcus punctate or slightly scrobiculate. Scutoscutellar sulcus scrobiculate. Mesoscutellum longitudinally strigulate laterally. Metapleural-propodeal suture with same microsculpture as rest of integument. Mesosoma mostly slightly microareolate and with silky sheen, becoming coarsely punctate on declivitous surface of propodeum; with decumbent to suberect pubescence and suberect hairs, distance between each hair usually less than



**Fig. 14.** *Dinoponera gigantea* (Perty, 1833), ♂ (specimen from Benevides, Pará, Brazil; MPEG HHY03034653). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

half its length. Legs densely covered by decumbent pubescence; also with sparse suberect long hairs, greater than femur diameter, from coxa to tibia. Protibial apex with at least one robust seta.

**METASOMA.** Petiolar node microareolate and shining, densely covered by decumbent pubescence and abundant suberect hairs. Abdominal tergite VIII spiniform. Gaster very slightly microareolate and shining; tergites densely covered by appressed to decumbent pubescence and sparse suberect hairs.

**GENITALIA.** Basal ring in dorsal view having slightly concave lateral margins, anteriorly narrower than posteriorly; fenestra rounded to slightly transversally directed; median invagination U-shaped; in lateral view, dorsal margin broadly convex to straight; anteroventral process rounded or slightly subquadrate. Gonostylus narrow and sharp. Dorsal margin of volsella in lateral view anteriorly straight to broadly convex and posteriorly concave; anteroventral corner with two anterior teeth; posteroventral margin strongly concave and forming sharp, triangular posterior lobe; digitus volsellaris with posterior margin straight or with a slight concavity. In lateral view, penisvalva with continuous dorsal and posterior margins, ending in rounded apex; ventral margin even and serrated; concave; anteroventral corner sharply pointed.

**COLOR.** Body mostly chestnut brown.

### Remarks

A robust set of characters separate females of *D. gigantea* from the other species of the genus. It differs from *D. hispida*, *D. longipes*, *D. mutica* and *D. nicinha* sp. nov., all species with either an overlapping or close distribution, by the opaque and microareolate pronotal dorsum and abdominal tergite III. Additionally, *D. gigantea* usually has the anteroventral pronotal corner with a tooth or an acute angle in lateral view. The other species with a toothed pronotum are *D. lucida* and *D. grandis*. *Dinoponera lucida* has bluish iridescence on abdominal tergite III and striae on the malar area that reach the anterior eye margin. *Dinoponera grandis* has a body length (BL) less than 27 mm and a relatively shorter petiolar node in lateral view (DPI > 0.8), besides the presence of well-marked striae on the malar area.

Rarely, some specimens may either have a small tooth or obtuse angle on the anteroventral pronotal corner or the third abdominal tergite with very sparse piligerous punctulae, and occasionally both. In such cases, *D. gigantea* may be confused with *D. quadriceps*, but this may be avoided by examining the ventral surface of head, which has arched strigulae covering the entire surface or at least the anterior half in *D. gigantea*. These variants are more commonly found in Maranhão and Tocantins, where the distribution of these species may overlap. *Dinoponera gigantea* and *D. quadriceps* are nevertheless maintained separate, as argued in the remarks for *D. quadriceps*.

Additional support for this separation is provided by the huge differences between their habitats, as *D. gigantea* is typically from the Amazon and *D. quadriceps* is from the Caatinga (IBGE 2019). It is worth noting that Maranhão and Tocantins, where the ‘problematic’ specimens are found, are mostly within the Cerrado Biome, which is located between the Amazon and Caatinga Biomes (IBGE 2019).

The lectotype and two paralectotypes of *D. gigantea* from the ZSM were examined. Diller (1990) designated the only labelled specimen as the lectotype in the type series of six ants. One of the examined paralectotypes (ZSM HYM-25183) is unusual in having a body length (BL) less than 2.7 cm, a straight metapleural-propodeal suture, a relatively short petiolar node in lateral view (DPI = 0.79), the ventral cephalic surface weakly strigulate, abdominal tergite III with sparse piligerous punctulae and relatively short and thick body hairs, especially on the cephalic venter. Collectively these characters do not correspond with the typical characterization of any species in this genus. Nevertheless, recognizing a

new species was not considered, as the exact collection locality is unknown. Perhaps this specimen is an atypical variant of *D. gigantea*. The worn integument and caked dirt may have abraded some hairs or made others appear more rigid than they should be, potentially complicating character interpretation. The specimen designated as lectotype by Diller (1990) is the one that better represents the forms described as *D. gigantea* and more resembles the specimens found in the North of Brazil.

Kempf (1971: 372) gave a diagnostic description of the male based on specimens from Belém, and Lenhart *et al.* (2013) described the genitalia of a male from Belém. Tozetto & Lattke (2020) described the genitalia of 3 males, all from different sites in Pará. This last study found greater similarities between the basal ring, gonopod, volsella and penisvalva of *D. gigantea* and *D. quadriceps* than between other species. Lenhart *et al.* (2013), in their identification key to the males of the genus, separated *D. gigantea* and *D. quadriceps* from those of other species by the long and erect hairs of the funiculus. Kempf (1971) noted the similarities between these two species on account of eye and ocellus size. The aforementioned similarities between these two species suggest they are more closely related to each other than with any of the other known species. Nevertheless, males of *D. gigantea* can easily be separated from *D. quadriceps* by the presence of a notaulus on the mesoscutum and the abundant hairs on the body.

### Biology

Within their known range these ants are found in areas where the average temperature of the coldest month is higher than 18°C and the annual precipitation is higher than 1000 mm (Alvares *et al.* 2013). They may be found at sites with different phytophysionomies, ranging from dense forests to savannas with small woody plants (IBGE 2012). Their nests, which may be polydomic, are usually built at the base of trees and may be up to 40 cm deep (Fourcassié *et al.* 1999; Fourcassié & Oliveira 2002). Each nest has from one to eight entrances surrounded by loose soil never piled into a mound (Fourcassié & Oliveira 2002). On average, each nest has some 41 adult workers (Monnin *et al.* 2003).

Workers forage alone searching for a broad variety of resources such as seeds, fruits, and dead or live arthropods (Fourcassié & Oliveira 2002). Foraging may be diurnal or nocturnal, with activity decreasing during the hottest hours of the day (Fourcassié *et al.* 1999; Fourcassié & Oliveira 2002). Workers exhibit general fidelity, with minor deviations, to a foraging route (Fourcassié *et al.* 1999). Spatial orientation during foraging apparently uses relatively large-scale reference points in the landscape, as minor changes, such as sweeping the leaf litter, do not change their path (Fourcassié *et al.* 1999). Workers from different colonies may find themselves at the edge of their foraging routes and exhibit territoriality, beating each other with their antennae (Fourcassié & Oliveira 2002). Hierarchical relationships within a colony are determined by the same agonistic interactions described for *D. quadriceps*, although with a lower frequency (Monnin *et al.* 2003).

### Distribution (Fig. 28A)

*Dinoponera gigantea* has been recorded in northern Brazil and eastern Peru. In Brazil, the northernmost record is the type-locality along the Rio Negro (probably close to Barcelos, Amazonas, according to Kempf 1971). It is important to note that, except for the type-series, *D. gigantea* has only one record for Amazonas. All other records are mostly from Pará and Maranhão, with the southernmost record from Rio Tapirapé, Mato Grosso. The examined records from Peru date from 1966 and are close to the border with Brazil, more than 900 km from any other record. This may indicate a much more extensive distribution in the recent past. Lenhart *et al.* (2013) examined a specimen from Bartica, Cuyuni-Mazaruni, Guiana but this single record may be an artefact of a misplaced label, as it is 500 km from any other record for the genus. Despite numerous surveys and collecting, *Dinoponera* has yet to be recorded from the Guiana Shield (Wheeler 1916, 1918; Lapolla *et al.* 2007; Alonso 2012; Alonso & Helms 2013; Helms *et al.* 2016; Groc *et al.* 2014; Franco *et al.* 2019).

***Dinoponera grandis*** (Guérin-Méneville, 1838). **Revived species**  
Figs 15–18, 28A

*Ponera grandis* Guérin-Méneville, 1838: 206 (♀).

*Dinoponera grandis australis* Emery, 1901: 48 (♀). **syn. nov.**

*Dinoponera australis brevis* Borgmeier, 1937: 227 (♀).

*Dinoponera australis bucki* Borgmeier, 1937: 228, fig. 7 (♀, ♂). **syn. nov.**

*Dinoponera australis nigricolor* Borgmeier, 1937: 228, figs 5–6, 8 (♀, ♂). **syn. nov.**

*Dinoponera snellingi* Lenhart, Dash & Mackay, 2013: 152, figs 4d, i, n, 5b, 7, 9b, 10b, 11b (♂).  
**syn. nov.**

*Dinoponera grandis* – Roger 1861: 38 (combined in *Dinoponera*, synonym of *D. gigantea*). — Bequaert 1926: 188 (junior synonym of *D. gigantea*).

*Dinoponera grandis australis* – Santschi 1921: 85 (male description). — Borgmeier 1937: 227 (raised to species, lectotype designated). — Kempf 1975: 382, figs 6, 17–18 (redescription, key). — Lenhart, Dash & Mackay 2013: 135, figs 4e, j, o, 5d, 9d, 10d, 11d (redescription, male genitalia, key). — Tozetto & Lattke 2020: 5, figs 2–3, 6 (male genitalia).

*Dinoponera australis brevis* – Kempf 1971: 382 (junior synonym of *D. australis*).

*Dinoponera australis nigricolor* – Kempf 1971: 387 (lectotype male designated).

Non *Dinoponera grandis australis brevis* – Santschi 1928: 416 (invalid name).

## Diagnosis

### Female

Malar area with longitudinal to oblique striae that reach anterior ocular margin. Abdominal tergite III microareolate and opaque to slightly silky, never smooth and shining. Hind basitarsus length less than 6 mm long. Petiolar node short,  $DPI \geq 0.8$ .  $BL \leq 27$  mm.

### Male

Body, including antenna, without long hairs. Basal ring in lateral view with dorsal margin declining and extending anteriorly to form a broad lobe. Penisvalva in lateral view with a posterior rounded apex, projecting ventrolaterally.

## Material examined

### Lectotype of *Ponera grandis*

BRAZIL – Minas Gerais • ♀; ZSM.

### Other type specimens (13 ♀♀, 2 ♂♂)

BRAZIL – Goiás • ♂, lectotype of *D. australis nigricolor*; Campinas; 5 May 1933; Schwarzmaier leg.; MZSP 65801 • 1 ♀, paralectotype of *D. australis nigricolor*; Campinas; 6–8 Feb. 1936; R. Spitz leg.; MZSP 67063 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding; MZSP 67064 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding; MZSP 67066 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding; MZSP 67067 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding; MZSP 67068 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding; MZSP 67069 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding; MZSP 67070 • 1 ♀, paralectotype of *D. australis nigricolor*; same locality as for preceding; 4 Nov. 1937; Schwarzmaier leg.; MZSP 67071 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding; MZSP 67072 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding; MZSP 67073 • 1 ♀, paralectotype of *D. australis nigricolor*; same collection data as for preceding.

for preceding; MZSP 67074. – **Rio Grande do Sul** • ♂, lectotype of *Dinoponera australis bucki* (here designated); Palmeira das Missões; 27 Jan. 1929; P. Buck leg.; MZSP 65800 • 1 ♀, paralectotype of *D. australis bucki*; same collection data as for preceding; MZSP 67061 • 1 ♀, paralectotype of *D. australis bucki*; same collection data as for preceding; MZSP 67062.

**Non-type specimens** (234 ♀♀, 9 ♂♂)

ARGENTINA – **Missiones** • 1 ♀; Bruch leg.; MZSP • 2 ♀♀; Iguazú; Oct. 1964; A. Martinez leg.; MZSP.

BOLÍVIA – **Icnilo** • 1 ♀; Buenavista; Feb. 1950; A. Martinez leg.; MZSP. – **Santa Cruz** • 1 ♀; Gutierrez, Nueva Moka [Moca]; 23 Nov. 1951; A. Martinez leg.; MZSP • 1 ♀; “Samaipata - balneário mama Pascuala”; 3 Jan. 1989; F.J.A. Peralta and Hansen leg.; INPA • 1 ♀; San José de Chiquitos; 3–5 Mar. 1954; C. Gans and F. Pereira leg.; MZSP • 1 ♀; Sara, Nueva Moka; Feb. 1950; A. Martinez leg.; MZSP • 1 ♀; Nueva Moka; Mar. 1956; A. Martinez leg.; MZSP.

BRAZIL – **Distrito Federal** • 1 ♀; APA Gama Cabeça de Veado; 2 Mar. 2000; Pic. Mireille leg.; CPDC • 2 ♀♀; Brasília; Oct. 1961; R.L. Araújo leg.; MZSP • 1 ♀; Brasília; 15.96565° S, 47.91626° W; 8 Apr. 2011; H.L. Vasconcelos and T. Frizzo leg.; 1157, T5-6S; UFU • 1 ♀; Brasília, Ceilândia; 15 Oct. 1976; 499; DZUP • 1 ♀; Brasília, E. Ecol. Águas Emendadas; 15 Dec. 1992; A. Reis leg.; MZSP • 1 ♀; same locality as for preceding; 19 May 1993; J.H. Schoederer leg.; UFV LabEcol 437 • 1 ♀; same collection data as for preceding; UFV LabEcol 438 • 1 ♀; Brasília, FAL; 15°57'47.4" S, 47°55'35.7" W; 16 Oct. 2010; M.C. Galego-Roperero and P. Rezende leg.; “cupinzeiro *C. cumulans*”; MZSP • 1 ♀; Brasília, Reserva Ecológica do IBGE (RECOR), Fisionomia campo limpo; 15.9166° S, 47.8666° W to 15.9500° S, 47.8833° W; 2009; F.A. Schmidt leg.; P:5 E:E; UFV LabEcol 445 • 1 ♀; Brasília, Reserva Ecológica do IBGE, cerrado sensu stricto; 6 Feb. 2008; J. Maravalhas leg.; MZSP • 1 ♀; same collection data as for preceding; 7 Feb. 2008; MZSP • 1 ♀; UnB Campus; 10 Nov. 1974; Bittencourt leg.; 11756, 500; DZUP • 1 ♀; same collection data as for preceding; 11756, 501; DZUP. – **Goiás** • 1 ♀; 7 km NW of Alto Paraíso, Morro das Cobras; 1–7 Jul. 1991; C.R.F. Brandão, M.L. Françoso and A.A. Reis leg.; pitfall stn 1; MZSP • 1 ♀; Abadia de Goiás; 6 Nov. 1980; C.R. Krigger leg.; UFSC • 1 ♀; Anápolis; Nov. 1938; M. Souza leg.; MZSP • 1 ♀; Anápolis, UEG, Campus CCET; 16.3826° S, 48.9446° W; 5 Oct. 2010; H.F. Cunha leg.; UEG • 6 ♀♀; same collection data as for preceding; 18 Oct. 2010; UEG • 1 ♀; same collection data as for preceding; 20 Oct. 2010; UEG • 1 ♀; same collection data as for preceding; 27 Oct. 2010; UEG • 1 ♀; same collection data as for preceding; 1 Nov. 2010; UEG • 1 ♀; same collection data as for preceding; 12 Nov. 2010; UEG • 2 ♀♀; same collection data as for preceding; 8 Dec. 2010; UEG • 2 ♀♀; same collection data as for preceding; 14 Dec. 2010; UEG • 1 ♀; same collection data as for preceding; 21 Dec. 2010; UEG • 4 ♀♀; same collection data as for preceding; 13 Jan. 2011; UEG • 4 ♀♀; same collection data as for preceding; 20 Jan. 2011; UEG • 3 ♀♀; same collection data as for preceding; 3 Feb. 2011; UEG • 2 ♀♀; same collection data as for preceding; 17 Feb. 2011; UEG • 1 ♀; same collection data as for preceding; 24 Feb. 2011; UEG • 3 ♀♀; same collection data as for preceding; 17 Mar. 2011; UEG • 1 ♀; Caiapônia, Cerradão; 17°19'40" S, 52°19'50" W; 27 Jan. 2007; Vitor M. Carvalho leg.; Coleção Diniz; 8-9h A7; DZUP • 2 ♀♀; same collection data as for preceding; 8-9h A9; DZUP • 2 ♀♀; same collection data as for preceding; 15-16h A6; DZUP • 1 ♀; same collection data as for preceding; 19-20h A7; DZUP • 2 ♀♀; same collection data as for preceding; 10 Feb. 2007; 19-20h A9; DZUP • 1 ♀; same collection data as for preceding; 24 Feb. 2007; 15-16h A6; DZUP • 1 ♀; same collection data as for preceding; 15-16h A7; DZUP • 1 ♀; same collection data as for preceding; 19-20h A6; DZUP • 1 ♀; same collection data as for preceding; 10 Mar. 2007; 15-16h A8; DZUP • 1 ♀; same collection data as for preceding; 19-20h A9; DZUP • 1 ♀; Caiapônia, pasto; 17°19'40" S, 52°19'50" W; 27 Jan. 2007; Vitor M. Carvalho leg.; Coleção Diniz, 15-16h A4; DZUP • 1 ♀; Caldas Novas; 1 Nov. 2011; H.L. Vasconcelos and T. Frizzo leg.; 952, T31-11S; DZUP • 1 ♀; same collection data as for preceding; 1020, T32-11S; DZUP • 1 ♀; same collection data as for preceding; 983, T33-17S; DZUP • 1 ♀; same collection data as for preceding; 1020, T32-17S; DZUP • 1 ♂; Campinas; 1935;

R. Spitz leg.; MZSP 62281 • 1 ♀; Chapada dos Veadeiros; 13 Apr. 2015; J.B. Maravalhas leg.; 1088, T67-15S; DZUP • 1 ♀; same collection data as for preceding; 1187, T68-3S; DZUP • 1 ♀; same collection data as for preceding; 1187, T68-15S; DZUP • 1 ♀; Cocalzinho de Goiás, cerrado rupestre; 15°47'43" S, 48°49'45.76" W; alt. 1321 m; 31 Jan. 2010; Eduardo de Oliveira Emery leg.; DZUP • 2 ♀♀; Goiânia, campus Euc. De veterinária; 23 Dec. 2001; Luciano Lozi leg.; Coleção Diniz; DZUP • 1 ♀; Goiás Velho; 2 Jan. 1976; Guiflora leg.; MZSP • 1 ♂; Jataí; Dec. 1972; F.M. Oliveira leg.; 8843; MZSP 62282 • 1 ♀; Mineiros; 8 Feb. 2012; T. Frizzo leg.; 849, T38-11S; DZUP • 1 ♀; Mineiros, Parque Nacional das Emas; 17°54'30.3" S, 53°00'29.6" W; 8 Feb. 2012; F. Camarota, T. Frizzo and R. Pacheco leg.; DZUP • 1 ♀; Niquelândia, Anglo American; 14°28'26" S, 48°27'35" W; 23 Jan. 2006; M. Vilela leg.; Coleção Diniz, IDSC (right) 19; DZUP • 1 ♀; same collection data as for preceding; INSC (right) 82; DZUP • 2 ♀♀; same collection data as for preceding; INSC (left) 65; DZUP • 1 ♀; same collection data as for preceding; INSC (left) 23; DZUP • 1 ♀; same collection data as for preceding; IDSC (left) 77; DZUP • 1 ♀; same collection data as for preceding; 22 Mar. 2006; IDSC (right) 88; DZUP • 1 ♀; same collection data as for preceding; 24 May 2006; INSC (right) 52; DZUP • 1 ♀; Parque das Emas; 11 Nov. 1990; C.R. Krigger leg.; UFSC • 1 ♀; P.E. Serra de Jaraguá; 15.7964° S, 49.3335° W; 3 Jan. 2017; D.E. Oliveira leg.; DEO 843; DZUP • 1 ♀; same collection data as for preceding; DZUP 549812 • 1 ♀; P.N. Emas, Mineiros; 25 Oct.–2 Nov. 1986; Bechara, Viviani, Ferro and Sanche leg.; MZSP • 1 ♀; Santa Bárbara; 9 Dec. 2014; H.L. Vasconcelos and J.B. Maravalhas leg.; 643, T61-19S; DZUP • 1 ♀; same collection data as for preceding; 631, T63-11S; DZUP. – **Mato Grosso** • 1 ♀; Barra do Garça; 6 May 2011; H.L. Vasconcelos and T. Frizzo leg.; 539, T11-7S; UFU • 1 ♀; Bonito; 10 Jul. 2012; T. Frizzo leg.; 436, T43-11S; DZUP • 1 ♀; Buriti; 15 Feb. 1967; N. Tangerini leg.; DZUP • 1 ♀; Cachoeira da Fumaça; 9 May 2011; H.L. Vasconcelos and T. Frizzo leg.; 330, T13-3S; DZUP • 1 ♂; Chapada dos Guimarães; 23 Nov. 1983; Dep. Zool - UFPR (polonoroeste) exped.; DZUP • 1 ♀; same locality as for preceding; 24 Nov. 1983; Depto. Zool. (polonoroeste) exped.; DZUP • 1 ♀; same collection data as for preceding; 1–4 Feb. 1965; Sebastião Laroca leg.; DZUP • 1 ♀; same collection data as for preceding; 27 Jan. 1965; DZUP • 6 ♀♀; same collection data as for preceding; Nov. 1963; Alvarenga and Werner leg.; MZSP • 1 ♀; same collection data as for preceding; May 1959; Fr. Cannto leg.; MZSP • 4 ♀♀; Jan. 1960; C. Amann leg.; MZSP • 3 ♀♀; Jan. 1961; C. Amann leg.; MZSP • 1 ♀; 27 Oct. 1961; F.M. Oliveira leg.; DZUP • 1 ♀; same locality as for preceding; 15°27'11" S, 55°44'23" W; Oct. 2007; R. Silvestre *et al.* leg.; manual UFGD • 1 ♀; Chapada dos Guimarães, Fazenda Buriti; 18 Nov. 1982; Márcio Zanuto; MPEG HYM11513596 • 1 ♀; same collection data as for preceding; MPEG HYM11513598 • 1 ♀; Chapada dos Guimarães, Buriti; Oct. 1972; G.R. Kloss and F. Val leg.; MZSP • 1 ♂; Itaum; Mar. 1974; M. Alvarenga leg.; 10877; MZSP 62284 • 1 ♂; same data as for preceding; 10878; MZSP • 1 ♂; Maracaju; Shannon Lane leg.; DZUP • 1 ♀; Nova Xavantina; 10 May 2011; T. Frizzo leg.; 321, T16-7S; DZUP • 1 ♀; same collection data as for preceding; 311 T17-3S; DZUP • 1 ♀; PARNA Chapada dos Guimarães, Trilha do Cerrado; 15°24' S, 55°50' W; alt. 617 m; Mar. 2016; R. Silvestre *et al.* leg.; UFGD • 1 ♀; Vale dos Sonhos, Barra do Garças; alt. 400 m; 22 Jun. 1972; Mielke and Brown leg.; DZUP 548841 • 1 ♀; Vale dos Sonhos, S. pr. B. do Garças; 14 Jan. 1977; Kunze leg.; Coleção Diniz; 1394; DZUP • 1 ♀; Xavantina; 28 Nov. 1949; W. Bollermann leg.; MZSP • 1 ♀; same locality as for preceding; 10 Jan. 1977; Kunze leg.; Coleção Diniz, 1392; DZUP. – **Mato Grosso do Sul** • 1 ♀; Bodoquena, Parque Nacional da Bodoquena, mata ciliar; 10 Apr. 2008; T. Marques, J.H. Schoereder, R. Silvestre and interns leg.; arm 1 solo; UFV LabEcol 442 • 1 ♀; Bonito; 9 Oct. 1989; Paiva R. leg.; MZSP • 1 ♀; Bonito, PARNA Serra da Bodoquena, Faz. Boqueirão; 21°07'14.7" S, 56°43'08.2" W; 18–22 Dec. 2005; R. Silvestre *et al.* leg.; Hym 93-F; UFGD • 1 ♀; Bonito, PARNA Serra da Bodoquena, Faz. Harmonia; 21°17'09.8" S, 56°41'45.5" W; Oct. 2006; R. Silvestre *et al.* leg.; Hym 85F; UFGD • 1 ♀; Bonito, RPPN Brazil Bonito, Rio Taquaral; 21°06'27" S, 56°38'14" W; Nov. 2009; R. Silvestre *et al.* leg.; Hym 75-F; UFGD • 1 ♀; Campo Grande; 9 Oct. 1989; C.R.F. Brandão leg.; MZSP • 1 ♀; Campo Grande, Universidade Federal de Mato Grosso do Sul, RPPN UFMS; 21 Oct. 2017; P.R. Souza leg.; ZUFMS 3064 • 1 ♀; Morraria do Sul, PN Serra da Bodoquena, Faz. Califórnia; 20°42'07" S, 56°52'47.7" W; Nov. 2009; R. Silvestre *et al.* leg.; UFGD • 1 ♀; Paranaíba, R. Paranaíba; 14 Aug. 1972; em solo 506; Coleção Diniz;



DZUP • 1 ♀; PARNA Serra da Bodoquena, Faz. Sta Laura da Vicunha, Rio Salobra; 20°46'56.2" S, 56°44'31.2" W; 22–29 Jun. 2006; 3° exp., R. Silvestre *et al.* leg.; pitfall A-10, Hym 83-F; UFGD • 1 ♀; P [Porto] Murtinho, Chaco Forest, Faz. Patolá; 21°42'02" S, 57°42'60" W; 7 Mar. 2012; P.R. Souza *et al.* leg.; busca ativa; UFGD • 1 ♀; same collection data as for preceding; DZUP 548837 • 1 ♀; S do Paranaíba [Santana do Parnaíba], Fazenda Olho D'água; 21 Feb. 1972; Diniz leg.; Coleção Diniz, 512, Em 9010; DZUP • 1 ♀; snt.do Paranaíba [Santana do Parnaíba], Faz. Olho D'Água; 12 Jul. 1971; Diniz leg.; Coleção Diniz, 499, Em 9010; DZUP • 1 ♀; same locality as for preceding; 12 Jul. 1972; Diniz leg.; em solo; MZSP • 2 ♀♀; Serra da Bodoquena, Cara da Onça RPPN; 20°44'24" S, 56°44'11" W; alt. 196 m; Dec. 2011; R. Silvestre leg.; manual; UFGD • 1 ♀; Serra da Bodoquena, Faz. Campo Verde; 21.3755° S, 56.7177° W; alt. 444 m; Dec. 2008; R. Silvestre leg.; manual; UFGD • 2 ♀♀; Três Lagoas, Jardim Alvorada; 3 Aug. 1985; J.L.M. Diniz leg.; Coleção Diniz, 2194; DZUP. – **Minas Gerais** • 1 ♀; Campo Florido; 12 Feb. 1964; H.M. Canter leg.; MZSP • 1 ♀; Monte Carmelo; 18.8000° S, 47.8000° W (3 min error); 23–25 May 2016; J.J.M. Aguiar leg.; amostra 355/176; ANTWEB 1038256; UFV • 1 ♀; S do Salito [Serra do Salitre]; 4 Apr. 1965; C. Elias leg.; DZUP • 1 ♀; Uberaba; Oct. 1961; C. Elias leg.; DZUP • 1 ♀; Uberlândia; Jan. 1999; W.L. de Melo leg.; DZUP 548840; DZUP. – **Paraná** • 1 ♀; C Mourão [Campo Mourão]; Jul. 1950; coleção F. Justus; DZUP • 1 ♀; F do Iguaçu, Foz de Iguaçu cataratas; 24 Aug. 2000; J.O. Schmidt leg.; MPEG • 1 ♂; Guarapuava; Mar. 1947; 4380, Coleção F. Justus Jr; DZUP 548845 • 1 ♀; Guarauna; Dec. 1940; coleção F. Justus, DZUP 548839; DZUP • 1 ♀; Laranjeira do Sul; Mar. 1947; coleção F. Justus, 4384; DZUP • 1 ♂; same locality as for preceding; Jan. 1962; S. Sakagami leg.; DZUP 548844 • 1 ♀; same collection data as for preceding; DZUP 548838 • 1 ♀; Palmas; Dec. 1928; F. Schroer leg.; MZSP. – **Santa Catarina** • 1 ♀; Chapecó; 2004; Funir leg.; P06; UFSC • 3 ♀♀; Nova Teutonia; Fritz Plaumann leg.; MZSP • 1 ♀; same locality as for preceding; 30 Dec. 1940; Diringe leg.; MZSP • 1 ♀; same locality as for preceding; May 1957; Fritz Plaumann leg.; MZSP. – **São Paulo** • 1 ♀; Agudos; May 1959; C. Gilbert leg.; 3524; MZSP • 3 ♀♀; same collection data as for preceding; Mar. 1960; MZSP • 1 ♀; Boa Esperança do Sul, Faz. Itaquerê; 28 Nov. 1963; K. Lenko leg.; 2946; MZSP • 1 ♀; Botucatu; 1 Sep. 1963; Mantovan leg.; MZSP • 1 ♀; same locality as for preceding; 18 Oct. 1968; M. Artamiro leg.; 6423; MZSP • 2 ♀♀; same locality as for preceding; 4 Dec. 1968; M. Artamiro leg.; 6422; MZSP • 1 ♀; Botucatu, CESP; 15 Apr. 1991; B.H. Dietz leg.; MZSP • 12 ♀♀; Corumbataí; 30 Dec. 1962; H.A. Britski leg.; MZSP • 1 ♀; Corumbataí, Fac. Fil. Rio Claro; 1 Nov. 1963; DZUP • 1 ♂; Itirapina; 10 Apr. 1990; R. Paiva leg.; MZSP 62283 • 2 ♀♀; same locality as for preceding; 27 Feb. 1968; D. Dias leg.; 4857; MZSP • 1 ♀; same locality as for preceding; 24 Oct. 1987; H.G. Fowler leg.; CPDC • 1 ♀; same locality as for preceding; 18 Nov. 1999; Thibaud Monnin leg.; MZSP • 1 ♀; Jundiaí; Nov. 1929; J. Lane leg.; MZSP • 1 ♀; Rio Claro; 1 Jul. 1962; S. Laroca leg.; DZUP • 1 ♀; same locality as for preceding; 18 Nov. 1983; Caetano and Brandão leg.; MZSP • 1 ♀; same locality as for preceding; Feb. 1992; E. Tomatake leg.; 4530; CPDC • 1 ♀; S [São] Carlos, Faz. Canchiu; 9 Jun. 1987; R.R. Martins leg.; MZSP. – **Rio Grande do Sul** • 1 ♀; Derrubadas, Parque Estadual do Turvo, Floresta Semidecídua; 25 Apr. 2009; T. Marques leg.; pitfall hipogeico; UFV LabEcol 441 • 1 ♀; Derrubadas, Parque Estadual do Turvo, mata seca; 25 May 2009; T. Marques and interns leg.; arm 10 estrato sol; MZSP • 2 ♀♀; Sto [Santo] Ângelo; 23 Feb. 1974; R.L. Araújo leg.; MZSP • 1 ♀; Santa Bárbara [Santa Bárbara do Sul]; 23 Dec. 1944; C.R. Gonçalves leg.; MZSP • 2 ♀♀; Soledade, PPBio, Natural Grassland Ecosystem, campo; 28.8725° S, 52.4588° W; Nov. 2013; L.R. Podgaiski leg.; manual collection; UFRGS • 1 ♀; Tem [Tenente] Portela, P. Est. Rio Turvo; Oct. 1978; E.P. Albuquerque leg.; MZSP • 1 ♀; Uruguaiana; Aug. 2014; E. Gazbe leg.; MZSP. – **Tocantins** • 1 ♀; Paranã, cerrado sensu stricto; 12.8140° S, 47.8980° W; 13 Oct. 2004; R.R. Silva and B.H. Dietz leg.; at night; MZSP.

PARAGUAY – **Amambai** • 1 ♀; Parque Nac. Cerro Corá; 2 Nov. 1983; T. Bonace leg.; ibn0070; MNHNP HX68 • 1 ♀; same locality as for preceding; 24 Feb. 1981; ibn0066; MNHNP HX62 • 1 ♀; same locality as for preceding; 7–27 Mar. 1982; H. Ferreira da Cunha leg.; ibn0062; MNHNP HX66 • 1 ♀; same locality as for preceding; 5 Nov. 1983; H. Ferreira da Cunha leg.; MNHNP HX63 • 1 ♀; same collection

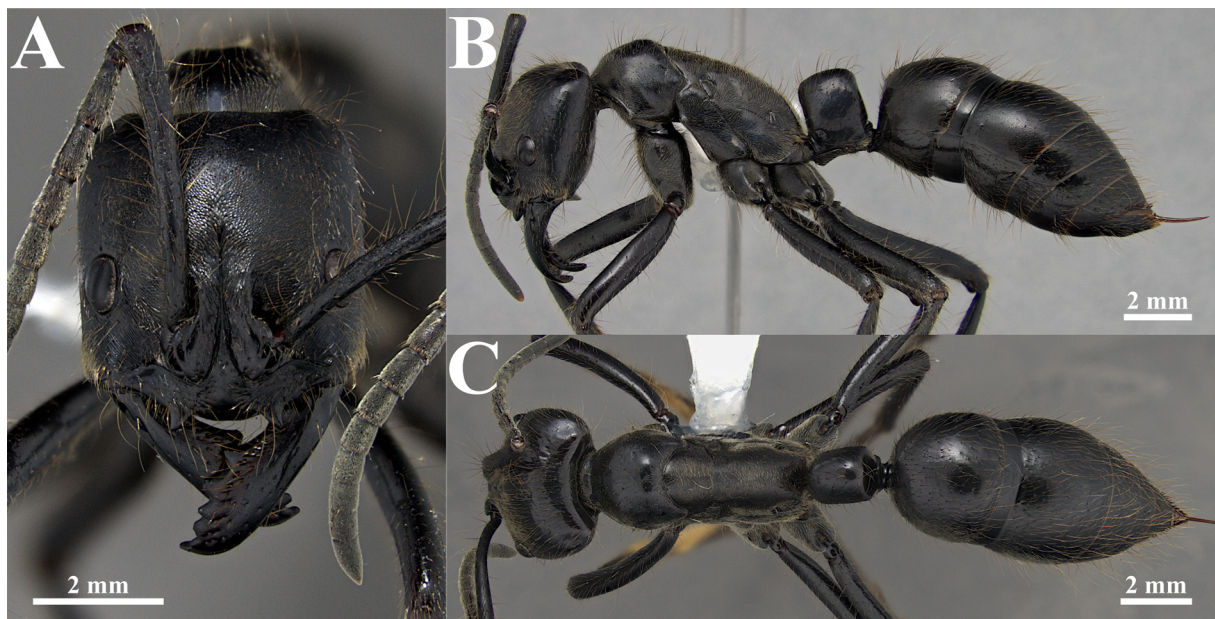
data as for preceding; ibn0065; MNHNP HX64 • 1 ♀; same collection data as for preceding; ibn0063; MNHNP HX67 • 1 ♀; same locality as for preceding; 5 Jun. 1984; T. Bonace leg.; ibn0059; MNHNP HX65 • 1 ♀; same collection data as for preceding; ibn0067; MNHNP HX69 • 1 ♀; same locality as for preceding; 2 Nov. 1985; P. Muller leg.; MNHNP HX55 • 1 ♀; same collection data as for preceding; MNHNP HX56 • 1 ♀; same collection data as for preceding; MNHNP HX57 • 1 ♀; same collection data as for preceding; MNHNP HX58 • 1 ♀; PN Cerro Corá; 12–16 Oct. 1981; J.A. Kolchaka leg.; MNHNP HX53 • 1 ♀; same collection data as for preceding; MNHNP HX54 • 1 ♀; same locality as for preceding; 22°38'19" S, 56°01'12" W; alt. 269 m; 3 Apr. 2015; R. Silvestre *et al.* leg.; UFGD. – **Itapúa** • 1 ♀; Alto Verá; 10 Nov. 1999; J.A. Kolchaka leg.; MNHNP HX59 • 1 ♀; same collection data as for preceding; MNHNP HX60 • 1 ♀; same collection data as for preceding; MNHNP HX61 • 1 ♀; Encarnación; n° 2646 coll Borgm.; MZSP • 1 ♀; same locality as for preceding; 2 Oct. 1898; C. Schrottky leg.; MZSP. – **Misiones** • 1 ♀; Santiago; Oct. 1975; H. Fowler leg.; HFXXX, 13418; MZSP. – **San Pedro** • 1 ♀; Choré; 25 Feb. 1988; Maria Noce de Meza leg.; MNHNP HX52.

## Redescription

### Female

MEASUREMENTS. Lectotype: HL 5.1; HW 4.97; MDL 3.85; SL 4.78; MSL 7.36; HFL 6.4; HBL 5.6; PL 1.93; PH 2.99; PW 1.89; ATS 6.72; BL 24.97 (mm); CI 0.97; SI 0.96; DPI 0.97. Non-types (n = 61): HL 4.38–5.63; HW 4.04–5.35; MDL 3.05–4.28; SL 4.08–5.48; MSL 6.28–7.8; HFL 5.6–6.88; HBL 4.72–5.9; PL 1.67–2.23; PH 2.48–3.2; PW 1.48–1.92; ATS 5.68–7.72; BL 22.06–27 (mm); CI 0.88–1.03; SI 0.85–1.07; DPI 0.8–1.

HEAD. Malar area with longitudinal to oblique striae that always reach anterior eye margin, sometimes extending to gena. Gena microareolate and opaque, sometimes silky, never smooth and shining, usually without rugulae. Apressed pubescence present between eye and frontal lobe, extending posteriorly to frons. Frons microareolate and opaque or with weak silky sheen; with flexuous, brownish and decumbent to suberect hairs, longer than scape diameter; pubescence short, appressed and scarce. Occipital corner varying from strongly microareolate and opaque to smooth and silky. Antennal scape microareolate



**Fig. 15.** *Dinoponera grandis* (Guérin-Méneville, 1838), ♀ (specimen from Jaraguá, Goiás, Brazil; DZUP549812). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

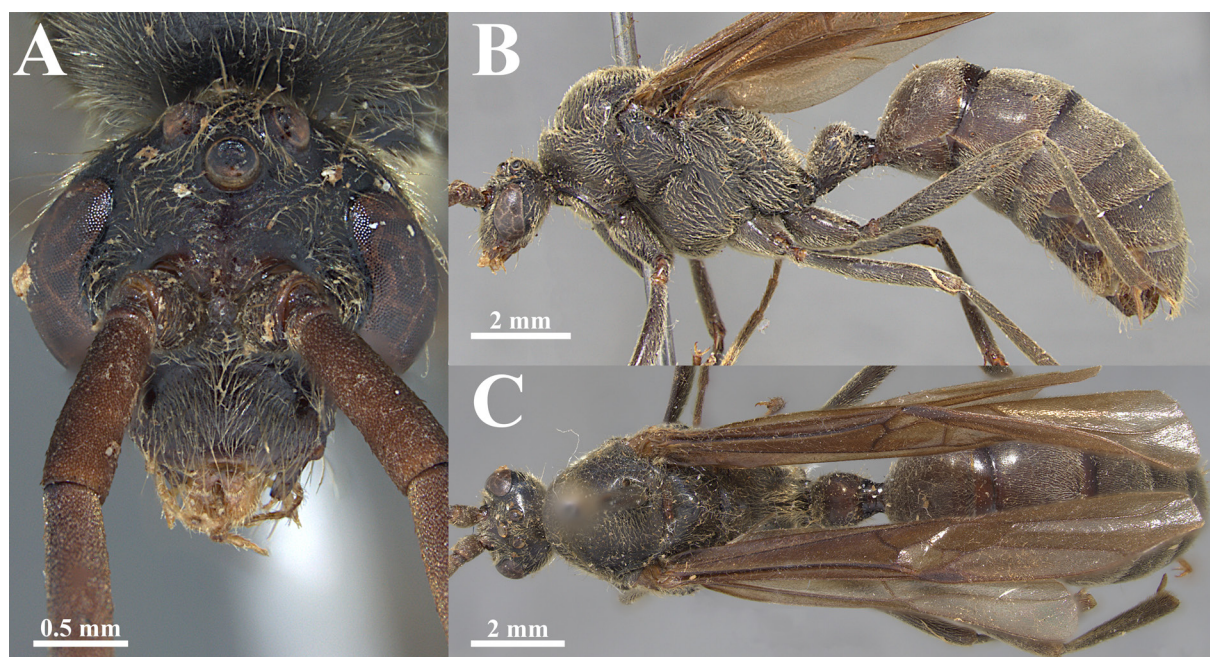
and silky, suberect and long hairs usually present on antennal segments 1–3. Ventral surface of head microareolate with arched strigulae covering entire surface or just close to postgenal suture (rarely absent). Hypostomal tooth longitudinally strigulate. Labrum with median longitudinal sulcus weakly marked; with transverse rugulae. Mandibular dorsum weakly longitudinally strigulate on inner base, sculpture gradually fading apicad.

**MESOSOMA.** Dorsal margin of pronotum in lateral view broadly convex, usually with no pronounced dorsoposterior swelling; anteroventral corner of pronotum toothed or forming acute angle, rarely obtuse. Pronotal dorsum strongly microareolate and opaque to weakly microareolate and silky. Metapleural-propodeal suture sinuous, with at least one curve ventral to position of propodeal spiracle.

**METASOMA.** Petiolar node in lateral view relatively short ( $DPI \geq 0.8$ ); anterodorsal corner at same level as posterodorsal corner, sometimes slightly lower; anterior margin straight or slightly concave, forming blunt angle with dorsal margin; dorsal and posterior margin each varying from broadly convex to straight and forming blunt to slightly rounded angle. Node lateral face usually microareolate and opaque, rarely slightly smooth and silky. Node anterior margin in dorsal view convex; posterior margin straight to broadly convex; lateral margins broadly convex and converging anterodorsally. Abdominal tergite III strongly microareolate and opaque to weakly microareolate and silky; punctulae in variable density, always denser laterally than dorsally; densely covered with brownish, flexuous, decumbent to suberect hairs on entire surface; appressed pubescence very sparse on dorsum, denser laterally.

#### Male

**MEASUREMENTS.** *D. a. nigricolor* lectotype: HL 2.07; HW1 2.3; MDL 0.56; SL 0.55; EL 1.19; MOD 0.31; LOD 0.33; MSL 5.93; HFL 4.6; PL1 1.34; PH 1.14; PW 1.12; ASL 3.25; BL1 13.16 (mm); CI1 1.1; SEI 2.14; SI1 0.24. *D. a. bucki* lectotype: HL 2.17; HW1 2.25; MDL 0.55; SL 0.62; EL 1.06; MOD 0.26; LOD 0.3; MSL 5.62; HFL 4.5; PL1 1.27; PH 1.09; PW 1; ASL 3.22; BL1 12.85 (mm); CI1 1.03; SEI 1.7; SI 10.27. Non-types (n = 7): HL 1.9–2.12; HW1 2.15–2.37; MDL 0.51–0.68; SL 0.46–0.68; EL 1.11–1.3; MOD 0.31–0.43; LOD 0.27–0.43; MSL 5.37–6.66; HFL 3.74–4.68; PL1 1.3–1.48; PH



**Fig. 16.** *Dinoponera grandis nigricolor* Borgmeier, 1937 syn. nov., lectotype, ♂ (Campinas, Goiás, Brazil; MZSP 65801). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

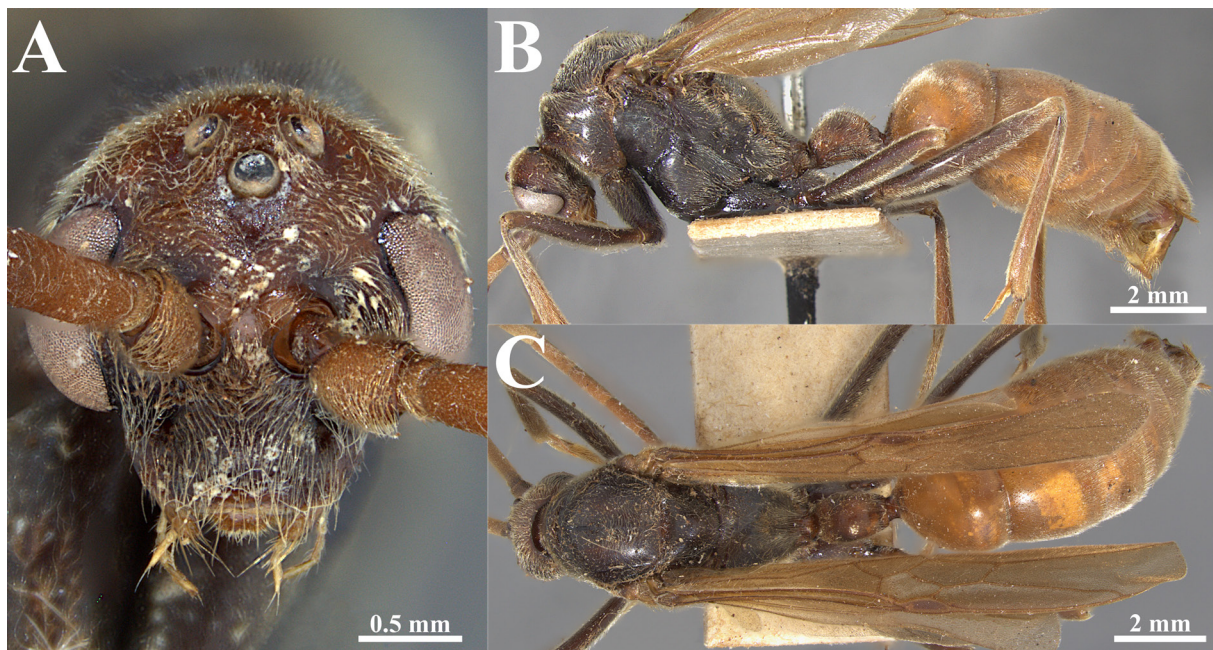
1.14–1.42; PW 1.06–1.25; ASL 3.06–4.12; BL1 12.39–14.9 (mm); CI1 1.04–1.24; SEI 1.83–2.53; SI1 0.2–0.31.

**HEAD.** Frontal carina forming a short longitudinal line. Lateral ocellus usually reduced, sometimes not surpassing posterior head margin in full-face view. Head punctulate, very slightly microareolate and with silky sheen; with pallid decumbent pubescence and very few decumbent hairs only on clypeus and vertex. Antenna with very short appressed pubescence, without hairs. Ventral surface of head punctulate and slightly microareolate with silky sheen.

**MESOSOMA.** Mesoscutum without notaulus. Mesopleural sulcus usually mostly smooth. Scutoscuteellar sulcus scrobiculate. Mesoscutellum usually longitudinally strigulate laterally to variable degrees. Metapleural-propodeal suture with same microsculpture as rest of integument. Mesosoma varying from microareolate and subopaque to smooth and shining, not becoming coarsely punctate on declivitous surface of propodeum; with short decumbent pubescence; without hairs. Legs densely covered by decumbent pubescence; without long hairs. Protibial apex usually without a stout seta.

**METASOMA.** Petiolar node usually slightly microareolate and with silky sheen; densely covered by decumbent to suberect pubescence, without hairs. Abdominal tergite VIII triangular, sometimes with a very sharp apex. Gaster usually microareolate and subopaque; tergites densely covered by appressed to decumbent pubescence; without long hairs.

**GENITALIA.** Basal ring in dorsal view with slightly concave lateral margins, anteriorly narrower than posteriorly; maximum diameter of fenestra longitudinally directed; median invagination usually V-shaped; in lateral view dorsal margin declining and extending anteriorly to form a broad lobe; anteroventral process subtriangular to trapezoid. Gonostylus broad and rounded. Dorsal margin of volsella in lateral view anteriorly straight to broadly convex and posteriorly concave; anteroventral corner projecting ventrally as a subtriangular, subquadrate or rounded lobe; rarely as a narrow and sharp process; posteroventral margin usually continuous, broadly concave and forming a discrete posterior



**Fig. 17.** *Dinoponera grandis bucki* Borgmeier, 1937 syn. nov., lectotype, ♂ (Palmeiras das Missões, Rio Grande do Sul, Brazil; MZSP 65800). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

rounded to acute lobe; digitus volsellaris with posterior margin straight to broadly convex. In lateral view, penisvalva with continuous dorsal and posterior margins, usually ending in a rounded apex which projects ventrolaterally; ventral margin uneven, usually with a concavity containing a short tooth or a spiniform projection; posteriorly with serrated rounded or triangular ventral lobe of variable size; anteroventral region concave or with a short triangular lobe.

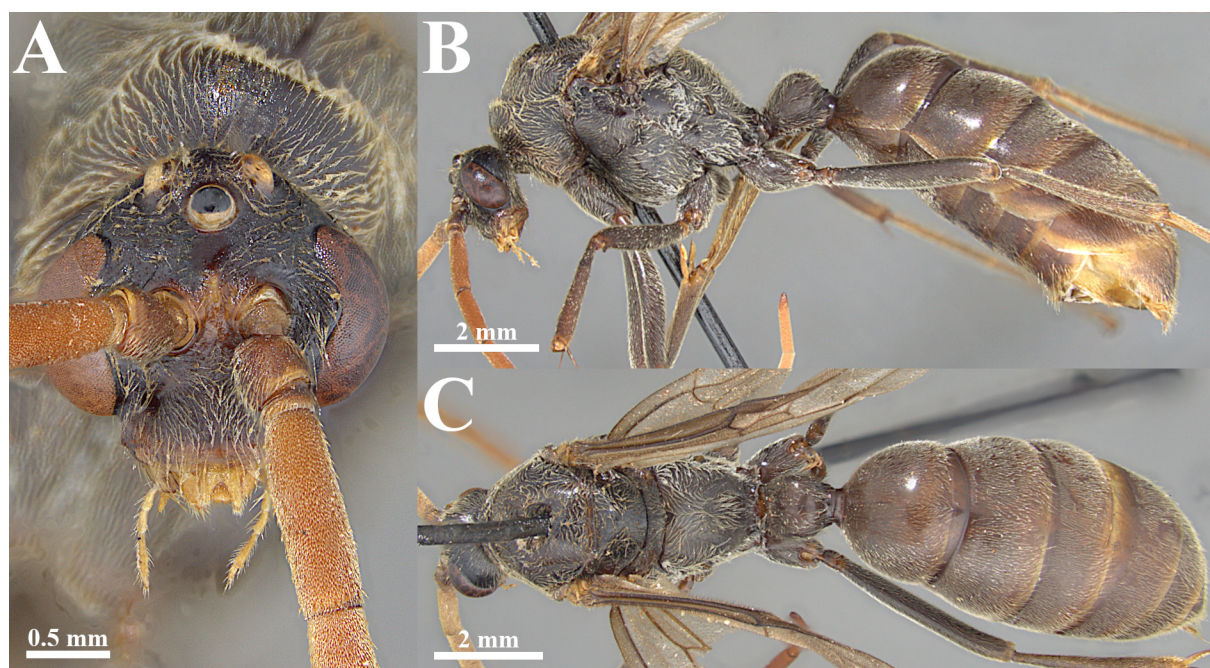
**COLOR.** Body varying from completely light brown to black, sometimes with gaster much lighter-colored.

### Remarks

*Dinoponera grandis*, as discussed below, is strongly polymorphic. The paradox about this species is that females and males tell different histories when examined separately. While males of *D. grandis* will vary discretely in some characters, variation is more continuous in females. Because of this, even recognizing that *D. grandis* may represent a complex of several cryptic species, this is not tenable, based on the current information that separates these forms.

Females from southwestern Mato Grosso do Sul, Brazil, to Amambai, Paraguay, tend to have abdominal tergite III strongly microareolate and opaque and the anteroventral pronotal tooth long and acute, almost spiniform. Ants from Distrito Federal to the northeast of Goiás, Brazil, usually have the pronotal dorsum and abdominal tergite III weakly microareolate and with a silky sheen, and the anteroventral pronotal margin obtusely angular, edentate. Some specimens from southern Brazil have the pronotal dorsum and abdominal tergite III weakly microareolate and with a silky sheen. Some specimens from Paraná could be tentatively identified as *D. lucida* on account of their having the anterodorsal petiolar node angle slightly lower than the posterior angle, but in *D. lucida* this character is more pronounced plus the pubescence on the frons is abundant and long, quite different from *D. grandis*.

Besides the above-mentioned variation, all examined females of *D. grandis* have the malar striae reaching the eye, a relatively short petiolar node ( $DPI \geq 0.8$ ), a body length of less than 27 mm and a



**Fig. 18.** *Dinoponera grandis* (Guérin-Ménéville, 1838), ♂ (specimen from Itahum, Mato Grosso do Sul, Brazil; MZSP 62284). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

hind basitarsus less than 6 mm long. Occasionally, *D. quadriceps* and *D. lucida* may have some of these characters, but besides being usually larger, the following traits will also separate them. The petiolar node of *D. lucida* is anterodorsally lower than the posterodorsal corner and its abdominal tergite III is very smooth, with bluish iridescence. In *D. quadriceps*, the malar striae clearly fail to reach the eye and the petiolar node often has a higher anterodorsal corner.

Santschi (1928) described a form from Paraguay as *Dinoponera grandis australis brevis* based on female characters such as a scape length as long as the head length and a short petiolar node, one third higher than long. Borgmeier (1937) considered it as a subspecies, making the name *D. australis brevis* valid. However, Kempf (1971) did not consider these differences to be significant and he synonymized *brevis* under *D. australis*. Scape length in the studied specimens of *D. grandis* ranges from being longer to shorter than the head length. The node length was found to be one third higher than long in several specimens, leading to the conclusion that such differences are intraspecific.

Guérin-Méneville (1838) apparently described *D. grandis* based on two specimens. In the original description, the author referred to the extremely smooth and shining integument and to the petiolar node shape, which is rounded “up and forward”. These characters could refer to what is now considered *D. longipes*; however, Guérin-Méneville also mentioned the type locality, probably in Minas Gerais, Brazil. Roger (1861) analyzed Guérin-Méneville’s specimens and recognized that one ant had somewhat sculptured and opaque integument, while the other was mostly smooth and shining. Roger also noted that one specimen had the petiolar node relatively narrower in lateral view, but despite this he synonymized *D. grandis* and *D. gigantea*. *Dinoponera grandis*, the more recent name, thus became a junior synonym of *D. gigantea*. In recent revisions, neither Kempf (1971) nor Lenhart *et al.* (2013) were able to study the types of these two species, so doubts lingered as to the status of *D. grandis*.

One of Guérin-Méneville’s syntypes in the ZSM was designated as the lectotype by Diller (1990). It corresponds to the form Roger described as opaque and with a short petiolar node, collected in Minas Gerais, Brazil.

Examining this type, we saw that it is definitely a different species than *D. gigantea*, its current synonym. It thus became obvious we had to separate these two species. Based on the type locality, it would be possible that *D. grandis* was a synonym of *D. australis*, *D. lucida* or *D. quadriceps*. These last two species, however, are easily separated from *D. grandis*. In addition, the lectotype of *D. grandis* was revealed to have the same characters used by Emery (1901) to describe *D. grandis australis* and later used by Borgmeier (1937) to raise *D. australis* to species level: body size smaller than in other species of *Dinoponera*; anteroventral pronotal tooth present; integument less shining than in either *D. longipes*, *D. lucida* or *D. mutica* but more so than in *D. gigantea*; short petiolar node, slightly longer than broad; short legs and antennae; and the scape surpassing the posterior head margin.

Due to the similarities between the lectotype of *D. grandis* and the description and the known forms of *D. australis*, allied with the fact that both occur in sympatry, these two species are synonymized. *Dinoponera grandis*, which is the oldest name, thus becomes the valid name (senior synonym) and *D. australis* becomes the junior synonym. Although the type of *D. australis* has not been examined, choosing not to synonymize these names would mean that there would be two names with the same diagnosis.

In this study three other names are synonymized under *D. grandis*: the species *D. snellingi* Lenhart, Dash & Mackay, 2013, and the subspecies *Dinoponera australis nigricolor* Borgmeier, 1937 and *Dinoponera australis bucki* Borgmeier, 1937. This decision is discussed below.

Borgmeier (1937) described *D. australis nigricolor* and *D. australis bucki* based on females and males taken from their respective nests, the former in central Goiás and the latter in Rio Grande do Sul, Brazil. He found *D. a. nigricolor* females to be identical to *D. a. bucki* females except for having the dorsal margin of the petiolar node margin slightly convex, a difference we consider as intraspecific. However, he considered male characters to be more reliable indicators, particularly gonostylus width. Other male differences he also considered diagnostic included the petiolar node shape, body color, shade of wing color and slight differences in the relative scape length. Unfortunately, he only had one male for each subspecies.

Lenhart *et al.* (2013) described *D. snellingi* based on 3 males collected at a light in Campo Grande, Mato Grosso do Sul, Brazil. The ants were initially identified as *D. australis* because they were collected at the same locality and on the same day as some females of *D. australis*. They compared these males with the descriptions by Kempf (1971) and found similarities in the short pygidial spine and bicolored body, but they also discerned a number of differences. They recognized it as a different species on account of the following combination of characters: bicolored body; head with bulging compound eyes and ocelli; penisvalva with a large ventral lobe and finger-like serrated flange; a short and broad digitus volsellaris with a finely toothed basal lobe; and a distinctively shaped paramere.

The present study was able to gather the largest number of *D. grandis* male specimens with the widest geographic coverage until now (11 male specimens, contrasting with five and four in Lenhart *et al.* 2013 and Kempf 1971, respectively). Below we discuss variation in the diagnostic characters given by Borgmeier (1937) and Lenhart *et al.* (2013), finding many of them to be ineffective for species delimitation and thus weakening the validity of these names.

Node shape, in general, is convex as seen laterally, but it can vary from evenly convex to unevenly convex, with the highest point shifting from mid-petiolar distance to points just anterior or posterior to it. Variability was found even in the relative height of the node. Given such variation, the differences in node shape used by Borgmeier to distinguish *D. a. bucki* from *D. a. nigricolor* becomes ineffective when more specimens are compared.

The male specimen of the *D. a. bucki* type series is designated here as the lectotype, given the apparent greater discreteness of male characters. It is strikingly bicolored with the gaster light chestnut and the rest of the body dark brown, but the bicolor pattern is also present in a male from Goiás (Jataí) and in another from São Paulo (Itirapina), the latter with a more yellowish gaster and darker body. Lenhart *et al.* (2013) described *D. snellingi* as having the same colors, but a male from Mato Grosso do Sul (Itaum), with genitalia very similar to those of *D. snellingi*, is entirely chestnut. The lectotype male of *D. a. nigricolor* is entirely black, with the gaster slightly lighter. This pattern was also found in males from Paraná (Guarapuava and Laranjeiras do Sul) and Mato Grosso do Sul (Itaum). Another male collected at the type locality of *D. a. nigricolor* is entirely light chestnut, as well as a specimen from Mato Grosso (Chapada dos Guimarães).

The relative scape length was found to be slightly less in *D. nigricolor* than in *D. a. bucki* by Borgmeier (1937). The ratio of scape width divided by scape length varies from 0.73 to 0.93 in six males, including the types, so this variation becomes muddled when studying more specimens.

In general, all males studied here have reduced eyes and ocelli compared with other species of *Dinoponera*, but only in the lectotype of *D. a. bucki* are they as small as those of the *D. grandis* male of fig. 4e in Lenhart *et al.* 2013. The lectotype of *D. a. nigricolor*, a topotypic male, and a specimen from Itirapina, São Paulo, all have the lateral ocelli surpassing the posterior head margin in dorsal view, as in the description of *D. snellingi* and fig. 4d in Lenhart *et al.* 2013. Therefore, this character is not exclusive to *D. snellingi* and its usefulness in separating species becomes doubtful.

Borgmeier (1937) found the gonostylus in *D. a. nigricolor* to be relatively wider than in *D. a. bucki*. Lenhart *et al.* (2013) described the gonostylus shape in *D. snellingi* as distinct from that in *D. grandis*. We detected differences in the shape and relative width of the gonostylus of other *D. grandis* males that are similar to those in *D. a. bucki* and *D. a. nigricolor*. Thus, these observed differences prove continuous among specimens, rendering them useless for diagnosis.

The anteroventral corner of the volsella in lateral view usually varies from rounded to subtriangular between specimens, with no evident pattern. An exception is provided by the lectotype of *D. a. nigricolor* and a topotype male, which have their anteroventral process narrow and sharp (spiniform). The posteroventral margin of the volsella of these specimens also differs by having a small subquadrate lobe close to the apex. All other males have a continuous margin. In the Itirapina male this margin is more strongly convex, giving the whole volsella an arched appearance.

All the observed males have a large anteroventral lobe on the penisvalva. The anteroventral corner, however, has two different states: either a concavity or a short triangular lobe. The latter state was found only in the Itaum and Itirapina males. The penisvalva illustration of *D. snellingi* in Lenhart *et al.* (2013) does not show this triangular lobe; instead it shows a more rounded and convex corner, which is also different from the concave corner found in other *D. grandis* males.

Penisvalva shape is the most variable character among examined males. In *D. snellingi* it is described by Lenhart *et al.* (2013) as having a large triangular ventral lobe with a vertical ridge running through the middle. This ventral lobe is longer than wide and is strikingly different from that of other *Dinoponera* males. Additionally, the ventral margin of the penisvalva has a small tooth. Males from Itaum and Itirapina have a very similar penisvalva shape, although the vertical ridge is inconspicuous. The penisvalva in the type of *D. a. nigricolor* and the topotypic specimen have a ventrally pronounced posteroventral lobe that forms a blunt angle, but it is never longer than wide, as in the illustration of the type of *D. snellingi* (Lenhart *et al.* 2013: fig. 11b). The penisvalva of *D. a. bucki* has a rounded posteroventral lobe and a long, acute ventral spine, as do the other *D. grandis* males. It is very similar to the description of males from Argentina (Lenhart *et al.* 2013).

Most of the characters mentioned above are not solid enough to justify the validity of *D. snellingi*, *D. a. nigricolor* or *D. a. bucki*. Even though the shape of the anteroventral corner in the volsella and penisvalva seems to vary discretely in *D. a. nigricolor* and *D. snellingi*, there are more gaps than certainties about the delimitation of these entities.

These males were taken during the same collection events as *D. grandis* females, but these few males do not allow us to know whether these seemingly distinct characters simply represent extremes of continuous variations.

A last consideration is that the validity of *D. snellingi*, *D. a. nigricolor* and *D. a. bucki* would imply we know the form of the *D. grandis* male, a tenuous assumption. The first description of a *D. grandis* male (Santschi 1921: 85) was based on specimens from Argentina, very far from the type locality in Minas Gerais, Brazil. It is much more likely that the male of *D. grandis* corresponds to one of the specimens described as *D. snellingi*, *D. a. nigricolor* or *D. a. bucki*, all of which occur much closer to the type locality.

Based on all of this evidence, we argue for the synonymy of these names; however, we strongly encourage future studies on *D. grandis*, as the high variability of this species can be a sign of the existence of a complex of cryptic species. For future studies, we recommend that the first question addressed be: what is the form of the *D. grandis* male? The next step must be to gather fresh specimens by extensive fieldwork in all distribution areas, the results of which would also enable molecular and



phylogeographic studies. In the light of human-induced climate change, and continuing deforestation and forest fires, we consider such fieldwork to be of utmost importance. Not only would it help elucidate the questions surrounding the situation of *D. grandis*, but it would also inform conservation measures that could help preserve the remaining populations of these giant ants.

### Biology

*Dinoponera grandis* is found in a wide variety of environments, with predominance in savannas, at least for Brazilian records. Nests have a random spatial distribution and may have a density of up to 180 nests per hectare (Tillberg *et al.* 2014). Each nest has an entrance without a surrounding mound and may reach a depth of 143 cm (Paiva & Brandão 1995). Despite the relatively large nest size, colonies have on average only 14 workers, which indicates that nests are constantly reused and not completely constructed every generation (Paiva & Brandão 1995; Monnin *et al.* 2003). *Pheidole dinophila* Wilson, 2003 has been recorded as nesting within nests of *D. grandis* at more than one locality (Wilson 2003).

They are omnivorous, but favor hunting other invertebrates (Tillberg *et al.* 2014). Foraging strategies involve route fidelity for individual workers and the distribution of different routes among workers, favoring greater efficiency in the area being covered (Tillberg *et al.* 2014). Organization inside the nest reflects division of tasks, with foraging workers occupying chambers closer to the surface and higher status workers occupying deeper chambers (Paiva & Brandão 1995). This nest occupation dynamic was confirmed by Smith *et al.* (2011), demonstrating that workers of deeper chambers have up to 39% of their dry body mass composed of fat, while workers found in shallow chambers may have less than 1% body fat. Dominance hierarchy is determined by agonistic conflicts similar to those in *D. quadriceps*, guaranteeing colony monogyny (Monnin *et al.* 2003).

### Distribution (Fig. 28A)

*Dinoponera grandis* is a widely distributed species, occurring in most of the Central West, South and Southeast regions of Brazil as well as Paraguay, Argentina and Bolivia. The northernmost record is in Paranã (Tocantins) and the southernmost Brazilian record is in Uruguaiana (Rio Grande do Sul). These ants are not present in eastern Brazil.

### *Dinoponera hispida* Lenhart, Dash & Mackay, 2013 Figs 19, 28B

*Dinoponera hispida* Lenhart, Dash & Mackay, 2013: 141, figs 1c, g, 2 (♀).

### Diagnosis

#### Female

Body covered by thick and stiff hairs. Ventral surface of head posteriorly with transverse strigulae. Anteroventral pronotal corner in lateral view rounded or forming obtuse angle, never toothed. Dorsum of pronotum and abdominal tergite III mostly smooth and with bluish iridescence. Petiolar node in dorsal view usually slender (DPI < 0.71).

### Material examined

#### Holotype

BRAZIL – Pará • 1 ♀; Tucuruí; Jan. 1979; coll. M. Alvarenga; examined by images; MCZC.

#### Non-type specimens (21 ♀♀)

BRAZIL – Pará • 1 ♀; Curionópolis, Faz. Serra Grande; 9 Jul. 1991; C. Melo and F. Melo leg.; 1385/1/79; DZUP • 1 ♀; FloNa Carajás, Parauapeba; Mar. 2016; V.C. Rocha leg.; UFSC • 1 ♀; Marabá; 2017; DZUP • 1 ♀; Marabá, Gruta do Gavião; 5 Oct. 1986; GEP; MZSP • 1 ♀; Melgaço, Caxiuanã, ECFPn;

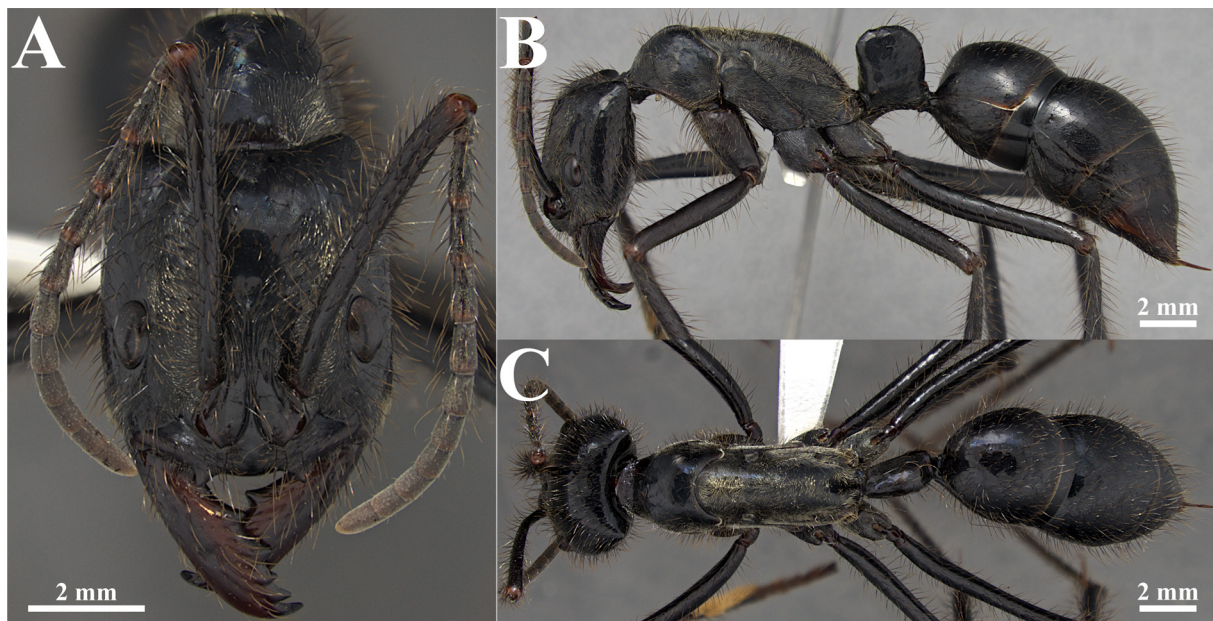
1.7815° S, 51.5919° W; 5–7 Nov. 2003; A.Y. Harada, E.P. Fagundes and C. Renato leg.; VI: transecto 16-900; MPEG • 1 ♀; Melgaço, Caxiuana, Estação Científica Ferreira Penna; 1°45' S, 51°31' W; 30 Oct. 2003; J. Souza and C. Moura leg.; plote VI transecto 5-600, pitfall 05; INPA • 1 ♀; Novo Repartimento, Fazenda Arataú; 25–26 Jun. 2003; A.M. Elizabeth leg.; CPDC • 1 ♀; Parauapebas, FLONA de Carajás; 24 Feb. 2010; A.A. Matias leg.; “isca de sardinha, 10 trilha F Canga Controle – solo”; INPA • 1 ♀; same collection data as for preceding; “5 trilha F Canga Controle – solo”; INPA • 1 ♀; Portel, Igarapé Banã; 2.0522° S, 50.7313° W; 26 Jan. 2016; MPEG • 1 ♀; Serra dos Carajás; J.C. Freitas leg.; 1501, Coleção Diniz; DZUP • 1 ♀; Serra Norte, Carajás; Jul.–Aug. 1985; Brandão and Benson leg.; Unicamp Ecol. Campo exped.; N3 mata trilha; MZSP • 1 ♀; same collection data as for preceding; N3 canga Arrm. Berlese; MZSP • 1 ♀; same collection data as for preceding; N1 Canga gramínea; MZSP • 1 ♀; same collection data as for preceding; N1 Canga gramínea #4; MZSP • 1 ♀; Serra Norte, Manganês; 16 Aug. 1984; W. França leg.; lote 2550; MPEG HYM11506519 • 1 ♀; same locality as for preceding; 17 Jun. 1985; R.D. Thomaz leg.; lote 2552; MPEG HYM11506521 • 1 ♀; Serra Norte, N-1 Canga; 24 Oct. 1984; Márcio Zanuto leg.; lote 2537; MPEG HYM11506495 • 1 ♀; Serra Norte, N-3 mata; 6 Oct. 1986; M. Martins leg.; lote 2536; MPEG HYM11506496 • 1 ♀; Tucuruí; 7 Jul. 1978; P. Maurício leg.; MPEG HYM11513011 • 1 ♀; same locality as for preceding; 8 Jul. 1978; W. França leg.; MPEG HYM11513016.

## Redescription

### Female

MEASUREMENTS. Non-types (n = 10): HL 4.8–6.17; HW 4.6–5.73; MDL 3.95–4.66; SL 5.67–6.42; MSL 7.52–8.7; HFL 7.24–8.5; HBL 6.08–7.1; PL 2.17–2.51; PH 2.75–3.5; PW 1.36–1.64; ATS 6.96–8.4; BL 25.4–30.12 (mm); CI 0.87–0.96; SI 1.13–1.27; DPI 0.6–0.71.

HEAD. Malar area with longitudinal to oblique striae which gradually fade posteriorly, sometimes not reaching anterior eye margin. Gena smooth or weakly microareolate, with bluish iridescence, usually without rugulae. Appressed pubescence present between eye and frontal lobe, extending posteriorly to frons. Frons smooth to weakly microareolate, with bluish iridescence; integument slightly irregular close to hair insertions; decumbent to suberect thick, stiff hairs; pubescence densest laterally. Occipital corner



**Fig. 19.** *Dinoponera hispida* Lenhart, Dash & Mackay, 2013, ♀ (specimen from Parauapebas, Pará, Brazil; UFSC). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

smooth and with bluish iridescence. Antennal scape weakly microareolate and shining; antenna with suberect, thick, stiff hairs except for 4–5 apical segments. Ventral surface of head weakly microareolate to smooth; arched, weakly impressed strigulae present on anterior half; well-marked transverse strigulae posteriorly. Hypostomal tooth with longitudinal strigulae. Labrum with weak median longitudinal sulcus that extends from anterior margin to half its length; with transverse rugulae. Mandibular dorsum with longitudinal strigulae along inner margin, gradually fading apicad.

**MESOSOMA.** Dorsal margin of pronotum in lateral view broadly convex, with no pronounced dorsoposterior swelling; anteroventral corner of pronotum rounded or forming obtuse angle, never toothed. Pronotal dorsum smooth, with bluish iridescence. Metapleural-propodeal suture well-marked and straight, rarely sinuous.

**METASOMA.** Petiolar node in lateral view elongate ( $DPI < 0.8$ ); anterodorsal corner usually higher than posterodorsal corner; anterior margin slightly concave, forming blunt angle with dorsal margin; dorsal and posterior margins each broadly convex and forming rounded angle. Node lateral face smooth or weakly microareolate with bluish iridescence. Node anterior margin in dorsal view strongly convex; posterior margin broadly convex; lateral margins broadly convex, slightly converging anterodorsally. Abdominal tergite III smooth or weakly microareolate, with bluish iridescence; punctulae sparse, slightly denser laterally than dorsally; covered by suberect thick, stiff hairs on entire surface; appressed pubescence very sparse on dorsum, denser laterally.

#### **Male**

Unknown.

#### **Remarks**

The diagnostic characters easily separate *D. hispida* from any other *Dinoponera*. This species occurs in sympatry with *D. gigantea*, which differs by having a microareolate and opaque integument with slender, flexuous hairs. It may be confused with either *D. longipes*, *D. mutica*, or *D. nicinha* sp. nov., which also have a shining integument and occur in northern Brazil. *Dinoponera mutica* and *D. nicinha* sp. nov. can be separated by not having the petiolar node with a blunt anterodorsal angle or a rounded posterodorsal angle in lateral view. *Dinoponera longipes* may have the node slightly similar to that of *D. hispida*, but it lacks strigulae on the head venter and has flexible golden hairs throughout the body. Another species with smooth and shining integument is *D. lucida*, but it differs by having the anterodorsal node angle lower than the posterodorsal angle in lateral view. *Dinoponera lucida* only occurs in the Atlantic forest of eastern Brazil.

The holotype of *D. hispida* was examined by images available in the online database of the MCZC (<https://mczbase.mcz.harvard.edu>, Identifiers: Entomology, 36191) and additional images. Besides that, the description of Lenhart *et al.* (2013) is very complete and detailed, permitting a clear recognition of the species.

#### **Biology**

The life history of this species is unknown. It is restricted to the Amazon, characterized by humid forests and large trees (IBGE 2012). According to the Köppen classification system, the predominant climate in southeastern Pará is Tropical Monsoon, with the average temperature of the coldest month over 18°C and high annual precipitation (Alvares *et al.* 2013).

#### **Distribution** (Fig. 28B)

*Dinoponera hispida* has a relatively restricted distribution, known only from a few sites in Pará that are being affected by large-scale mining, a large hydroelectric plant (Tucuruí Hydroelectric Power Plant) and

extensive deforestation. This combination of habitat disturbance makes the species a likely candidate for being considered as threatened. However, its distribution could be greater if there are more specimens in collections presently misidentified as the sympatric *D. gigantea*.

*Dinoponera longipes* Emery, 1901

Figs 20, 29A

*Dinoponera grandis longipes* Emery, 1901: 48 (♀).

*Dinoponera longipes* – Kempf 1971: 375 (raised to species). — Lenhart, Dash & Mackay 2013: 143, figs 1a, b, 3, 4c, h, m, 5e, 8, 9e, 10e, 11e (redescription, male description, key).

**Diagnosis**

**Female**

Anteroventral corner of pronotum in lateral view unarmed, forming obtuse angle. Petiolar node in lateral view with anterodorsal corner clearly higher than posterodorsal corner. Abdominal tergite III smooth and with bluish iridescence; covered with sparse golden pubescence. Body covered with flexible golden hairs.

**Material examined**

**Holotype**

PERU – **Cumbase** • 1 ♀; examined by images; MCSN.

**Non-type specimens (15 ♀♀)**

BRAZIL – **Acre** • 1 ♀; Cruzeiro do Sul; Dec. 1963; P.L. Herbst leg. MZSP • 1 ♀; same collection data as for preceding; Coleção Diniz; DZUP • 2 ♀♀; Marechal Thaumaturgo, Vila Thaumaturgo; Feb. 1962; Pe.L. Herbst leg.; MZSP • 1 ♀; Porto Acre, Humaita; 15 Jun.–2 Jul. 1992; Gorayeb, Pena Henriques and Edmar leg.; MPEG • 1 ♀; Rio Branco, mata terra firme; 25 Oct.–8 Nov. 1991; F. Ramos, A. Henrique, I. Gorayeb and N. Bittencourt leg.; MPEG.

COLOMBIA – **Amazonas** • 1 ♀; Leticia, 7 km via Tarapacá; 4 Dec. 1971; S. Franky leg.; CPDC. – **Caquetá** • 1 ♀; Florencia; alt. 266 m; 10–20 Oct. 1990; G. Medina and C. Rodriguez leg.; ICN 078906; ICNC.

PERU – **Amazonas** • 2 ♀♀; Montenegro, Rio Marañon; 16 Apr. 1960; alt. 350 m; V. Weyrauch leg.; MZSP. – **Leoncio Prado** • 1 ♀; Tingo Maria, Rio Huallaga; 26 Jul. 1955; alt. 670 m; Weyrauch leg.; 212; MZSP • 1 ♀; Upper Rio Huallaga; 1 Nov. 1930; F6123; MZSP. – **San Martin** • 2 ♀♀; Taropoto; A. Velásquez leg.; MZSP. – **Tocache** • 1 ♀; Uchiza, Palmas del Espino; 19 Aug. 1987; G. Couturier leg.; DZUP 549808.

**Redescription**

**Female**

MEASUREMENTS. Non-types (n = 6): HL 5.54–6.07; HW 5.22–5.73; MDL 4.22–4.97; SL 5.92–6.17; MSL 8.1–8.9; HFL 8.08–8.8; HBL 7–7.6; PL 2.32–2.69; PH 2.97–3.4; PW 1.55–1.82; ATS 7.8–8.5; BL 28.31–31.02 (mm); CI 0.91–0.98; SI 1.04–1.18; DPI 0.63–0.67.

HEAD. Malar area with weak longitudinal to oblique striae that do not reach anterior eye margin. Gena weakly microareolate with bluish iridescence, usually without rugulae. Golden appressed pubescence present between eye and frontal lobe, extending posteriorly to frons. Frons smooth and with bluish iridescence; with flexuous, golden and decumbent to suberect hairs, longer than scape diameter;

pubescence densest laterally. Occipital corner smooth and with bluish iridescence. Antennal scape weakly microareolate and silky; antenna with decumbent to suberect and long hairs, except for 4–5 apical segments. Ventral surface of head smooth, with silky sheen; longitudinal strigulae mostly absent or, if present, only near hypostomal tooth. Labrum without median longitudinal sulcus, transverse rugulae absent. Mandibular dorsum weakly longitudinally strigulate on inner base, sculpture gradually fading apicad.

**MESOSOMA.** Dorsal margin of pronotum broadly convex in lateral view, usually with no pronounced dorsoposterior swelling; anteroventral corner of pronotum forming obtuse angle, never toothed. Pronotal dorsum smooth, with bluish iridescence. Metapleural-propodeal suture well-marked and slightly sinuous, with at least one curve ventral to position of propodeal spiracle.

**METASOMA.** Petiolar node in lateral view elongate ( $DPI < 0.8$ ); anterodorsal corner higher than posterodorsal corner; anterior margin slightly concave, forming blunt angle with dorsal margin; dorsal and posterior margins broadly convex, forming rounded angle. Node lateral face smooth with bluish iridescence. Node anterior margin in dorsal view strongly convex, posterior margin straight to broadly convex, lateral margins broadly convex and converging anterodorsally. Abdominal tergite III smooth with bluish iridescence; punctulae in variable density, evenly distributed laterally and dorsally; covered by flexuous, golden suberect hairs and appressed pubescence evenly distributed on dorsal and lateral surfaces, ranging from dense to sparse.

#### Male

Not examined.

#### Remarks

*Dinoponera longipes* may occur in sympatry with *D. gigantea*, but the females are easily separated by the microareolate and opaque integument and anteroventral pronotal tooth of *D. gigantea*. Females of *D. mutica* and *D. nicinha* sp. nov. are the most similar to *D. longipes* as both have a shining integument



**Fig. 20.** *Dinoponera longipes* Emery, 1901, ♀ (specimen from Uchiza, Peru; DZUP 549808). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

and a toothless anteroventral pronotal margin in lateral view. However, the node shape of *D. longipes* separates it from these two species. *Dinoponera quadriceps* may have a similar node shape, but differs by having abdominal tergite III microareolate and opaque with brownish, not golden, hairs.

Images of the holotype (AntWeb, CASENT 0903861) were examined. The original description includes some characters that are at odds for all the examined specimens, such as the length of the legs and the antennae being longer in comparison with other *Dinoponera*. Despite this, the node shape and golden pilosity were considered sufficient to maintain the validity of this species. The density of the pilosity and pubescence on abdominal tergite III varies greatly. A specimen from Rio Branco, Acre State, has the body completely covered by dense long and appressed pubescence, but specimens from Colombia have sparse pubescence. The availability in Brazil of *D. longipes* in collections is meagre and several female specimens identified as *D. longipes* actually belong to *D. nicinha* sp. nov.

The male was described by Lenhart *et al.* (2013) based on 2 specimens from Tingo María, Peru. According to these authors, *D. longipes* can be separated from other species by the thick decumbent antennal setae and by the shape of abdominal tergite VIII, which is shorter than in *D. gigantea* and *D. quadriceps* and longer than in *D. grandis* and *D. snellingi*. Comparing the description and illustrations of *D. longipes* with the males of *D. lucida*, it seems that they are similar, but the shape of the penisvalva is very different, not forming a rounded ventral lobe in *D. longipes*.

### Biology

*Dinoponera longipes* occurs in regions with dense tropical rainforests, but Morgan (1993) found most nests in areas with sparse understory vegetation. Each nest can have one to thirty entrances with soil particles forming mounds around each (Morgan 1993). Most nests are close to roots or in areas shaded by vegetation and the distance between them averages 35 m (Morgan 1993). In two nests observed by Morgan (1993), the number of workers was seven in a young colony and 120 in a mature colony.

The diet is predominantly carnivorous and foraging is solitary and mainly nocturnal (Morgan 1993). The ants interact, displaying agonistic behaviors similar to those described in other species, such as immobilization and antennal beating (Morgan 1993; Monnin *et al.* 2003).

### Distribution (Fig. 29A)

*Dinoponera longipes* is present in Brazil, Colombia and Peru. Lenhart *et al.* (2013) also examined specimens from Ecuador. In this study, the northernmost record is from Florencia, Caquetá, Colombia, and the southernmost record is from Porto Acre, Acre State. This species has not been collected in Brazil in over 25 years.

### *Dinoponera lucida* Emery, 1901

Figs 21–22, 29A

*Dinoponera grandis lucida* Emery, 1901: 48 (♂).

*Dinoponera lucida* – Kempf 1971: 376: figs 1–2 (raised to species). — Lenhart, Dash & Mackay 2013: 146, fig. 1h (redescription, key, male genitals). — Escárraga *et al.* 2017 (male description). — Tozetto & Lattke 2020: 5, figs 2–3, 6 (male genitals).

### Diagnosis

#### Female

Malar area with longitudinal to oblique striae that always reach entire anterior ocular margin and extend to gena until at least half of eye length. Anteroventral corner of pronotum in lateral view with tooth or

acute angle. Dorsum of pronotum and abdominal tergite III smooth, with bluish iridescence. Anterodorsal corner of petiolar node in lateral view lower than posterodorsal corner.

### Male

Antenna with stiff decumbent hairs shorter than maximum scape diameter. Gastral tergites with long hairs. Abdominal tergite VIII triangular, with a very sharp apex. Penisvalva ending in a rounded ventral lobe.

### Material examined

#### Non-type specimens (324 ♀♀, 26 ♂♂)

BRAZIL – **Bahia** • 1 ♀; Barrolândia; 16–23 Jul. 1994; S. Lacau leg.; CPDC • 2 ♂♂; same locality as for preceding; 4 Aug. 2004; J.R.M. Santos leg.; CPDC • 1 ♀; Faz. Amaralina, Guaratinga; 27 Aug. 1993; O.S.A. Paula leg.; 4675c; CPDC • 1 ♀; Fazenda Limeira, Itapebi; 25 Apr. 1988; J. Raimundos leg.; 4369; CPDC • 2 ♂♂; Ibirapuã; 5 Jul. 2004; J.R.M. Santos leg.; CPDC • 1 ♀; Itamaraju, Faz. Pau Brasil; 10 May 1969; Ventocilla leg.; 2744; INPA • 2 ♂♂; Itamaraju; 8 Jul. 2004; J.R.M. Santos leg.; CPDC • 1 ♀; Itanhem; 12 Nov. 2009; Jonathas leg.; 5580; CPDC • 1 ♀; Jacobina; 1996; J. Jardim leg.; CPDC • 5 ♀♀; Jequié; 15 Nov. 1964; C. and T. Elias leg.; DZUP • 1 ♂; Lajedão; 6 Jul. 2004; J.R.M. Santos leg.; CPDC • 1 ♀; same locality as for preceding; 21 Jul. 1967; K. Brown leg.; DZUP • 1 ♀; Monte Pascoal; 20 Jan. 1994; J.C. Nascimento leg.; 4795; CPDC • 1 ♀; Mucuri; 1–10 Mar. 1971; C. Elias leg.; DZUP • 1 ♀; Pau Brasil; 14 Jan. 1998; L.A. Matos Silva leg.; 5220; CPDC • 1 ♀; Porto Seguro; 13 Dec. 1992; A.B. Casimiro leg.; 4600b; CPDC • 1 ♀; Porto Seguro, E.E. Pau Brazil; 16°23'17" S, 39°10'55" W; 13 Nov. 2014; DZUP • 8 ♀♀; Prado; 5 Mar. 1971; C. Elias leg.; DZUP • 1 ♀; R. [Rio] Mucuri Sul; 23 Jul. 1967; K. Brown leg.; DZUP • 1 ♀; T [Teixeira] de Freitas, zona rural; 30 Jul.–3 Aug. 2007; F.B. Fraga leg.; UFES 55843. – **Espírito Santo** • 1 ♀; Alfredo Chaves; 20°27'53" S, 40°42'35" W; alt. 714 m; 15 Oct. 2007; C.O. Azevedo and team leg.; UFES 39348 • 1 ♂; Alfredo Chaves, Matilde, RPPN Oitrem; 20°33' S, 40°48' W; 14–21 Oct. 2009; C.O. Azevedo and team leg.; Malaise 600–800 m; UFES • 1 ♂; same collection data as for preceding; UFES 74864 • 1 ♀; Aracruz, Faz. Rio Verde; 23 Jan. 1994; Delabie leg.; 4788; CPDC • 3 ♀♀; Baixo Guandu; 17 May 1970; C. and C.T. Elias leg.; DZUP • 7 ♀♀; same locality as for preceding; 24–31 Aug. 1970; Tadeu and C. Elias leg.; DZUP • 12 ♀♀; same locality as for preceding; 25 Apr. 1970; C. and C.T. Elias leg.; DZUP • 2 ♀♀; same locality as for preceding; 29 Jun. 1970; C. and C.T. Elias leg.; DZUP • 3 ♀♀; same locality as for preceding; 7–13 May 1970; Tadeu and C. Elias leg.; DZUP • 5 ♀♀; same locality as for preceding; 1 Jun. 1970; C.T. and C. Elias leg.; DZUP • 1 ♀; same locality as for preceding; 10–16 Aug. 1970; C. and C.T. Elias leg.; DZUP • 4 ♀♀; same locality as for preceding; 16–22 Sep. 1971; C. Elias leg.; DZUP • 1 ♀; same locality as for preceding; 17–22 Aug. 1970; C. and C.T. Elias leg.; DZUP • 4 ♀♀; same locality as for preceding; 1–8 Aug. 1970; C. and C.T. Elias leg.; DZUP • 1 ♀; same locality as for preceding; 22 Jun. 1970; Claudionor Elias leg.; DZUP • 5 ♀♀; same locality as for preceding; 23–30 Apr. 1970; C. and C.T. Elias leg.; DZUP • 23 ♀♀; same locality as for preceding; 23–30 Sep. 1970; C. and C.T. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; DZUP 549807 • 1 ♀; same locality as for preceding; 26–30 Apr. 1970; C. and C.T. Elias leg.; DZUP • 4 ♀♀; same locality as for preceding; 29 Apr.–6 May 1970; C. and C.T. Elias leg.; DZUP • 2 ♀♀; same locality as for preceding; 6 Jul. 1970; C. and C.T. Elias leg.; DZUP • 4 ♀♀; same locality as for preceding; 8 Jun. 1970; C.T. and C. Elias leg.; DZUP • 1 ♀; Buenos Aires, 10 km W of Guarapari; alt. 500 m; 6 Jan. 1996; G.A.R. Melo leg.; DZUP • 1 ♀; Cariacica, Res. Biol. De Duas Bocas; 16 Sep. 2006; R. Kawada and team leg.; UFES 124428 • 1 ♂; same locality as for preceding; 28 Feb. 2004; R. Kawada leg.; UFES 132366 • 2 ♀♀; Colatina; Jan. 1962; C. Elias leg.; DZUP • 5 ♀♀; Conc [Conceição] da Barra; 1 Nov. 1969; C.T. and C. Elias leg.; DZUP • 5 ♀♀; same locality as for preceding; 11 Oct. 1969; C.T. and C. Elias leg.; DZUP • 1 ♀; same locality as for preceding; 15 Nov. 1968; C. and C.T. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; DZUP 548835 • 2 ♀♀; same locality as for preceding; 1–6 Jul. 1968; C. and C.T. Elias leg.; DZUP • 2 ♀♀; same locality as for preceding; 16–22 Jan. 1970; C. and C.T. Elias leg.; DZUP • 1 ♀; same locality as for

preceding; 16–22 Mar. 1969; C. and C.T. Elias leg.; DZUP • 1 ♀; same locality as for preceding; 16–23 Apr. 1969; C. and C.T. Elias leg.; DZUP • 5 ♀♀; same locality as for preceding; 17 Sep. 1969; C.T. and C. Elias leg.; DZUP • 3 ♀♀; same locality as for preceding; 17–22 Mar. 1969; C. and C.T. Elias leg.; DZUP • 24 ♀♀; same locality as for preceding; 18 Aug. 1969; C.T. and C. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; DZUP 548824 • 4 ♀♀; same locality as for preceding; 18 Oct. 1969; C.T. and C. Elias leg.; DZUP • 1 ♀; same locality as for preceding; 19 Jun. 1969; C.T. and C. Elias leg.; DZUP • 4 ♀♀; same locality as for preceding; 20 Dec. 1969; C.T. and C. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; DZUP 548826 • 1 ♀; same collection data as for preceding; DZUP 548827 • 1 ♀; same collection data as for preceding; DZUP 548828 • 1 ♀; same collection data as for preceding; DZUP 548829 • 1 ♀; same collection data as for preceding; DZUP 548830 • 8 ♀♀; same locality as for preceding; 25 Sep. 1969; C.T. and C. Elias leg.; DZUP • 1 ♀; same locality as for preceding; 26 May 1968; C.T. and C. Elias leg.; DZUP • 4 ♀♀; same locality as for preceding; 27 Mar. 1969; C.T. and C. Elias leg.; DZUP • 18 ♀♀; same locality as for preceding; 27 Dec. 1969; C.T. and C. Elias leg.; DZUP • 3 ♀♀; same locality as for preceding; 29 Nov. 1969; C.T. and C. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; DZUP 548833 • 1 ♀; same locality as for preceding; 4 Jul. 1969; C.T. and C. Elias leg.; DZUP 548825 • 5 ♀♀; same locality as for preceding; 4 Aug. 1969; C.T. and C. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; DZUP 548821 • 1 ♀; same collection data as for preceding; DZUP 548822 • 1 ♀; same collection data as for preceding; DZUP 548823 • 2 ♀♀; same locality as for preceding; 4–8 Apr. 1969; Tadeu and C. Elias leg.; DZUP • 1 ♀; same locality as for preceding; 5 May 1968; C.T. and C. Elias leg.; DZUP 548834 • 4 ♀♀; same locality as for preceding; 6 Dec. 1969; C.T. and C. Elias leg.; DZUP • 1 ♀; same collection data as for preceding; DZUP 548831 • 1 ♀; same collection data as for preceding; DZUP 548832 • 1 ♀; same locality as for preceding; 6–22 Jan. 1970; C. and C.T. Elias leg.; DZUP • 2 ♀♀; same locality as for preceding; 8 Nov. 1969; C.T. and C. Elias leg.; DZUP • 2 ♀♀; same locality as for preceding; 9–15 Apr. 1969; C. and C.T. Elias leg.; DZUP • 1 ♂; Domingos Martins, Mata do Pico do Eldorado; 20°22'17" S, 40°39'29" W; 26 Nov.–3 Dec. 2004; M.T. Tavares and team leg.; Malaise T1; UFES 107891 • 1 ♂; same locality as for preceding; 3–10 Dec. 2004; M.T. Tavares and team leg.; Malaise T1; UFES 106427 • 1 ♂; same collection data as for preceding; Malaise B4; UFES 104604 • 1 ♂; same collection data as for preceding; Malaise T7; UFES 64441 • 1 ♂; same collection data as for preceding; Malaise B4; UFES 104603 • 1 ♂; same collection data as for preceding; Malaise T1; UFES 106426 • 1 ♂; same collection data as for preceding; Malaise T1; UFES 106425 • 5 ♀♀; Domingos Martins; Jan. 1962; Claudionor Elias leg.; DZUP • 2 ♀♀; Itaguaçu; 19 Mar. 1970; C.T. and C. Elias leg.; DZUP • 1 ♂; Itaguaçu, Alto Lajinha, Fazenda Binda; 22–29 Sep. 2008; M.T. Tavares and team leg.; Malaise; UFES 82143 • 1 ♂; same collection data as for preceding; UFES 82138 • 1 ♀; Laranja da Terra, Joatuba, Faz. Betzel; 19°50'25" S, 40°49'40" W; 5–12 Oct. 2012; Tavares and team leg.; UFES137307 • 1 ♂; same collection data as for preceding; Malaise B-1; UFES 135693 • 1 ♂; same collection data as for preceding; Malaise B-4; UFES 135132 • 1 ♂; Santa Leopoldina, Suíça, mata; 20.08183° S, 40.59413° W; alt. 361 m; 05–12 Nov. 2007; C.O. Azevedo and team leg.; Malaise; UFES 68910 • 1 ♀; Linhares; 19 Oct. 1967; Kloss leg.; Coleção Diniz; DZUP • 1 ♀; same locality as for preceding; 24–31 Jul. 1972; C. Elias leg.; DZUP • 17 ♀♀; same locality as for preceding; 8–14 Aug. 1972; Claudionor Elias leg.; DZUP • 15 ♀♀; same locality as for preceding; 8–14 Dec. 1972; Claudionor Elias leg.; DZUP • 1 ♀; same locality as for preceding; 20 Sep. 1983; M.A. Penha leg.; UFES 39355 • 1 ♀; same locality as for preceding; 10 Oct. 1993; Ademar Luz leg.; 1392; CPDC • 1 ♂; Linhares, Fz. Goitacazes; 20 Oct. 1967; Vantocilla leg.; 1865; CPDC • 1 ♀; Linhares, Res. Vale Rio Doce; 19.2461° S, 39.9611° W; alt. 12 m; 5–6 May 2007; J.A. Rafael and F.F. Xavier F. leg.; manual; INPA • 1 ♀; Res. de Linhares; 20 Oct. 1999; C. Villemant leg.; DZUP • 1 ♀; Morro Mestre Alvaro, Serra; 16 Apr. 1987; A.P. Aguiar leg.; UFES 39363 • 1 ♂; Pancas, Faz. Juliberto Stur; 19.21958° S, 40.77327° W; 24–31 Jan. 2003; Tavares, Azevedo and team leg.; Malaise T4; UFES 99293 • 1 ♀; Piúma, ilha; 6 Nov. 2007; R.S. Ferreira leg.; CPDC • 1 ♀; Regência; 23 Jan. 1994; J.C. Nascimento leg.; 4794; CPDC • 1 ♀; Sta. Tereza [Santa Teresa]; 13 Jan. 1970; C.T. and C. Elias leg.; DZUP • 16 ♀♀; same locality as for preceding; 7 Dec. 1964; C. Elias leg.; DZUP • 1 ♀; Santa Teresa, Est. Biológica de Santa Lúcia;



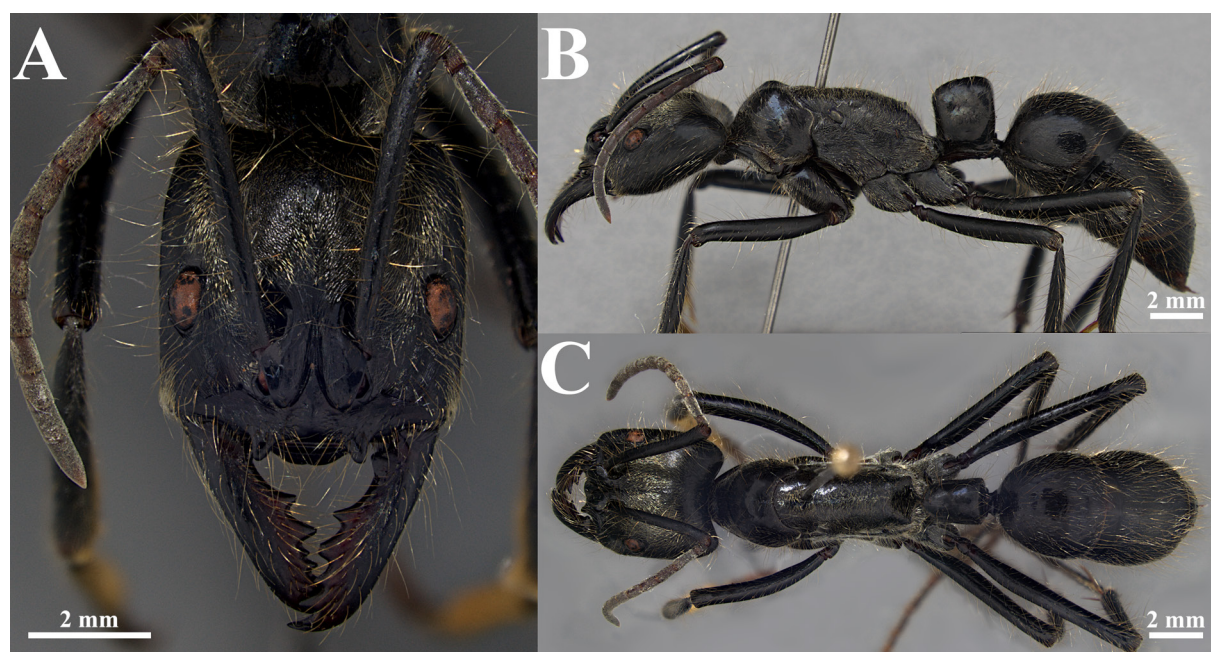
20–24 Oct. 2007; M.T. Tavares and team leg.; UFES 70534 • 1 ♀; same collection data as for preceding; UFES 70535 • 1 ♂; same locality as for preceding; 17–23 Oct. 2011; M.T. Tavares and team leg.; Malaise; UFES 118173 • 1 ♀; Serra Mestre Alvaro; 27 Jul. 2002; T.S. Soares leg.; UFES 39347 • 1 ♀; Soretama, Reserva Natural Vale; 19.1333° S, 40.0500° W; Feb. 2015; T. Vargas leg.; UFV LabEcol 43 • 1 ♀; same collection data as for preceding; UFV LabEcol 432 • 1 ♀; Vila Valério, Sítio Benincá; 18°58' S, 40°27' W; 14–28 Sep. 2011; C.O. Azevedo and team leg.; UFES 119467 • 1 ♀; Vitória, Fradinhos; 18 Sep. 1986; R.P. Moure leg.; UFES 38457 • 1 ♀; Vitória, Maruípe; 14 Aug. 2002; Silva, A.S. leg.; UFES 21962 • 1 ♀; Vitória, Morro TV Gazeta; 6 Oct. 1993; H. José leg.; UFES 39362 • 1 ♀; Parque Fonte Grande; 25 Apr. 1987; R.B. Frigeri leg.; UFES 39529 • 1 ♀; Vitória, Pq. Estadual Fonte Grande; alt. 290 m; 20.3091° S, 40.3413° W; 3 May 2007; J.A. Rafael and F.F. Xavier F. leg.; light; INPA. – **Minas Gerais** • 2 ♀♀; Aimorés; 1–7 Apr. 1970; C. and Tadeu Elias leg.; DZUP • 1 ♀; Ataleia; 27 Jan. 1994; I. Cardoso leg.; 4772; CPDC • 1 ♀; Ponto dos Volantes, margem BR 116; 10 Jul. 2009; Isac H. Cordeiro leg.; 5563; CPDC • 1 ♀; Salto da Divisa; 10 Feb. 2004; Andre Amorim leg.; 160142653955172; CPDC • 1 ♀; Serra dos Amóres; 7 Jul. 2004; J.R.M. Santos leg.; CPDC • 1 ♂; same collection data as for preceding; CPDC. – **São Paulo** • 1 ♀; Cruzeiro; 26 Sep. 1933; Pedro S. de Myra leg.; MZSP. – **Rio de Janeiro** • 1 ♀; Rio das Ostras; Jan. 1989; M.L. Rets leg.; DZUP.

## Redescription

### Female

MEASUREMENTS. Non-types (n = 34): HL 4.9–5.71; HW 4.5–5.33; MDL 3.8–4.33; SL 5.15–5.58; MSL 7.2–8.13; HFL 6.78–7.62; HBL 6–7.2; PL 2.13–2.96; PH 2.91–3.35; PW 1.55–1.98; ATS 6.88–8.7; BL 25.7–29.46 (mm); CI 0.87–1; SI 1.01–1.16; DPI 0.61–0.81.

HEAD. Malar area with longitudinal to oblique striae that always reach entire anterior eye margin, striae extend to gena until at least half of eye length. Gena weakly microareolate and silky, usually without rugulae. Longitudinal to oblique striae and brownish appressed pubescence present between eye and frontal lobe, pubescence extends posteriorly to frons. Frons slightly microareolate and silky; with



**Fig. 21.** *Dinoponera lucida* Emery, 1901, ♀ (specimen from Baixo Guandu, Espírito Santo, Brazil; DZUP 549807). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

flexuous, brownish, suberect hairs, longer than scape diameter. Occipital corner slightly microareolate and silky. Antennal scape microareolate and silky, antenna with long suberect hairs, except for 4–5 apical segments. Ventral surface of head microareolate with arched strigulae that may cover entire surface or just anterior half. Hypostomal tooth with longitudinal strigulae. Labrum with weak transverse rugulae, without median longitudinal sulcus. Mandibular dorsum longitudinally strigulate, irregularly impressed along inner margin, gradually fading apicad.

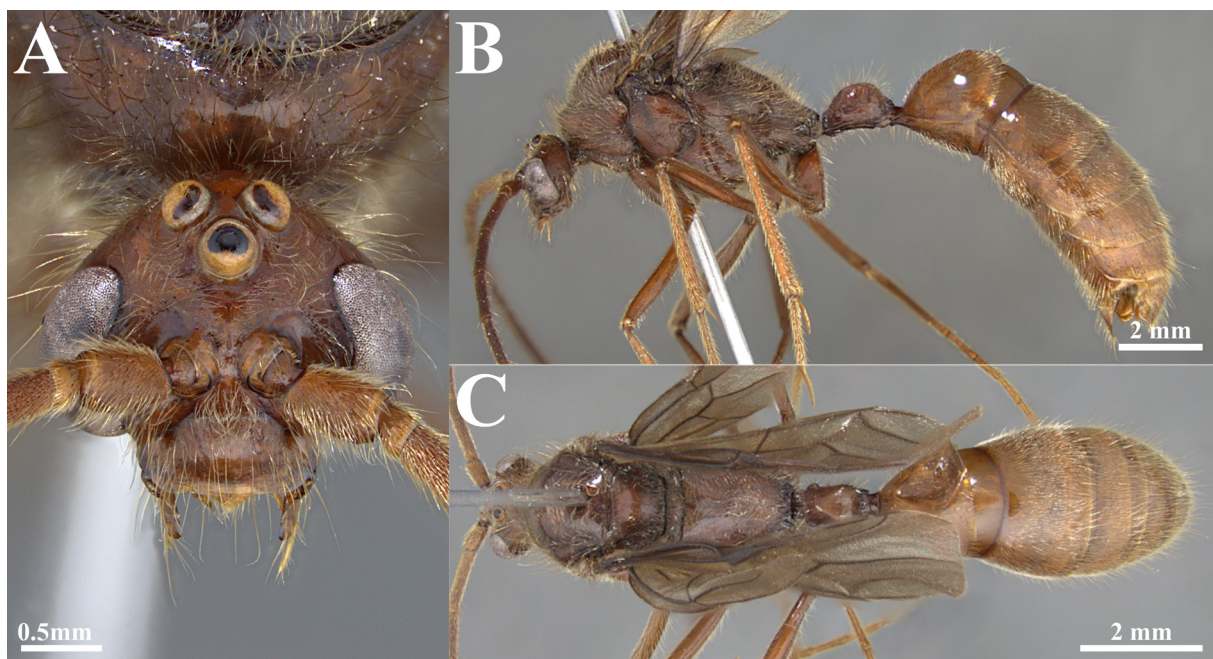
**MESOSOMA.** Dorsal margin of pronotum in lateral view sharply convex, usually with very pronounced dorsoposterior swelling; anteroventral corner of pronotum toothed or forming acute angle. Pronotal dorsum smooth, with bluish iridescence. Metapleural-propodeal suture weak and sinuous, with at least one curve ventral to position of propodeal spiracle.

**METASOMA.** Petiolar node in lateral view elongate (usually  $DPI < 0.8$ ), anterodorsal corner lower than posterodorsal corner; anterior margin straight to slightly concave and forming blunt angle with dorsal margin, dorsal and posterior margins broadly convex to straight and forming blunt angle. Node lateral face slightly microareolate and silky. Node anterior margin in dorsal view convex, posterior margin broadly convex to straight, lateral margins broadly convex, slightly converging anterodorsally. Abdominal tergite III mostly smooth with bluish iridescence, usually with anterior rugulosity; punctulae denser laterally than dorsally; densely covered by brownish, flexuous, suberect hairs on entire surface; decumbent pubescence very sparse on dorsum, denser laterally.

#### Male

**MEASUREMENTS.** Non-types ( $n = 5$ ): HL 1.85–2; HW1 2.21–2.32; MDL 0.53–0.6; SL 0.62–0.7; EL 1.17–1.26; MOD 0.38–0.41; LOD 0.36–0.38; MSL 5.87–6.25; HFL 4.56–4.87; PL1 1.57–1.58; PH 1.23–1.38; PW 0.92–1.08; ASL 4–4.05; BL1 14.04–14.35 (mm); CII 1.1–1.21; SEI 1.7–1.92; SII 0.28–0.3.

**HEAD.** Frontal carina forming a longitudinal line. Lateral ocellus clearly surpassing posterior head margin in full-face view. Head punctulate, very slightly microareolate and shining; with yellowish suberect



**Fig. 22.** *Dinoponera lucida* Emery, 1901, ♂ (specimen from Domingos Martins, Espírito Santo, Brazil; UFES 106427). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

pubescence and long suberect to erect hairs, longer than ocellus height in full-face view. Antenna with appressed pubescence and stiff decumbent hairs shorter than maximum scape diameter. Ventral surface of head punctulate and slightly microareolate with silky sheen.

**MESOSOMA.** Mesoscutum without notaulus. Mesopleural sulcus usually scrobiculate. Scutoscutellar sulcus scrobiculate. Mesoscutellum longitudinally strigulate laterally. Metapleural-propodeal suture usually slightly scrobiculate. Mesosoma mostly smooth and shining, becoming coarsely punctate on declivitous surface of propodeum; with decumbent to suberect pubescence and suberect hairs, distance between each hair usually less than half its length. Legs densely covered by suberect pubescence; with sparse suberect long hairs, greater than femur diameter, ranging from coxa to tibia. Protibial apex without a stout seta.

**METASOMA.** Petiolar node smooth and shining; with sparse suberect pubescence and abundant suberect hairs. Abdominal tergite VIII triangular, with a very sharp apex; mostly smooth and shining. Tergites with sparse suberect pubescence and abundant suberect hairs.

**GENITALIA.** Basal ring in dorsal view with lateral margins slightly convex, anteriorly narrower than posteriorly; maximum diameter of fenestra longitudinally directed; median invagination V-shaped; in lateral view, dorsal margin broadly concave and extending anteriorly to form a lobe; anteroventral process subquadrate to rounded. Gonostylus broad and rounded. In lateral view, dorsal margin of volsella anteriorly convex and posteriorly slightly concave; anteroventral corner projecting anteriorly as a rounded to subquadrate lobe; posteroventral margin concave, sometimes forming a posterior subtriangular lobe; digitus volsellaris usually with posterior margin broadly convex. In lateral view, penisvalva with continuous dorsal and posterior margins, ending in a rounded ventral lobe; ventral margin uneven and serrated, with a short median spine placed in a concavity; anteroventral corner rounded to subquadrate.

**COLOR.** Body mostly chestnut brown.

### Remarks

Females of *Dinoponera lucida* are distinct from other *Dinoponera* by having the anterodorsal corner of the petiolar node in lateral view lower than the posterodorsal corner. Additionally, *D. lucida* also has longitudinal to oblique striae on the malar area that reach the entire anterior ocular margin, extending on to the gena until at least half of eye length. Rarely, *D. grandis* may exhibit a similar node shape, but the anterodorsal corner is not as low as in *D. lucida*. *Dinoponera lucida* may also be separated from *D. grandis* by the bluish iridescence of the dorsum of abdominal tergite III, with no visible microsculpturing. Besides that, *D. lucida* and *D. grandis* are allopatric. *Dinoponera mutica* may have the anterodorsal node corner slightly lower than the posterodorsal corner, but it does not have well-marked striae on the malar area that reach the entire anterior ocular margin and no anteroventral pronotal tooth. *Dinoponera lucida* is currently considered endangered according to the red book of threatened Brazilian fauna (ICMBio 2018).

Escárraga *et al.* (2017) described the male of *D. lucida*. It differs from *D. gigantea* and *D. quadriceps* mainly by not having long antennal hairs. Besides that, in these two species and in *Dinoponera* morphospecies 1, the dorsal margin of the genital basal ring in lateral view does not form an anterior lobe as in *D. lucida*. *D. longipes* may be similar to *D. lucida*, but they can be separated by the penisvalva shape, which forms a ventral rounded lobe only in *D. lucida*. In *D. grandis* and *D. snellingi*, the ventral penisvalva lobe is curved laterally and not continuously rounded; neither does the antenna have stiff hairs.

## Biology

*Dinoponera lucida* occurs mainly in dense ombrophilous forest, characterized by high humidity, medium to large trees, and large numbers of epiphytes (Campanili & Schaffer 2010). These forests are predominantly hot and humid, with average temperatures varying from 20 to 26°C (Alvares *et al.* 2013). Nests of *D. lucida* are found always in the soil, usually less than 1 m away from trees and in shaded areas (Peixoto *et al.* 2010). Each nest can contain one to four entrances with small sticks, leaves and loose soil all around (Peixoto *et al.* 2010). The distribution pattern of the nests is aggregated, with local densities varying from 20 to 52 nests per hectare (Peixoto *et al.* 2010). On average, each nest is 35 cm deep, with four to five chambers (Paiva & Brandão 1995; Peixoto *et al.* 2010). The number of adult workers per colony can vary from 22 to 106, but rarely exceeds 50 (Paiva & Brandão 1995; Peixoto *et al.* 2008, 2010). Peixoto *et al.* (2010) suggested that the number of workers tends to be higher before and at the beginning of summer, the period before nest fission. The number of males, however, does not seem to have seasonal variation, since a gamergate can be substituted at any time of the year (Peixoto *et al.* 2010).

*Dinoponera lucida* is omnivorous, feeding mainly on small dead invertebrates or angiosperm seeds (Peixoto *et al.* 2010). The workers forage alone during the day, even at warmer hours (Peixoto *et al.* 2010). During foraging, a worker may forage up to 20 m from the nest entrance (Paiva & Brandão 1995; Peixoto *et al.* 2010). However, the distance traveled may be higher when local nest density is smaller, suggesting intraspecific competition for territory (Peixoto *et al.* 2010).

Founding of new colonies occurs by fission, i.e., some workers (among them a newly fertilized one) migrate to a nearby nest probably doing tandem running (Hölldobler & Wilson 1990; Peixoto *et al.* 2008, 2010). This process can happen gradually, since the older colony goes through a polydomic stage before the total separation (Peixoto *et al.* 2010). Newly founded colonies are monogynous and with age exhibit polyethism, the older ants foraging and younger ones taking care of the brood (Hölldobler & Wilson 1990; Peixoto *et al.* 2008, 2010). In contrast to *D. quadriceps*, agonistic interactions among workers are uncommon in colonies with gamergates and when they occur the gamergate does not participate in the interactions (Peixoto *et al.* 2008). The existence of a dominance hierarchy within the colonies of *D. lucida* has not yet been clearly determined by researchers (Peixoto *et al.* 2008).

Many arthropods live in *D. lucida* nests, including a species of *Pheidole* Westwood, 1839 which occurs only in this association (Paiva & Brandão 1995; Peixoto *et al.* 2010). Buys *et al.* (2010) recorded a wasp of the genus *Kapala* Cameron, 1884 (Eucharitidae) parasitizing a pupa of *D. lucida*, which had about 70 to 90% of the body consumed.

## Distribution (Fig. 29A)

*Dinoponera lucida* is endemic to the Atlantic Forest biome of eastern Brazil, occurring throughout Espírito Santo State, south of Bahia, the eastern boundary of Minas Gerais and north of São Paulo. The northernmost record for this study is Jacobina, Bahia, and the southernmost is in Cruzeiro, São Paulo dating from 1933. This is the only known record for São Paulo and could imply that *D. lucida* had a wider distribution or that this is a labeling error. The state of Rio de Janeiro, which is between the states of São Paulo and Espírito Santo, does not have records of *Dinoponera*. A specimen was received with a label from Rio das Ostras, Rio de Janeiro, but it is a probable labeling error for two reasons: (1) no published records of *Dinoponera* were found for the state, despite being a heavily collected region for insects in general; and (2) before the fire at the National Museum of Rio de Janeiro, consultation with researchers there found that the collection of ants did not have any *Dinoponera* from the state. For these reasons, this record was not included in the distribution map.

*Dinoponera mutica* Emery, 1901

Figs 23, 28B

*Dinoponera grandis mutica* Emery, 1901: 48 (♀).

*Dinoponera mutica* – Kempf 1971: 378, fig. 4 (raised to species). — Lenhart, Dash & Mackay 2013: 148, figs 1e, f, 12b (redescription, key).

**Diagnosis**

**Female**

Anteroventral corner of pronotum in lateral view forming obtuse angle. Petiolar node in lateral view with dorsal margin straight. Abdominal tergite III smooth and shining. Sparse brownish pubescence on dorsum, denser laterally. Body with brownish hairs.

**Material examined**

**Non-type specimens** (80 ♀♀)

BOLÍVIA – **Santa Cruz** • 1 ♀; ‘7W’ P [Puerto] Juarez, ‘n’ cerrito; 1938; Wittmer leg.; MZSP • 1 ♀; San Ignacio [San Ignacio de Velasco]; 1 Jan. 1963; L.J. Hammerschmidt leg.; MZSP.

BRAZIL – **Goiás** • 3 ♀♀; Aragarças, R. Araguaia; Sep. 1946; H. Sick leg.; MZSP • 1 ♀; Parque Nacional das Emas; 10 Nov. 1990; Cesar Kriger leg.; UFSC • 2 ♀♀; same locality as for preceding; 25 Oct.–2 Nov. 1986; Bechara, Viviani, Ferro and Sanches leg.; MZSP • 13 ♀♀; same locality as for preceding; 15–30 Oct. 1994; MZSP • 1 ♀; Parque Nacional das Emas, torre; 1 Jun. 2008; Valentim, Schmidt, Pereira and Ribas leg.; parcela 8 armadilha E; MZSP. – **Mato Grosso** • 1 ♀; “Eot. Da Colônia R. Itumbolt”; 3 Oct. 1975; L.P. Albuquerque and J.B. Moraes leg.; MPEG HYM11513005 • 1 ♀; Barra dos Bugres; 1 Jul. 1973; B. Dias leg.; MZSP • 1 ♀; Barracão Queimado; Nov. 1960; M. Alvarenga leg.; DZUP • 1 ♀; Itiguira [Itiquira]; 2013; T. Semido leg.; coleta manual; DZUP • 1 ♀; Juara; 11°5’21.3” S, 57°43’26” W; Feb. 2015; Santo R. leg.; M1L2 pitfall 8; DZUP • 1 ♀; same collection data as for preceding; DZUP 549809 • 1 ♀; Juara, UHE Castanheira, floresta secundária; 11.0892° S, 57.7238° W; M1L2; MPEG • 1 ♀; Novo Mundo, PE Cristalino; May 2013; R.E. Vicente leg.; parcela 12 pitfall 6; DZUP • 1 ♀; Poconé; 1 May 1948; C. Valette leg.; MZSP • 1 ♀; Rio Correntes; 5 Mar. 1978; Olavo Seifert leg.; 6228; MZSP • 1 ♀; Ricardo Franco; 2 Jun. 2014; H.L. Vasconcelos and J.B. Maravalhas leg.; 518, T58-9S; DZUP • 1 ♀; same collection data as for preceding; 629, T59-1S; DZUP • 3 ♀♀; Rondonópolis; Diringe leg.; MZSP • 1 ♀; Sto [Santo] Antônio de Leverger, Águas Quentes; 26 Oct. 1984; J.C. Trager leg.; isca carne, High cerrado, 169; MZSP • 1 ♀; Tangará da Serra; 2003; CPDC • 1 ♀; Utiariti, Rio Papagaio; 1 Aug. 1961; K. Lenko leg.; MZSP • 1 ♀; same locality as for preceding; 1 Nov. 1966; Lenko and Pereira leg.; 4917; MZSP • 1 ♀; same locality as for preceding; 23 Oct. 1966; Lenko and Pereira leg.; MZSP • 1 ♀; same collection data as for preceding; Coleção Diniz; DZUP • 1 ♀; Vila Bela da Santíssima Trindade, Serra Ricardo Franco; 14.9076° S, 60.0644° W; 7 Feb. 2014; J. Maravalhas *et al.* leg.; T59 11S; DZUP • 3 ♀♀; Xingu; Nov. 1961; Alvarenga and Werner leg.; MZSP. – **Mato Grosso do Sul** • 1 ♀; Camapuã; 15 Oct. 1960; Evangelista leg.; MZSP • 1 ♀; Rio Verde de Mato Grosso; Diringe leg.; MZSP • 1 ♀; Serra do Urucum, Corumbá; 25 Nov. 1960; K. Lenko leg.; 940; MZSP. – **Pará** • 1 ♀; Altamira, Castelo de Sonhos; 8.2033° S, 55.0202° W; alt. 265 m; 10 Nov. 2005; A.L. Nunes leg.; área 18; MPEG • 1 ♀; Jacareacanga, Rio Teles Pires; 6°58’03” S, 57°39’00” W; Jun. 2009; N. Rodrigues leg.; UFGD. – **Rondônia** • 1 ♀; Alto Alegre dos Parecis, linha 24-RO 370; 12°14’23.2” S, 61°47’26.7” W; 24 Jun. 2016; I.O. Fernandes leg.; coleta manual; INPA • 1 ♀; “EXTEX”; 10°19’17” S, 64°33’47” W; 13 Mar. 1998; J.R.M. Santos leg.; CPDC • 1 ♀; same collection data as for preceding; DZUP • 8 ♀♀; Forte Príncipe da Beira; 10 Nov. 1961; F.M. Oliveira leg.; MZSP • 1 ♀; same locality as for preceding; 1 Nov. 1952; Coleção Campos Seabra; MZSP • 1 ♀; Ji-Paraná; 11 Aug. 1984; R.B. Neto leg.; MPEG HYM11513006 • 1 ♀; Monte Negro-Cacaulândia, mata na margem, direita do Rio Jamari; Jul. 2001; S.E. Favorito

*et al.* leg.; pitfall; MZSP • 1 ♀; Ouro Preto do Oeste; 1997; O. Trevizan leg.; “in. natural de *Monalonia* spp”; CPDC • 1 ♀; Ouro Preto do Oeste, Sítio Deus é amor; 26 Mar. 1985; M.F. Torres leg.; MPEG HYM11513007 • 4 ♀♀; Ouro Preto do Oeste, Reserva Biológica de Ouro Preto do Oeste; 10°42'59.3" S, 62°14'39.3" W; 13–18 Jul. 2009; I.O. Fernandes leg.; alt. 287 m; INPA • 1 ♀; Pres [Presidente] Médici; 23 Aug. 1984; MPEG • 1 ♀; R [Rio] Urupá, Ji-Paraná; 1 Jul. 1983; C.E.R. Coimbra leg.; MZSP • 1 ♀; Rio Madeira, M. Três Praias; 7 Oct. 2001; F.D. Santana leg.; #5696; CPDC • 1 ♀; V [Vila] Rondônia, 378 km from P [Porto] Velho; 25 Jan.–9 Feb. 1961; Pereira and Machado leg.; MZSP • 2 ♀♀; Vilhena; Nov. 1960; M. Alvarenga leg.; DZUP.

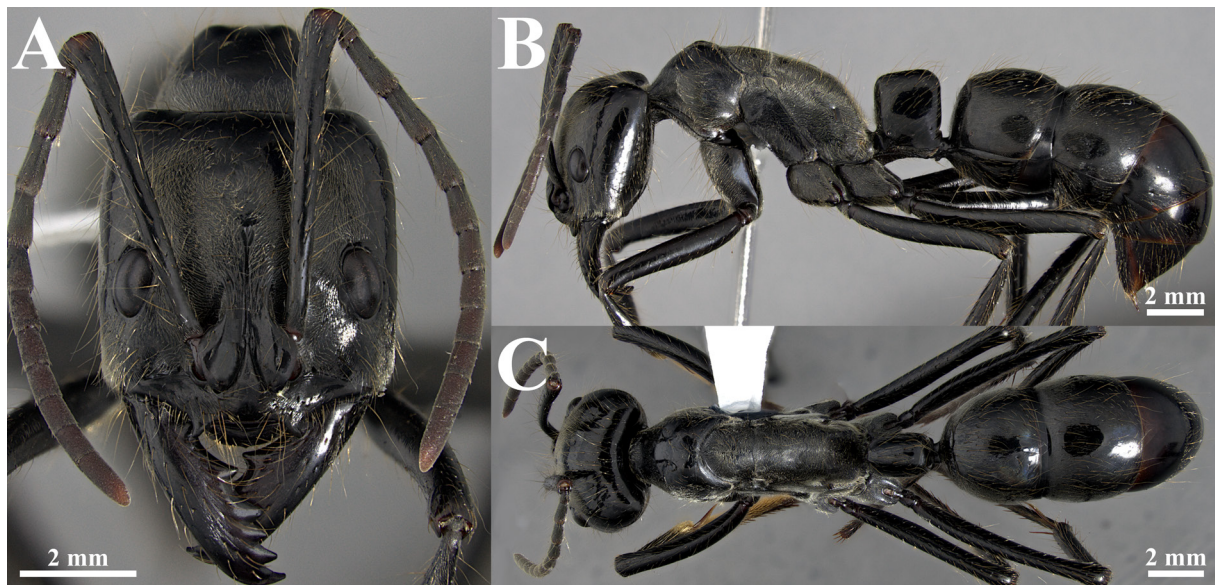
PARAGUAY – **Alto Paraguai** • 1 ♀; Parque Nacional Defensores del Chaco, Cruce, 4 de Mayo; 20°18'03" S, 60°33'02" W; 18 Jan. 2001; B. Garcete leg.; MNHNP HX70. – **Boquerón** • 1 ♀; Parque Nacional Teniente Enciso; 21°11' S, 61°40' W; 16–18 Sep. 2002; B. Garcete leg.; MNHNP HX71.

## Redescription

### Female

MEASUREMENTS. Non-types (n = 24): HL 4.85–6.23; HW 4.55–6.3; MDL 4.05–4.97; SL 5.1–6.07; MSL 7.52–8.8; HFL 7.2–8.1; HBL 6–7.3; PL 2.13–2.57; PH 2.1–3.55; PW 1.55–1.86; ATS 7.24–8.8; BL 23.72–30.66 (mm); CI 0.9–1.01; SI 0.95–1.16; DPI 0.67–0.78.

HEAD. Malar area punctulate and weakly striate; striae longitudinal to oblique, usually not reaching anterior eye margin. Gena smooth (rarely weakly microareolate) with bluish iridescence; usually transversely rugulose in median area. Appressed brownish pubescence present between eye and frontal lobe, extending posteriorly to frons. Frons smooth, with bluish iridescence; with flexuous, brownish, suberect to erect hairs, longer than scape diameter; pubescence densest laterally. Occipital corner smooth and with bluish iridescence. Antennal scape weakly microareolate and silky; antenna with long decumbent to suberect hairs, except for 5–6 apical segments. Ventral surface of head mostly smooth and silky; longitudinal strigulae present on anterolateral cephalic margin, including hypostomal tooth. Labrum usually without median longitudinal sulcus; transverse rugulae absent. Mandibular dorsum with well-marked longitudinal strigulae on inner base that gradually fade apicad.



**Fig. 23.** *Dinoponera mutica* Emery, 1901, ♀ (specimen from Juara, Mato Grosso, Brazil; DZUP 549809). A. Full-face view. B. Full body in lateral view. C. Full body in dorsal view.

MESOSOMA. Dorsal margin of pronotum in lateral view convex, usually with pronounced dorsoposterior swelling; anteroventral corner of pronotum forming obtuse angle, never toothed. Pronotal dorsum smooth, with bluish iridescence. Metapleural-propodeal suture well-marked, straight to slightly sinuous.

METASOMA. Petiolar node in lateral view elongate (DPI<0.8); anterodorsal corner at same level or slightly lower than posterodorsal corner; anterior, dorsal and posterior margins straight; antero and posterodorsal corners forming blunt angle. Node lateral face smooth with bluish iridescence. Node anterior posterior and lateral margins in dorsal view broadly convex. Abdominal tergite III smooth with bluish iridescence; punctulae denser laterally than dorsally; covered by flexuous, brownish, decumbent to suberect hairs on all surfaces; brownish appressed pubescence sparse on dorsum, denser laterally.

#### Male

Unknown.

#### Remarks

*Dinoponera mutica* may resemble the sympatric *D. nicinha* sp. nov. The most useful diagnostic traits are the golden pilosity, the sparse pubescence on the dorsum of abdominal tergite III and the petiolar node in lateral view with its convex dorsal margin in *D. nicinha* sp. nov. *Dinoponera grandis* may also occur in sympatry, but has DPI>0.8, while *D. mutica* usually has DPI<0.8. Besides that, *D. mutica* has no visible microsculpturing on abdominal tergite III, unlike *D. grandis*. The petiolar node of *D. mutica* in lateral view can present an anterodorsal angle slightly lower than the posterodorsal angle, sometimes resembling *D. lucida*. However, *D. lucida* has an anteroventral pronotal tooth and strigulae on the cephalic ventral surface. *Dinoponera quadriceps* and *D. gigantea* are different on account of their predominantly microareolate and opaque integument.

#### Biology

Little is known about the habits of *D. mutica*. Although apparently occurring in sympatry with *D. grandis*, a species more common in savanna environments, Meurer *et al.* (2015) suggested that *D. mutica* may be restricted to forest environments.

#### Distribution (Fig. 28B)

This species is distributed in the midwest and part of northern Brazil, as well as Bolivia and Paraguay. The northernmost record is in Jacareacanga, Pará, Brazil, and the southernmost Brazilian record is in Camapuã, Mato Grosso do Sul.

#### *Dinoponera nicinha* sp. nov.

[urn:lsid:zoobank.org:act:4BCDB67F-8944-4BE4-A613-BCC4AB018C27](https://zoobank.org/act:4BCDB67F-8944-4BE4-A613-BCC4AB018C27)

Figs 24, 29B

#### Diagnosis

##### Female

Anteroventral corner of pronotum in lateral view forming obtuse angle. Petiolar node in lateral view with convex dorsal margin, anterodorsal corner at same level as posterodorsal corner. Abdominal tergite III smooth and with bluish iridescence, covered with sparse golden pubescence. Body covered by golden hairs.

#### Etymology

This species epithet is a matronym in memory of Nilce de Souza Guimarães, locally known as Nicinha. She was an environmental and human rights activist that took to task consortiums that constructed

hydroelectric dams and displaced entire villages to new sites with dismal living conditions. She lived in Rondônia State, near the type locality, and was murdered in 2016.

### Material examined

#### Holotype

BRAZIL – **Rondônia** • 1 ♀; Porto Velho, Área Abunã; 9°38'03.3" S, 65°26'23.9" W; 17–27 Jul. 2013; G.R. Mazão and R.S. Probst leg.; DZUP 549810.

#### Paratypes (25 ♀♀)

BRAZIL – **Rondônia** • 1 ♀; Porto Velho, Nova Teotônio; 8.85071° S, 64.0679° W; 29 Feb.–5 May 2016; TPI Network exped.; 105 Forest, 10T T06; MZSP 65802 • 1 ♀; same collection data as for preceding; MZSP 65803 • 1 ♀; same collection data as for preceding; MZSP 65804 • 1 ♀; same locality as for preceding; 8.86987° S, 64.0546° W; 29 Feb.–5 May 2016; TPI Network exped.; 117 Forest, 11C T04; MPEG HHY03034650 • 1 ♀; same collection data as for preceding; MPEG HHY03034651 • 1 ♀; same collection data as for preceding; MPEG HHY03034652 • 1 ♀; same locality as for preceding; 8.85071° S, 64.0679° W; 29 Feb.–5 May 2016; TPI Network exped.; 105 Forest, 10T T05; CASENT 0887850; INPA • 1 ♀; same collection data as for preceding; CASENT 0887851; INPA • 1 ♀; same locality as for preceding; 8.87762° S, 64.0623° W; 29 Feb.–5 May 2016; TPI Network exped.; 115 Forest, 9C T05; CASENT 0887852; CASC • 1 ♀; same collection data as for preceding; CASENT 0887853; CASC • 1 ♀; same collection data as for preceding; CASENT 0887854; CASC • 1 ♀; same locality as for preceding; 29 Feb.–5 May 2016; TPI Network exped.; 115 Forest, 9C T04; CASENT 0887855; MCZC • 1 ♀; same collection data as for preceding; CASENT 0887856; MCZC • 1 ♀; same collection data as for preceding; CASENT 0887857; MCZC • 1 ♀; same locality as for preceding; 8.86987° S, 64.0546° W; 29 Feb.–5 May 2016; TPI Network exped.; 117 Forest, 11C T05; DZUP 550208 • 1 ♀; same collection data as for preceding; DZUP 550209 • 1 ♀; same collection data as for preceding; DZUP 550210 • 1 ♀; same locality as for preceding; 8.85071° S, 64.0679° W; 29 Feb.–5 May 2016; TPI Network exped.; 105 Forest, 10T T08; DZUP 550211 • 1 ♀; same collection data as for preceding; DZUP 550212 • 1 ♀; same collection data as for preceding; DZUP 550213 • 1 ♀; same locality as for preceding; 8.86987° S, 64.0546° W; 29 Feb.–5 May 2016; TPI Network exped.; 117 Forest, 11C PPT08; CASENT 0887848; DZUP • 1 ♀; same collection data as for preceding; CASENT 0887849; DZUP • 1 ♀; same locality as for preceding; 8.86432° S, 64.063° W; 29 Feb.–5 May 2016; TPI Network exped.; 131 Forest, 9T T08; DZUP 550215 • 1 ♀; same collection data as for preceding; DZUP 550216 • 1 ♀; same locality as for preceding; 8.86987° S, 64.0546° W; 29 Feb.–5 May 2016; TPI Network exped.; 117 Forest, 11C T03; DZUP 550214.

#### Non-type specimens (24 ♀♀)

BRAZIL – **Amazonas** • 5 ♀♀; Lábrea, Ramal Apaeral, km 09 sítio São Raimundo; 7°19'10" S, 64°40'07" W; Jun. 2006; F.F. Xavier F. leg.; coleta manual; INPA • 1 ♀; Humaitá, Galego; 12 Apr. 1975; V.P. da Silva leg.; 11944; MZSP • 2 ♀♀; Manaus, Uypiranga, Rio Negro, 14 km from Manaus; alt. 81 m; Oct. 1941; August Rabaut leg.; MZSP. – **Rondônia** • 1 ♀; Ariquemes, Rio Ji-Paraná; 9°44' S, 61°52' W; 28 Oct. 1986; J.A. Rafael leg.; arm. Malaise; INPA • 3 ♀♀; Nova Colina; 30 Oct.–4 Nov. 1984; Polonoroeste exped.; MZSP • 10 ♀♀; Porto Velho; 8°45'43" S, 63°54'14" W; 21 May 2011; Carmo *et al.* leg.; pitfall; INPA • 1 ♀; Guaporé; 1 Nov. 1954; F. Pereira, Werner Dente and M. Alvarenga leg.; MZSP • 1 ♀; Rio Madeira, M. Teotônio; 15 Oct. 2011; F.D. Santana leg.; #5696; CPDC.

### Description

#### Female

MEASUREMENTS. Holotype: HL 5.73; HW 5.6; MDL 4.53; SL 5.54; MSL 8; HFL 7.8; HBL 6.5; PL 2.35; PH 3.3; PW 1.7; ATS 7.76; BL 28.38 (mm); CI 0.97; SI 1.03; DPI 0.62. Non-types (n = 10): HL 5.48–6.64; HW 5.54–5.96; MDL 4.47–5.04; SL 5.98–6.64; MSL 8.2–9.2; HFL 7.92–8.8; HBL 6.4–7.5;



PL 2.38–2.63; PH 3.32–3.42; PW 1.59–1.89; ATS 7.6–9.2; BL 28.86–32.51 (mm); CI 0.89–0.98; SI 1.05–1.13; DPI 0.63–0.72.

**HEAD.** Malar area with weak longitudinal to oblique striae that do not reach anterior eye margin. Gena smooth, with bluish iridescence; usually without rugulae. Golden appressed pubescence present between eye and frontal lobe, extending posteriorly to frons. Frons smooth, with bluish iridescence; with flexuous, golden, decumbent to suberect hairs, longer than scape diameter; pubescence densest laterally. Occipital corner smooth and with bluish iridescence. Antennal scape weakly microareolate and silky; antenna with decumbent to suberect hairs, except for 5–6 apical segments. Ventral surface of head mostly smooth, with bluish iridescence; longitudinal strigulae present on anterolateral cephalic margin, including hypostomal tooth. Labrum without median longitudinal sulcus, transverse rugulae absent. Mandibular dorsum weakly longitudinally strigulate on inner base, sculpture gradually fading apicad.

**MESOSOMA.** Dorsal margin of pronotum in lateral view convex, dorsoposterior swelling sometimes very pronounced, anteroventral corner of pronotum forming obtuse angle, never toothed. Pronotal dorsum smooth, with bluish iridescence. Metapleural-propodeal suture well-marked and straight.

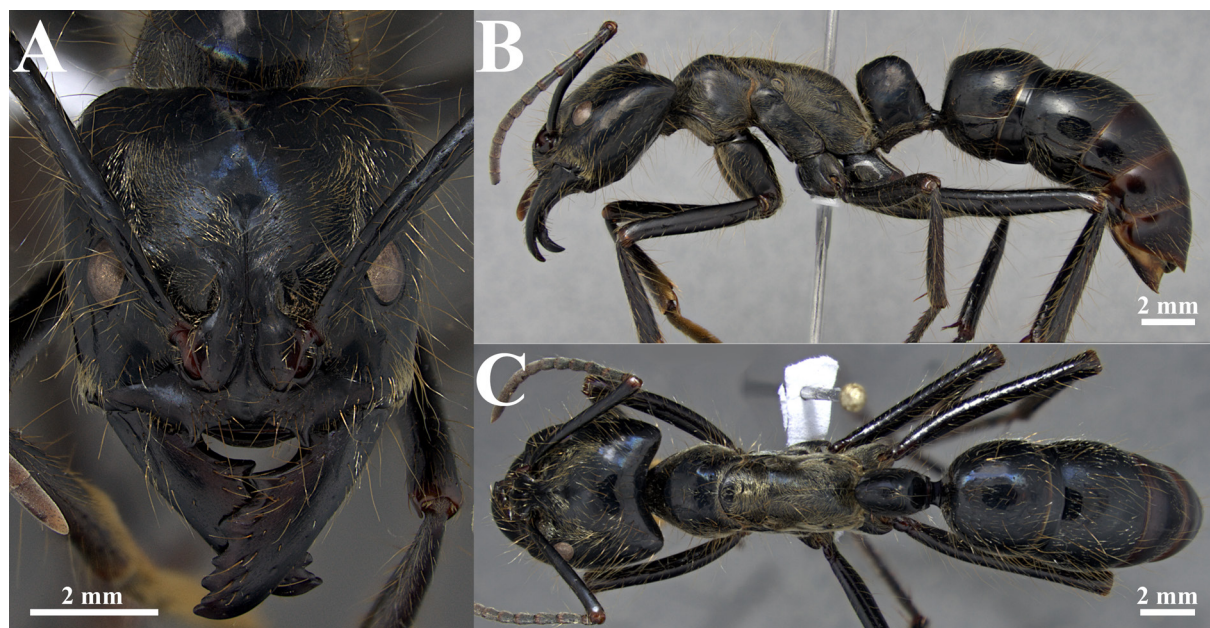
**METASOMA.** Petiolar node in lateral view elongate (DPI < 0.8), antero- and posterodorsal corners at same level, anterior and posterior margins broadly convex, dorsal margin convex, antero- and posterodorsal corners rounded. Node lateral face smooth, with bluish iridescence. Node lateral margin in dorsal view broadly convex, anterior and posterior margins convex. Abdominal tergite III mostly smooth, with bluish iridescence; laterally and dorsally with evenly distributed punctulae; densely covered by golden, flexuous, suberect hairs and sparse pubescence evenly distributed on dorsal and lateral surfaces.

#### Male

Unknown.

#### Remarks

The main difference between *D. nicinha* sp. nov. and other species of *Dinoponera* is in the shape of the petiolar node. This character has proven to be useful for separating species in this genus, as its shape is



**Fig. 24.** *Dinoponera nicinha* sp. nov., holotype, ♀ (Porto Velho, Rondônia, Brazil; DZUP 549810). A. Full-face view. B. Full body in lateral view. C. Full body in dorsal view.

generally constant within the species. Specimens of this species were found in collections identified as *D. longipes*, but besides the node shape they can also be separated by the ratio of the length of the hind basitarsus to the head width, which in *D. longipes* is greater (always  $>1.3$  in *D. longipes* and  $<1.3$  in *D. nicinha* sp. nov.). *Dinoponera nicinha* sp. nov. can also be confused with the sympatric *D. mutica*, but the pilosity is not golden in *D. mutica* and abdominal tergite III has dense pubescence on its side (sparse in *Dinoponera nicinha* sp. nov.). The node in *D. mutica* has the anterior and dorsal margins in lateral view meeting at a blunt angle, slightly lower than the posterodorsal angle. *Dinoponera nicinha* sp. nov. has rounded antero- and posterodorsal node angles, both at the same level.

## Biology

*Dinoponera nicinha* sp. nov. occurs in forest environments with high rainfall and dense coverage of medium to large trees, with a maximum of six months of drought during the year (IBGE 2012). Its natural history is unknown, except for the fact that most specimens were collected in pitfall soil traps.

## Distribution (Fig. 29B)

*Dinoponera nicinha* sp. nov. is only known from the Brazilian states of Amazonas and Rondônia. The northernmost record is Manaus, Amazonas, and the southernmost record is in Ji-Paraná, Rondônia.

### *Dinoponera quadriceps* Kempf, 1971

Figs 25–26, 29B

*Dinoponera quadriceps* Kempf, 1971: 380, figs 5, 13–16 (♂).

*Dinoponera opaca* Kempf, 1971: 379 (♂).

*Dinoponera quadriceps* – Mann 1916: 409. — Borgmeier 1937: 226 (male description). — Lenhart, Dash & Mackay 2013: 149, figs 4b, g, l, 5a, 6a, 10a, 11a, 12b (redescription, key, male genitalia). — Tozetto & Lattke 2020: 5, figs 2–3, 6 (male genitalia).

*Dinoponera opaca* – Kempf 1975: 344 (junior synonym of *D. quadriceps*).

Non *Dinoponera grandis mutica quadriceps* – Santschi 1921: 84 (invalid name).

Non *Dinoponera grandis mutica opaca* – Santschi 1921: 84 (invalid name).

## Diagnosis

### Female

Malar area without striae or with weak longitudinal to oblique striae that do not reach anterior eye margin. Ventral head surface without strigulae. Head with short to inconspicuous pubescence. Anteroventral corner of pronotum in lateral view forms an obtuse angle. Abdominal tergite III microareolate and opaque, with sparse pubescence on dorsum.

### Male

Antenna with long suberect to erect hairs, clearly longer than maximum scape diameter. Mesoscutum without notaulus. Gastral tergites without long hairs. In lateral view, dorsal margin of basal ring broadly concave to straight.

## Material examined

### Non-type specimens (200 ♀♀, 17 ♂♂)

BRAZIL – Bahia • 1 ♀; Aramari, ex Distrito de Alagoinhas; MZSP • 1 ♀; Banaê; 10°34'37" S, 38°36'54" W; Mar. 2009; M.D. Dantas leg.; 01; CPDC • 1 ♀; Barragem de Anagé [Amajés]; 19 Oct. 1996; Argôro Santos leg.; 5126; CPDC • 1 ♀; Barreiras, Serra do Mimo; 5 Aug. 2010; S. Souza and B. Santos leg.; #5657; CPDC • 1 ♀; Bendegó, próx. Canudos; 19–22 Nov. 1965; Exp. DZ Fapesp leg.;

MZSP • 2 ♀♀; Lapa [Bom Jesus da Lapa]; 1 Dec. 1948; Gonçalves leg.; MZSP • 1 ♀; Bonfim; 6 Dec. 1948; C.R. Gonçalves leg.; “Let OT Borgmeier set 1953”; MZSP • 7 ♀♀; Buritirama; 22 Mar. 1958; E. Dente leg.; MZSP • 1 ♀; Caatinga do Moura; 24 Jan. 1980; M.T.U. Rodrigues leg.; MZSP • 1 ♀; same locality as for preceding; 24–29 Jan. 1980; P.E. Vanzolini leg.; MZSP • 2 ♀♀; Caculé; Jul. 1961; S. Laroca leg.; DZUP • 1 ♀; Caetitê; Nov. 2009; Jaqueline leg.; 8593; CPDC • 1 ♀; Camisão; 8 Apr. 1905; E. Bondas leg.; n 3401 Coll Borgmeier; MZSP • 1 ♀; Campo Formoso; 20 Apr. 1974; R.L. Araújo leg.; n5534; MZSP • 1 ♀; same locality as for preceding; Jun. 1995; C. Moura leg.; 4940; CPDC • 1 ♀; Contendas do Sincorá; 13°55'20" S, 41°06'57" W; alt. 375 m; 3 Jun. 2014; Santos Silva leg.; UFGD • 5 ♀♀; Contendas do Sincorá, F.N.C. Sincorá; 14°00' S, 41°10' W; 3 Jun. 2014; G. Santos Silva leg.; DZUP • 2 ♀♀; Cruz das Almas; 1 Apr. 1988; C.A.L. Carvalho leg.; 704 188 (2/2) ME 014; MZSP • 2 ♀♀; Feira de Santana; 23 Feb. 1993; J. Ricardo leg.; 4611; CPDC • 1 ♀; same locality as for preceding; 19 Jun. 2006; J.J. Resende leg.; 11, ninho 1 F07; CPDC • 1 ♀; Feira de Santana, UEFS; 30 Nov. 1993; I.M.F. Soares leg.; 4899; CPDC • 1 ♀; Guanambi, EAFG; Apr. 1997; A.J.S. Argolo leg.; CPDC • 3 ♀♀; Ibiraba; 1 Mar. 1989; Pedro Rocha leg.; “noite, ninho pé arbusto”; MZSP • 1 ♀; Ibotirama; 21 Jul. 1969; W. Silva leg.; MZSP • 1 ♀; Igaporã; 9 Nov. 2011; J.A. Jesus leg.; CPDC • 1 ♀; Itaberaba; 19 Aug. 2008; Antônio Alves leg.; CPDC • 1 ♀; Itaberaba, Amparo Br28; 16 May 1965; R. Grantsan leg.; MZSP • 4 ♀♀; Itaberaba, Faz. Riacho do Uruçu 1; 5 Dec. 1990; C.R.F. Brandão, J.L.M. Diniz and O.S. Oliveira leg.; 9 pm; MZSP • 3 ♀♀; Itaberaba, Faz. Riacho do Uruçu; 1 Dec. 1990; S.T.P. Amarante leg.; “bandeja d’água”; MZSP • 1 ♀; Itatim; 6 Jul. 1996; G.M. Santos leg.; 5105b; CPDC • 1 ♀; Itauçu, FLONA Contendas do Sincorá; 9 Sep. 2005; Daniela and Péricles leg.; TR pt 14; CPDC • 1 ♀; Jandaíra, Costa Azul; 11°56'58" S, 37°36'34" W; 6 Oct. 2010; M.L.O. Travassos leg.; H1430; CPDC • 1 ♀; Juazeiro; 11 Jul. 1989; M. Cristiano leg.; CPDC • 7 ♀♀; Lagoa Itaparica; 8 Oct. 1990; Jorge L.M. Diniz leg.; coleção Diniz; DZUP • 1 ♀; Marcionílio Souza; 24 Jul. 1993; N.S. Laca leg.; 4664; CPDC • 1 ♂; Manoel Vitorino; 26–27 Jan. 2006; R.R. Hora leg.; CPDC • 1 ♀; Milagres; 12°54'54.2" S, 39°51'27.9" W; 22–26 Oct. 2010; M.A. Ulysses, A.M. Medina and E.M. Campos leg.; T1F 3H1; MZSP • 1 ♀; same collection data as for preceding; T2F 2H5; MZSP • 1 ♀; same collection data as for preceding; T3F 4H4; MZSP • 1 ♀; same collection data as for preceding; 23–25 Oct. 2010; M.A. Ulyssés leg.; MuBio-CE Hym 507; UFGD • 1 ♀; Milagres, Br 116 km 561, caatinga arbórea; 12°52'12" S, 39°11'31" W; 4 May 2009; J.J. Resende leg.; DZUP • 1 ♀; Monte Santo; 19 Jul. 1995; Cardoso leg.; 4945A; CPDC • 1 ♀; Morro do Chapéu; 25 Mar. 1990; J. Roseira leg.; #278; CPDC • 2 ♀♀; Morro do Cruzeiro; 31 Jan. 1993; André leg.; 4610; CPDC • 1 ♀; Mucugê; 6 Jul. 2009; Thomas Strwtzel leg.; UFSC • 1 ♀; Paulo Afonso, APA Serra Branca; 19 Mar. 2009; Layla Marques leg.; #5596<sup>a</sup>; DZUP • 1 ♀; Pilão Arcado, Barra Zacarias; 9°59' S, 42°48' W; alt. 416 m; 5 Dec. 2005; P.P. Lopes and G.M.M. Santos leg.; CPDC • 1 ♀; same locality as for preceding; 3 Oct. 2006; J.J. Resende leg.; ninho 1 F30, 08; CPDC • 1 ♀; Poções, Faz. São João; 9 feb. 1964; Eduardo leg.; CPDC • 1 ♀; Rio Real; 27 Jun. 1994; Carmo leg.; 4859F; CPDC • 1 ♀; Rui Barbosa; 16 Nov. 2012; Juliana Alves leg.; CPDC • 1 ♀; Sambaíba; 24 Aug. 1993; C. Ivan leg.; 4512; CPDC • 1 ♂; same locality as for preceding; Mar. 2001; D.C. Nascimento leg.; CPDC • 1 ♀; S [Santa] Rosa; 18 Jul. 1995; Cardoso leg.; 4944; CPDC • 1 ♀; Santa Maria da Vitória, Serra do Ramalho; 13°23'52" S, 44°11'52" W; Jun. 2009; J. Castro leg.; CPDC • 2 ♀♀; Sr do Bonfim [Senhor do Bom Fim]; 20 Jul. 1974; S. Laroca leg.; DZUP • 1 ♀; Serra da Jiboia; 20 Jul. 2004; R.M. Rodrigues leg.; CPDC • 1 ♀; Tucano, caatinga; 10.7798° S, 38.8928° W; 15 Nov. 2010; E.M. Campos, A.M. Medina, P.L. Paixão and P.L.O. Rebouças leg.; MZSP • 2 ♀♀; Vila Nova; 1 Feb. 1908; E. Gazbe leg.; MZSP. – **Ceará** • 1 ♀; Araripe; 10 Nov. 1975; R.L. Araújo leg.; MZSP • 1 ♀; Chapada do Araripe; 5 Apr. 1962; D. Zajuwawl leg.; MZSP • 1 ♀; Crateús, Croátia; 5.1333° S, 40.9166° W; 20–30 Apr. 2003; Y. Quinet leg.; MZSP • 1 ♂; Crateús, Serra das Almas; 5.14170° S, 40.91620° W; 19 May 2014; G. Melo and B. Rosa leg.; DZUP • 1 ♂; same locality as for preceding; 19–20 May 2014; G. Melo and B.B. Rosa leg.; Mini-luminosa; DZUP 549801 • 1 ♂; same collection data as for preceding; DZUP 548847 • 6 ♀♀; Fazenda Malhada Arcoverde; Jul. 1974; MZSP • 1 ♀; Fortaleza; 3°43'01" S, 38°32'34" W; Sep. 2008; Y. Quinet leg.; 04; CPDC • 1 ♀; Maranguape, Serra de Maranguape; 14 Nov. 2003; A.A. Tavares leg.; MZSP • 1 ♀; same locality as for preceding;

3.8809° S, 38.6958° W; alt. 100 m; 16. Oct. 2017; Y.P. Quinet leg.; manual; DZUP • 1 ♀; Pacatuba; 10 May 2016; G. Melo and B. Rosa leg.; DZUP • 1 ♀; Tianguá; 18 Dec. 1948; C.R. Gonçalves leg.; MZSP. – **Distrito Federal** • 1 ♂; Brasília; Sep. 1972; N. Simões leg.; MZSP. – **Minas Gerais** • 1 ♀; Poções de Sta Cruz, 10 km SE of Janaúba; 16°53' S, 43°16' W; alt. 660 m; 19 Jan. 2005; Melo and Costa leg.; DZUP • 1 ♀; Viçosa, UFV; 30 Oct. 1975; J. Freire leg.; CPDC. – **Paraíba** • 1 ♀; Areia; 1 Jul. 1955; Pe. Pereira leg.; MZSP • 1 ♀; Barra do Rio Mamanguape, Rio Tinto; 10 Jan. 2018; Marília Costa leg.; DZUP • 1 ♀; Brandão [Caldas Brandão]; 22 Sep. 1955; Aristóteles Silva leg.; MZSP • 1 ♀; Estrela Dalva, S [São] Sebastião do Umbuzeiro; 24 Aug. 1954; A. Silva leg.; MZSP • 1 ♀; Fazenda Almas; 20 Dec. 2006; J. Paulo leg.; pitfall A5; CPDC • 1 ♀; forest near Areia; alt. 630 m; 24 Jan. 1981; Robert Davidson leg.; primary forest, sweeping day; MPEG • 1 ♀; João Pessoa; 28 Nov. 2008; Linsmara Nunes leg.; CPDC • 1 ♀; same locality as for preceding; 23 Jan. 1988; M. Kammers and I.L. Oliveira leg.; MZSP • 1 ♀; same locality as for preceding; 4 Nov. 1955; C.A. Gonçalves leg.; MZSP • 2 ♀♀; same locality as for preceding; 9 Sep. 2002; A. Vasconcelos leg.; CPDC • 1 ♂; same collection data as for preceding; CPDC • 1 ♀; same locality as for preceding; 7°7'9.2" S, 34°50'41.67" W; alt. 41 m; 4 Sep. 2014; J.M. Churata S. leg.; DZUP • 1 ♀; João Pessoa, UFPB; 2–5 Apr. 1995; M.F.S. Santos leg.; 4921; CPDC • 1 ♀; João Pessoa, Cabo Branco; 18 Jul. 1993; N. Rabet leg.; CPDC • 1 ♀; João Pessoa, forest of Gargau; alt. 45 m; 22 Jan. 1981; R. Davidson leg.; primary forest, sweeping day; MPEG • 5 ♀♀; Mamanguape; 1 Jul. 1957; Dep. Zoologia exped.; MZSP • 1 ♀; Mata do campus UFPB; 24 Apr. 1977; V.Py Daniel leg.; INPA • 1 ♀; same collection data as for preceding; Dec. 1976; INPA • 1 ♂; Matureia, Pico do Jabre; 7.25250° S, 37.38472° W; 19 Feb. 2018; A. Ferreira leg.; “armadilha de luz”; DZUP • 1 ♂; same collection data as for preceding; DZUP 5488852 • 1 ♂; same collection data as for preceding; DZUP 5488853 • 2 ♀♀; Olivados; 20 Aug. 1954; Aristóteles Silva leg.; MZSP • 1 ♀; Rebio Sema 3; 2 Jul. 2015; L. Brisa leg.; pitfall; UEMS • 1 ♀; Rio Tinto; 6°47'56.5" S, 35°05'04" W; alt. 83 m; 5 Jul. 2015; R. Silvestre leg.; pinça; UFGD • 2 ♀♀; São José Cordeiros, Faz. Almas; 2 May 2003; A. Vasconcelos leg.; CPDC • 1 ♀; São José da Mata, Sítio São Miguel; 12 Apr. 1997; A.D. Brescovit leg.; at night; MZSP • 1 ♀; Tabuleiro, N Sta Rita; 7 Feb. 1968; Dr. Dardano leg.; 9; MZSP. – **Pernambuco** • 3 ♀♀; Oct. 1929; Pickel leg.; MZSP • 1 ♀; Afrânio; alt. 500 m; 16 May 2007; J.A. Rafael and F.F. Xavier F. leg.; light; INPA • 1 ♀; Araripina; 2 Jan. 1973; R. Montenegro leg.; #324, 8430; MZSP • 2 ♀♀; Arcoverde; 17 Jul. 1974; R.L. Araújo leg.; MZSP • 1 ♀; Brejão, Faz. Matary, R Maranhão; 24 Apr. 1974; 932; MZSP • 1 ♀; same collection data as for preceding; coleção Diniz; DZUP • 6 ♀♀; Carnaubeira; 20 May 1971; ABC MZUSP exped.; MZSP • 13 ♀♀; Floresta, Faz. Campos Bons; 20–27 Jun. 1971; ABC MZUSP exped.; MZSP • 3 ♀♀; Garanhuns; 13 Jan. 1967; F.B. Galinda leg.; DZUP • 1 ♀; same locality as for preceding; 29 Oct. 1938; A. Silva leg.; 5314; MZSP • 1 ♀; Itambé; 13 Feb. 1976; C.J. Rosetto leg.; 931; DZUP • 1 ♀; Olinda; Reichensperger leg.; 34; MZSP • 1 ♀; Parque Nacional do Catimbau; 8°30'40.561" S, 37°16'37.133" W; 27 Dec. 2017; Katherine B. Haedo leg., R27; DZUP • 1 ♀; same locality as for preceding; 8°32'48.38" S, 37°15'21.74" W; alt. 938 m; 27 Dec. 2017; Katherine B. Haedo leg.; R4; DZUP • 1 ♀; same locality as for preceding; 8°28'29.71" S, 37°21'22.36" W; alt. 987 m; 27 Dec. 2017; Katherine B. Haedo leg.; R23; DZUP • 1 ♀; same locality as for preceding; 8°31'32.41" S, 37°14'57.62" W; alt. 910 m; 27 Dec. 2017; Katherine B. Haedo leg.; R45; DZUP • 1 ♀; Pesqueira; 5 Aug. 1928; B. Pickel leg.; MZSP • 1 ♀; Petrolina; 18 Jul. 1974; R.L. Araújo leg.; MZSP • 1 ♀; Recife; 21 Apr. 1905; L. Lima Castro leg.; 2376; MZSP • 1 ♀; Salgueiro; 17 Jul. 1974; P.L. Araújo leg.; MZUSP 5502 • 1 ♀; same collection data as for preceding; MZSP. – **Piauí** • 1 ♀; Bom Jesus; 9°28'52.3" S, 44°72'12.1" W; 8 Nov. 2010; T. Frizzo and H. Vasconcelos leg.; T2 PI 10S; DZUP • 1 ♂; Caracol, P.N. da Serra das Confusões; 9.22637° S, 43.46331° W; 3–7 Mar. 2016; R.M. Feitosa, G.P. Camacho and M.F.O. Martins leg.; DZUP 549804 • 1 ♂; Colônia do Piauí; 27 Mar.–1 Apr. 1994; Boussard leg.; CPDC • 1 ♀; same collection data as for preceding; 4914; CPDC • 2 ♀♀; Curimatá, Espinhos; 10°6'19" S, 44°13'08" W; 20 Apr. 2000; M.P.D. Santos leg.; coleta manual; MPEG • 1 ♀; Faz. Sta. Paz; 19 Jun. 1992; Argolo leg.; 4635; CPDC • 1 ♀; Ribeirão Gonçalves, Est. Ecol. Uruçuí-Una, cerrado; 10 Dec. 1980; A.I. Almeida leg.; MZSP • 1 ♀; São Raimundo Nonato, P.N. Serra da Capivara, Zabelê; 12 Apr. 2011; A.C.A. leg.; pitfall; MZSP. – **Rio Grande do Norte** • 1 ♀; FLONA de Nísia; Jun. 2017; Dina leg.; UFRN • 1 ♀;

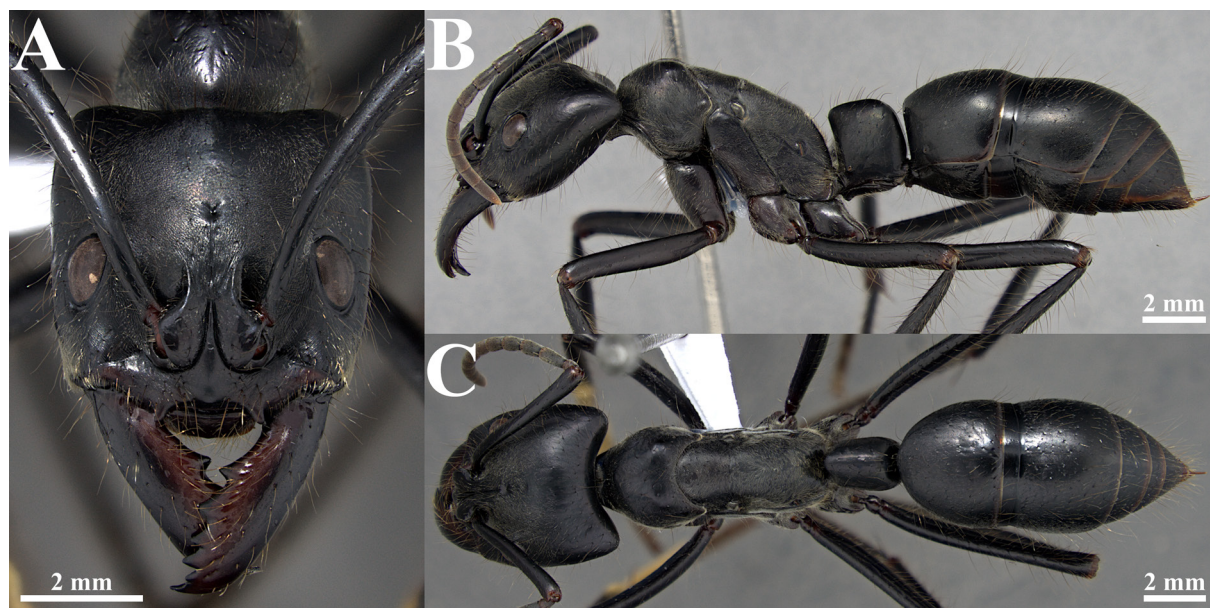
same locality as for preceding; 15 Sep. 2005; R.R. Hora leg.; 5457; CPDC • 1 ♀; Natal; 24 May 2008; Pitfall F4; CPDC • 1 ♀; Natal, Campus Central UFRN; Jun. 2014–Jan. 2016; Dina leg.; “4 ninhos”; UFRN • 1 ♀; same collection data as for preceding; DZUP 549811 • 3 ♂♂; Campus Central UFRN, Jul. 2012–Jan. 2016, Dina leg., “4 ninhos”; DZUP • 1 ♂; same collection data as for preceding; DZUP 548850 • 1 ♂; same collection data as for preceding; DZUP 548851 • 1 ♀; Natal, Lagoa de Jenipabu; Oct. 2010; R. Silvestre leg.; CPDC • 1 ♀; Parnamirim, Mata do Jiqui; Oct. 2009; Dina leg.; UFRN. – **Sergipe** • 1 ♀; Estância; 15 Jun. 1994; J. Jardim leg.; CPDC • 1 ♀; Itabaianinha, Mata Verde; 15 Dec. 1991; B. Santos leg.; 4492; CPDC • 1 ♀; Pirambu, Pov. Aguilhada, restinga; 10°41'37" S, 36°50'37" W; 8 Jun. 2017; D.S. Mesquita and team leg.; pitfall; MPEG • 1 ♀; Poço Redondo, Angico, alto sertão; 9°41' S, 38°31' W; Jun. 2008; F.S. Nascimento leg.; MZSP • 1 ♀; São Cristóvão; 11°00'54" S, 37°12'21" W; 16 Apr. 2009; J.O. Dantas leg.; “ninho 2, 12”; CPDC • 1 ♀; Serra de Itabaiana; Mar. 2008; T.J. leg.; CPDC. – **Tocantins** • 1 ♀; Jalapão, 19 Nov. 2012; H.L. Vasconcelos and T. Frizzo leg.; 405, T49-19S; UFU • 1 ♀; same locality as for preceding; 409, T49-17S; DZUP • 1 ♀; same locality as for preceding; 409, T50-11S; DZUP • 1 ♀; same locality as for preceding; 452, T51-2S; DZUP.

## Redescription

### Female

MEASUREMENTS. Non-types (n = 32): HL 4.95–5.76; HW 4.9–5.73; MDL 3.9–4.66; SL 4.95–5.73; MSL 7.52–8.47; HFL 6.78–7.71; HBL 5.84–6.48; PL 2.15–2.59; PH 2.85–3.35; PW 1.45–1.95; ATS 7.04–8.4; BL 25.71–29.39 (mm); CI 0.93–1.04; SI 0.96–1.09; DPI 0.64–0.81.

HEAD. Malar area without striae or with weak longitudinal to oblique striae that do not reach anterior eye margin. Gena microareolate and opaque, usually without rugulae. Brownish, appressed and very short pubescence present between eye and frontal lobe, extending posteriorly to frons. Frons microareolate, opaque to silky; with very sparse brownish, flexuous, suberect to erect hairs, longer than scape width; pubescence densest laterally. Occipital corner microareolate and opaque (sometimes silky). Antennal scape microareolate and silky; long, suberect hairs usually present on antennal segments 1–3. Ventral surface of head microareolate, generally without strigulae, sometimes present only on anterolateral margin and extending to hypostomal tooth. Labrum without median longitudinal sulcus; very shallow



**Fig. 25.** *Dinoponera quadriceps* Kempf, 1971, ♀ (specimen from Natal, Rio Grande do Norte, Brazil; DZUP 549811). **A.** Full-face view. **B.** Full body in lateral view. **C.** Full body in dorsal view.

transverse rugulae sometimes present. Mandibular dorsum weakly longitudinally strigulate on inner base, sculpture gradually fading apicad.

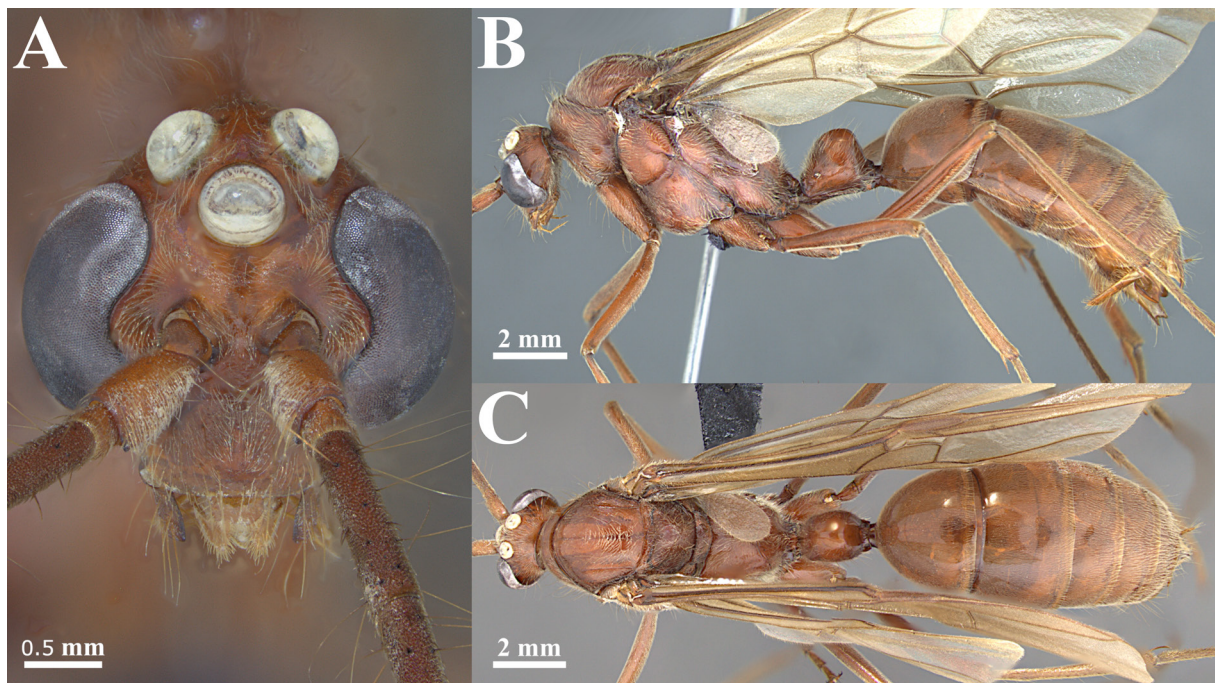
**MESOSOMA.** Dorsal margin of pronotum in lateral view broadly convex, with no pronounced dorsoposterior swelling; anteroventral corner of pronotum forms obtuse angle. Pronotal dorsum weakly microareolate, opaque to silky. Metapleural-propodeal suture well-marked and usually straight.

**METASOMA.** Petiolar node in lateral view elongate (usually  $DPI < 0.8$ ); anterodorsal corner usually higher than posterodorsal corner; anterior margin slightly concave to straight, forming blunt angle with dorsal margin; dorsal and posterior margins broadly convex and forming rounded angle. Node lateral face microareolate and usually opaque, rarely silky. Node anterior margin in dorsal view strongly convex, posterior margin broadly convex to straight, lateral margins broadly convex and converging anterodorsally. Abdominal tergite III microareolate and opaque; punctulae in variable density, usually denser laterally than dorsally; covered by brownish, flexuous, suberect hairs on entire surface; appressed pubescence usually sparse on dorsum, denser laterally.

### Male

**MEASUREMENTS.** Non-types ( $n = 5$ ): HL 2.13–2.32; HW1 2.56–2.84; MDL 0.52–0.58; SL 0.87–0.97; EL 1.5–1.58; MOD 0.53–0.58; LOD 0.51–0.57; MSL 6.75–7.16; HFL 5.5–6; PL1 1.8–1.9; PH 1.44–1.54; PW 1.17–1.27; ASL 4.35–4.75; BL1 15.56–16.53 (mm); CII 1.13–1.24; SEI 1.59–1.77; SII 0.33–0.36.

**HEAD.** Frontal carina usually forming short longitudinal swelling. Lateral ocellus clearly surpassing posterior head margin in full-face view. Head punctulate, weakly microareolate and with silky sheen; with yellowish decumbent pubescence and scarce long suberect to erect hairs, longer than ocellus height in full-face view. Antenna with appressed pubescence and long suberect to erect hairs clearly longer than maximum scape diameter; third to fourth most apical antennomeres without hairs. Ventral surface of head punctulate and slightly microareolate; with subopaque to silky sheen.



**Fig. 26.** *Dinoponera quadriceps* Kempf, 1971, ♂ (specimen from Caracol, Piauí, Brazil; DZUP 549804). A. Full-face view. B. Full body in lateral view. C. Full body in dorsal view.

**MESOSOMA.** Mesoscutum without notaulus. Mesopleural sulcus punctate or slightly scrobiculate. Scutoscutellar sulcus scrobiculate. Mesoscutellum longitudinally strigulate laterally. Metapleural-propodeal suture with same microsculpture as rest of integument. Mesosoma mostly slightly microareolate and with silky sheen, becoming coarsely punctate on declivitous surface of propodeum; with decumbent to suberect pubescence and suberect hairs, distance between each hair usually greater than half its length. Legs densely covered by decumbent pubescence; coxae with suberect long hairs, greater than femur diameter. Protibial apex with at least one stout seta.

**METASOMA.** Petiolar node microareolate and shining; densely covered by decumbent to suberect pubescence and sparse suberect hairs. Abdominal tergite VIII spiniform. Gaster very slightly microareolate and shining; tergites densely covered by appressed to decumbent pubescence, without long hairs.

**GENITALIA.** Basal ring in dorsal view with slightly concave lateral margins, anteriorly slightly narrower than posteriorly; fenestra rounded to slightly transversally directed; median invagination U-shaped; dorsal margin in lateral view broadly concave to straight; anteroventral process subquadrate. Gonostylus narrow and sharp. Dorsal margin of volsella in lateral view anteriorly straight and posteriorly concave; anteroventral corner with two anterior teeth; posteroventral margin strongly concave and forming sharp triangular posterior lobe; digitus volsellaris with posterior margin straight or with a slight concavity. In lateral view, penisvalva with continuous dorsal posterior margins, ending in a subacute apex; ventral margin even and serrated, with slight concavity; anteroventral corner sharply pointed.

**COLOR.** Body mostly chestnut brown.

### Remarks

Females of *Dinoponera quadriceps* have a robust set of characters that usually permit easy separation from those of other species of the genus. However, *D. quadriceps* and *D. gigantea*, geographically close species, can sometimes cause confusion. The main characters dividing the two species are: (1) in *D. quadriceps* the anteroventral pronotal margin forms an obtuse angle, but in *D. gigantea* it is toothed or forms an acute angle; (2) the metapleural-propodeal suture in *D. quadriceps* is well-marked and straight, but in *D. gigantea* it is weaker and sinuous; (3) the cephalic venter is mostly strigulate in *D. gigantea* but in *D. quadriceps* the strigulae are absent or sometimes present just anterolaterally; (4) the dorsal region of abdominal tergite III in *D. quadriceps* is sparsely punctulate, but densely so in *D. gigantea*; and (5) the anterodorsal corner of the petiolar node is higher in *D. quadriceps* than in *D. gigantea*. Some specimens of *D. quadriceps* can present one or two *D. gigantea* characters, and vice-versa, so the use of all these characters affords the most reliable identifications. It is worth noting that the difficult cases are more common among specimens from Maranhão and Tocantins, as in *D. gigantea*. Notwithstanding these complications, we consider the aforementioned set of diagnostic characters to provide stronger support for maintaining *D. quadriceps* and *D. gigantea* as separate species than for synonymizing them. The alternative of describing a new species from Tocantins and Maranhão is not possible because the characters seem to vary randomly. Determining the degree of expression of each character is also important. Species differences are frequently a degree of difference one from another, as in the case of the anteroventral pronotal corner in *D. quadriceps*, which may be strongly angular but not toothed or forming an acute angle.

A specimen from Itabaianinha (Sergipe) has a short and robust petiolar node ( $DPI > 0.8$ ), characteristic of *D. grandis*. However, these two species differ in the absence of: (1) the pronotal anteroventral tooth; (2) striae in the malar area and (3) strigulae on the ventral head surface in *D. quadriceps*. The other species of *Dinoponera* can be easily distinguished by having abdominal tergite III smooth and shining.

It was not possible to examine the holotype of *D. opaca*. It is kept as a junior synonym of *D. quadriceps*, on account of the examination of the holotype by C. Baroni Urbani in 1974 at the request of W. Kempf (1975: 344). Dr Baroni Urbani found that the type agreed with the description of *D. quadriceps*. Lenhart *et al.* (2013) examined the type and found total coincidence with *D. quadriceps*. The Rio de Janeiro record for *D. opaca* is undoubtedly a labelling error, as there are no other records of *Dinoponera* for Rio de Janeiro, a heavily collected area for ants, and if there were any *Dinoponera*, the expected species would either be *D. lucida* or *D. australis*.

Males of *D. quadriceps* are different from those of *D. lucida*, *D. longipes*, *Dinoponera* morphospecies 1 and *D. grandis* by having hairs on the antennae that are clearly longer than the scape diameter and the gonostylus narrow, with a sharp apex. As mentioned before, males of *D. gigantea* and *D. quadriceps* are similar in many characters, but the former is longer, more pilose and has a visible notaulus on the mesoscutum.

### Biology

The species occurs mainly in arid or savanna areas with the temperature of the coldest month greater than 18 °C and the precipitation of the driest month less than 60 mm (Alvares *et al.* 2013). Nests are usually built in the ground, near roots and often in direct contact with termite mounds (Araujo *et al.* 1990; Paiva & Brandão 1995). However, Vasconcellos *et al.* (2004) found nests more than 3 m from trees in a remnant of Atlantic Forest, indicating nesting habits may vary with the environment. Each nest can have two to ten entrances surrounded by branches and some loose earth (Araujo *et al.* 1990; Paiva & Brandão 1995). Nest depth varies from 10 to 120 cm and the number of chambers can reach 16 (Araujo *et al.* 1990; Paiva & Brandão 1995; Vasconcellos *et al.* 2004). Assis *et al.* (2017) recorded *D. quadriceps* reusing nests of *Atta sexdens* (Linnaeus, 1758), which are deep enough to ensure protection against hot and dry weather. The density of nests varies from 15 to 40 per hectare (Vasconcellos *et al.* 2004).

The size of the colony can vary from 12 to 141 workers (Paiva & Brandão 1995; Monnin & Peeters 1997, 1998; Vasconcellos *et al.* 2004; Nascimento *et al.* 2012; Asher *et al.* 2013). Vasconcellos *et al.* (2004) found males almost every month of the year, suggesting male production is not seasonal.

Their diet is omnivorous, with a preference for arthropods found dead on the soil (Araújo & Rodrigues 2006). Foraging is solitary and occurs during the day, avoiding the hottest hours (Medeiros *et al.* 2012). The size of food items varies, but regardless of its weight there is no recruitment of other workers (Araújo & Rodrigues 2006). Before finding food, the worker is usually slow and meanders about its usual route, moving up to 35 m from the nest. Foraging tends to be faster during the return trip and follows a relatively straight line (Araújo & Rodrigues 2006; Azevedo *et al.* 2014). Araújo & Rodrigues (2006) suggested that spatial orientation during foraging may follow chemical and visual cues.

Medeiros & Araújo (2014) divided the life cycle of the colony into stages. The first stage is monodomic, with the ants occupying a single nest. Subsequently the colony becomes polydomic, until gradually the ants stop visiting the parental nest and the colonies become isolated, completing the fission. The newly separated colonies go through a period of territorial conflict that results in the extinction or migration of the old colony (Medeiros & Araújo 2014). Vasconcellos *et al.* (2004) also pointed out that intraspecific territorial competition may be one of the main factors responsible for the spatial arrangement of nests.

Colonies of *D. quadriceps* are predominantly monogynous (Monnin & Peeters 1997, 1998, 1999), though Araujo *et al.* (1990) found colonies with more than one gamergate. The dynamics that determine the hierarchy of dominance in this species is well studied, mainly by Monnin & Peeters (1999). Hierarchical position is determined by age and agonistic interactions involving mainly the ants with high status in the colony (Monnin & Peeters 1999). Newly emerged workers usually replace older ones in the highest



positions of the hierarchy. Agonistic interactions are usually related to the stability of monogyny in the colony, and can be performed by the gamergate itself, inhibiting other workers (Monnin & Peeters 1999). After copulation, gamergates chew away the end of the male abdomen, which remains trapped in the female genitalia, preventing further copulation (Monnin & Peeters 1998).

### Distribution (Fig. 29B)

*Dinoponera quadriceps* is endemic to northeastern Brazil, occurring predominantly in the Caatinga. The northernmost record is in Fortaleza, Ceará and the southernmost record is in Viçosa, Minas Gerais. However, Viçosa is more than 500 km away from the next southernmost record (Janaúba, Minas Gerais), leaving doubts as to the reliability of the former record. Another unexpected record is from Brasília, which is also more than 500 km distant from any other record. These records may reflect a wider distribution in a recent past (both date from the 1970s) or just labeling errors. Lenhart *et al.* (2013) cited records of *D. quadriceps* in the cities of Santarém and Óbidos, as well as along the Tapajós River, all in the state of Pará. However, we found no records of this species within at least 1000 km of that region. This discrepancy may be due to either wrong labeling or differences in the criteria used for species identification in each study. The latter is most probably the case, given the similarity between *D. quadriceps* and *D. gigantea*.

### *Dinoponera* morphospecies 1

Figs 27, 28B

### Preliminary considerations

The morphology of this single male is described because it is significantly different from that of all other known males of *Dinoponera*. However, the lack of an associated female does not allow us to identify this specimen. This male may belong to either one of the sympatric species, *D. mutica* or *D. nicinha* sp. nov., both of which do not have described males. Given the present impossibility of associating this specimen with an available name, we present it here with the intention of increasing our knowledge about *Dinoponera* males, but avoiding a wrong association. We also feel compelled to present it due to the recent significantly increased rate of deforestation and bush fires that have ravaged vast swathes of potential distribution range for *Dinoponera*, including the species represented by this male. In view of this calamity, it is not unreasonable to expect dwindling opportunities to collect additional specimens of *Dinoponera* in many parts of the Brazilian Amazon. This male is evidence of the wonderful biodiversity that is literally turning into ashes before our very eyes, and we have no certainty that more specimens will come to light.

### Diagnosis

#### Male

Antenna with thick and stiff decumbent hairs, as long as or slightly longer than maximum scape diameter. Abdominal tergite VIII spiniform. Penisvalva ending in a rounded apex, without a ventral lobe. Anteroventral corner of penisvalva in lateral view with long and very sharp spine.

### Material examined

BRAZIL – Rondônia • 1 ♂; Porto Velho, Rio Madeira, Area Mutum, Ahe Jirau; 9°35'29.5" S, 65°02'57.6" W; 7–20 Feb. 2013; F. Fernandes leg.; malaise, MZSP 62285.

### Description

#### Male

MEASUREMENTS (n = 1). HL 2.23; HW1 2.68; MDL 0.57; SL 0.88; EL 1.47; MOD 0.45; LOD 0.43; MSL 6.91; HFL 5.41; PL1 1.82; PH 1.5; PW 1.25; ASL 4.45; BL1 15.99 (mm); CI1 1.19; SEI 1.64; SII 0.33.

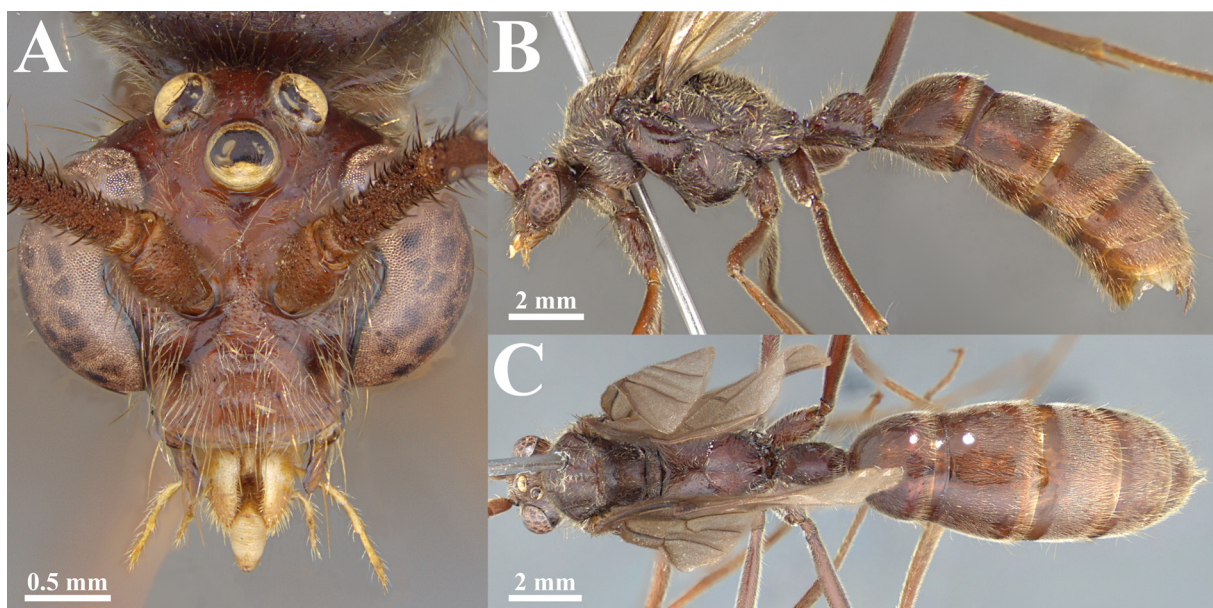
**HEAD.** Frontal carina forming short longitudinal swelling. Lateral ocellus clearly surpassing posterior head margin in dorsal view. Head punctulate, weakly microareolate and shining; with yellowish suberect pubescence and long decumbent to suberect hairs, longer than ocellus height in dorsal view. Antenna with appressed pubescence and thick, stiff decumbent hairs as long as or slightly longer than maximum scape diameter. Ventral surface of head punctulate and slightly microareolate with silky sheen.

**MESOSOMA.** Pronotum with weak transverse rugulae on posterior margin, mesoscutum without notaulus. Mesopleural sulcus slightly scrobiculate. Scutoscutellar sulcus smooth. Mesoscutellum longitudinally strigulate laterally. Metapleural-propodeal suture slightly scrobiculate. Mesosoma mostly smooth and shining, becoming coarsely punctate on declivitous surface of propodeum; with decumbent to suberect pubescence and suberect hairs; distance between each hair usually less than half its length. Legs densely covered by suberect pubescence; also with long suberect hairs, longer than femur diameter. Protibial apex without a stout seta.

**METASOMA.** Petiolar node smooth and shining; densely covered by decumbent pubescence and abundant suberect hairs. Abdominal tergite VIII spiniform. Gaster mostly smooth and shining; tergites densely covered by appressed to decumbent pubescence and sparse suberect hairs.

**GENITALIA.** Basal ring in dorsal view with slightly concave lateral margins, anteriorly much narrower than posteriorly; maximum diameter of fenestra longitudinally directed, median invagination V-shaped; dorsal margin of ring in lateral view anteriorly concave, anteroventral process subquadrate. Gonostylus broad and rounded. Dorsal margin of volsella in lateral view straight; anteroventral corner rounded; posteroventral margin strongly concave and forming a posterior triangular lobe; digitus volsellaris with posterior margin with a slight concavity. In lateral view, penisvalva with continuous dorsal and posterior margins, ending in rounded apex; ventral margin even and serrated, concave; anteroventral corner with long, very sharp spine.

**COLOR.** Body mostly brown, with head and gaster apex slightly clear.



**Fig. 27.** *Dinoponera* morphospecies 1, ♂ (specimen from Porto Velho, Rondônia, Brazil; MZSP 62285). A. Full-face view. B. Full body in lateral view. C. Full body in dorsal view.

### Remarks

*Dinoponera* morphospecies 1 is different mainly because of the shape of the anteroventral corner of the penisvalva, which ends in a long, sharp spine. It also differs from *D. gigantea* and *D. quadriceps* by the antennal hairs, which are shorter and thicker. An additional character that distinguishes this male from *D. lucida* and the *D. grandis* is the concavity of the basal ring in lateral view, much weaker in *Dinoponera* morphospecies 1. In *D. longipes* the penisvalva is wedge-shaped, not rounded, in lateral view, and the spine is shorter (observations made from the illustrations and description in Lenhart *et al.* 2013). Hopefully, additional specimens will be collected in the future, permitting the association of this male with its conspecific females. This could be done directly by collecting nest series of both sexes of the same species, or indirectly by collecting those of another species, making apparent which species it does not belong to.

### Biology

Unknown.

### Distribution (Fig. 28B)

This morphospecies is only known from Porto Velho, Rondônia, Brazil.

### Discussion

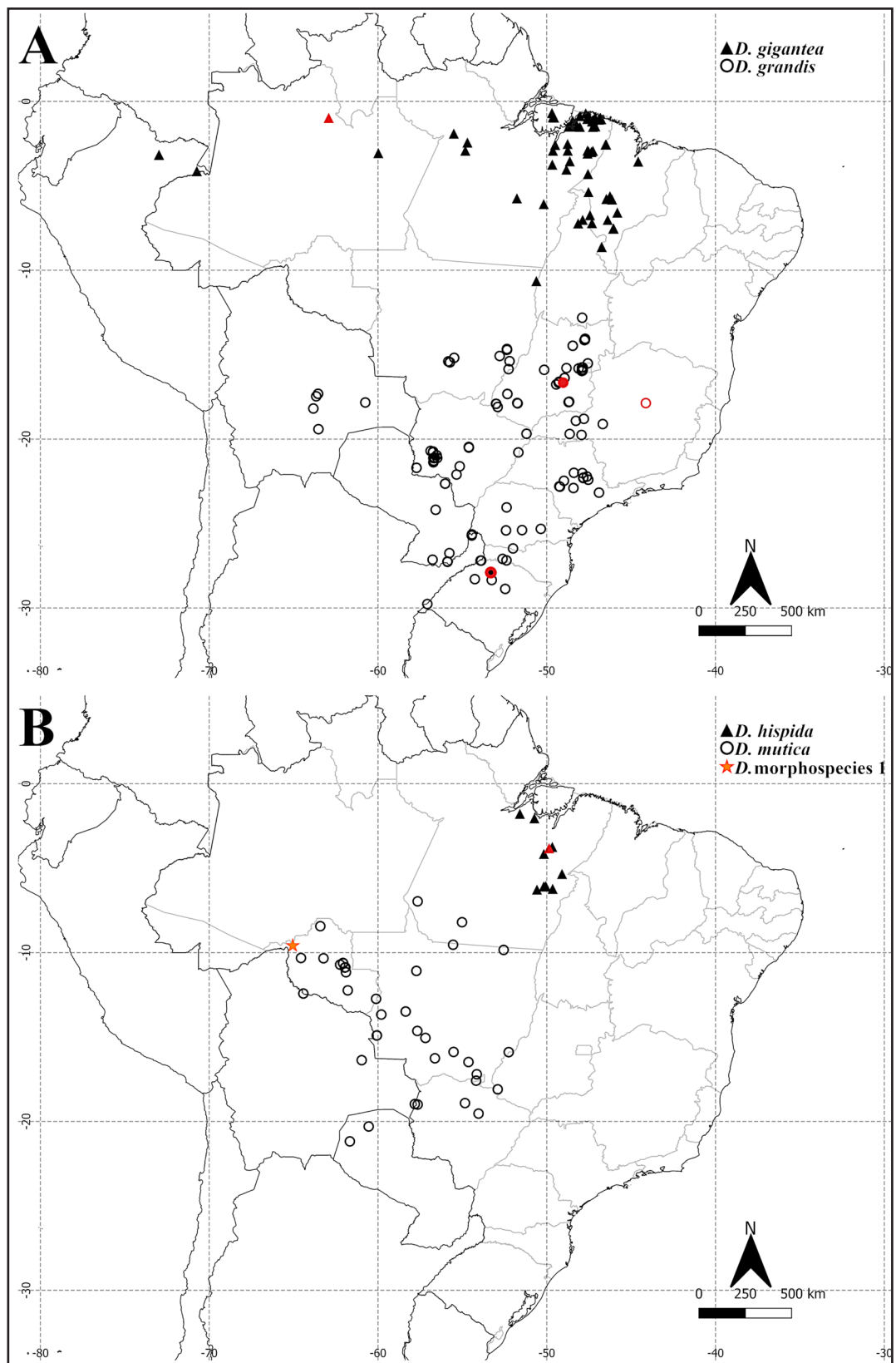
We have redescribed all known species of *Dinoponera* and described a new species using the largest amount yet available of specimens for a study of this group, particularly from Brazilian institutional collections. Due to the large size of these ants, a trait that would make them attractive for even generalist insect collections, we expected to find more of these ants in collections. Especially surprising and worrying is the paucity of recent collecting events for several of these species.

It was possible to note that males are morphologically more variable than females. In *D. grandis*, males seem to be discreetly variable, in sharp contrast with the continuous variability of females. This offers the hope of permitting less challenging identifications than when using the females, but in practice this is cold comfort as males are harder to come by, and the apparent greater discreteness of male characters may be an artefact of the few males examined.

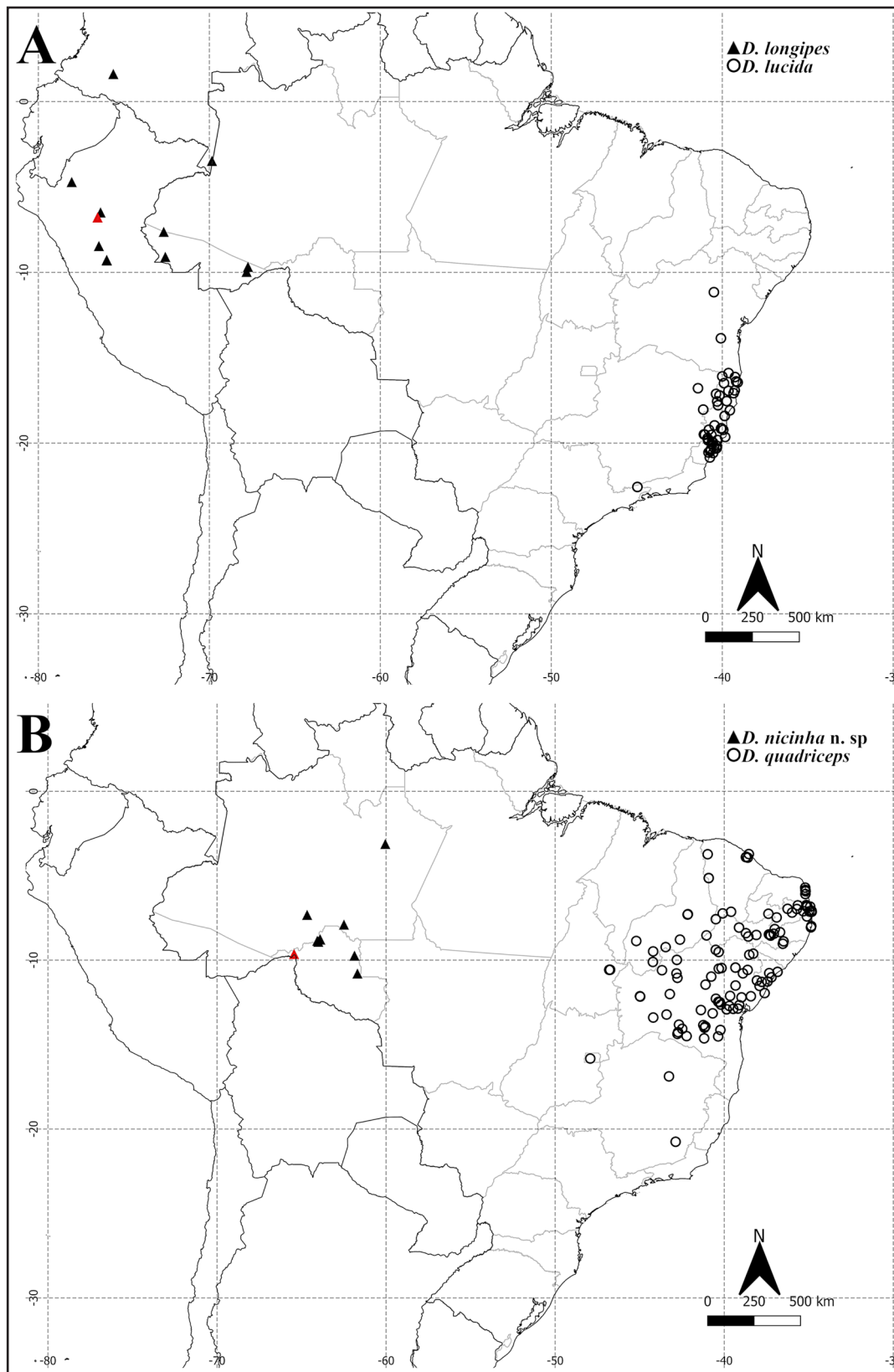
While we believe that we have been able to significantly improve the alpha taxonomy of these species, there is still much to be done. The application of molecular methods could give us valuable insights into the phylogenetic relationships amongst the different lineages and provide additional evidence for taxonomic decisions. During the course of this study we unsuccessfully tried to extract and amplify DNA from several specimens. Given the paucity of museum specimens, particularly from recent collecting events, we advocate for field work specifically targeting the known populations and searching localities where some populations may still remain; this is especially urgent for *D. grandis*. The long history of deforestation, fragmentation and conversion of natural landscapes into agricultural landscapes has probably complicated matters even further, both for the survival of these ants and the opportunities for studying them. Particularly worrying is the dramatic increase in bush fires in recent times. Even though one species, *D. lucida*, figures in the Brazilian Red list of endangered species (ICMBio 2018), it is possible that other species and populations, such as *D. hispida*, are arguably in even more dire straits.

### Acknowledgements

We would like to thank all those responsible for specimen loans or donations, and support: Jacques Delabie, Fernando Fernández, Bolívar Rafael Garcete-Barrett, Rogério R. Silva, Livia Pires do Prado, Rogério Silvestre, Carlos Roberto Ferreira Brandão, Mônica Ulysea, Héli da Ferreira da Cunha, Daniel



**Fig. 28.** Distribution maps for species of *Dinoponera* Roger, 1861. Red symbols indicate type specimens examined here. **A.** *D. gigantea* (Perty, 1833) and *D. grandis* Guérin-Ménéville, 1838. **B.** *D. hispida* Lenhart, Dash & Mackay, 2013, *D. mutica* Emery, 1901 and *Dinoponera* morphospecies 1.



**Fig. 29.** Distribution maps for species of *Dinoponera* Roger, 1861. Red symbols indicate type specimens examined here. **A.** *D. longipes* Emery, 1901 and *D. lucida* Emery, 1901. **B.** *D. nicinha* sp. nov. and *D. quadriceps* Kempf, 1971.

Burckhardt, William Fernando Antonialli Junior, Stefan Schmidt, Marcelo Teixeira Tavares, Priscila Hanisch, Iracenir Andrade dos Santos, Luciana Regina Podgaiski, Arrilton Araújo, Benedito Cortês Lopes, José Henrique Schoereder, Heraldo Vasconcellos, Gustavo Graciolli, Mariah Tibcherani, Itanna Fernandes and Marília Costa. We also thank Flavia Esteves and Alexandre Ferreira for imaging specimens, Leonardo Tozetto for helping with dissections, and Rodrigo Feitosa, Monica Ulysea, Itanna Fernandes and Gabriel Melo for critical reviews of the first version of this manuscript. To Marcio Pie and André Olivotto we are grateful for all their support in our attempts to include molecular data in this study. Finally, we thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the financial support that made this study possible. We also thank the reviewers for their valuable suggestions.

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*Manuscript received: 28 February 2021*

*Manuscript accepted: 14 October 2021*

*Published on: 21 December 2021*

*Topic editor: Nesrine Akkari*

*Section editor: Gavin Broad*

*Desk editor: Danny Eibye-Jacobsen*

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