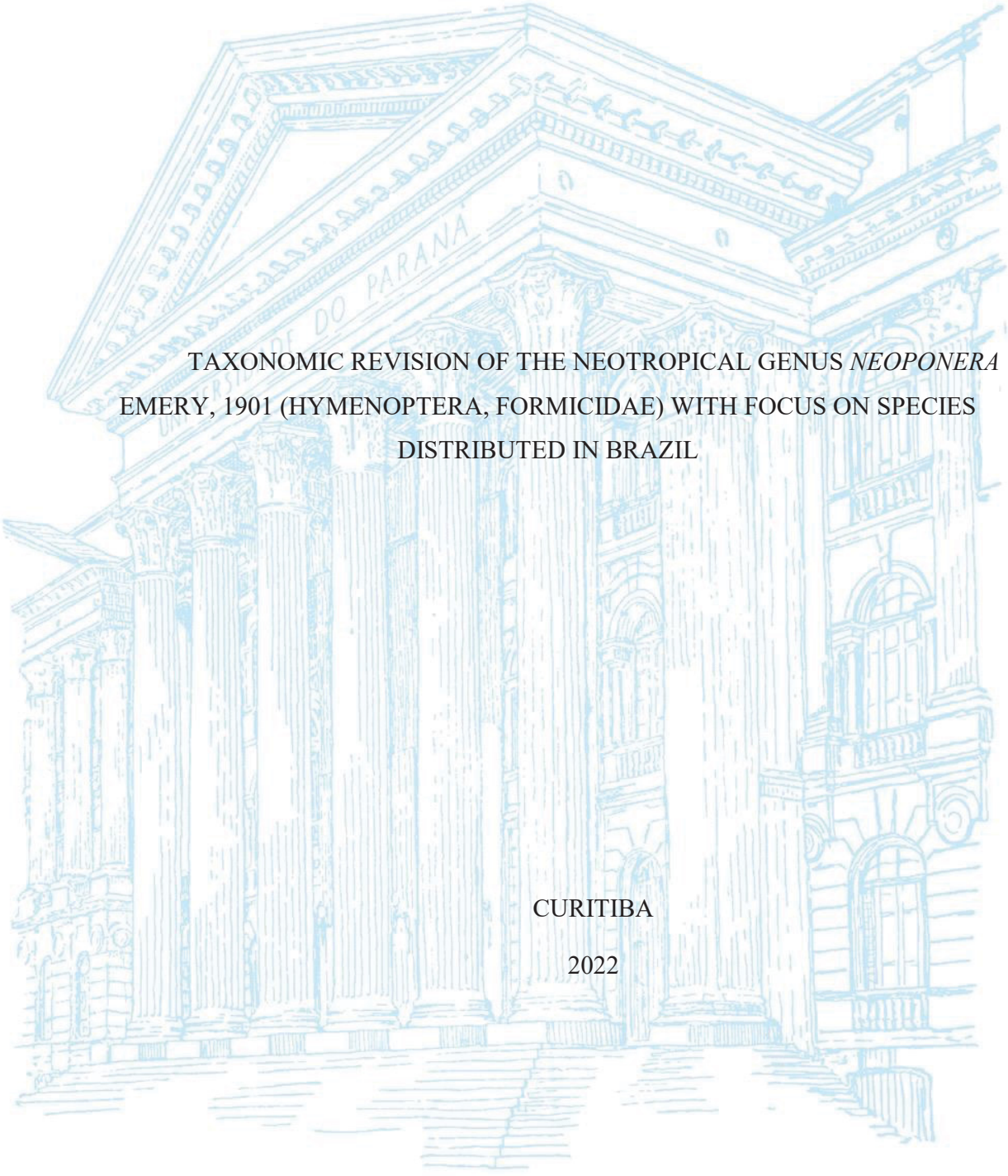
UNIVERSIDADE FEDERAL DO PARANÁ

ADRIAN ESTEBAN TROYA PROAÑO



TAXONOMIC REVISION OF THE NEOTROPICAL GENUS *NEOPONERA* EMERY, 1901 (HYMENOPTERA, FORMICIDAE) WITH FOCUS ON SPECIES DISTRIBUTED IN BRAZIL

CURITIBA

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Tese de Doutorado apresentada à Coordenação do Programa de Pós-Graduação em Ciências Biológicas (Área de concentração em Entomologia), do Setor de Ciências Biológicas da Universidade Federal do Paraná, como requisito parcial para a obtenção do título de doutor em Ciências Biológicas.

Orientador: Prof. Dr. John Lattke Bravo

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A outorga do título de doutor está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

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To my mother, Eli

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My eternal gratitude to my mom to whom I owe everything in life, and possibly after I leave this planet. I learnt from her to gain courage even if the world turns against you. No matter how dark or hard, everything will be fine in the end. Thank you so much, mom.

To my brothers Carlos, Hernán, and even to Andrés, with whom I have shared extremes like joy and sadness. Thank you Carlungui and Shurita, despite being separated for such a long time during these years, you both were always in my thoughts.

Thank you, John for accepting me as your student. I enjoyed the short but fruitful bate-papos (dialogues) we had while at your Lab. Although we could not know each other as much as I would like to, let's leave the coming years to fill that gap! In this same line I extend my gratitude to my ex labmates Erik, Román, Fred, Leo, Eder, Joshua, and Amanda. I really hope we meet again in the future, and I know we will!

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Finally, I thank the following institutions from which I received additional funding which significantly aided in developing the present work: The Association of Systematic Biologists, USA; The Society for the Study of Evolution, USA; Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (Projeto 140995/2020– 0), Brazil; and Escuela Politécnica Nacional, Ecuador.

"Nomine si nescis, perit et cognitio rerum" – If you ignore the names of things, what you know of them also disappears.

(Carolus Linnaeus, 1755)

And the ant cried out ¡cannot carry it all! then she retracted while watching the army behind her. (The author)

RESUMO

O gênero *Neoponera* Emery, 1911, ou como eu gosto de chamar às espécies "formigas-tigre" ou, em alguns casos, "formigas-tigre douradas", é composto por 58 táxons válidos, todos habitam na Região Neotropical. Entre os Ponerinae, este é um gênero emblemático devido à sua alta diversidade comportamental, que pode variar desde a especialização na predação de cupins, até a caça solitária; algumas espécies também são consideradas modelos para estudar a evolução da eusocialidade. Wild (2005), Mackay e Mackay (2010), e Fernandes et al (2014) fizeram contribuições taxonômicas anteriores ao gênero. No entanto, inúmeras questões taxonômicas vêm se acumulando, algumas delas relacionadas exclusivamente à nomenclatura de novos táxons encontrados durante este estudo, e outras mais complexas, como o lidar com as espécies crípticas para as quais não havia material tipo disponível. Além disso, identificar a maioria dos *Neoponera*, em particular aqueles adaptados à vida arbórea, é complexo ou mesmo impossível com a literatura atualmente disponível. Além disso, uma hipótese filogenética para o gênero estava faltando, até agora. Neste trabalho abordo a maioria dessas questões revisando exemplares de toda a área de distribuição do gênero. Eu incluo uma quantidade relativamente grande de exemplares do Brasil, a maioria dos quais não foram examinados em tratamentos taxonômicos anteriores. Como resultado, descrevo 12 novas espécies, e pelo menos cinco espécies ficam pendentes de descrição futura; eu propor nove sinônimos; reviso os grupos de espécies *crenata*, *emiliae*, *foetida* e *laevigata*; um novo gênero é erguido e outro é detectado cuja morfologia documento através de imagens de microscópio de varredura. Todos os tratamentos são baseados nas castas de operária, rainha e, quando disponível, do macho. Finalmente, com base em elementos ultraconservados, reconstruo uma hipótese de relações evolutivas entre as linhagens de *Neoponera* usando a maioria dos taxa atualmente válidos; a filogenia resultante fornece forte suporte para a monofilia do gênero, conforme aqui definido. O género ainda precisa de trabalho no futuro, principalmente a descoberta de machos não descritos, e a que pode ser a última grande questão taxonômica do gênero: desvendar linhagens ocultas em complexos de espécies, como por exemplo, em *N. apicalis* e *N. verenae*.

Palavras-chave: Espécies crípticas. Caçadoras. Região Neotropical. Ponerinae. Elementos ultraconservados.

ABSTRACT

The genus *Neoponera* Emery, 1911, or as I like to call its species "tiger ants" or, in some cases, "golden tiger ants", is composed of 58 valid taxa, all inhabiting the Neotropical Region. Among the Ponerinae, this is a flagship genus due to its high behavioral diversity ranging from extreme specialization on termite raiding, to solitary hunting; some species are also considered models to study the evolution of eusociality. Wild (2005), Mackay and Mackay (2010), and Fernandes et al (2014) made prior taxonomic contributions to the genus. However, numerous taxonomic issues have been piling up, some of these are exclusively related to naming new taxa found during this study, and others are more complex, like grappling with cryptic species for which no type material was available. Furthermore, identifying most *Neoponera*, in particular those adapted to arboreal life, is complex or even impossible with currently available literature. In addition, a phylogenetic hypothesis for the genus was missing, until now. Here, I address most of these issues by revising exemplars from the entire distribution range of the genus. I also included a relatively great amount of material from Brazil, most of which was not examined in past taxonomic treatments. As a result, I describe 12 new species, with at least five pending future description; propose nine synonyms; revise the *crenata*, *emiliae*, *foetida*, and *laevigata* species-groups; propose a new genus, and detect another whose morphology I documented through SEM images. All treatments are based on the worker, queen, and, when available, the male castes. Finally, based on ultraconserved elements, I reconstruct a hypothesis of lineage relationships for *Neoponera* using most of the currently valid species; the resulting phylogeny provides strong support for the monophyly of the genus, as here defined. Future work is still ahead, especially finding undescribed males, as well as addressing what could be the last major taxonomic issues in the genus: unveiling hidden lineages in species complexes, like *N. apicalis* and *N. verenae*.

Keywords: Cryptic species. Huntresses. Neotropical Region. Ponerinae. Ultraconserved elements.

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NOTE TO THE READER

In the following text, except for subchapter I, a number of new nominal species are mentioned. All of them are described in correspondent treatments. However, new species names in subchapters II and III are not published, therefore they are not officially part of the taxonomic literature. Nevertheless, I consider useful including them in this work so as to facilitate associating these entities with terms and theory here mentioned, rather than just citing alphanumeric codes, except for few cases where descriptions are pending, and/or species-group names, i.e., specific epithets have not yet been assigned. Although this manuscript represents the so called gray literature (Auger 1975, Paez 2017), such new species names must not be cited in any printed or digital, scientific or non-scientific work, since they are not yet registered in the Zoological Record (ICZN 1999, Appendix B). If the interested user wants to mention this information, it is preferable using, for example, "*Neoponera* new species".

The author.

CHAPTER I

Phylogeny and evolution of *Neoponera* Emery, 1901 (Hymenoptera: Formicidae)

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ABSTRACT

Evolutionary trees are a way to understand the past and present of life: how organisms change, generally from simple to more complex forms. The ants are a good example upon to illustrate this process due to their broad array of behavioral and morphological traits. In recent years research on the ant tree of life advanced steadily mostly boosted by new genome- and phenomic-based techniques. Currently, the higher classification of the ants, at the subfamily level, mostly reflects phylogeny. However, the systematics of tribes and especially of genera still requires attention. In this work we reconstruct the phylogeny of one of the most behaviorally rich groups of the subfamily Ponerinae, the genus *Neoponera* Emery. Based on ultraconserved elements (UCE), which are genome-scale markers that allow recovering evolutionary relationships at both shallow and deep levels, and using a recently discovered Dominican amber fossil that is assignable to the *Neoponera foetida* species-group, we unveil a new perspective about the origin of the genus, and inform precedent morphology-based taxonomic work. The resulting phylogeny can be used as a tool to trace the evolution of behavior, and in general, the natural history of *Neoponera* in regards to current or future hypotheses; for example, the role of certain body traits enabling many species to shift from ground-nesting to arboreal-nesting. As a result of this study, we make minor taxonomic adjustments in the internal classification of the genus, and propose new_genus_B, a new ponerine lineage that in our tree come out as sister to *Neoponera*. Finally, we confirm that *N. bucki* Borgmeier, does not belong to this genus, but is rather distantly related, and placed it for now as *incertae sedis* in Ponerinae.

Keywords: Amber fossil, arboreal, molecular phylogenetics, Neotropics, Ponerinae.

INTRODUCTION

Phylogenetic systematics is a dominant paradigm of systematic biology and for several decades has influenced the study of evolution across the tree of life (Wiley and Lieberman 2011). Major advances in ant systematics have been published recently, e.g., Branstetter et al. (2017), Borowiec et al. (2019), Camacho et al. (2022), most of which go in hand with fast-evolving molecular techniques and bioinformatics methods. Active research around resolving the phylogenetic backbone of the ants led to a currently more stable classification in monophyletic subfamilies (Branstetter et al. 2017, Borowiec et al. 2019), and a number of tribes (Ward et al. 2015, 2016). Yet, multilocus DNA (Schmidt 2013, Ward et al. 2015), and most recently phylogenomic data (Camacho et al. 2022), showed that some generic and tribal classifications may not reflect evolutionary relationships. As this work continues, inconsistencies become evident between new molecular-based findings with respect to traditional, usually morphology-based classifications (Solomon et al. 2019, Branstetter and Longino 2022), with homoplasy and convergence at intergeneric (Ward and Boudinot 2021) and intraspecific levels (Branstetter 2013) also playing a role.

Ponerinae, one the four largest ant subfamilies which currently holds 1274 valid species (AntCat 2022), was reviewed by Schmidt and Shattuck (2014); prior to their work this group was subject to some taxonomic confusion since a number of species in some genera, like *Bothroponera*, *Mesoponera*, *Pseudoponera*, and in particular *Pachycondyla* showed significant interspecific morphological variation, thus rendering them para- or even polyphyletic. Based on the molecular phylogeny of Schmidt (2013) they reorganized the internal ponerine classification, and solved numerous taxonomic inconsistencies. Yet, a number of genera, if not most, requires further taxonomic revisions at the specific level since additional issues exist, many of which were identified by Schmidt and Shattuck (2014).

Neoponera Emery, was among the resurrected genera by Schmidt and Shattuck (2014), priorly considered part of the then polyphyletic *Pachycondyla*, which prior to their work was revised by MacKay and Mackay (2010) who described numerous new species (now assigned to various independent genus lineages), proposed new synonyms, and overall established sub groups they called “species-complexes”, which we here call species-groups, as follows: *aenescens*, *apicalis*, *crenata*, *emiliae*, *foetida*, *laevigata*, *rostrata*, and *stigma*. Except for *Pachycondyla* (=

Neoponera) *procidua* Emery these groups remained valid in the genus. Since then Fernandes et al. (2014), and Troya and Lattke (2022) incorporated two new species assigned to the *foetida* group, and two to the *laevigata* group, respectively. The latter authors, also provide a new key to *Neoponera* species-groups, thus tacitly validating Mackay and Mackay's (2010) classification, except for three species which they unofficially "transfer" to a potential new genus they called "*N. emiliae* 2" (without argumentation), although some characters and images representing "*N. emiliae* 2" are shown. Troya and Lattke (2022) also noted that *N. bucki* Borgmeier is not a *Neoponera*, again without argumentation, but decide to leave it in their taxonomic key until formalizing its new status.

Neoponera is behaviorally and morphologically diverse among the Ponerinae; the shape of the petiole probably best illustrates this richness in forms (Fig. 1) and is a key feature for identifying its taxa. Few species have been heavily studied in several lines of knowledge, but probably most in regards to foraging behavior (see review in Schmidt and Shattuck 2014). As with many ponerines they are particularly useful as research models (e.g., *N. apicalis, N. villosa*) to comprehend and unravel "incipient" traits in the evolution of social interactions (Kolmer 2002, Yagound et al. 2015). In the Ponerinae, perhaps, this might be amongst the few lineages where epigeic highly specialized foragers (e.g., species in the *laevigata* group), underground/surface nesters, solitary foragers (e.g., *N. magnifica*), obligate arboreal nesters (e.g., *N. insignis*, *N. luteola*), and arboreal generalist nesters (e.g., *N. villosa*, *N. goeldii*) converge. In order to gain evolutionary insights of these array of behavioral strategies we, 1) Reconstruct the phylogeny of the *Neoponera* so as to produce a base on where future research relies on; 2) Infer the times of divergence of most of its currently valid lineages; and as consequence of the previous two, 3) Propose changes in nomenclature, including the erection of a new genus.

MATERIALS AND METHODS

Taxon sampling

The data set is composed of 77 terminals representing 59 species depicting outgroup and ingroup lineages belonging from a number of sites across the Neotropics (Appendix A). This material is dry-mounted and preserved in various institutions harboring ant collections (see further below); collection information about all examined specimens is supplemented online

(Supp_table_1). The outgroup comprises *Dinoponera longipes* Emery, *Pachycondyla procidua* Emery, and *Neoponera bucki* (Borgmeier). The first two are closely related to *Neoponera*, while *N. bucki* is not part of this genus but distantly related to it (see results); this is also supported by morphological evidence (Troya, pers. obs.).

Representatives from other ponerine lineages belonging to the *Pachycondyla* genus-group sensu Schmidt and Shattuck (2014), the ponerine clade where *Neoponera* is placed in, namely *Belonopelta*, *Igaponera*, *Mayaponera*, *Simopelta*, and *Thaumatomyrmex*, were not included as part of the outgroup since these were either not available before writing this manuscript, or the available DNA sequences showed inconsistencies (probably machine-originated) that precluded complete background analyses, e.g., reads assembling, before proceeding with the phylogenetic inference. In any case, *Dinoponera* and *Pachycondyla* which are closely related to *Neoponera* were successfully incorporated into the working matrix. The DNA material from the single known specimen of *Igaponera*, which is *Neoponera's* putative siter genus, was too degraded for sequencing.

The ingroup includes 48 out of the 58 valid *Neoponera* sensu AntCat.org (2022), it contains specimens representing the seven currently recognized species-groups sensu Troya and Lattke (2022), as follows (included species/valid species): *aenescens* group (9/9), *apicalis* group (4/4), *crenata* group (14/17), *emiliae* group (4/6), *laevigata* group (5/5), *foetida* group (12/13), and *rostrata* (1/2). Those not included were *N. agilis* Forel (represented by rostrata under which *N. agilis* will be synonymized, A. Troya, pers. obs.), *N. billemma* (Fernandes et al.) (degraded DNA, though represented through *N. curvinodis* (Forel) under which *N. billemma* will be synonymized, A. Troya, pers. obs.), *N. commutata* (Roger) (not available), *N. concava* (Mackay and Mackay) (degraded DNA), *N. coveri* (Mackay and Mackay) (not available), *N. latinoda* (Mackay and Mackay) (represented by *N. fiebrigi* under which *N. latinoda* will be synonymized, A. Troya, pers. obs.), *N. magnifica* (Borgmeier) (degraded DNA), *N. unidentata* (Mayr) (sequence with unresolved issue).

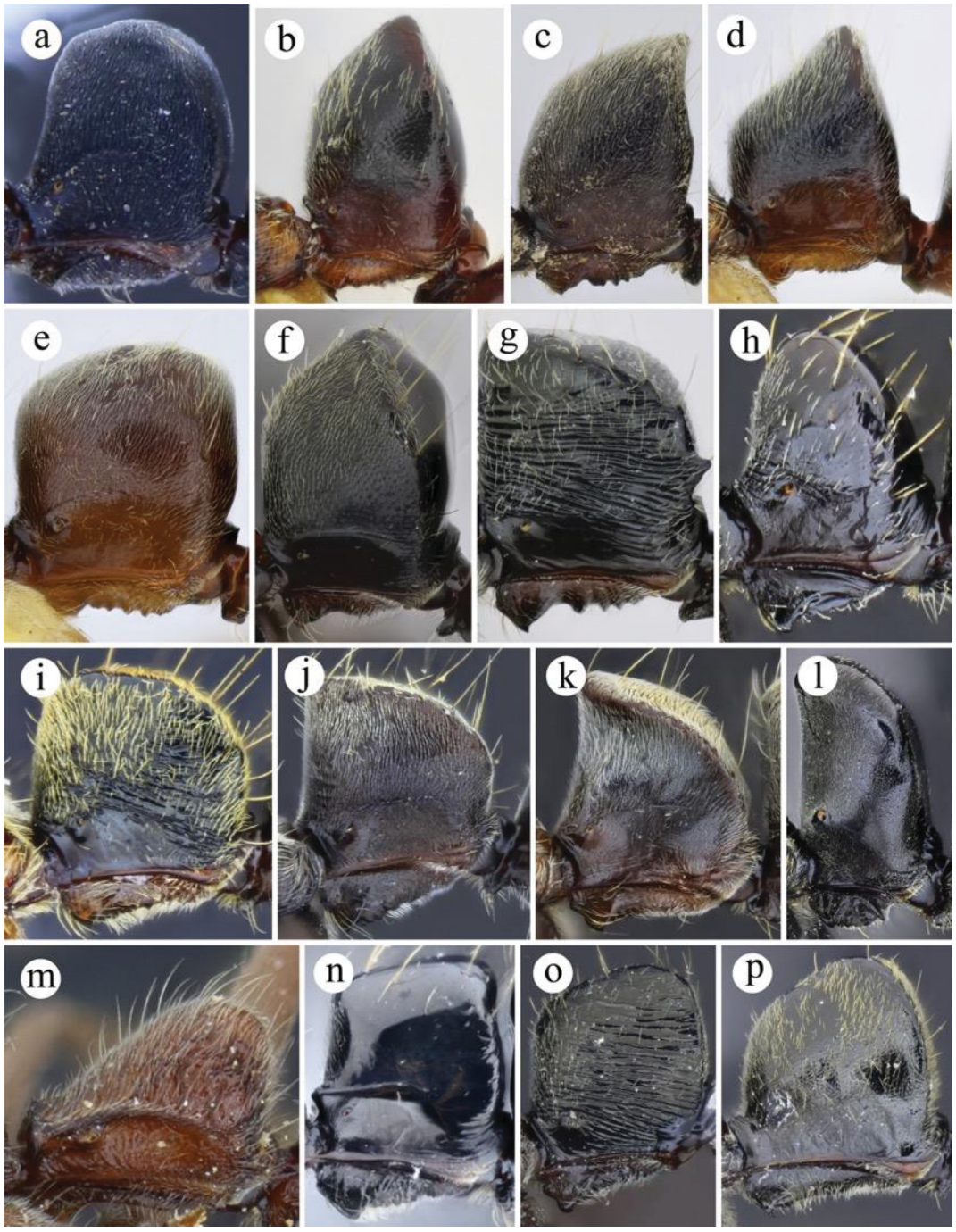


Fig. 1. Morphological diversity in *Neoponera* (petioles in lateral view). **a.** *N.* bra549385 (☿ DZUP549385); **b.** *N. oberthueri* (♀ATPFOR2083); **c.** *N. cavinodis* (☿ ATPFOR0855); **d.** *N. oberthueri* (☿ MEPN2944); **e.** *N. globularia* (☿ INB0003607588); **f.** *N. carinulata* (☿ DZUP549406); **g.** *N. striatinodis* (☿ GO-E-02-1-05); **h.** *N. fisheri* (☿ CASENT0843089); **i.** *N. theresiae* (☿ GO-E-08-1-03); **j.** *N. insignis* (☿ JTL9077-1); **k.** *N. curvinodis* (☿ INPA); **l.** *N. caxiuana* (☿ INPA); **m.** *N. rostrata* (♂DZUP549351); **n.** *N. mashpi* (☿ ATPFOR2054–2); **o.** *N. holcotyle* (☿ HOR1321); **p.** *N. fusca* (☿ CASENT0649890). Images: A. Troya.

In addition, the following undescribed lineages were included in the working set: *N.* ecu33723 (DZUP549355) which belongs to the *aenescens* group, and *N.* bra549385 (DZUP549385) belonging to the *apicalis* group; and the following which are recent additions to the genus (Troya, unpublished): *N. dorsilinea* Troya, *N. dropsy* Troya., and *N. glabra* Troya. assigned to the *emiliae* group; *N. cylindrinodis* Troya., and *N. dejeani* Troya, assigned to the *crenata* group; and *N. prasiosomis* Troya, assigned to the *foetida* group.

Morphology

The material examined here is preserved in the following institutions: CASC – California Academy of Sciences, USA; CPDC – Coleção do Laboratório de Mirmecologia, Centro de Pesquisas do Cacau, Ilhéus, Bahia, Brazil; DZUP – Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil; ICN – Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; INBC – Instituto Nacional de Biodiversidad, San José, Costa Rica; INPA – Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil; JTLC – John T. Longino Collection, University of Utah, Salt Lake City, UT, USA; MEPN – Museo de Colecciones Biológicas Gustavo Orcés, Escuela Politécnica Nacional, Quito, Ecuador; MPEG – Museu Paraense Emílio Goeldi, Belém, Pará, Brazil; MZSP – Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; PSWC – Philip S. Ward Collection, University of California, Davis, CA, USA; UCDC – University of California, Davis; UTIC – University of Texas El Paso, Texas, USA.

All specimens were identified based on comparisons with correspondent type material, either examined in person or through images from: AntWeb (2022) available at www.antweb.org; the MCZ Database of Zoological Collections, available at www.mczbase.mcz.harvard.edu; and those directly supplied by museum curators. The type material of the new species will be deposited at the institutions cited in the Supp_table_1; images of all species cited in this work are available at AntWeb.

Morphometric variables

All observations and measurements of the following morphological variables were taken at magnifications from 8X to 50X with an ocular micrometer incorporated to a Zeiss® Stemi SV6 stereo microscope. Measurements are presented in mm with an accuracy of two decimal places, minimum and maximum values are indicated when more than one specimen was measured. We

selected specimens for measurement based on the distribution of each species by picking up a number of differently sized specimens per collection site, when available.

HL Head length. In frontal view, maximum distance from the posterior margin of head to the anterior margin of clypeus.

HW Head width. In frontal view, maximum width of head, excluding the eyes.

EL Eye length. In lateral view, measured along its maximum length.

SL Scape length. In frontal view, maximum length of scape excluding its basal condyle and neck.

PrW Pronotum width. In dorsal view, maximum width of pronotum.

WL Weber's length. In lateral view, distance between the anterior margin of pronotum, excluding collar, to the posteroventral margin of metapleuron.

MsW Mesonotum width. In dorsal view, maximum width of mesonotum.

MsL Mesonotum length. In a dorsal view, the maximum distance from the anterior margin of the mesonotum to its posterior margin.

PW Petiolar width. In dorsal view, maximum width of the petiolar node.

PH Petiolar height. In lateral view, the perpendicular distance from the posteroventral lobe of the petiolar tergite to its maximum dorsal margin.

PL Petiolar length. In a lateral view, the distance between the anteriormost margin of petiole to its posterior margin, excluding the posteroventral ridge.

GL Gaster length. In lateral view, the oblique distance between the anterior margin of abdominal segment III to the posterior margin of the pygidium, excluding the sting. This is a relative measure since it can vary in relation to the extension or contraction of abdominal segments IV to VII.

A3L Abdominal segment III length. In dorsal view, the distance between the anterior and posterior margin of abdominal tergite III.

A3W Abdominal segment III width. In dorsal view, maximum width of tergite of abdominal segment III.

A4L Abdominal segment IV length. In dorsal view, the distance between the anterior and posterior margins of abdominal tergite IV.

A4W Abdominal segment IV width. In dorsal view, maximum width of tergite of abdominal segment IV.

TLa Total accurate length of body: HL + WL + PL + A3L + A4L

TLr Total relative length of body: HL + WL + PL + GL

Indices

The following ratios were multiplied by 100:

CI Cephalic index: HW/HL

OI Ocular index: EL/HW

SI Scape index: SL/HW

MsI Mesonotum index: MsW/MsL

LPI Lateral petiolar index: PL/PH

DPI Dorsal petiolar index: PW/PL

DNA extraction

DNA was extracted from adults or pupae in the Longino lab (by Rodolfo Probst and Toby Hays), School of Biological Sciences, University of Utah, USA. Extractions were non-destructive in most cases. Destructive sampling using whole specimens was carried out when at least one voucher belonging to the same nest series was available. We used DNeasy Blood and Tissue Kit

(Qiagen, Valencia, CA). Muscle tissues were digested with Proteinase K overnight. DNA elution was done in two washes of 65 uL for a final volume of 130 uL. Input DNA was sheared to a target size of ~600 bp using a QSonica Q800R3-110 (Qsonica Inc., Newtown, CT). This product served as input for a modified genomic DNA library preparation protocol (Kapa Hyper Prep Library Kit, Kapa Biosystems) that included SPRI bead cleanup using a generic substitute (Rohland and Reich 2012) and custom dual-indexing barcodes (Glenn et al. 2019).

DNA sequence generation

We based our analyses on ultraconserved elements (UCE), using the methodology for target enrichment and multiplex NGS sequencing described in Faircloth et al. (2012), and Branstetter et al. (2017). Library preparation, UCE enrichment, sample pooling, and sequencing was performed at RAPiD Genomics (Gainesville, Florida). The ant-specific UCE bait set " hym-v2", which targets 2524 hymenopteran conserved loci (Branstetter et al. 2017), was used to enrich the UCE raw material. The sequencing facility demultiplexed and converted raw data from BCl to FASTQ using BCL2FASTQ. Low-quality nucleotides and adapter-contaminated end regions from these initial sequence reads were removed (or cleaned) using Illumipricessor (Faircloth et al. 2013) around TRIMMOMATIC (Bolger et al. 2014).

UCE matrix assembly

Once the reads were cleaned, we prepared a matrix before phylogenetic inference; this process is carried out through a sequence of scripts implemented in Phyluce package v. 1.7.1 (Faircloth 2016), as follows: 1) *De novo* read assembly into contig sequences was performed using SPAdes (Bankevich et al. 2012); 2) To find UCE loci from each of these contigs we run the script *match_contigs_to_probes* which aligns them to the bait set hym-v2; 3) With *assembly_get_match_counts* we created a data matrix configuration file, which is a list of the taxa containing UCE loci we want in the analyses; 4) We then extracted FASTA files from each of those loci contained in each taxa, and calculated general statistics, like # of contigs, # of base pairs, mean length, for each taxon with *get_fasta_lengths*; 5) These FASTA sequences were then aligned using MAFTT (Katoh et al. 2009) with *seqcap_ align*, which also performs a trimming round of the flanking (external) regions on each aligned locus, this step is called "edge trimming". Note: According to Brant Faircloth comment on his Phyluce site (phyluce.readthe docs.io) edge trimming is usually efficient enough to produce well-aligned blocks for closely related lineages

which diverged approximately between 30 – 50 ; whereas internal trimming (see below) is used for more broadly diverging lineages (> 50 my). We tested this assumption by producing three matrices: edge- and internally-trimmed, edge-trimmed, and internally-trimmed. We concluded that for the present data set both edge and internal trimming produced much better results since their combined action more effectively get rid of gaps and ambiguous sites than by using each method separately. 6) We then made internal trimming using the same script above (*seqcap_align*) but adding the *no-trim* option; 7) Using the program Gblocks (Talavera and Castresana 2007), with the script *get_gblocks_trimmed_ alignments_from_untrimmed*, and default stringency parameters (b1: 0.5, b2: 0.85, b3: 8, b4: 10), potentially problematic or difficult to align blocks were removed; 8) Following a final cleaning of each alignment with *remove_locus_name_from_files*, we used *get_ only_loci_with_min_taxa/ --percent 0.75*, and *get_ only_loci_with_min_taxa/ --percent 0.95*, so as to produce two final data matrices containing locus data for 75% and 95% of the taxa, respectively, and then we got summary statistics for those data sets with *get_align_summary_data*, which are summarized in Supp_table_2; 9) Lastly, we created concatenated PHYLIP files containing the aligned loci using *concatenate_alignments*, which was used for inferring the phylogeny.

Phylogenomic inference

We used IQ-TREE v2.12 (Nguyen et al. 2015) through the CIPRES Science Gateway v3.3 (phylo.org). The following parameters were used: node support calculated with 1000 ultrafast bootstrap replicates (UFB) (Minh et al. 2013, Hoang et al. 2018), also referred to as “samples”, using 1000 iterations with a minimum correlation coefficient of 0.99, in a scale between 0.9 – 1. According to Minh et al. (2013), a high correlation coefficient. i.e., 0.99 or higher, is indicative that no further substantial changes in node support values are likely to show up as the search progresses. We limited the tree search to 100 unsuccessful iterations with default nearest neighbor interchange (NNI) perturbation strength of 0.5; to infer single-branch supports we chose the SH-approximate likelihood ratio test (SH-aLRT) (Guindon et al. 2010), and the approximate Bayes test (aBayes) (Anisimova et al. 2011); Model Finder (Kalyaanamoorthy et al. 2017) tested 34 models of evolution based on a total sample size of 887 641 base pairs, under the Akaike information criterion (AIC) (Akaike 1973), the AICc (AIC corrected) (Hurvich and Tsai 1993), and the Bayesian information criterion (BIC) (Schwarz 1978). The best model selected was

TVM+F+R9 showing a LogLikelihood value of 4 142 733 according to BIC (see full models tested in Supp_table_3.

We did not attempt a partitioned-scheme analysis since the resulting tree was overall well-supported, and most importantly, depicting coherent relations between species-groups (see extended details in the discussion).

Tree dating

Bias in estimation of divergence times under both Maximum Likelihood (ML) and Bayesian frameworks is associated with incorrect calculation of branch lengths (Swofford et al. 2001, Schwartz and Mueller 2010), which, among other factors, is thought to be influenced by ambiguous sites (Lemmon et al. 2009), and excess of insertions-deletions (Löytynoja and Goldman 2008). In our data set, one outgroup and six ingroup taxa show gaps and ambiguities in about 50% or more of their total length (Supp_table_5); these lineages are differentiated from the others in the tree by their comparatively long branches (Fig. 2). We thus pruned from our matrix these terminals, and also all remaining outgroups but *Pachycondyla procidua* because this is the closest genera to *Neoponera* from which we have UCE sequences; this is also a requirement of RelTime (Tamura et al. 2012), an ML method we used for divergence inference implemented in MEGA11 (Tamura et al. 2021), because the program allows selection of only one lineage as outgroup, which preferably should be sister or closely related to the most recent common ancestor (MRCA) of the ingroup. This reduced data set is composed of 68 terminals.

Node calibration

We used a recently discovered Dominican amber fossil which is confidently assignable to *Neoponera* (Fiorentino et al. 2023). Due to its well-preserved external body features it can also be assigned to the *foetida* group; within this clade, this specimen is most similar to two extant species, *N. insignis* and *N. dismarginata*, with which it shares, among some features, the shape of the head, and the petiolar node, respectively. It has a metallic, greenish cuticle which is quite rare in the *foetida* group. Only one extant, recently described lineage from Panama shows some resemblance, *N. prasiosomis*. Based on this information we added node constraints on two nodes in the *foetida* group: the first located on the node including *N. prasiosomis* + (*N. bugabensis* + *N. insignis*), with a minimum bound of 16 my; while the other node was constrained on the MRCA of all the *foetida* group lineages, except *N. fisheri* (Fig. 3), using a maximum bound of 18 my.

Ages of Dominican amber are based on Seyfullah et al. (2018). *Neoponera fisheri* was not constrained under these boundaries because this species emerged in our phylogeny as sister to all others in said species-group; the morphology of *N. fisheri* is also distinctive from that of any other congener. We performed the ML analysis based on the Tamura-Nei model of evolution with five categories, and Gamma distribution of evolutionary rates; all sites of the concatenated alignment were used. Computer calculations were performed on an Intel processor with 12 cores using 6 GB in ram; four threads were used by default in MEGA11.

In order to compare the performance of such analysis, we made additional fast-processing, and less computing-intensive runs based on RelTime's Ordinary Least Squares (OLS) (To et al. 2016) which is generally recommended for large genomic-based alignments; we constrained the same nodes as in those of the ML analysis, as well as others shown in Supp_table_4; these analyses were based on both single-node constraints (with a minimum bound of 16 my), and two-node constraints (with minimum/maximum bounds).

RESULTS & DISCUSSION

UCE capture summary information

Our final Gblocks-trimmed 75% complete UCE matrix (see below) is composed of 77 terminals, representing 60 species, three of these in the outgroup, and 56 in the ingroup; of these latter, 48 are valid taxa, six are new additions to *Neoponera* (publication pending), and two are undescribed. Altogether, 2,517 loci with a length of 1,003,352 bp were captured; of these, 157,970 are informative sites. The reduced 68-terminal matrix is composed of 2,513 loci, with a length of 1,151,145 bp, of which 152,675 are informative sites. Missing data post edge-trimming (after removing flanking regions) in the 75% matrix summed ca. 10% nucleotides. An average of 2,143.5 loci were captured per taxon, with a range of 1036 – 2415 (see complete information in Supp_table_2). Interestingly, both matrices, 75% and 95%, returned exactly the same amount of extracted loci, additional statistics are supplied in the supplementary material (Supp_table_2).

After some trimming runs with Gblocks, building data matrices with varying proportions of queried loci/taxa, namely 50%, 75%, and 95%, we noted that while increasing the percentage queried, the number of gaps and ambiguous sites slightly decreased in each taxon. Both 75% and

95% matrices, however, resulted in identical gaps and ambiguous sites per taxon, with their tree topologies yielding mostly fully supported nodes (UFB = 100), and showing identical internal clade (= species groups) arrangements (Appendix B). Yet, the tree based on the 95% matrix besides differing slightly in the nodes support as compared to that produced with the 75% matrix, depicts *N. rostrata* as sister to the *apicalis* group, whereas the tree originated from the 75% matrix depicts *N. rostrata* as siter to the clade formed by the groups *crenata* + *foetida* (Fig. 2). Since this latter result makes more sense in light to our current knowledge of the morphology and natural history of the genus as a whole, we chose this topology for illustrating evolutionary relationships between *Neoponera* lineages.

Phylogenetic relations

The ingroup in our phylogeny is structured in seven fully supported (UFB = 100), monophyletic groups, plus *N. rostrata* representing the nominotypical group which is composed of two taxa (the other is *N. agilis* for which no specimens were available). *Neoponera*, as here considered, is recovered as a clade with respect to a new genus here erected (see further below), and is internal classification is largely in agreement to morphological observations of MacKay and Mackay (2010), and is coherent to ours as well, save for the taxa of the *emiliae* group whose overall body shape, with big heads and small eyes placed anteriorly on head (e.g., *N, magnifica*) moderately departs from the "typical" ground plan found in the genus (e.g., *N. crenata* Roger). This is reflected in our phylogeny because species in this clade have a longer evolutionary history than most in the genus (Fig. 3).

Most within-clade lineage relationships are also fully supported, and among those that are not (values in red in Fig. 2), the effect of long branches of lineages like *N. dejeani* or *N. rostrata* are possibly playing a role; in *N. dejeani*, for example, approximately 70% of its sequence contains ambiguities and gaps which are likely the cause for such abnormally long branches (Lemmon et al. 2009). Despite issues like these, which are minority, almost all within-clade relations can be reasonably explained through morphology, but in certain cases, for example, between the sympatric *N. mashpi* and *N. laevigata* (belonging to the *laevigata* group), this task becomes challenging as they are quite similar. These two species come out as paraphyletic in our phylogeny (Fig. 2), but not in the dated tree (Fig. 3) where *N. laevigata* appears to be the youngest lineage of this species-group, with *N. mashpi* coming out less divergent and close to *N. gojira*. Either this

result is biased due to, for example, errors during the bioinformatic processing and phylogenetic inference; these two forms represent a single but highly polymorphic species; or these are recently divergent species, perhaps a case of incomplete lineage sorting, which is particularly likely during rapid speciation events (Pollard et al. 2006, Feng et al. 2022). The former seems not likely, otherwise at least several more cases would have been detected; whereas the other two hypotheses seem reasonably coherent, and are perhaps part of the same problem, because *N. mashpi* is morphologically more variable in size and shape than *N. laevigata*, in particular in the striae of the petiolar node which progressively disappear in populations from Atlantic regions in Central America (Troya and Lattke 2022). *Neoponera mashpi* also has a broader range than that of *N. laevigata* which occurs only in northern South America, mostly in Amazonia. We believe both are indeed good species, with a potentially paraphyletic and older *N. mashpi* from which *N. laevigata* diverged in Amazonia as their possible center of origin. If this scenario holds with future empirical evidence, then it would support Brown's theory of centrifugal speciation (Brown 1957) which basically states that novelties come from the center of origin, leaving older (partent) populations at the periphery.

Neoponera bucki and a male that is a putative conspecific come out in our analyses at the base of the phylogeny. Troya and Lattke (2022) noted the morphological mismatch of this lineage with respect to other *Neoponera*, as well as to all other known lineages of the subfamily. Current molecular evidence confirms our supposition that this is a separate lineage, not close to *Neoponera*, but possibly placed in an isolated branch as sister to many genera in the Odontomachus genus-group (Branstetter, pers. obs.). In this work we leave it as *incertae sedis* in *Neoponera* but do not include it in the morphological diagnosis of the genus nor consider it further, pending future work characterizing it as a separate genus.

The ingroup taxa emerging at the base of the tree (marked by green dashed line, Fig. 2), formerly classified in the *emiliae* group by MacKay and Mackay (2010), are not related with currently recognized species belonging to said group (green shaded in Fig. 2), with respect to which show genetic distances higher than 4% (Supp_table_4), and their morphology is also different, with the former being much smaller than the latter (see details in the taxonomic account). These taxa, and their conspecifics form a clade which was recently identified by Troya and Lattke (2022) as different to all known *Neoponera*, but also not fitting the diagnostic features of currently valid ponerine genera. Based on present molecular and morphological evidence we propose

new_genus_B **gen. nov.** (see details in taxonomic account). This genus lineage is recovered with high support (UFB = 100) in our phylogeny as sister to the *Neoponera*, with a mean divergence time of its MRCA occurring about 70 mya (range = 107 – 46 mya); the ancestors of both new_genus_B and *Neoponera* are separated by some 16 my (Fig. 3). Extant lineages of new_genus_B would have appeared much later during perhaps the early Neogene (Fig. 3). See synoptic species list in the taxonomic account.

Internal classification and origin of clades

The genus can be classified in two major groups (Figs. 1, 2): the first is formed by the *aenescens* and the *laevigata* groups (in blue and gray shades, respectively), and the second is composed by the *emiliae* (green), *apicalis* (red), *rostrata*, *crenata* (cyan), and *foetida* (beige) groups. The ancestor of these two major groups appeared during the early – middle Paleogene, about 54 mya (range: 75 – 39 mya), which represents the origin of the genus. Schmidt and Shattuck (2014) refer to this division as "basal split", and use the term *sensu stricto* (s.s.) as a tag for the second major group, which is represented mostly by arboreal lineages, since prior to their study most species in this clade were considered "true" *Neoponera* based on the classification of Emery (1911).

The first major group is characterized by predominantly ground nesters, epigeic foragers, possibly generalist predators like the taxa composing the *aenescens* group which share at least two apomorphies that are also diagnostic for this group: a homoplastic carina-less malar region that also characterizes most species of the *laevigata* group (except *N. commutata*) , and a vertically-oriented carina at the base of the metapleural gland orifice, this latter is possibly a unique trait among the *Neoponera*. All species of the quite diverged *laevigata* group (Fig. 3), on the other hand, are specialist termite predators, and the worker caste shows a jet-black, highly polished cuticle (Wheeler 1936, Mill 1982, Leal and Oliveira 1995, Troya and Lattke 2022), both considered non-homoplastic apomorphies in the genus. *Neoponera commutata* (which is missing in our data set) belongs to this clade, and despite sharing a number of behavioral and morphological traits with its clade partners it also shows some differing features as compared to them, like a homoplastic malar carina, present in most *Neoponera* lineages, and a very large body size, approximately twofold (or more) larger than that of its group partners.

The placement of *N. commutata* in the *laevigata* clade is still uncertain due to the lack molecular data. However, we believe it could come out as the base of its clade because it is monomorphic, while the other clade members are polymorphic, in particular *N. mashpi* and *N. laevigata* which show the highest level of polymorphism, with the smallest workers being approximately two times smaller than the largest workers (Wheeler 1936, Troya and Lattke 2022). *Neoponera marginata*, which appears in our phylogeny at the base of the clade, shows a less marked polymorphism than *N. mashpi* and *N. laevigata*. Therefore, it seems that polymorphism in this *Neoponera* clade evolved from a non-polymorphic state. Some studies found that emergence of polymorphism in ant workers is associated with larger colonies, because it promotes the division of labor which otherwise may be too costly for smaller colonies (Oster and Wilson 1978, Tschinkel 1988, Wheeler 1991). Blanchard and Moreau (2017), on the other hand, found a negative association of polymorphism with predacious habits; according to them is more likely to polymorphism to be gained in stingless ants. More recently, Lecocq de Pletincx et al. (2021) concluded that polymorphism in *Cataglyphis* (a stingless group) is positively correlated with mature, larger colonies. When compared to most species in the genus, species of the *laevigata* group have relatively large colonies easily reaching 1000 or more individuals, for example, *N. marginata* (Leal and Oliveira 1995) or *N. laevigata* (Longino 2010), while colonies of *N. commutata* are apparently smaller, according to Mill (1984) between 400 – 1000 individuals. This aspect would support, at least in part, the hypothesis of colony size-age, but contrasts with the findings of B&M (2017). Whether size-polymorphism in species of this clade is related to intrinsic factors of a species (Wills et al. 2018, Lecocq de Pletincx et al. 2021), like colony size-age, or it is a product of the evolutionary pathway of species in this group in response to their predation habits, or maybe is an interplay of both biological and evolutionary aspects, it warrants future research.

The *laevigata* and the *aenescens* groups split in the mid Paleogene, about 42 mya (range: 63 – 29 mya), and despite both displaying ground foraging behavior, their strategies are quite diverging; we know scant aspects about foraging habits of the *aenescens* lineages (MacKay and Mackay 2010), nonetheless, they can be considered generalist predators, a habit that is found in virtually all the *Neoponera*, since they are equipped with the features typically present in predaceous ants.

At the base of the second major group emerge the lineages of the *emiliae* group (in green shade, Fig. 2), all of which are also epigeic foragers, litter (and potentially underground) nesters. They share two apomorphies: an anteroventral well-marked, cross ribbed pronotal groove, and a raised posterolateral, propodeal carina. The first is unique in the genus, and the second is present in other *Neoponera*, e.g., *N.* curvinodis, although here are less raised. The ancestor of the *emilae* group represents the earliest branching node in the genus (Fig. 3), and as hypothesized by Schmidt and Shattuck (2014) it possibly evolved from a ground forager, scavenger which is the supposed ancestral behavior of the *Neoponera*; this behavior is retained in all the lineages of the *aenescens* and *laevigata* groups. This clade is formed by seven species, five of which were here included, and is formed by two sister groups; the first is composed by *N. emiliae* and *N. metanotalis*, and a second more divergent and diverse clade is composed of five lineages, of which only *N. magnifica* (not included here) was previously known. No unique apomorphies were identified in the potentially monophyletic *N. emiliae* + *N. metanotalis*, though probably the easiest recognizable diagnostic trait is a feebly-impressed malar carina. The second group, also called the "*N. magnifica* subclade" by Troya (unpublished revision of the *N. emiliae* group) is composed of five, morphologically similar lineages, four of which are recent additions to *Neoponera*: *N. caxiuana*, *N. dorsilinea*, *N. dropsy*, and *N. glabra*. This a singular group in the genus because it significantly differs from all other known taxa; this is better exemplified in three unique apomorphies: costae (raised longitudinal ridges) on the head and pronotal dorsum, the proximal corner of the masticatory mandibular margin is round and unarmed, and a medially coriaceous epipygium. *Neoponera emiliae* + *N. metanotalis*, and the *magnifica* subclade share a common origin about 40 mya (range: 59 – 27 mya), and they show ca. 2.5% of genetic divergence (Supp_table_4), which is reflected in about 10 my (mean age between the *N. dropsy* + *N. glabra* and the ancestor of the magnifica subclade) of evolutionary distance between them. It is also worth noting that *N. emiliae* is the oldest *Neoponera* lineage.

The ancestor of the *apicalis* group (in red shade, Fig. 2) is the second oldest branching node of the genus, it may have appeared between 68 – 34 mya (mean = 48.3 mya, node #132 in Supp_Figure_1_online_only), however, extant lineages derived from that hypothetical ancestor are comparatively young, and all retain the ancestral epigeic foraging, aspect that was noted before by Schmidt and Shattuck (2014); among their morphological apomorphies, perhaps the large eyes of workers and queens (the biggest proportionally to head length in the genus), located slightly

posterad to head midline, is the most notorious, and could also be regarded amongst the newest adaptations for ground living emerging in the genus around the early Neogene (Fig. 3). All five included lineages (one of these still undescribed, *N.* bra549385) are closely related, in particular *N. apicalis* and *N. verenae* which show less than 1% of genetic divergence (Supp_table_4), and its split took place about 5 mya (Fig. 3); during this period the populations of these two species expanded their range across the Neotropics like few other *Neoponera*, only compared to that of *N. curvinodis* and *N. villosa* (*foetida* group), with the latter depicting the largest range in the genus (central Texas to northern Argentina), and also showing a remarkable homogeneous morphology (Fernandes et al. 2014, Mendoza-Ramírez et al. 2019, Troya, unpublished). This is not the case with *N. apicalis*, and *N. verenae*, whose populational variants, especially from Mexico, strongly suggest these forms represent two species complexes (Delabie et al. 2008).

The placement of *N. rostrata* in our phylogeny is still uncertain since the bootstrap resampling is comparatively low (= 77). The relative high amount of ambiguous sites and gaps in its sequence (ca. 50%, Supp_table_5) is probably contributing to underestimate its true branch length, and therefore its true placement on the actual topology. As pointed out before, different placements for this lineage were obtained in the analyses of both 75% and 95% matrices, however, the result illustrated in Fig. 2 seems more congruent to us since *N. rostrata* is more attributable as being arboreal than a ground forager, despite specimens being found sometimes on or near the ground surface. Yet, their large aroliae, which are proportionally larger than most arboreal *Neoponera*, probably best reflects an adaptation to the floating arboreal environment because adhesion to the usually smooth leaf surfaces is required (Federle et al. 2002), but see Freeland et al. (1982) since this may be the norm but not a requirement. Although the node between *N. rostrata* + (crenata group + foetida group) is low-supported, it seems more likely that arboreal life progressively evolved from the ground to the trees, than the opposite (but see further below).

The *crenata* (cyan shaded, Fig. 2) and the *foetida* (orange shaded, Fig. 2) groups come out as sister from the shallower node in our phylogeny, and here few within-clade nodes are poorly supported, for example the node linking *N. dejeani* Troya + *N. carinulata* Roger to a diverse group of more divergent species. Since *N. dejeani* shows a long branch (ca. 70% ambiguities, Supp_table_5) its placement as sister to *N. carinulata* is possibly biased, and therefore the branching at this node is also not accurately estimated. However, both *N. dejeani* and *N. carinulata* share more traits (in particular the shape of the petiolar node) between each other, than with

remaining taxa in this group. Additional bioinformatic treatment of the sequence of *N. dejani* is needed to get rid of ambiguities, or whenever available, generating new sequences. Since *N. unidentata* and a new species (*N. yasuni* Troya) were not included in the analyses, further reorganization is expected in this group, but we anticipate it will be only at the shallow nodes of this clade since these two lineages are morphologically similar to the subgroup conformed by *N. striatinodis* Emery, *N. antecurvata* Mackay & Mackay, and *N. rugosula* Emery.

Despite the few low-supported nodes, overall evolutionary relations in the *crenata* group depict our expectations, with most lineages coherently grouped, and also reflecting geographic distribution, as for example, *N. donosoi* Mackay & Mackay + *N. recava* Mackay & Mackay whose range is restricted to southwestern Colombia and northwestern Ecuador; also *N. fiebrigi* Forel + (*N. cylindrinodis* + *N. crenata*) whose range spans *grosso modo* across the mid-southern Atlantic Forest and southern Cerrado, except for *N. crenata* for which scant records exist from northern and northwestern Amazonia (Troya & Lattke, unpublished). One interesting finding is the placement of *N. moesta* Mayr at the base of the clade; this species is remarkably similar to the closely related and sympatrically occurring *N. crenata* and *N. fiebrigi* (Troya & Lattke, unpublished), which are more derived in the phylogeny. *Neoponera moesta* reaches the mid-eastern Atlantic Forest, however, we have no strong evidence supporting contact between its populations with those of *N. crenata* or *N. fiebrigi*, which would explain, in part, through for example, hybridization, their morphological resemblance. Further field explorations in central-eastern Brazil are required in order to gain additional insights into this issue. Since *N. moesta* is older than *N. crenata* and *N. fiebrigi*, and given that scarce records of such species have been found thus far in southern Brazil (Troya & Lattke, unpublished), it would be coherent hypothesizing that the latter species diverged from *N. moesta* which in the past was perhaps more abundant in Atlantic Forest habitats.

Relationships between lineages of the *foetida* group come out in our phylogeny, in general, as expected; and also, as in the *crenata* clade, these are reflective of current geographic distribution, for example, a group of lineages is found mostly in Central America (Fig. 3), expect for *N. insignis* Mackay & Mackay which occurs in northwestern South America. The remaining lineages form a group broadly distributed in the Neotropics, among these *N. villosa* holds the record: from central Texas to northern Argentina (Fernandes et al. 2014). This latter group includes some of the most hard-to-separate species in the genus; for some of these no consensus is yet

reached in regards to taxonomic identity (Troya, pers. obs.), this is why they were treated as variants in the revision of the *foetida* and *emiliae* groups (Troya, unpublished); while others, like the triad *N. curvinodis*, *N. zuparkoi* (Mackay and Mackay), and *N. inversa* (Smith) are extremely similar; *N. curvinodis* and *N. inversa* are also morphologically quite variable, with no effective diagnosis currently available. Fernandes et al. (2014), described two species: *N. bactronica* and *N. billemma*, but these are indeed variants of *N. curvinodis* (Troya, unpublished). We sequenced two *N. bactronica* specimens, one of which (INPAHYM033801-2) showed a long branch (ca. 70% ambiguities, Supp_table_5), and is recovered as siter to a *N. curvinodis* specimen (IPAHYM033800) also with a relatively long branch (Fig. 2). Despite this, we believe they belong to a single species, i.e., *N. curvinodis*, because we could not separate them morphologically (although they show expected variations proper of this species), and they are part of a larger, carefully examined sample set representing a number of sites in the Neotropics.

In our phylogeny *N. inversa* and *N. curvinodis* come out as closely related, with *N. zuparkoi* + *N. zuparkoi*-var as sister to *N. inversa*, with low support though (UFB = 69). *Neoponera zuparkoi* can be reasonably diagnosed by at least two traits, based on the only three specimens known (lamella-shaped anterior mesopleural margin, and humeral carina not salient), however, these are apparently subject to plasticity, as is the case for various "diagnostic" traits in *N. curvinodis* and *N. inversa* (Troya, unpublished). The specific status of *N. zuparkoi* is doubtful, even more considering the short genetic distance between it and *N. inversa* (ca. 0.3 – 0.5%, Supp_table_4). Since scant specimens of this form are currently available (from Peru and Ecuador), no final taxonomic decision is possible. In any case, it seems reasonable *N. zuparkoi* be synonymized under *N. inversa* based on its genetic and morphological proximity.

The *foetida* and *crenata* clades diverged in the mid-Paleogene, about 40 mya (range: 61 – 26 mya), but their oldest extant lineages, e.g., *N. fisheri* (*foetida* group) diverged about 19 mya (range: 19 – 17 mya). The foetida group contains the fastest diverging lineages in the genus (in black and green in Fig. 3), and two of these are also broadly ranged, e.g., *N. villosa*. These two groups contain similar forms, in certain cases very similar at first sight, for example, between *N. insignis* or *N. prasiosomis* (*foetida* group) and *N. unidentata* (*crenata* group). As such, these groups share multiple traits, for example, the malar carina (except for *N. fisheri* and *N. dismarginata* which have a vestigial malar carina), the medially placed eyes on head, the arboreal nesting behavior, among others. However, no unique apomorphies are recognized for each clade,

but several symplesiomorphies are. In the foetida group: a shallowly grooved notopropodeal suture, malar carina, abundant erect hairs (most species). In the crenata group: vestigial to highly reduced notopropodeal suture (except *N. donosoi*), malar carina, lobes of metasternal process distally acute (fang-shaped) and closely approximated, with distance between each lobe shorter than apical width of each lobe. This latter may potentially be apomorphic for this group, if not for certain variations found in species of the Neotropical-distributed clade.

From the ground to the trees: a hypothesis of shifting behavior in Neoponera

Evolutionary transitions involving a change in site nesting preference (underground, soil surface, or arboreal strata), either unidirectional (with no return) or bidirectional (gains and losses) are not rare in ant evolution, although transitions to and from soil are very infrequent (Lucky et al. 2013). The *rostrata* group, conformed by *N. rostrata* and its siter lineage *N. agilis* are probably arboreal foragers; they have relatively large aroliae, and in most examined specimens these are at least 2/3 length of correspondent pretarsal claws, as compared to typical epigeic foragers in this genus and other ponerine genera where these structures are either tiny or vestigial, as in members of the *emiliae* group; also, specimens in this group appear to be more frequently collected through canopy-aimed techniques, like fogging or arboreal Malaise, than directly by hand or ground pitfall traps (A. Troya, pers. obs.). Similarly, almost all members of the *crenata* and *foetida* groups are well-adapted to arboreal life, like *N. insignis* (Mackay and Mackay) which occurs exclusively on *Cecropia* (Urticaceae) plants (Longino 2010), or like the South American *N. luteola* which also prefers nesting in a number of *Cecropia* species, and apparently is beginning to replace *Azteca* spp. in the association with *C. membranacea* Trécul (Gutiérrez-Valencia et al. 2017). Since all members of the *emiliae* and *apicalis* groups are epigeic, it seems plausible therefore, arboreal life in *Neoponera* occurred through a single evolutionary jump, with the ancestor of the *rostrata* clade potentially dwelling on arboreal strata but possibly also on the ground surface. Under this hypothesis, *N. rostrata* and *N. agilis*, the sole members of this group, would represent the link between underground and litter-living to arboreality, thus emerging as a prominent life strategy in other diverging lineages like those of the *crenata* group and most of the *foetida* group. An exception with respect to this latter is perhaps *N. villosa*, and potentially also *N. curvinodis*, which have been collected (rarely though) in soil nests near tree roots in a lowland Amazonian forest in Ecuador (Troya, pers. obs.).

The change in habitat preference for colony foundation, from the underground or soil surface to complete arboreality, maybe emerged among the drivers explaining the high species diversity within the *crenata* and *foetida* groups as compared to remaining groups in this genus. The pace of rate of evolution as a proxy for lineage diversification (Eo and DeWoody 2010) helps explain why some groups are more diverse than others, especially in the Neotropics where this hypothesis has been tested for various organisms (Colinvaux et al. 2000, Hughes and Eastwood 2006, Price et al. 2014). In the *foetida* clade, the lineages with broad distribution (black in Fig. 3), as well as those restricted to South America (green in Fig. 3), are perhaps the clearest examples of relatively fast diversification in *Neoponera*, in particular *N. villosa*, *N. curvinodis* and *N. zuparkoi* which, apparently, evolved in a time span of ca. 1 my, showing moderately high rates of evolution, between 0.6 – 0.8 sites/my (Supp_table_4), with *N. inversa*, probably the youngest lineage of the genus, showing the highest rate (2 sites/my, specimen from Costa Rica, Supp_table_4).

Since these two clades encompass approximately half of the species richness found in the genus, probably more if we consider the recent discoveries, among the hypotheses potentially explaining this relatively rapid radiation of forms, the availability of resources of the tropical canopy strata could find support. The heterogeneous tropical canopy provide habitat for arguably most organisms than any other (Erwin 2001); ants are not only diverse in these habitats (Schonberg et al. 2004) but the most abundant insect group, especially the trophobionts which acquire nitrogen through sap-feeding insects (Davidson et al. 2010). Once reaching the trees, arboreal *Neoponera* may also adapted to this resource-rich environment, ultimately leading to the lineage diversity we see today. During this habitat shifting, a reversal to their original state was apparently unlikely because transitions back to litter or to the underground would require additional physiological and/or behavioral changes (Lucky et al. 2013).



Fig. 2. Maximum likelihood consensus tree of *Neoponera* and outgroups (gray branches) based on UCE 75% complete matrix, with 77 terminals, representing 59 species. All nodes are 100% supported by ultrafast bootstrap (UFB), except those with red numbers. Figure obtained in IQ-TREE with model TVM+F+R9, using 1000 UFB iterations, with 0.99 correlation coefficient. Shaded regions represent *Neoponera* species-groups. Dashed green square represents a new genus here proposed (see text). Terminals with *: new *Neoponera* species (pending submission); and in bold: undescribed lineages.

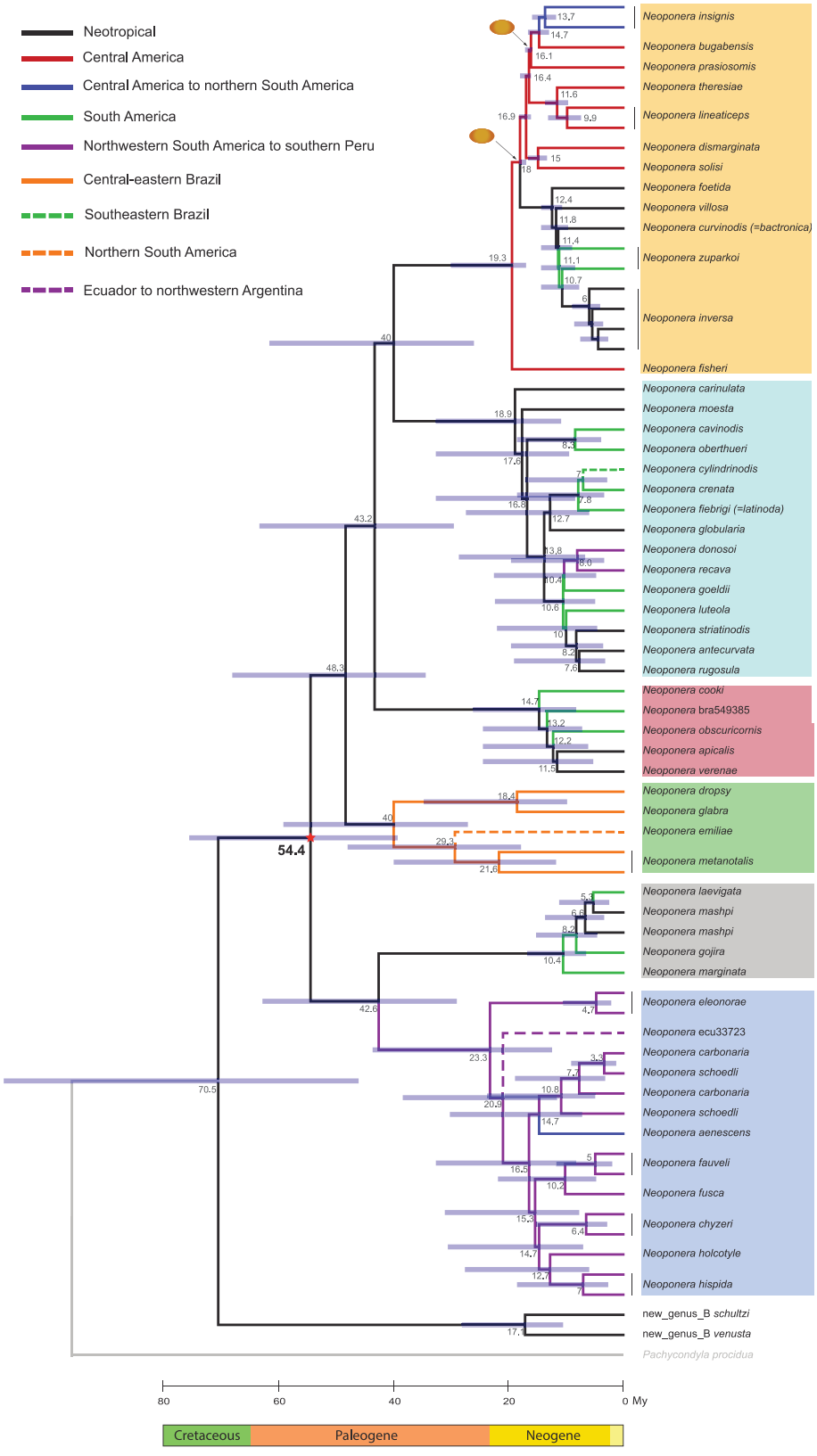


Fig. 3. RelTime´s maximum likelihood timetree based on UCE 75% complete matrix, using local clocks, and Tamura-Nei model with five discrete Gamma categories; all sites considered. Blue bars: error representing age (in million years – my) 95% confidence intervals; shaded names: *Neoponera* species-groups; colored branches: geographic distribution; yellow ovals point to fossil-constrained nodes; node numbers are ages in my. The node with a red star indicates origin of *Neoponera* (mean age). The tree is rooted with *Pachycondyla procidua*.

CONCLUSION

Based on both morphology examination and molecular phylogenetics we have shown that *Neoponera*, as here defined, is a monophyletic- though morphologically highly variable lineage. Current distribution of species-groups in our phylogeny, as well as most included lineages, representing ca. 85% of the valid taxa, is in agreement with past and current knowledge of their natural history and distribution. Most of the internal clade-based arrangements proposed in the pioneering work of W. MacKay and E. Mackay (2010), largely fit with the new taxonomic boundaries presented in this study; and, together with the input of Wild's (2005) and Fernandes et al's (2014) contributions, form the basis on which we have continued generating knowledge.

The inferred age for the origin of *Neoponera* significantly departs from the results of Schmidt (2013). However, using as calibration tool a confidently identified, well-preserved amber fossil belonging to a well-known lagerstätte, allowed us to more accurately constrain nodes in the tree topology, as compared to, for example, using fossil impressions whose identity is usually conjectural. While no divergence times analysis is error-free, and accounting for the broad range of the confidence interval (about 36 my) at *Neoponera*'s MRCA known node, we consider plausible a mid-Paleogene origin for this genus. Something to additionally consider are the relatively long branches of the members of the emiliae clade, the oldest lineages of the genus, today distributed in eastern Brazil, which we believe could represent vestiges of a greater past diversity, and that also contributed pushing back the age estimates.

By detecting new_genus_B as the new *Neoponera* sister; providing support that extant lineages in the *emilae* group are the closest known forms to ancestral *Neoponera*; confirming that *N. bucki* (*incertae sedis*) does not belong to this genus, but is distantly related to it, we endorse the use of ultraconserved elements (UCE) in combination with morphology-based arguments, as promising tools for disentangling complicated issues and unveiling new research frontiers in insect systematics.

TAXONOMIC ACCOUNT

Updated diagnosis of Neoponera

The following is added to the diagnosis proposed by Schmidt and Shattuck (2014). We do not consider diagnostic the flap at the metapleural gland orifice, also called "U-shaped lip" by them, since it varies moderately even within species-groups (see Troya and Lattke 2022). The following characters apply to the worker and queen castes, except otherwise noted.

1. Head subquadrate in most species, e.g., *N. crenata*, otherwise either slightly narrowed posterior to eyes, e.g., *N. apicalis*, *N. aenescens*, or anterior to eyes, e.g., *N. rostrata*.
2. Eye suboval in most species; in some species of the aenescens group it is virtually round, e.g.,
3. Eye maximum length as compared to head length: relatively small, ca. 1/5, e.g., *N. carbonaria*, *N. fauveli*; medium-sized, ca. 1/4, e.g., *N. carinulata*, *N. commutata*; or large, ca. 1/3, e.g., *N. apicalis, N. verenae*.
4. Frontal carina not exceeding posterior eye margin, except for members of the *emiliae* group where carina slightly exceeds it.
5. Malar (pre-ocular) carina present in many species; completely absent in members of the *aenescens* and *laevigata* groups, except for *N. commutata*.
6. Notopropodeal suture present, shallowly grooved in most species; completely absent or vestigial in most species of the *crenata* group.
7. Propodeal spiracle slit-shaped in most species; oval in some species of the *emiliae* group.
8. Stridulitrum present on presclerite of AIV.
9. Aroliae well-developed, comparatively large in most species, longer than half pretarsal claw length; smaller in most members of the *aenescens* group.
10. Hypopygium without spine-like hairs at either side of the sting (many species), or showing them, e.g., most species in the *crenata* group.
11. Male: in lateral view, clypeus convex, sometimes globular (strongly convex, e.g., *N. marginata*) in most species, except for the only known male of the *emiliae* group where it is relatively flat; ocelli well-developed, each about as large as antennal acetabulum, except for

the *laevigata* group where these are smaller; triangular impression well-marked anteriorly on pronotum; jugal lobe present.

New_genus_B

Type species: *Neoponea venusta* Forel, 1912 [image link] **new combination**

Etymology. [pending]

Diagnosis

Worker. Eye globose, breaking lateral head margin, elliptical, placed slightly anterior to head midlength (this study: Fig.4e; MacKay and Mackay, 2010: Fig. 388, 634, 672; Troya and Lattke, 2022: Fig. 4d; eye facets comparatively prominent, slightly raised (Fig. 4a, c); antennal scape long, when pulled posterad, exceeding posterior head margin by three to four times apical scape width (present study: Fig. 4e; MacKay and Mackay, 2010: Figs. 388, 634, 672); malar carina present, running over anterointernal eye region, in lateral view (Fig. 4a, c; Troya and Lattke, 2022: Fig. 4d); notopropodeal suture well-marked, shallowly grooved, usually cross ribbed (Fig. 4d); propodeal spiracle circular (this study: Fig. 4d; MacKay and Mackay, 2010; Troya and Lattke, 2022: Fig. 4a), opening usually directed dorsolaterad; mesosternal process reduced to vestigial (Fig. 4b); metasternal process well-developed, lobes distally blunt, distance between them broader than width of each (Fig. 4b); in lateral view, petiolar node subtriangular to rectangular shaped (this study: Fig. 4d; MacKay and Mackay, 2010: Fig. 89, 387, 633); arolium small but well-developed (Fig. 4g); in ventral view, anterior margin of abdominal sternite III horizontally broadened (Fig. 3f); hypopygium armed with stout spine-like hairs (Fig. 3d); body black, dorsum of mandibles dark castaneous to dark yellowish, legs yellowish to castaneous, body dorsum with abundant erect hairs (Fig. 3d).

Queen. Wingless ergatoid; first, and second gastral segments feebly broader than in worker, in dorsal view. Remaining external structures as worker.

Male. Eye large, slightly longer than half head length (Fig. 5c); ocelli tiny, feebly protruding from cuticle, distance from anterior ocellus to posterior ocellus about five times anterior ocellus diameter; notauli present, feebly cross ribbed, not meeting posteriorly (Fig. 5b); mesopleural sulcus well-marked, cross ribbed, not extending to ventral pleural surface (Fig. 5a);

propodeal spiracle circular (Fig. 5a); posterior propodeal margin carina-less (Fig. 5a, b); metanotal dorsum with well-marked, raised longitudinal carina (Fig. 5b); anterodorsal propodeal groove absent; forewing: discoidal cell subquadrate, vein M about as long as vein 1m-cu (Fig. 5d); hindwing: vein 2M vestigial, jugal lobe absent (Fig. 5d); penisvalval ventral (serrate) margin relatively straight medially and posteriorly, distally feebly inclined (Fi. 5f).

Comments

New_genus_B is a small ponerine clade, composed by five species of relatively small, black ants (☿, ♀: TLa = 4.15 – 5.8 mm, WL = 1.4 – 2.15 mm;♂: WL = 1.7 mm, TLa = 4 – 4.4 mm), all restricted to eastern Brazil. This genus is sister to the more diverse *Neoponera*, from which it differs mainly in the following (*Neoponera* traits in parentheses): 1) The malar carina runs over the anterointernal eye margin (when present, always in front of the anterior eye margin); 2) Eye elliptical with raised facets (suboval, facets not raised, and more numerous); 3) Propodeal spiracle circular (slit-shaped in most species, or oval in few species); 4) Distance between anterior eye margin to mandibular insertion about half maximum eye length, or less, but never longer (in virtually all species that distance is longer, the only exception is *N. moesta*); 5) Discoidal cell in male´s forewing subquadrate (usually elongate, rectangular, or in rare cases, e.g., *N. apicalis*, subquadrate); 6) The male´s hindwing lacks jugal lobe (always present).

Arguably, 1 and 2 are autapomorphic among the Ponerinae; although the malar carina is also present in members of *Odontoponera* and *Bothroponera*, it does not go over the anterointernal eye margin. The reader can reach also the taxonomic key in Troya and Lattke (2022) to separate this genus from *Neoponera*.

New_genus_B *concava* and New_genus_B *venusta* are the most frequently collected species, and both occur in sympatry in southern Bahia (Fig. 8); the other three species are rarely found, and New_genus_B schultzi-2 is known only from four specimens in the state of Bahia. As far as we aware from collections labels and field annotations, all five species are epigeic, probably predacious, litter nesters, collected through pitfall traps (few times with feces-baited), Winkler, and through active search. Nothing else is known about their biology. Amidst the rampant human-induced modification of the landscape in the Bahia Coastal and Interior forests, as well as in the Cerrado and Caatinga biomes where populations of these species inhabit, we assume these have low chances to expand and diversify in the future, if the irruption tendency continues.

Synoptic species list

In parentheses known castes, and in brackets known distribution. AL: Alagoas, BA: Bahia, ES: Espírito Santo, MG: Minas Gerais, RJ: Rio de Janeiro, SE: Sergipe.

New_genus_B *concava* Mackay & Mackay, 2010 (☿, ♀) **comb. nov.** [Brazil: AL, BA, ES, SE]

New_genus_B *schultzi* Mackay & Mackay, 2010 (☿) **comb. nov.** [Brazil: ES]

New_genus_B *venusta* Forel, 1912 (☿, ♀) **comb. nov.** [Brazil: BA, ES, MG, RJ]

New_genus_B *schultzi*-2 Troya **sp. nov.** (☿) [Brazil: BA]

New_genus_B *schultzi*-3 Troya **sp. nov.** (☿) [Brazil: BA]

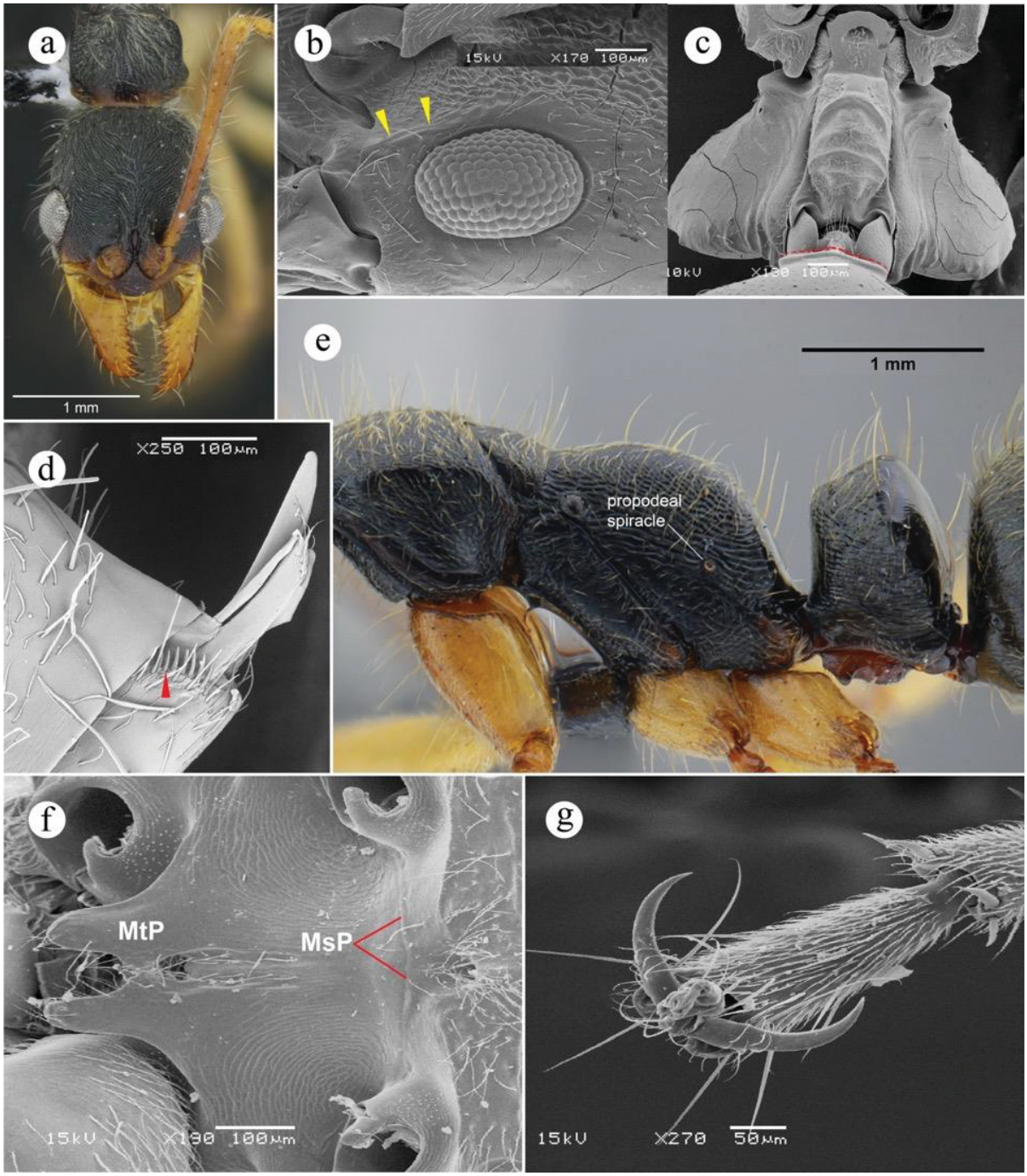


Fig. 4. new_genus_B. gen. nov. **a.** Head in frontal view (new_genus_B schultzi-3, ATPFOR2024); **b.** Eye in lateral view, arrows point to the malar carina (new_genus_B *concava*, ATPFOR2057); **c.** Sternite of AII in ventral view (new_genus_B *venusta*, ATPFOR2016); **d.** Hypopygium in lateral view (new_genus_B *concava*, ATPFOR2016); **e.** Mesosoma and petiole in lateral view (new_genus_B *schultzi*, UFV-LABECOL-000499); **f.** Mesosternum, **MtP**: metasternal process, **MsP**: mesosternal process (new_genus_B *venusta*, ATPFOR2016); **g.** Arolium and pretarsal claw (new_genus_B *venusta* ATPFOR2016). Images (♀): a, b, c, f, g (A. Troya); e (Julio Chaúl).

New_genus_B *concava* (Mackay & Mackay 2010) [image link]

Figs. 4: b, d (☿); 8 (distribution of examined records).

Worker diagnosis. Anterior clypeal margin tooth-like, protruding anterad over mandibles when closed; in lateral view, petiolar node subtriangular, anterior margin vertically straight, posterior margin convex, top of node anterior to nodal vertical midline; posterior nodal face polished and hairless, medially with patch of horizontal striae; in lateral view, subpetiolar process block-shaped; in lateral view, anterodorsal margin of tergite of AIII slightly concave; in dorsal view, anterior margin of tergite of AIII straight to slightly convex. See also Mackay and Mackay (2010).

Worker. Measurements (*n* = 9): HW: 0.85-1.0; HL: 1.0-1.25; EL: 0.25-0.3; SL: 1.0-1.35; WL: 1.4-1.75; PrW: 0.6-0.8; MsW: 0.4-0.6; MsL: 0.25-0.3; PW: 0.5-0.8; PH: 0.55-0.75; PL: 0.3-0.45; GL: 1.15-1.9; A3L: 0.6-1.1; A4L: 0.5-0.65; A3W: 0.9-1.1; A4W: 0.8-1.05; TLa: 4.15-4.9; TLr: 4.0-5.15. **Indices**. CI: 80.0-90.91; OI: 26.32-31.58; SI: 115.0-135.0; MsI: 160.0-220.0; LPI: 50.0-81.82; DPI: 111.11-250.0.

Queen. Measurements (*n* = 5): HW: 1.05-1.1; HL: 1.2-1.3; EL: 0.3-0.85; SL: 1.2-1.3; WL: 1.6-1.75; PrW: 0.85-1.0; MsW: 0.55-0.65; MsL: 0.25-0.35; PW: 0.7-0.95; PH: 0.65-0.85; PL: 0.35-0.5; GL: 1.55-1.95; A3L: 0.95-1.1; A4L: 0.65-0.8; A3W: 1.0-1.25; A4W: 0.9-1.15; TLa: 5.0-5.25; TLr: 4.85-5.3. **Indices**. CI: 80.77-87.5; OI: 27.27-80.95; SI: 113.64-123.81; MsI: 171.43-260.0; LPI: 41.18-69.23; DPI: 140.0-271.43.

Material examined. 181☿. **BRAZIL – Alagoas:** • 1☿; Quebrângulo; -9.3167, -36.4667; alt. 361m; 1999-07-28; do Carmo, J. C. S. leg.; (MZSP). • 1☿; Quebrângulo; -9.3167, -36.4667; alt. 362m; (CPDC). – **Bahia:** • 3☿; 0.5 km S of Sargi, Ponta do Ramo; -14.5116, -39.034; 1997-02-11; Santos, J. R. M. leg.; (CPDC). • 3☿; 1 km N of Côlonia; -15.25, -39.15; alt. 61m; 1997-06-12; Santos, J. R. M. leg.; (CPDC). • 3☿; 1 km S of Betânbia; -15.5, -39.2167; alt. 123m; 1999-10-21; Santos, J. R. M. leg.; (CPDC). • 3☿; 1.5km NE of Lençóis; -12.55, -41.8333; alt. 379m; 2001-03-24; Santos, J. R. M. leg.; (CPDC). • 3☿; 10 km SW of Maraú, Fazenda Água Boa; -14.1503, -39.1137; alt. 129m; 1997-07-01; Santos, J. R. M. leg.; (CPDC). • 2☿; 10 km W of Mascote; -15.5667, -39.4; alt. 95m; 1999-03-19; Santos, J. R. M. leg.; (CPDC). • 3☿; 11 km E of Itajuípe; -

14.7, -39.4833; alt. 377m; 1997-06-18; Carmo, J. C. S. leg.; (CPDC). • 9♀; 12 Km NW Porto Seguro; -16.3833, -39.1667; alt. 90m; 2000-06-16; Santos, J. R. M.; Soares, J. C. leg.; Winkler; (MZSP). • 3♀; 14 km SW of Una; -15.3833, -39.1833; alt. 75m; 1999-10-04; Santos, J. R. M. leg.; (CPDC). • 3♀; 18 km N of Itororò; -14.95, -40.0333; alt. 600m; 2000-08-08; Santos, J. R. M. leg.; (CPDC). • 1♀; 2 km SE of Itacaré; -14.3, -39.0; alt. 70m; 1998-06-25; Santos, J. R. M. leg.; (CPDC). • 3♀; 2 km SE of Itacaré; -14.3, -39.0; alt. 70m; 1998-06-25; Santos, J. R. M. leg.; hand collected; (MEPN). • 3♀; 2 km W of Itapitanga; -14.4167, -39.55; alt. 140m; 1997-05-30; Santos, J. R. M. leg.; (CPDC). • 3♀; 2.5 km E of Aurelino Leal; -14.3167, -39.35; alt. 108m; 1997-04-14; Santos, J. R. M. leg.; (CPDC). • 2km N Serra Grande; -14.45, -39.0333; alt. 102m; 1997-04-28; Carmo, J. C. S. leg.; (CPDC). • 2♀; 2km N Serra Grande; -14.45, -39.0333; alt. 102m; 1997-04-28; Carmo, J. C. S. leg.; (CPDC). • 3♀; 2km N Serra Grande; -14.45, -39.0333; alt. 102m; 1997-04-28; Santos, J. R. M. leg.; (CPDC). • 3♀; 3km of N São José da Vitória, Fazenda Puaias; -15.05, -39.3333; alt. 156m; 2000-05-22; Santos, J. R. M. leg.; (CPDC). • 1♀; 4 Km NNW Colônia; -15.2333, -39.1833; alt. 118m; 2000-03-21; Santos, J. R. M. leg.; (DZUP). • 2♀; 4km NE of Aritaguá; -14.65, -39.0667; alt. 6m; 1998-10-05; Carmo, J. C. S.; Santos, J. R. M. leg.; (CPDC). • 3♀; 4km NE of Pimenteira; -14.5333, -39.4167; alt. 306m; 1997-10-06; Santos, J. R. M. ; Carmo, J. C. S. leg.; (CPDC). • 3♀; 5km of NE of São José da Vitória; -15.05, -39.3; alt. 678m; 2000-09-14; Carmo, J. C. S. leg.; (CPDC). • 3♀; 6.5 km N of Ubaitaba; -14.25, -39.3167; alt. 104m; 1997-04-10; Carmo, J. C. S. leg.; (CPDC). • 3♀; 6km N of Gongogi; -14.2667, -39.4833; alt. 106m; 1997-04-17; Carmo, J. C. S. leg.; (CPDC). • 6♀; 6km NE of Santa Luzia; -15.3833, -39.3; alt. 106m; 1999-10-01; Carmo, J. C. S. leg.; (CPDC). • 4♀; 7 km W of Travessão; -14.1333, -39.2667; alt. 157m; 1997-04-28; Santos, J. R. M. leg.; (CPDC). • 2♀; 8 km E of Ubatã; -14.2167, -39.45; alt. 106m; 1996-12-27; Santos, J. R. M. leg.; (CPDC). • 3♀; Arataca; -15.2656, -39.4192; alt. 160m; 1999-05-25; Santos, J. R. M. leg.; (CPDC). • 1♀; Aritaguá; -14.65, -39.0667; alt. 6m; (CPDC). • 3♀; Barreiras; -12.1477, -44.9947; alt. 460m; 1999-10-25; Carmo, J. C. S. leg.; (CPDC). • 3♀; Buerarema; -14.9843, -39.2583; alt. 132m; 2002-10-28; Santos, J. R. M. leg.; (CPDC). • 3♀; Camaçã; -15.4203, -39.4961; alt. 160m; (CPDC). • 1♀; Camaçã; -15.4203, -39.4961; alt. 160m;

1999-03-19; Santos, J. R. M. leg.; (CPDC). • 1♀; Caminho Prainha; -14.2939, -38.9857; alt. 34m; 2015-10-23; Chaul, J. leg.; Winkler; (DZUP). • 1♀; Caminho prainha; -14.2939, -38.9857; alt. 7m; 2015-10-23; Chaul, J. leg.; Winkler; (DZUP). • 2♀; Canavieiras; -15.6777, -38.9417; alt. 7m; 1997-11-07; Santos, J. R. M. leg.; (CPDC). • 3♀; Castelo Novo; -14.65, -39.1833; alt. 33m; 2000-04-26; Santos, J. R. M. leg.; (CPDC). • 1♀; Chapada Diamantina, Lençois; -12.55, -41.3833; alt. 370m; 2001-03-25; Santos, J.R.M. leg.; Winkler; (CPDC). • 1♀; Coaraci; -14.6333, -39.55; alt. 234m; 2002-09-30; Santos, J. R. M. leg.; Winkler; (CPDC). • 1♀; Cruz das Almas; -12.671, 39.103; alt. 200m; (CPDC). • 2♀; Guaratinga; -16.5872, -39.7846; alt. 175m; 2002-12-06; Santos, J. R. M. leg.; pitfall; (CPDC). • 1♀; Ibicaraí, Km 41; -14.862, -39.5873; alt. 185m; (CPDC). • 1♀; Ibirapitanga, A2; -14.165, -39.379; alt. 80m; (CPDC). • 1♀; Ilhéus; -14.7472, -39.2272; alt. 138m; 2010-01-01; Silvestre R. leg.; Manual; (MuBio-UFGD). • 1♀; Ilhéus-Castelo Novo; -14.6416, -39.198; alt. 53m; (CPDC). • 1♀; Ilhéus-Olivença; -14.9504, -39.0111; alt. 34m; (CPDC). • 3♀; Inema; -14.5038, -39.4701; alt. 248m; 1997-10-13; Santos, J. R. M. leg.; (CPDC). • 1♀; Itambé Leoncio; -15.243, -40.619; alt. 300m; (CPDC). • 3♀; Itapebi; -15.9687, -39.5321; alt. 195m; 1996-11-19; Silveira, J. E. leg.; (CPDC). • 1♀; Jardim Botánico de Salvador; -12.9292, -38.4347; alt. 81m; (CPDC). • 1♀; Jussari; -13.8333, -39.1667; (CPDC). • 1♀; Lagoa Encantada; -14.6206, -39.1397; alt. 10m; (CPDC). • 2♀; Lençóis Trevo ; -12.4833, -41.2667; alt. 729m; 2011-03-28; Santos, J. R. M. leg.; (DZUP). • 1♀; Lomanto Júnior; -14.8, -39.4833; alt. 200m; (CPDC). • 22♀; Mata de boa esperança; -14.7833, -39.05; alt. 22m; 2000-11-09; Santos, J. R. M. leg.; Winkler; (MZSP). • 1♀; Milagres; -12.9, -39.85; alt. 753m; 2010-10-23; Ulysséa, M. A.; Medina, A. M.; Campos, E. M. leg.; Winkler; (MZSP). • 1♀; Monte Pascoal; -16.8667, -39.9167; alt. 119m; (CPDC). • 1♀; Parna do Paul Brasil; -16.4432, -39.6653; alt. 4m; 2015/05; Vargas, T. leg.; (UFVLABECOL). • 1♀; Parque Nacional do Pau Brasil; -16.4976, -39.256; alt. 117m; 2015-01-05; Vargas, T. leg.; pitfall; (JTLC). • 2♀; Reserva Ecológica Michelin, 5 km SSW Igrapiúna; -13.8, -39.1; alt. 44m; 2008-07-22; Benati, K.; et al. leg.; (CPDC). • 1♀; Reserva Ecológica Michelin, 5 km SSW Igrapiúna; -13.8, -39.1; alt. 44m; 2008-07-22; Benati, K.; et al. leg.; (JTLC). • 2♀; Reserva Ecológica Michelin, 5 km SSW Igrapiúna; -13.8, -39.1; alt. 44m; 2013-07-22; Benati, K.

leg.; (CPDC). • 1☿; Reserva Ecológica Michelin, 5 km SSW Igrapiúna; -13.8, -39.1; alt. 44m; 2013-07-22; Benati, K. leg.; (MEPN). • 4☿; Serra Grande ; -14.4649, -39.0406; alt. 106m; 1992-08-25; Nascimento, I. C. leg.; (CPDC). • 2☿; Serra da Jibólia; -12.7717, -39.522; alt. 219m; 2001-04-08; Soarez, I. M. F. leg.; (CPDC). • 1☿; Simões Filho; -12.7863, -38.4022; alt. 33m; (CPDC). • 3☿; Taboquinhas; -14.3568, -39.1752; alt. 51m; 1996-12-06; Santos, J. R. M. leg.; (CPDC). • 3☿; Una; -15.2172, -39.1282; alt. 80m; 1996-08-24; Santos, H. J. leg.; Winkler; (CPDC). • 1☿; Unacau; unknown coordinates; (CPDC). • 2☿; Uruçuca; -14.5976, -39.2854; alt. 102m; 2002-10-02; Santos, J. R. M. leg.; (CPDC). • 2☿; Uruçuca; -14.5976, -39.2854; alt. 102m; 2002-10-01; Santos, J. R. M. leg.; (CPDC). – **Espírito Santo:** • 1☿; Reserva Natural Vale; -19.1333, -40.05; alt. 48m; 2015/02; Vargas, T. leg.; pitfall; (DZUP). • 1☿; Reserva Natural Vale; -19.15, -40.0501; alt. 56m; 2009-03-08; Schmidt, F. leg.; (UFVLABECOL). – **Sergipe:** • 2☿; Castro; -11.3667, -37.4167; alt. 87m; 2001-07-29; Silva, R. R.; Brandão, C. R. F. leg.; Winkler; (MZSP). • 1☿; Crasto; -11.396, -37.411; alt. 11m; (CPDC).

Geographic range. Brazil: Alagoas, Bahia, Espírito Santo, Sergipe.

New_genus_B *schultzi* (Mackay & Mackay 2010) [image link]

Figs. 4e (☿); 8 (distribution of examined records).

Worker diagnosis. Anterior mid clypeal margin straight to concave; in lateral view, petiolar node block-shaped, anterior margin vertically straight, posterior margin convex, dorsal margin straight and inclined anterad; posterior nodal face glabrous; in lateral view, subpetiolar process block-shaped. See also Mackay and Mackay (2010).

Worker. Measurements (n = 3): HW: 1.15-1.2; HL: 1.3-1.4; EL: 0.35-0.35; SL: 1.5-1.7; WL: 2.0-2.15; PrW: 0.8-0.9; MsW: 0.6-0.6; MsL: 0.3-0.4; PW: 0.8-0.85; PH: 0.7-0.75; PL: 0.5-0.55; GL: 1.75-2.25; A3L: 0.75-0.95; A4L: 0.7-0.75; A3W: 1.25-1.35; A4W: 1.15-1.25; TLa: 5.4-5.6; TLr: 5.6-6.15. **Indices**. CI: 85.71-88.89; OI: 29.17-30.43; SI: 125.0-147.83; MsI: 150.0-200.0; LPI: 71.43-73.33; DPI: 145.45-170.0.

Material examined. 5☿. **BRAZIL – Espírito Santo:** • 1☿; Carrapato; -19.905, -40.555; alt. 853m; 2013/06; Simon, S. leg.; pitfall epigaeic; (UFVLABECOL). • 1☿; Estação Biológica Santa Lucia ; -19.9661, -40.5392; alt. 665m; 2015-01-30; Vargas, T. leg.; (MEPN). • 1☿; Estação Biológica Santa Lucia ; -19.9661, -40.5391; alt. 666m; 2015-01-30; Vargas, T. leg.; (UFVLABECOL). • 1☿; Rebio Augusto Ruschi, Carrapato; -19.905, -40.555; alt. 853m; 2013/01; Simon, S. leg.; pitfall; (UFVLABECOL). • 1☿; Regência; -19.6357, -39.8786; alt. 17m; 2013/02; Simon, S. leg.; pitfall epigaeic; (UFVLABECOL).

Geographic range. Brazil: Espírito Santo.

New_genus_B *venusta* Forel, 1912 [image link]

Figs. 4: c, f, g (☿); 5: a – f (♂); 8 (distribution of examined records).

Worker and queen diagnosis. Anterior mid clypeal margin straight to feebly convex; in lateral view, petiolar node subtriangular, anterior margin vertically straight, posterior margin convex, top of node anterior to nodal vertical midline; posterior nodal face polished and hairless, medially with patch of horizontal striae; in lateral view, subpetiolar process block-shaped; in dorsal view, anterior margin of tergite of AIII feebly concave medially. See also Mackay and Mackay (2010).

Worker. Measurements (*n* = 11): HW: 0.95-1.05; HL: 1.1-1.25; EL: 0.25-0.35; SL: 0.9-1.5; WL: 1.5-2.0; PrW: 0.7-0.9; MsW: 0.45-0.6; MsL: 0.2-0.75; PW: 0.5-0.9; PH: 0.6-0.85; PL: 0.4-0.5; GL: 1.5-2.25; A3L: 0.75-1.0; A4L: 0.55-0.8; A3W: 1.0-1.25; A4W: 0.95-1.2; TLa: 4.5-5.45; TLr: 4.5-5.8. Indices. CI: 80.0-91.3; OI: 26.32-35.0; SI: 94.74-150.0; MsI: 66.67-225.0; LPI: 52.94-66.67; DPI: 111.11-200.

Male (first description). Measurements (*n* = 3): HW: 0.55-0.6; HL: 0.75-0.8; EL: 0.45-0.45; SL: 0.2-0.25; WL: 1.7-1.7; PrW: 0.65-0.7; MsW: 0.6-0.75; MsL: 0.6-0.7; PW: 0.45-0.5; PH: 0.45-0.5; PL: 0.3-0.45; GL: 1.65-2.25; A3L: 0.6-0.65; A4L: 0.65-0.85; A3W: 0.8-0.85; A4W: 0.95-1.0; TLa: 4.05-4.4; TLr: 4.6-5.15. Indices. CI: 68.75-80.0; OI: 75.0-81.82; SI: 33.33-45.45; MsI: 100.0-107.14; LPI: 60.0-100; DPI: 100-166.67.

Head. *Frontal view*: Subrhomboid. Mandible spatulate, longer than wide, acute apically. About 1.5 oval pits (maximum length) fit on mandibular dorsum, mandibular apex, when mandible is closed, barely touches lateral margin of labrum. Prementum with reduced transverse dome. Palp formula: 6,4. Stipes smooth, internal longitudinal groove absent. Labrum dorsum smooth. Clypeus anteromedially convex, not projecting anterad. Area between posterior margin of clypeus and supraclypeal area without depression. Posterior supraclypeal area acute. Supraclypeal area even. Distance between internal margins of antennal sockets approximately one socket diameter. Torular lobe small but well-developed, projecting vertically dorsad, not covering antennal socket acetabulum. Malar carina absent. Eye suboval, slightly notched near dorsal third, maximum length slightly more than half head length, convex, globose, placed at cephalic mid-length. Ocellar area not protruding from cuticle. Ocellar area placed slightly posterad to vertex. Anterior ocellus maximum length subequal to that of posterior ocelli. Ocelli not equidistant to each other, distance between anterior ocellus to posterior ocelli longer than interposterior ocellar distance. Distance from posterior ocellar margin to posterior margin of head roughly one apical scape width. Distance between anterior and posterior ocelli approximately 5 times anterior ocellus maximum length. Occipital carina reduced. Scape cylindrical, about twice as long as pedicel. Length of first flagellomere subequal to second flagellomere. **Mesosoma**. *Lateral view*: Dorsal margin convex. Pronotum lacking humeral carina, completely rounded. Anterior subalar area approximately as broad as tegular maximum width. Anapleural sulcus well-developed, running laterally only on mesopleuron, not reaching ventral mesopleural region. Metanotal trough weakly impressed. Metapleuropropodeal suture relatively shallow. Posterolateral margin of propodeal declivity carinate, with carina vanishing at propodeal mid length. Anterolateral propodeal corner marginate. Propodeal spiracle circular. Posteroventral cuticular flap at metapleural gland opening well developed, forming a vertically-oriented, salient carina, gland orifice completely visible in posterolateral view. Pheromone venting canal at metapleural gland opening absent, replaced by cricular groove surrounded by strong, salient carinae. *Dorsal view*: mesoscutum about as long as broad, close to three times length of mesoscutellum. Mesoscutum anterior triangular impression vestigial or absent. Parapsidal lines weakly impressed, slightly divergent. Notauli present, strongly impressed, weakly cross ribbed, meeting posteriorly, not extending to transcutal line. Transscutal sulcus feebly developed. Scutoscutellar sulcus present, slightly arched posterad, strongly impressed, cross ribbed, completely separating mesoscutum from mesoscutellum. Mesoscutellum

subtrapezoid, convex. Metascutellum well-developed, clearly discernible dorsally, surface with slightly salient longitudinal carina. Anterodorsal median propodeal sulcus absent. Posterior face of propodeal declivity flat. Propodeal lateral margins subparallel, not converging dorsomedially. *Ventral view*: probasisternum horseshoe-shaped. Mesosternal process absent. Metasternal process well-developed, inclined posterad, 20°-30° in lateral view, lobe-shaped, flattened anteroposteriorly, apex shorter than half height of metacoxal internal margin, space between lobes wider than width of each, internal margins running parallel. Metasternal process external margins slightly convergent. **Wings**. Hyaline. Moderately iridescent. Forewing venation Ogata type Ia: submarginal cells 1, 2 and discoidal present, vein 2M vestigial, 2r-rs offset from Rs+m, setose layer evenly covering surface. Hindwing venation Cantone and Von Zuben Type I: basal and subbasal cells and vein 2M present, 1R present but hardly discernible, 1Rs well-developed. Jugal lobe absent. Hindwing bearing 8 hamuli. **Legs**. Mesofemur roughly equally thick as metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora convex from base to apex. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur slightly longer than half-length of posterior spur. Anterior hind tibial spur half-length of posterior spur. Pretarsal claw proximal two thirds straight, distal third arched, unarmed (without accesory teeth on surface). Arolium present, roughly 0.5 times length of pretarsal claw. **Petiole**. *Lateral view*: Petiolar node anterior margin straight, inclined ca. 30° posterad; posterior margin straight, inclined ca. 20° anterad, anterior and posterior margins reaching approximately same level dorsally, middorsal margin convex, highest point posterior to nodal longitudinal midline, posterior face slightly convex. Subpetiolar process subtriangular, with blunt, keel-shaped, grooved anterior cusp, followed posteriorly by straight dome, dome with pair of irregular longitudinal carinae. Lateral projection of anteroventral nodal carina well-developed, with blunt tip feebly projecting dorsad. Lateral nodal carina well-impressed but short, not reaching nodal midlength. Anteroventral nodal carina incomplete, strongly concave medially. **Gaster**. Lateral view: Prora poorly developed, similar to cuticular lip, hardly discernible laterally; posterior region flattened and broadened. Anterior margin of tergum of A3 straight. Meeting region of anterior margin of tergum of A3 with its dorsal margin broadly convex. Anterodorsal margin of tergum of A3 slightly convex. Cinctus well-impressed, cross ribbed. *Dorsal view*: Tergum of A3 longer than A4. Abdominal sternum 7 weakly concave, glabrous. Spine at posterior margin of tergum of A8 well-developed, extending posterad, beyond posterior margin of sternum of A9, acute, slightly flattened laterally. Sternum of A9 roughly as long as

broad, posterior margin convex. Pygostyles present, about three times longer than broad. **Color**. Appendages whitish to pale yellowish, antennae yellowish. **Pilosity**. Body with sparse, flexuous, whitish to golden, erect and suberect hairs. Appressed pubescence present, mostly fine small hairs distributed across integument which is easily discernible. Most erect hairs on body dorsum approximately to scape length. Meso- and metatarsi bearing abundant suberect setae. **Sculpture**. Integument polished, with abundant, shallowly impressed piligerous punctures, except propodeal dorsum which has a mix of rugae and more densely impressed punctures. Striae on head absent, mesosoma mostly devoid of striae, except for axilar area and metapleuropropodeal groove. Striae on petiolar node absent.

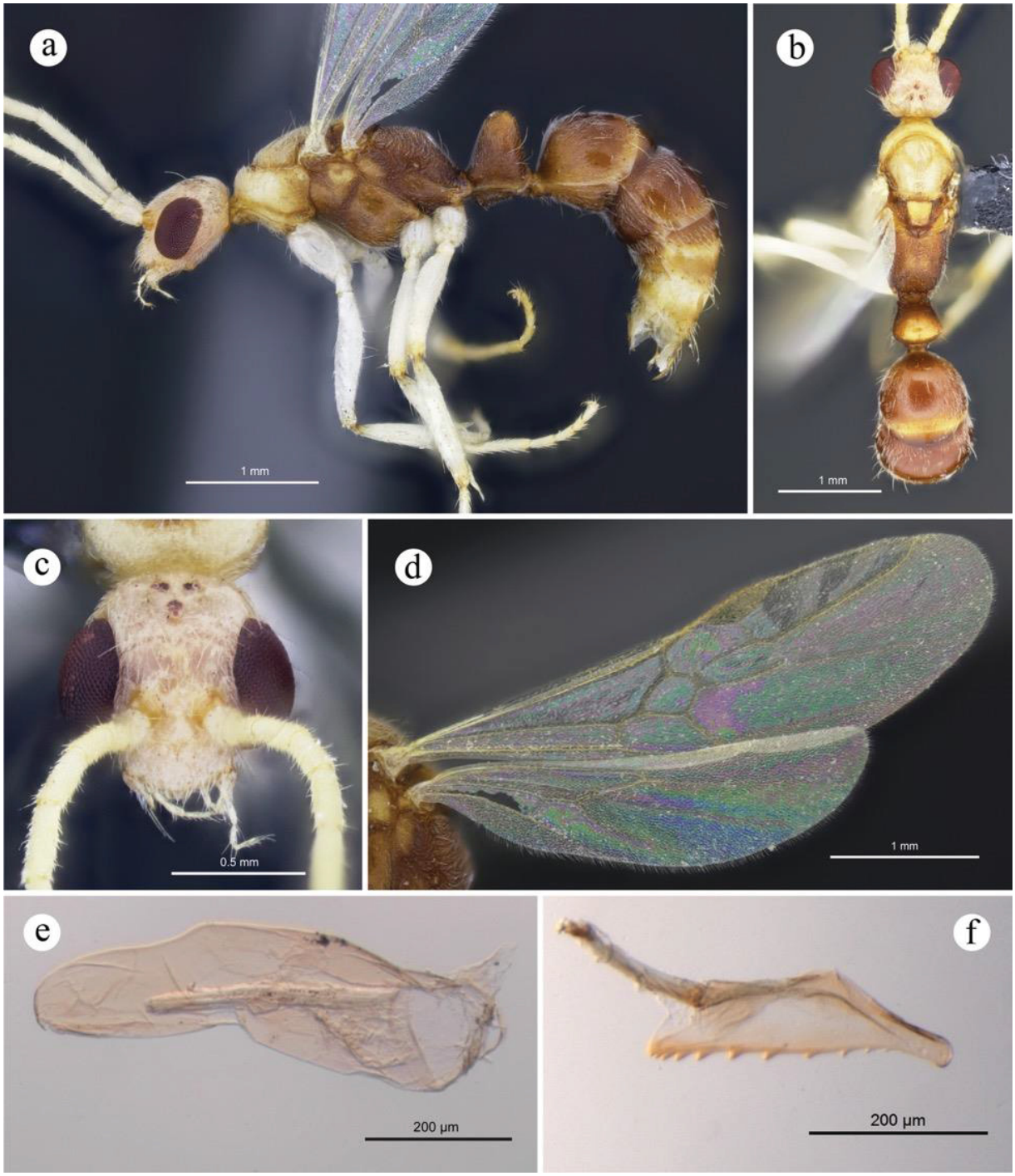


Fig. 5. new_genus_B *venusta* (♂CPDC: ATPFOR2075). **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Fore- and wing; **e.** Right gonopod; **f.** Left penisvalva.

Material examined. 80☿, 4♂. **BRAZIL – Bahia:** • 2☿; 1.5 km E of Guaratinga; -16.5833, -39.7667; alt. 151m; 2002-12-06; Santos, J. R. M. leg.; (CPDC). • 1☿; Itamaraju; -17.0391, -39.5293; alt. 103m; (CPDC). • 1☿; Monte Pascoal; -16.8667, -39.9167; alt. 119m; 1999-07-18; Santos, J. R. M. leg.; (DZUP). • 1☿; Monte Pascoal; -16.8667, -39.9167; alt. 119m; (CPDC). • 2♂; Mucuri; -18.157, -39.7344; alt. 41m; 2004-03-30; Mariano, C. F. S leg.; (CPDC). • 1☿; Mucuri; -18.157, -39.7344; alt. 41m; (CPDC). • 1☿; Mucuri; -18.157, -39.7344; alt. 41m; 2004-03-30; Mariano, C. F. S leg.; (CPDC). • 1☿; Parna do Paul Brasil; -16.4432, -39.6653; alt. 4m; 2015/05; Vargas, T. leg.; (UFVLABECOL). – **Espírito Santo:** • 27☿; Estación Bilógica Santa Lucia, 5 Km W Santa Teresa; -19.9667, -40.5333; alt. 706m; 2002-01-20; Schoereder, J. H. L.; Ribas, C. R. leg.; Winkler; (MZSP). • 1☿; Estaçao Biológica de Santa Lucia; -19.95, -40.5333; alt. 600m; 2018-11-18; Grupo 4 formigas do Brasil leg.; (JTLC). • 1☿; Estaçao Biológica de Santa Lucia; -19.95, -40.5333; alt. 600m; 2018-11-18; Grupo 4 formigas do Brasil leg.; (DZUP). • 1☿; Estação Biológica Santa Lucia ; -19.9661, -40.5392; alt. 667m; 2015-01-30; Vargas, T. leg.; (UFVLABECOL). • 1☿; Flona Goytacazes; -19.4354, -40.072; alt. 22m; 2013/02; Simon, S. leg.; pitfall; (MEPN). • 1☿; Linhares; -19.4, -40.0667; alt. 35m; (CPDC). • 1☿; Linhares; -19.3974, -40.0646; alt. 32m; 1972/09; Alvarenga, M. leg.; (MZSP). • 2☿; RFVC Rio Doce; -19.4001, -40.0667; alt. 25m; Pezon, A. leg.; (CPDC). • 4☿; Reserva Biológica Sooretama; -19.0667, -39.9333; alt. 47m; 2002-05-14; Schoereder, J. H. L.; Ribas, C. R. leg.; Winkler; (MZSP). • 1☿; Santa Teresa; -19.9368, -40.5983; alt. 617m; (MZSP). • 1☿; [no locality given]; -19.5748, -40.6859; Göldi leg.; (MHNG). – **Minas Gerais:** • 1☿; Cocais da Estrela; -19.4433, -42.8468; alt. 923m; 2007-06-19; Braga, D. L. leg.; (CPDC). • 1♂; Mata do Paraiso, Universidade Federal do Viçosa; -20.806, -42.8514; alt. 758m; 2019-03-08; Chaul, J.; et al. leg.; Malaise aerial; (UFVLABECOL). • 1☿; Mata do Paraiso, Universidade Federal do Viçosa; -20.75, -42.85; alt. 704m; (CPDC). • 3☿; Mata do Paraiso, Universidade Federal do Viçosa; -20.75, -42.85; alt. 704m; 2000-11-25; (CPDC). • 1☿; Mata do Paraiso, Universidade Federal do Viçosa; -20.75, -42.85; alt. 704m; 1993/07; Ferreira, P. S. F. leg.; (CPDC). • 1☿; Samarco; -20.2305, -43.4473; alt. 778m; 2012-09-20; Paolucci, L. leg.; pitfall; (UFVLABECOL). • 1♂; Universidade Federal de Viçosa; -20.7589, -42.8695; alt. 710m; 2016-

03-28; Chaul, J. leg.; hand collected; (DZUP). • 1☿; Universidade Federal de Viçosa, Mata da Biologia; -20.7572, -42.8608; alt. 706m; 2013/03; Chaul, J. leg.; Winkler; (DZUP). • 1☿; Universidade Federal de Viçosa, Mata da Biologia; -20.7572, -42.8608; alt. 706m; 2012-12-01; Chaul, J.; Jesus, R. leg.; (MEPN). • 1☿; Viçosa; -20.7474, -42.8833; alt. 648m; (CPDC). • 1☿; Viçosa; -20.8167, -42.8833; alt. 760m; 1998-02-06; Soares, M. leg.; (DZUP). • 6☿; Viçosa; -20.8167, -42.8833; alt. 760m; 2001/02; Sobrinho, T. leg.; (UFVLABECOL). **– Rio de Janeiro: •** 3☿; Reserva Biológica Tinguá, 10 Km W Xerém; -22.55, -43.4; alt. 416m; 2002-02-04; Winkler; (MZSP). • 11☿; Santa Maria Madalena; -21.9614, -42.0076; alt. 690m; Winkler; (MZSP).

Geographic range. Brazil: Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro.

New_genus_B *schultzi*-2 sp. nov.

Figs. 6: a – c (☿); 8 (distribution of examined records).

[zoobank link]

Holotype*.** 1☿, Reserva Sapiranga, Mata de São João; -12.55, -38.0333; alt. 60m; 2001-07-21; Silva, R. R.; Brandão, C. R. F. leg.; Winkler; (MZSP: ATPFOR2192). ***Paratypes. 1☿ [same data as for holotype], (INPA: ATPFOR2167); 1☿ [same data as for holotype], (DZUP: ATPFOR1991).

Etymology. [pending]

Worker (and probably queen) diagnosis. In frontal view, antennal scape, exceeding posterior head margin by about four times apical scape width (Fig. 4a, 6b); anterior mid clypeal margin straight (Fig. 6b); humeral carina blunt, salient anteriorly; posterolateral propodeal margin with blunt, laterally expanded carina (Fig. 6a); in lateral view, petiolar node rectangular with dorsal margin horizontally straight, nodal height slightly more than two times longer than dorsal margin, anterior nodal face concave, posterolateral nodal margin with blunt carina (Fig. 6a); subpetiolar process shovel-shaped, ventral margin horizontally straight (Fig. 6a); prora not projected anterad (Fig. 6a); pronotum and mesonotum dorsally with fused foveae, forming irregular, raised

longitudinal striae (Fig. 6c), pronotum laterally lacking sculpture; propodeum laterally with gross, irregular horizontal striae (Fig. 6a).

Worker description. Measurements (n = 4; holotype in parenthesis): HW: 1.15-1.25 (1.19); HL: 1.3-1.4 (1.3); EL: 0.35-0.35 (0.35); SL: 1.6-1.65 (1.62); WL: 2.0-2.1 (2.1); PrW: 0.88-1.0 (0.98); MsW: 0.6-0.7 (0.6); MsL: 0.3-0.4 (0.3); PW: 0.85-0.95 (0.85); PH: 0.75-0.8 (0.8); PL: 0.5-0.5 (0.5); GL: 1.65-2.65 (1.7); A3L: 0.8-1.15 (0.8); A4L: 0.7-0.8 (0.7); A3W: 1.3-1.4 (1.3); A4W: 1.15-1.3 (1.15); TLa: 5.3-5.8 (5.4); TLr: 5.45-6.5 (5.6). Indices. CI: 88.46-92.31 (91.54); OI: 28.0-30.43 (29.41); SI: 132.0-143.48 (136.13); MsI: 150.0-233.33 (200.0); LPI: 62.5-66.67 (62.5); DPI: 170.0-190.0 (170.0).

Head. *Frontal view*: subquadrate. Mandible triangular, longer than wide, distal region slightly bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with four to five teeth distally, slightly decreasing in size, followed by four to five denticles proximally. Prementum with reduced transverse dome. Prementum and feebly grooved region distally. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially straight to slightly convex, slightly projected anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina surpassing ocular mid-length but not reaching ocular posterior margin medially. Torular lobe subtriangular, covering approximately 40% of acetabulum of antennal socket, posterolateral margin straight. Malar carina well-developed, not touching eye margin. Eye oval, maximum length ca. one-third head length, convex, slightly globose, surpassing lateral margin of head, placed anterior to cephalic mid-length. Posterior margin of head straight to slightly concave. Occipital carina vestigial. Scape, when pulled posterad, surpassing posterior margin of head by more than three times apical scape width. **Mesosoma**. *Lateral view*: Dorsal margin concave at the meeting region of mesonotum and propodeum. Pronotum carinate, with carina moderately projecting from cuticle. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum. Posterolateral margin of propodeal declivity with blunt, salient carina. Propodeal spiracle circular. Ventrolateral propodeal declivity with shallow groove just dorsad to metapleural gland opening. Posteroventral cuticular flap at metapleural gland opening well developed, forming a vertically-oriented, salient carina, gland orifice completely visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Notopropodeal suture present, relatively shallowly grooved. Posterior face of propodeal declivity mostly flat. Propodeal

lateral margins subparallel, not converging dorsomedially. *Ventral view*: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process poorly developed, tooth-shaped, internal margins of lobes running parallel, relatively flattened anteroposteriorly, space between lobes broader than width of each. Metasternal process well-developed, inclined posterad, ca. 45° in lateral view, triangular-shaped, slightly flattened anteroposteriorly, apex about as long as mid height of metacoxal internal margin, space between lobes wider than width of each, internal margins divergent. Metasternal process external margins straight to slightly convergent. **Legs**. Mesofemur roughly equally thick as metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora slighlty flattened roughly on distad two thirds. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about 2.5 times shorter than posterior spur. Pretarsal claw arched, unarmed (without accesory teeth on surface). Arolium present, roughly three times shorter than pretarsal claw. **Petiole**. *Lateral view*: Petiolar node with slightly concave anterior margin and slighty convex posterior margin, posterior margin slightly higher than anterior margin, middorsal margin mostly flat, anterodorsal margin relatively angulate, posterior face mostly flat. Subpetiolar process shovel-shaped, with keel-shaped anterior cusp, followed by posterior horizontally straight region, dome with transverse, strongly impressed striae. Lateral projection of anteroventral nodal carina well-developed, with blunt tip feebly projecting dorsad. Lateral nodal carina weakly impressed. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. *Lateral view*: Prora poorly developed, similar to cuticular lip, partially hidden by helcium; posterior region flattened and broadened. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin slightly convex. Anterodorsal margin of tergum of A3 convex. Cinctus weak. *Dorsal view*: Tergum of A3 slightly longer than A4. Posterior dorsum of epipygium completely smooth. **Color**. Mandibles lighter than remaining body integument, occasionally legs yellowish, antennae brown to ferruginous brown. **Pilosity**. Body with moderately abundant, flexuous, whitish to golden, erect and suberect hairs. Appressed pubescence present, mostly fine small hairs distributed across integument which is easily discernible. Most erect hairs on body dorsum mostly longer than maximum eye length. Scape pilosity mostly composed of erect and suberect hairs and pruinose pubescence, erect hairs slightly longer than apical scape width. Meso- and metatarsi bearing stiff setae (ventraly only) interspersed with suberect and appressed fine

setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, longer than eye maximum length, and a row of tiny, stiff setae about one fifth length of those hairs. Posterior dorsum of epipygium surrounded by sparse, ca. 10 flexuous hairs, about same length of eye maximum length. **Sculpture**. Integument polished, with abundant, shallowly impressed piligerous punctures, except for head dorsum, pronotum and mesonotum where punctures are more densely and strongly impressed. Striae on head absent except on mid clypeal dorsum bearing longitudinal striae, mandibles without striae dorsally, mesosoma bearing strong striae on posterior and dorsal propodeal surface. Striae on petiolar node absent.

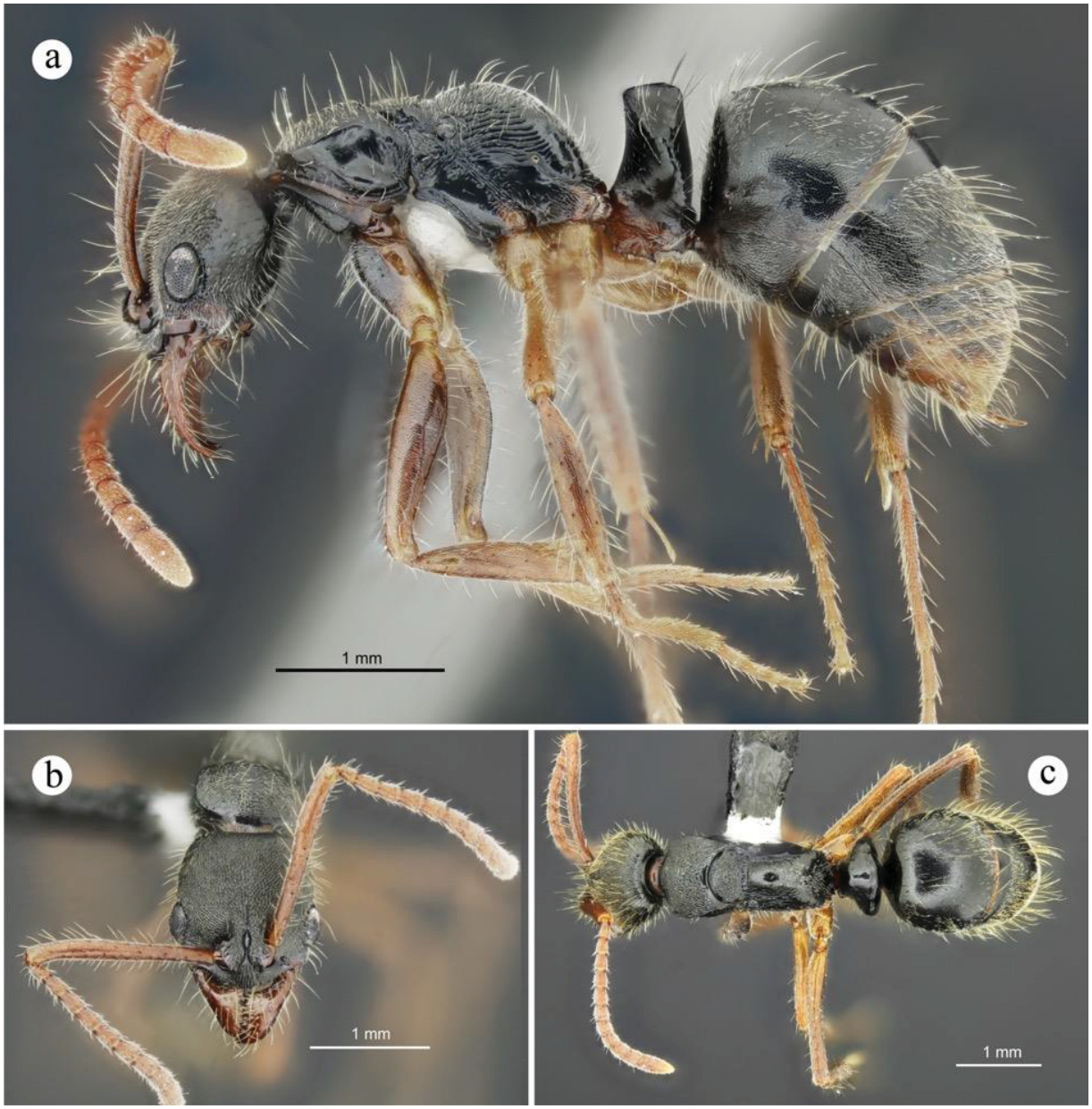


Fig. 6. new_genus_B *schultzi*-2. ☿ holotype (MZSP: ATPFOR2192). **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Comments. New_genus_B *schultzi*-2 is a relatively large species in the genus (☿ TLa = 5.30 – 5.8 mm). This form is quite distinct from other congeners, however, the reader can examine the following main characters present in new_genus_B *schultzi*-2 which allow its separation from others in the genus (in order of relative importance): 1) Shovel-shaped subpetiolar process; this is a unique trait (autapomorphy) for this species in this genus; 2) In lateral view, the petiolar node is rectangular and narrow, narrower than any other known species in new_genus_B, with the nodal height slightly more than two times longer than length of its dorsal margin; and 3) the mesonotum has fused foveae, thus forming irregular raised, longitudinal striae. The other congeners also show fused mesonotal foveae, but these do not for striae.

Since only six specimens were examined, though probably more are available at MZSP and CPDC collections in Brazil, no strong inferences are possible with respect to morphological variation. The specimens are externally identical, they likely belong from the same nest series, though this is not indicated on the collection labels.

New_genus_B *schultzi*-2 is the least commonly collected taxon in the genus; since it is known only from one site at the Bahia Coastal forests, eastern state of Bahia (Fig. 8), it also raises concerns about the current conservation status of its populations which are possibly under pressure due to the steady human-driven degradation of native ecosystems in such region. This species is possibly living in sympatry with *N. concava*, which is the commonest among all species in the genus.

Natural history notes. Nothing is known about the biology of new_genus_B *sultzi*-2, except that it is probably a litter nester. All six specimens were collected with Winkler extractors.

Other material examined. 3☿. **BRAZIL – Bahia:** • 1☿; Reserva Sapiranga, Mata de São João; -12.55, -38.0333; alt. 60m; 2001-07-21; Silva, R. R.; Brandão, C. R. F. leg.; Winkler; (MZSP).

Geographic range. Brazil: eastern Bahia.

New_genus_B *schultzi*-3 sp. nov.

Figs. 7: a – c (☿); 8 (distribution of examined records).

[zoobank link]

Holotype. 1 ☿, BRAZIL: Bahia, 112 km NW Uruçuca; -14.5, -39.2; alt. 198m; 2002-10-24; Santos, J. R. M. leg.; (MECN: ATPFOR2024). *Paratypes*. 1 ☿ [same data as for holotype]; (CPDC: ATPFOR2191); 1 ☿ [same data as for holotype]; (UFVLABECOL: ATPFOR2096).

Etymology. [pending]

Worker (and probably queen) diagnosis. Antennal scape, when pulled posterad exceeding posterior head margin by about four times apical scape width (Fig. 7b); humeral carina present blunt, not salient; pronotum mid laterally feebly deflate; posterolateral propodeal margin with blunt carina (Fig. 7a); in lateral view, petiolar node block-shaped, with dorsal margin horizontally straight and inclined anterad, anterior nodal margin straight and feebly inclined posterad, posterior nodal margin with oblique acute carina feebly projected posterad (Fig. 7a); posterior nodal face mostly flat; subpetiolar process dome-shaped (convex) (Fig. 7a); prora with tiny anterior projection, almost indistinguishable in lateral view; in dorsal view, anterodorsal margin of tergite of AIII medially slightly concave (Fig. 7c);

Worker description. Measurements (n = 3; holotype in parenthesis): HW: 1.05-1.2 (1.2); HL: 1.4-1.45 (1.45); EL: 0.35-0.45 (0.35); SL: 1.6-1.75 (1.75); WL: 2.0-2.1 (2.0); PrW: 0.8-0.9 (0.9); MsW: 0.5-0.6 (0.5); MsL: 0.25-0.35 (0.25); PW: 0.75-0.8 (0.8); PH: 0.65-0.75 (0.65); PL: 0.45-0.55 (0.55); GL: 1.95-2.3 (2.3); A3L: 0.8-1.05 (0.85); A4L: 0.6-0.9 (0.85); A3W: 1.2-1.25 (1.25); A4W: 1.1-1.1 (1.1); TLa: 5.6-5.7 (5.7); TLr: 5.9-6.3 (6.3). **Indices**. CI: 72.41-85.71 (82.76); OI: 29.17-37.5 (29.17); SI: 141.67-152.38 (145.83); MsI: 171.43-240.0 (200); LPI: 66.67-84.62 (84.62); DPI: 145.45-166.67 (145.45).

Head. Frontal view: subquadrate. Mandible triangular, longer than wide, distal region moderately bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with four to six teeth alternating with four to five smaller teeth, basal margin edentate. Prementum with reduced transverse dome. Prementum and feebly grooved region distally. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially straight to slightly convex, slightly projected anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina surpassing ocular mid-length but not reaching ocular posterior margin medially. Torular lobe subtriangular, covering

approximately 60% of acetabulum of antennal socket, posterolateral margin straight. Malar carina well-developed, not touching eye margin. Eye oval, maximum length ca. one-third head length, convex, slightly globose, surpassing lateral margin of head, placed anterior to cephalic mid-length. Posterior margin of head straight. Occipital carina strongly reduced. Scape , when pulled posterad, surpassing posterior margin of head by more than three times apical scape width. **Mesosoma**. Lateral view: Dorsal margin concave at the meeting region of mesonotum and propodeum. Pronotum carinate, with carina moderately projecting from cuticle. Anapleural sulcus well-developed, not completely dividing mesopleuron, usually masked by surrounded striae. Posterolateral margin of propodeal declivity with feeble, blunt, salient, slightly crenulated carina. Propodeal spiracle circular. Ventrolateral propodeal declivity with shallow groove just dorsad to metapleural gland opening. Posteroventral cuticular flap at metapleural gland opening well developed, forming a vertically-oriented, salient carina, gland orifice completely visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Notopropodeal suture present, relatively shallowly grooved. Posterior face of propodeal declivity feebly convex. Propodeal lateral margins subparallel, not converging dorsomedially. Ventral view: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process strongly reduced to vestigial. Metasternal process well-developed, inclined posterad, ca. 45° in lateral view, triangular- to lobe-shaped, slightly flattened anteroposteriorly, apex about as long as mid height of metacoxal internal margin, space between lobes approximately equal to- or shorter than width of each, internal margins divergent. Metasternal process external margins straight to slightly convergent. **Legs**. Mesofemur roughly equally thick as metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora slighlty flattened roughly on distad two thirds. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur slightly longer than half-length of posterior spur. Anterior hind tibial spur half-length of posterior spur. Pretarsal claw arched, unarmed (without accesory teeth on surface). Arolium present, roughly three times shorter than pretarsal claw. **Petiole**. Lateral view: Petiolar node with straight anterior margin and convex posterior margin, posterior margin higher than anterior margin, middorsal margin flat, anterodorsal margin angulate, posterior face flat at base and slightly concave middistally. Subpetiolar process subtriangular, with blunt, keel-shaped, grooved anterior cusp, followed posteriorly by slightly convex dome, dome with transverse, well-impressed striae. Lateral projection of anteroventral nodal carina well-developed, with blunt tip

projecting dorsad. Lateral nodal carina absent. Anteroventral nodal carina incomplete, strongly concave medially. **Gaster**. Lateral view: Prora poorly developed, similar to cuticular lip, usually hardly discernible laterally; posterior region flattened and broadened. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin relatively angled. Anterodorsal margin of tergum of A3 convex. Cinctus weak. Dorsal view: Tergum of A3 slightly longer than A4. Posterior dorsum of epipygium completely smooth. **Color**. Mandibles lighter than remaining body integument, legs yellowish or ferruginous brown, antennae brown to ferruginous brown. **Pilosity**. Body with moderately abundant, flexuous, dark golden to pale whitish, erect and suberect hairs. Appressed pubescence present, mostly fine small hairs distributed across integument which is easily discernible. Most erect hairs on body dorsum approximately equal to maximum eye length. Scape pilosity mostly composed of erect and suberect hairs and pruinose pubescence, erect hairs about as long as apical scape width. Meso- and metatarsi bearing stiff setae (ventrally only) interspersed with suberect and appressed fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, shorter than eye maximum length, and row of tiny, stiff setae about one fifth length of those hairs. Posterior dorsum of epipygium surrounded by sparse, ca. 10 flexuous hairs, shorter than eye maximum length. **Sculpture**. Integument polished, with abundant, shallowly impressed piligerous punctures, except for head dorsum, pronotum and mesonotum where punctures are more densely and strongly impressed. Striae on head absent except on mid clypeal dorsum bearing longitudinal striae, mandibles finely striate dorsally, mesosoma bearing strong striae laterally on propodeum, except metapleuron, and feebly impressed striae laterally on pronotum. Striae on petiolar node present, feebly impressed ventrolaterally.

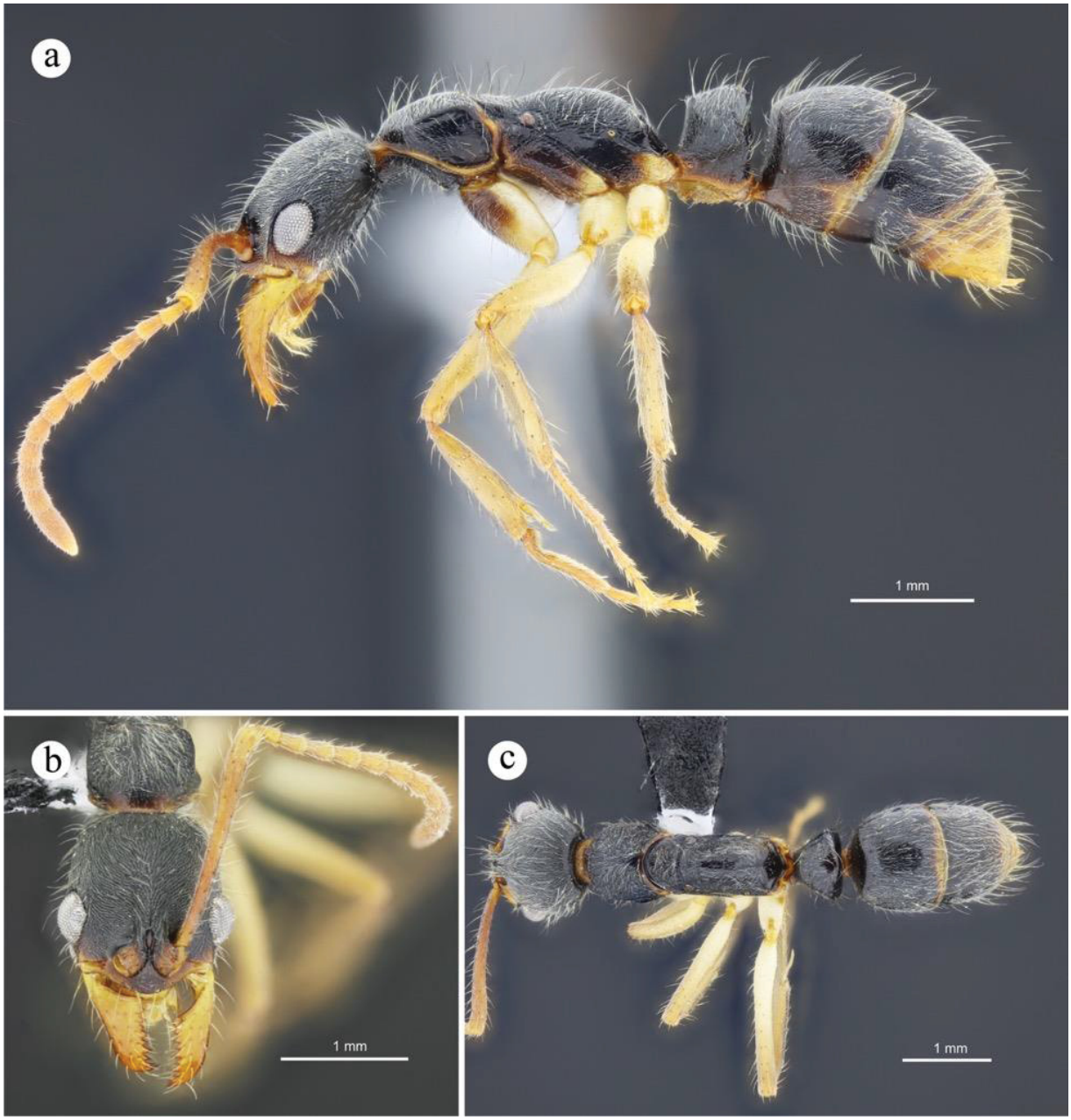


Fig. 7. new_genus_B *schultzi*-3 ☿ holotype (DZUP: ATPFOR2024). **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Comments. New_genus_B *schultzi*-3 is the largest species in the genus (TLa = 5.6 – 5.7 mm). The few examined specimens, from three sites in the state of Bahia, separated by between 40 – 150 km approximately, show slight variations mostly in color and sculpture; the holotype, has more feebly impressed striae laterally on the pronotum than the other specimens; in addition, the holotype shows pale yellowish legs, while in the other specimens the legs are brownish to castaneous, and the overall body color of these is darker than that of the holotype.

New_genus_B *schultzi*-3 is very similar only to *N. schultzi*, they are distinguished, however, by the following: the lateral side of pronotum, mesopleuron, metapleuron, and the dorsum of propodeum are smooth, while in *N. schultzi* these plates are completely punctate; the subpetiolar process of new_genus_B *schultzi*-3 is dome-shaped (feebly convex) in lateral view, while that of *N. schultzi* is block-shaped, with the ventral margin mostly straight; and the anterior margin of AIII is feebly concave in dorsal view, while that of *N. schultzi* is either straight or approximately convex. These two species occur in sympatry in eastern Bahia, the only site from where new_genus_B *schultzi*-3 is currently known, and they are likely closely related.

Based on the examined material, the populations of this species are also likely highly reduced, and restricted to a small region in southeastern Brazil. Although more material from unknown sites in Bahia is potentially vouchered in the Brazilian CPDC Collection, these unexamined specimens likely belong from the same sites here indicated.

Natural history notes. Virtually nothing is known about this epigeic forager; probably examined specimens were collected using pitfall traps, because this is one of the most frequent techniques researchers at CPDC use for collecting ants.

Other material examined. 4 ☿. **BRAZIL – Bahia:** • 3☿; 5 km NE São José da Vitória; -15.05, -39.3; alt. 678m; 2000-09-14; Carmo, J. C. S. leg.; (CPDC). • 1☿; Itapitanga; -14.4167, -39.55; alt. 141m; 1997-05-30; Santos, J. R. M. leg.; (DZUP).

Geographic range. Brazil: eastern Bahia.

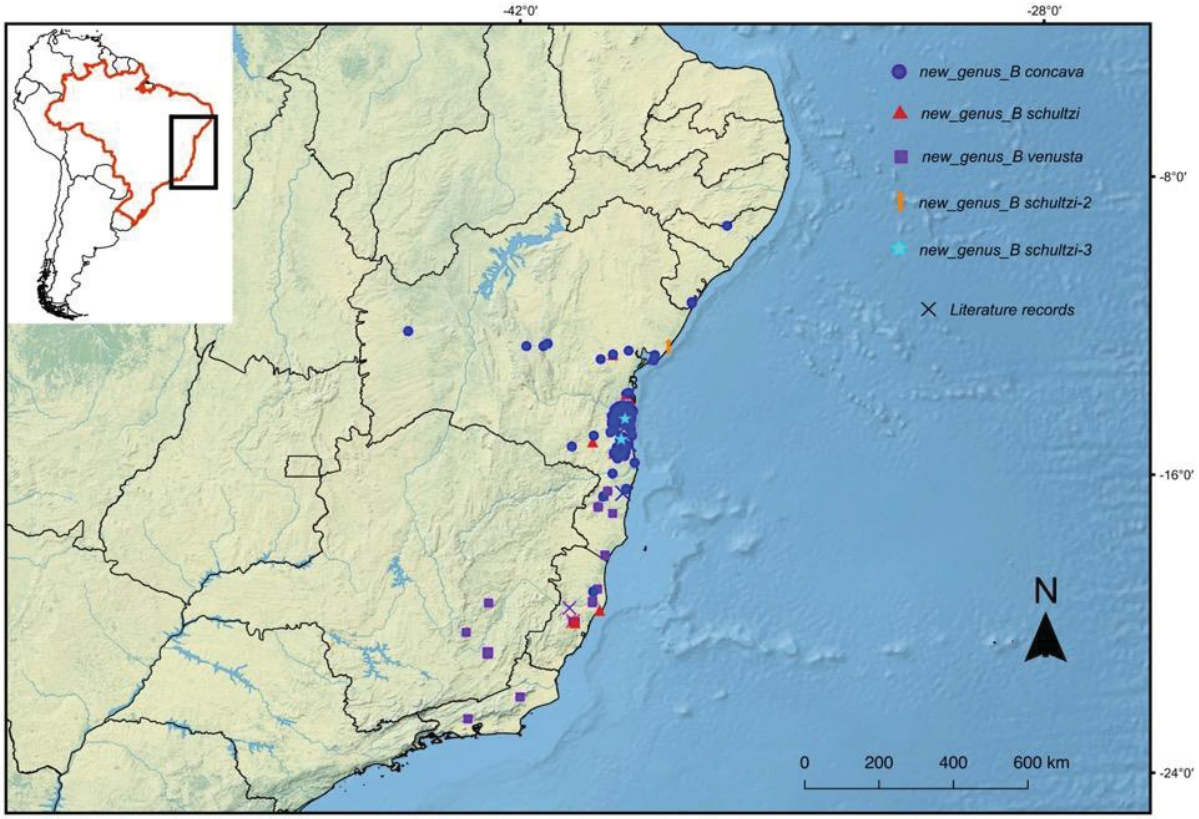


Fig. 8. Distribution of examined material of New_genus_B.

Appendix A. Voucher specimens sequenced in this study. Bold: new species (publication pending); *: undescribed new species.

Species-group	Species	Museum	Voucher ID	EX. ID	Caste	Country	Notes
aenescens	*Neoponera aenescens*	JTLC	CASENT0649098	EX2288	worker	CR	
aenescens	*Neoponera carbonaria*	MEPN	CASENT0649889	EX2402	worker	EC	
aenescens	*Neoponera carbonaria*	JTLC	CASENT0649898	EX2444	worker	EC	
aenescens	*Neoponera chyzeri*	MEPN	CASENT0649891	EX2410	worker	CO	
aenescens	*Neoponera chyzeri*	MEPN	CASENT0649892	EX2411	worker	EC	
aenescens	*Neoponera* ecu33723*	DZUP	DZUP549355	EX2418	worker	EC	
aenescens	*Neoponera eleonorae*	MEPN	MEPNINV30157	EX2405	worker	EC	
aenescens	*Neoponera eleonorae*	MEPN	CASENT0649895	EX2419	worker	EC	
aenescens	*Neoponera fauveli*	JTLC	CASENT0649899	EX2447	worker	CO	
aenescens	*Neoponera fauveli*	DZUP	ATPFOR1991	EX2439	worker	PE?	
aenescens	*Neoponera fusca*	MEPN	CASENT0649890	EX2408	worker	CO	
aenescens	*Neoponera hispida*	UTIC	UTIC00211977	EX2420	worker	EC	
aenescens	*Neoponera hispida*	ICN	ICN004347	EX2427	worker	CO	
aenescens	*Neoponera holcotyle*	ICN	ICN001374	EX2428	worker	CO	
aenescens	*Neoponera schoedli*	ICN	ICN003380	EX2399	worker	VE	
aenescens	*Neoponera schoedli*	MEPN	CASENT0649893	EX2412	worker	EC	
apicalis	*Neoponera apicalis*	JTLC	CASENT0649089	EX2302	queen	MX	
apicalis	*Neoponera* bra549385*	DZUP	DZUP549385	EX2414	queen	BR	
apicalis	*Neoponera cooki*	JTLC	CASENT0646173	EX2248	worker	FG	
apicalis	*Neoponera obscuricornis*	DZUP	DZUP549364	EX2436	worker	BR	
apicalis	*Neoponera verenae*	JTLC	CASENT0635079	EX2270	worker	CR	
crenata	*Neoponera antecurvata*	JTLC	CASENT0649083	EX2296	queen	HO	
crenata	*Neoponera carinulata*	JTLC	CASENT0640212	EX2245	worker	MX	
crenata	*Neoponera cavinodis*	JTLC	CASENT0649003	EX2246	worker	PE	
crenata	*Neoponera coveri*						not available
crenata	*Neoponera moesta*	JTLC	CASENT0631798	EX2282	worker	MX	
crenata	***Neoponera cylindrinodis***	JTLC	DZUP549354	EX2443	worker	BR	
crenata	***Neoponera dejeani***	CPDC	ATPFOR1978	EX2425	worker	FG	
crenata	*Neoponera donosoi*	MEPN	CASENT0649894	EX2416	worker	EC	
crenata	*Neoponera fiebrigi*						not available
crenata	*Neoponera globularia*	UCDC	CASENT0862739	D2111	queen	FG	
crenata	*Neoponera goeldii*	MEPN	MEPNINV37890	EX2448	worker	EC	

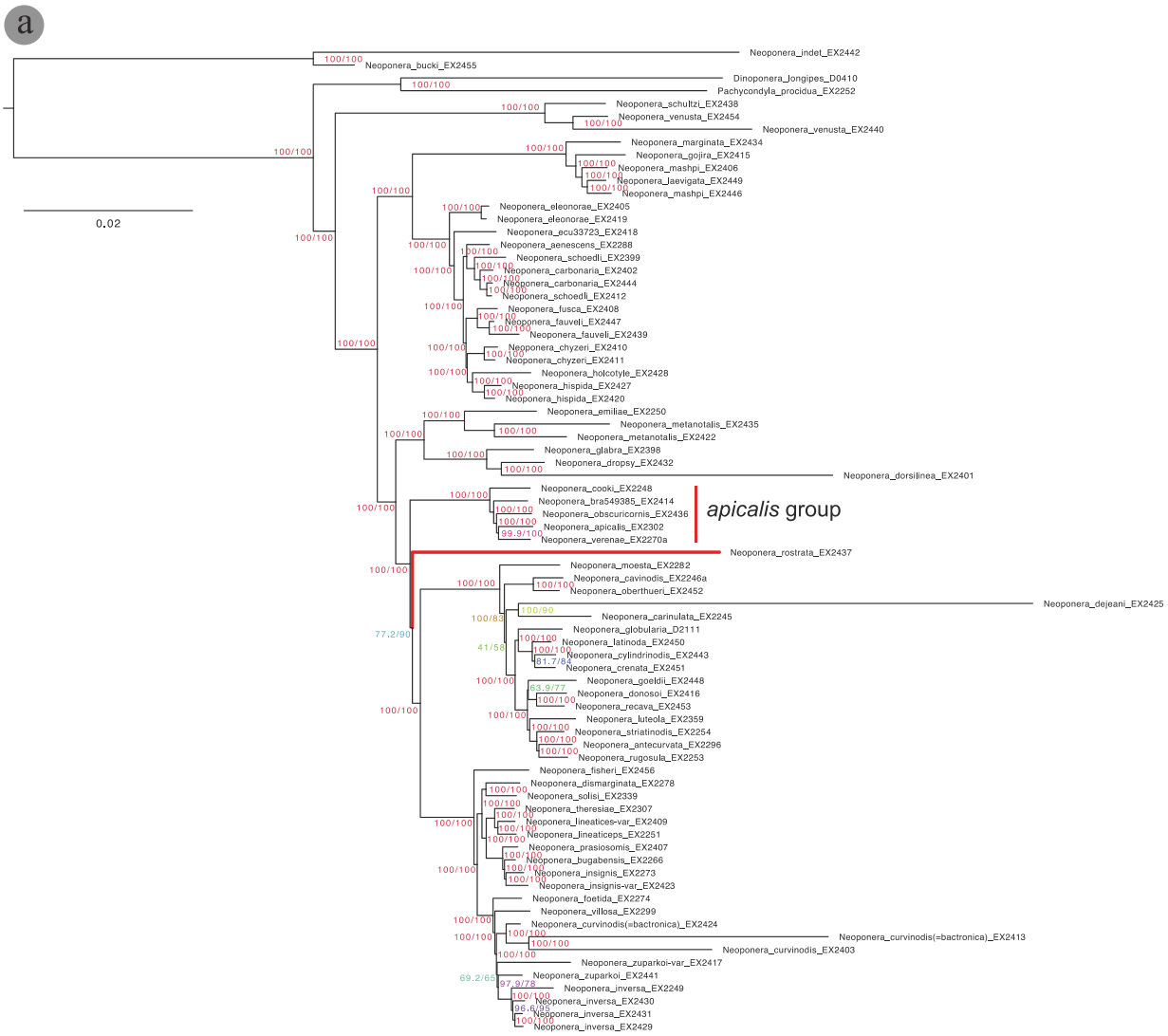
Appendix A. ***Continued*****.**

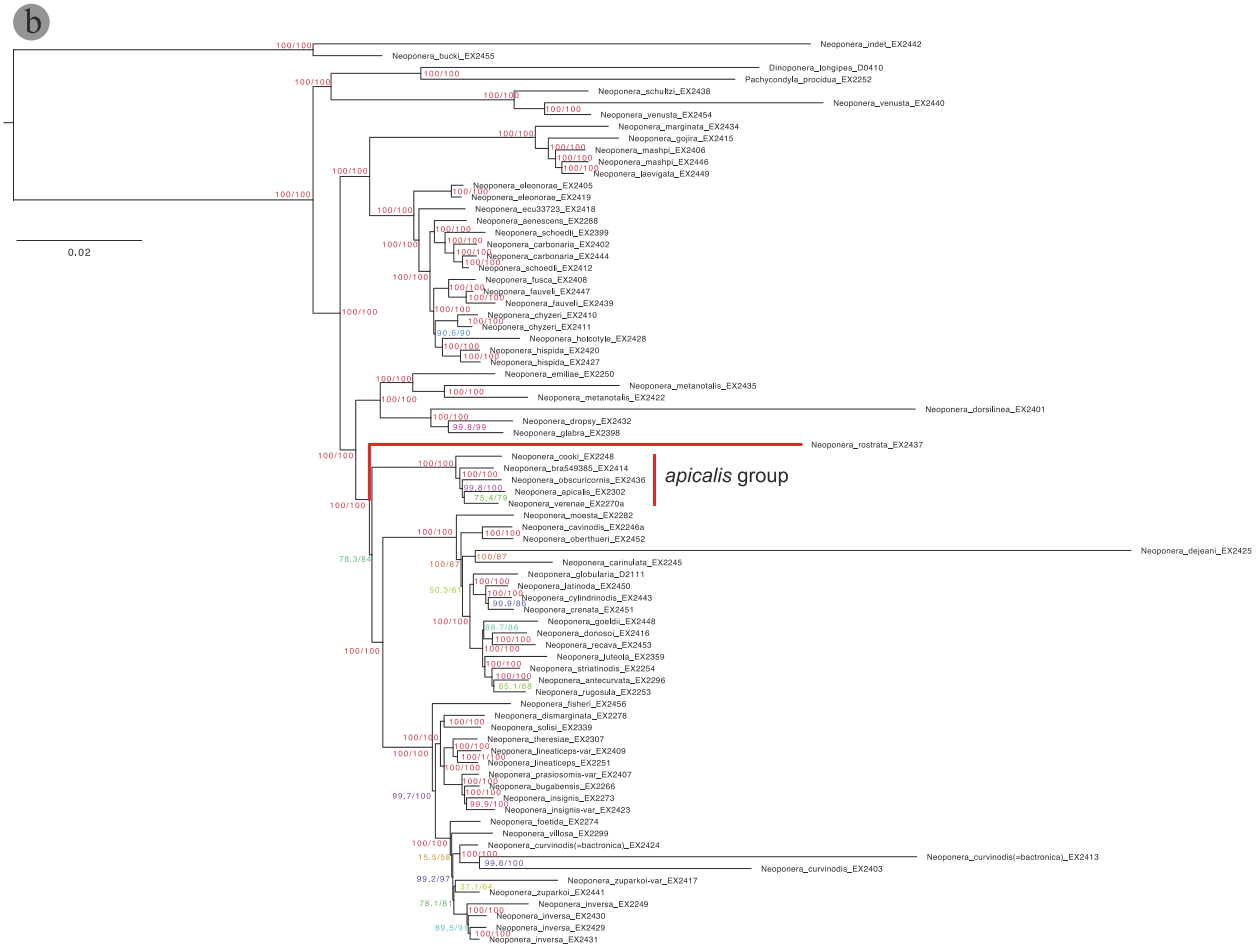
Species-group	Species	Museum	Voucher ID	EX. ID	Caste	Country	Notes
crenata	*Neoponera latinoda*	DZUP	DZUP549353	EX2450	worker	BR	
crenata	*Neoponera luteola*	JTLC	CASENT0649006	EX2359	worker	PE	
crenata	*Neoponera crenata*	MEPN	CASENT0649900	EX2451	worker	BR	
crenata	*Neoponera oberthueri*	DZUP	DZUP549437	EX2452	worker	BR	
crenata	*Neoponera recava*	UTIC	UTIC00212810	EX2453	worker	EC	
crenata	*Neoponera rugosula*	INBC	INB0003606252	EX2253	worker	CR	
crenata	*Neoponera striatinodis*	JTLC	CASENT0636953	EX2254	worker	CR	
crenata	*Neoponera unidentata*	JTLC	CASENT0636011	EX1650	worker	CR	unresolved issue in sequence
emiliae	*Neoponera concava*	JTLC	CASENT0649901	EX2445	worker	BR	degraded DNA
emiliae	*Neoponera concava*	JTLC	ANTWEB1032620	EX2247	worker	BR	degraded DNA
emiliae	***Neoponera dorsilinea***	CPDC	ATPFOR1965	EX2401	worker	BR	
emiliae	***Neoponera dropsy***	DZUP	ATPFOR1962	EX2432	worker	BR	
emiliae	*Neoponera emiliae*	JTLC	JTLC000015100	EX2250	worker	VE	
emiliae	***Neoponera glabra***	CPDC	ATPFOR1993	EX2421	worker	BR	degraded DNA
emiliae	***Neoponera glabra***	MEPN	CASENT0649888	EX2398	worker	BR	
emiliae	*Neoponera magnifica*	DZUP	DZUP549378	EX2433	worker	BR	degraded DNA
emiliae	*Neoponera metanotalis*	DZUP	UFVLABECOL000625	EX2435	worker	BR	
emiliae	*Neoponera metanotalis*	CPDC	ATPFOR1997	EX2422	worker	BR	
emiliae	*Neoponera schultzi*	MEPN	UFVLABECOL000500	EX2438	worker	BR	
emiliae	*Neoponera venusta*	DZUP	UFVLABECOL000492	EX2440	worker	BR	
emiliae	*Neoponera venusta*	JTLC	DZUP549414	EX2454	worker	BR	
foetida	*Neoponera bactronica*	INPA	INPAHYM033801-2	EX2413	worker	BR	
foetida	*Neoponera bactronica*	DZUP	DZUP549372	EX2424	worker	BR	
foetida	*Neoponera billemma*	INPA	INPAHYM033262	EX2404	worker	BR	degraded DNA
foetida	*Neoponera bugabensis*	JTLC	CASENT0619590	EX2266	worker	NI	
foetida	*Neoponera curvinodis*	JTLC	CASENT0636952	EX2249	queen	CR	
foetida	*Neoponera curvinodis*	INPA	INPAHYM033800	EX2403	worker	BR	
foetida	*Neoponera dismarginata*	JTLC	CASENT0637094	EX2278	worker	CR	
foetida	*Neoponera fisheri*	DZUP	CASENT0843090	EX2456	worker	PA	
foetida	*Neoponera foetida*	JTLC	CASENT0633624	EX2274	worker	PA	
foetida	*Neoponera insignis*	JTLC	CASENT0633623	EX2273	worker	PA	
foetida	*Neoponera insignis*	PSWC	CASENT0249167	EX2423	worker	PA	variety of *N. insignis*
foetida	*Neoponera inversa*	MEPN	CASENT0649896	EX2429	worker	BR	

Appendix A. ***Continued*.**

Species-group	Species	Museum	Voucher ID	EX. ID	Caste	Country	Notes
foetida	*Neoponera inversa*	MEPN	MEPNINV37891	EX2430	worker	EC	
foetida	*Neoponera inversa*	DZUP	DZUP549387	EX2431	worker	BR	
foetida	*Neoponera lineaticeps*	JTLC	CASENT0610994	EX2409	worker	GU	variety of *N. lineaticeps*
foetida	*Neoponera lineaticeps*	JTLC	CASENT0644884	EX2251	worker	CR	
foetida	***Neoponera prasiosomis***	DZUP	ATPFOR2001	EX2407	worker	PA	
foetida	*Neoponera solisi*	JTLC	INB0003238942	EX2339	worker	CR	
foetida	*Neoponera theresiae*	JTLC	CASENT0649094	EX2307	worker	CR	
foetida	*Neoponera villosa*	JTLC	CASENT0649086	EX2299	worker	MX	
foetida	*Neoponera zuparkoi*	MEPN	MEPNINV2923	EX2417	worker	EC	variety of *N. zuparkoi*
foetida	*Neoponera zuparkoi*	DZUP	DZUP549348	EX2441	worker	PE	
laevigata	*Neoponera commutata*	CASC	casent0217554		queen	VE	sequence not ready
laevigata	*Neoponera gojira*	DZUP	DZUP549444	EX2415	worker	BR	
laevigata	*Neoponera laevigata*	MPEG	ATPFOR2006	EX2449	worker	BR	
laevigata	*Neoponera marginata*	MEPN	CASENT0649897	EX2434	worker	BR	
laevigata	*Neoponera mashpi*	DZUP	DZUP549408	EX2406	worker	FG	
laevigata	*Neoponera mashpi*	JTLC	MEPNINV38315-1	EX2446	worker	EC	
rostrata	*Neoponera agilis*						not available
rostrata	*Neoponera rostrata*	DZUP	DZUP549441	EX2437	worker	BR	
outgroup	*Neoponera bucki*	DZUP	DZUP549431	EX2455	worker	BR	
outgroup	*Neoponera indet*	JTLC	CASENT0649902	EX2442	male	BR	
outgroup	*Pachycondyla procidua*	JTLC	CASENT0646046	EX2252	worker	FG	
outgroup	*Dinoponera longipes*			D0410	worker		

Appendix B. Maximum likelihood trees showing different placement of *N. rostrata* (red branch) with respect to the *apicalis* clade in *Neoponera*. Topologies based on, a. 75% complete matrix, and b. 95% complete matrix. Phylogenetic inference based on same parameters as those used for constructing Fig. 1.




b
Neoponera_indet_EX2442
Neoponera_buckl_EX2455
Dinoponera_longipes_D0410
Pachycondyla_procidua_EX2252
Neoponera_schultzi_EX2438
Neoponera_venusta_EX2440
Neoponera_venusta_EX2454
Neoponera_marginata_EX2434
Neoponera_gojira_EX2415
Neoponera_mashpi_EX2406
Neoponera_mashpi_EX2446
Neoponera_laevigata_EX2449
Neoponera_eleonorae_EX2405
Neoponera_eleonorae_EX2419
Neoponera_ecu33723_EX2418
Neoponera_senescens_EX2288
Neoponera_schoedli_EX2399
Neoponera_carbonaria_EX2402
Neoponera_carbonaria_EX2444
Neoponera_schoedli_EX2412
Neoponera_fusca_EX2408
Neoponera_fauveli_EX2447
Neoponera_fauveli_EX2439
Neoponera_chyzeri_EX2410
Neoponera_chyzeri_EX2411
Neoponera_holcotyle_EX2428
Neoponera_hispida_EX2420
Neoponera_hispida_EX2427
Neoponera_emiliae_EX2250
Neoponera_metanotalis_EX2435
Neoponera_metanotalis_EX2422
Neoponera_dorsilinea_EX2401
Neoponera_dropsy_EX2432
Neoponera_glabra_EX2398
Neoponera_rostrata_EX2437
Neoponera_cooki_EX2248
Neoponera_bra549385_EX2414
Neoponera_obscuricornis_EX2436
Neoponera_apicalis_EX2302
Neoponera_verenae_EX2270a
apicalis group
Neoponera_moesta_EX2282
Neoponera_cavinodis_EX2246a
Neoponera_oberthueri_EX2452
Neoponera_dejeani_EX2425
Neoponera_carinulata_EX2245
Neoponera_globularia_D2111
Neoponera_latinoda_EX2450
Neoponera_cylindrinodis_EX2443
Neoponera_crenata_EX2451
Neoponera_goeldii_EX2448
Neoponera_donosoi_EX2416
Neoponera_recava_EX2453
Neoponera_luteola_EX2359
Neoponera_striatinodis_EX2254
Neoponera_antecurvata_EX2296
Neoponera_rugosula_EX2253
Neoponera_fisheri_EX2456
Neoponera_dismarginata_EX2278
Neoponera_solisi_EX2339
Neoponera_theresiae_EX2307
Neoponera_lineaticeps-var_EX2409
Neoponera_lineaticeps_EX2251
Neoponera_prasiosomis-var_EX2407
Neoponera_bugabensis_EX2266
Neoponera_insignis_EX2273
Neoponera_insignis-var_EX2423
Neoponera_foetida_EX2274
Neoponera_villosa_EX2299
Neoponera_curvinodis(=bactronica)_EX2424
Neoponera_curvinodis(=bactronica)_EX2413
Neoponera_curvinodis_EX2403
Neoponera_zuparkoi-var_EX2417
Neoponera_zuparkoi_EX2441
Neoponera_inversa_EX2249
Neoponera_inversa_EX2430
Neoponera_inversa_EX2429
Neoponera_inversa_EX2431
0.02

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REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle, pp. 267–281. *In* Petrov, B.N., Csaki, F. (eds.), 2nd Int. Symp. Inf. Theory. Springer, Akademia Kiado, Budapest.

Anisimova, M., M. Gil, J. F. Dufayard, C. Dessimoz, and O. Gascuel. **2011**. Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. Syst. Biol. 60: 685–699.

AntCat. **2022**. AntCat (2022) An online catalogue of the ants of the world by Barry Bolton. Available from https//www. antcat.org. (accessed Mar 2022).

AntWeb. **2022**. AntWeb. Calif. Acad. Sci. online https//www.antweb.org. Accessed 14 July 2022.

Auger, C. P. 1975. Use of reports literature. London: Buttelworths.

Bankevich, A., S. Nurk, D. Antipov, A. A. Gurevich, M. Dvorkin, A. S. Kulikov, V. M. Lesin, S. I. Nikolenko, S. Pham, A. D. Prjibelski, A. V. Pyshkin, A. V. Sirotkin, N. Vyahhi, G.

Tesler, M. A. Alekseyev, and P. A. Pevzner. **2012**. SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. J. Comput. Biol. 19: 455–477.

Blanchard, B. D., and C. S. Moreau. **2017**. Defensive traits exhibit an evolutionary trade-off and drive diversification in ants. Evolution (N. Y). 71: 315–328.

Bolger, A. M., M. Lohse, and B. Usadel. **2014**. Trimmomatic: A flexible trimmer for Illumina sequence data. Bioinformatics. 30: 2114–2120.

Borowiec, M. L., C. Rabeling, S. G. Brady, B. L. Fisher, T. R. Schultz, and P. S. Ward. **2019**. Compositional heterogeneity and outgroup choice influence the internal phylogeny of the ants. Mol. Phylogenet. Evol. 134: 111–121.

Branstetter, M. G. 2013. Revision of the Middle American clade of the ant genus Stenamma Westwood (Hymenoptera, Formicidae, Myrmicinae). Zookeys. 295: 1–277.

Branstetter, M. G., and J. T. Longino. **2022**. UCE Phylogenomics of New World Cryptopone (Hymenoptera: Formicidae) Elucidates Genus Boundaries, Species Boundaries, and the Vicariant History of a Temperate–Tropical Disjunction. Insect Syst. Divers. 6.

Branstetter, M. G., J. T. Longino, P. S. Ward, and B. C. Faircloth. **2017**. Enriching the ant tree of life: enhanced UCE bait set for genome-scale phylogenetics of ants and other Hymenoptera. Methods Ecol. Evol. 8: 768–776.

Brown, B. Y. W. L. 1957. Centrifugal speciation. Q. Rev. Biol. 32: 247–277.

Camacho, G. P., W. Franco, M. G. Branstetter, M. R. Pie, J. T. Longino, T. R. Schultz, and R. M. Feitosa. **2022**. UCE Phylogenomics Resolves Major Relationships Among Ectaheteromorph Ants (Hymenoptera: Formicidae: Ectatomminae, Heteroponerinae): A New Classification For the Subfamilies and the Description of a New Genus. Insect Syst. Divers. 6.

Colinvaux, P. A., P. E. De Oliveira, and M. B. Bush. **2000**. Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. Quat. Sci. Rev. 19: 141–169.

Davidson, D., S. Cook, R. Snelling, and T. Chua. **2010**. Explaining the Abundance of Ants in Lowland Tropical Rainforest Canopies. ScienceScience. 300: 969–972.

Delabie, J. H. C., C. D. S. F. Mariano, L. F. Mendes, S. das Graças Pompolo, and D. Fresnau. **2008**. Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no gênero Pachycondyla na região neotropical: o caso do complexo apicalis.

Emery, C. 1911. Hymenoptera. Fam. Formicidae. Subfam. Ponerinae, p. 124. *In* Wytsman, P. (ed.), Genera Insectorum. Bologne.

Eo, S. H., and J. A. DeWoody. **2010**. Evolutionary rates of mitochondrial genomes correspond to diversification rates and to contemporary species richness in birds and reptiles. Proc. R. Soc. B Biol. Sci. 277: 3587–3592.

Erwin, T. L. 2001. Forest canopies, animal diversity. *In* Encicl. Biodiversityciclopedia Biodivers. 3.

Faircloth, B. C. 2016. PHYLUCE is a software package for the analysis of conserved genomic loci. Bioinformatics. 32: 786–788.

Faircloth, B. C., J. E. McCormack, N. G. Crawford, M. G. Harvey, R. T. Brumfield, and T. C. Glenn. **2012**. Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. Syst. Biol. 61: 717–726.

Faircloth, B. C., L. Sorenson, F. Santini, and M. E. Alfaro. **2013**. A Phylogenomic Perspective on the Radiation of Ray-Finned Fishes Based upon Targeted Sequencing of Ultraconserved Elements (UCEs). PLoS One. 8.

Federle, W., M. Riehle, A. S. G. Curtis, and R. J. Full. **2002**. An integrative study of insect adhesion: Mechanics and wet adhesion of pretarsal pads in ants. Integr. Comp. Biol. 42: 1100–1106.

Feng, S., M. Bai, I. Rivas-González, C. Li, S. Liu, Y. Tong, H. Yang, G. Chen, D. Xie, K. E. Sears, L. M. Franco, J. D. Gaitan-Espitia, R. F. Nespolo, W. E. Johnson, H. Yang, P. A. Brandies, C. J. Hogg, K. Belov, M. B. Renfree, K. M. Helgen, J. J. Boomsma, M. H. Schierup, and G. Zhang. **2022**. Incomplete lineage sorting and phenotypic evolution in marsupials. Cell. 185: 1646-1660.e18.

Fernandes, I. O., M. L. De Oliveira, and J. H. C. Delabie. **2014**. Description of two new species in the Neotropical Pachycondyla foetida complex (Hymenoptera: Formicidae: Ponerinae) and taxonomic notes on the genus. Myrmecological News. 19: 133–163.

Fiorentino, G., J. Lattke, A. Troya, C. Sosiak, M. Dong, and P. Barden. **2022**. Deep time extinction of largest insular ant predators and the first fossil Neoponera (Formicidae: Ponerinae) from Miocene age Dominican amber. BMC Biol. 1–12.

Forel, A. 1912. Formicides néotropiques. Part I. Ann. la Société Entomol. Belgique.

Freeland, J., R. H. Crozier, and J. Marc. **1982**. on the Occurrence of Arolia in Ant Feet. Aust. J. Entomol. 21: 257–262.

Glenn, T. C., R. A. Nilsen, T. J. Kieran, J. G. Sanders, N. J. Bayona-Vásquez, J. W. Finger, T. W. Pierson, K. E. Bentley, S. L. Hoffberg, S. Louha, F. J. Garcia-De Leon, M. A. Del Rio Portilla, K. D. Reed, J. L. Anderson, J. K. Meece, S. E. Aggrey, R. Rekaya, M. Alabady, M. Belanger, K. Winker, and B. C. Faircloth. **2019**. Adapterama I: Universal stubs and primers for 384 unique dual-indexed or 147,456 combinatorially-indexed Illumina libraries (iTru & iNext). PeerJ. 2019: 1–31.

Guindon, S., J. F. Dufayard, V. Lefort, M. Anisimova, W. Hordijk, and O. Gascuel. **2010**. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. Syst. Biol. 59: 307–321.

Gutiérrez-Valencia, J., G. Chomicki, and S. S. Renner. **2017**. Recurrent breakdowns of mutualisms with ants in the neotropical ant-plant genus Cecropia (Urticaceae). Mol. Phylogenet. Evol. 111: 196–205.

Hoang, D. T., O. Chernomor, A. Von Haeseler, B. Q. Minh, and L. S. Vinh. **2018**. UFBoot2: Improving the ultrafast bootstrap approximation. Mol. Biol. Evol. 35: 518–522.

Hughes, C., and R. Eastwood. **2006**. Island radiation on a continental scale : Exceptional rates of plant diversification after uplift of the Andes. 2006.

Hurvich, C. M., and C. - L Tsai. **1993**. A Corrected Akaike Information Criterion for vector autoregressive model selection. J. Time Ser. Anal. 14: 271–279.

ICZN. **1999**. International Code of Zoological Nomenclature. Int. Trust Zool. Nomencl.

Kalyaanamoorthy, S., B. Q. Minh, T. K. F. Wong, A. Von Haeseler, and L. S. Jermiin. **2017**. ModelFinder: Fast model selection for accurate phylogenetic estimates. Nat. Methods. 14: 587–589.

Katoh, K., G. Asimenos, and H. Toh. **2009**. Multiple Alignment of DNA Sequences with MAFFT. Springer.

Kolmer, H. 2002. Co-operation and conflict in societies of the ponerine ant genus Pachycondyla Kooperation und Konflikt in Staaten der Ameisengattung Pachycondyla. 109.

Leal, I. R., and P. S. Oliveira. **1995**. Behavioral ecology of the neotropical termite-hunting ant Pachycondyla (= Termitopone) marginata: colony founding, group-raiding and migratory patterns. Behav. Ecol. Sociobiol. 37: 373–383.

Lecocq de Pletincx, N., S. Dellicour, and S. Aron. **2021**. The evolution of ant worker polymorphism correlates with multiple social traits. Behav. Ecol. Sociobiol. 75.

Lemmon, A. R., J. M. Brown, K. Stanger-Hall, and E. M. Lemmon. **2009**. The effect of ambiguous data on phylogenetic estimates obtained by maximum likelihood and bayesian inference. Syst. Biol. 58: 130–145.

Longino, J. 2010. Ants of Costa Rica. (https://ants.biology.utah.edu/AntsofCostaRica.html).

Löytynoja, A., and N. Goldman. **2008**. Phylogeny-aware gap placement prevents errors in sequence alignment and evolutionary analysis. Science (80-.). 320: 1632–1635.

Lucky, A., M. Trautwein, G. Benoit, M. Weiser, and R. Dunn. **2013**. Tracing the Rise of Ants - Out of the Ground. PLoS One. 8: e84012.

MacKay, W., and E. Mackay. **2010**. The systematics and biology of the New World ants of the genus Pachycondyla (Hymenoptera: Formicidae). Edwin Mellen Press.

Mendoza-Ramírez, M., J. Gutiérrez-Rodríguez, C. Poteaux, P. Ornelas-García, and A. Zaldívar-Riverón. **2019**. Late Pleistocene genetic diversification and demographic expansion in the widely distributed neotropical ant Neoponera villosa (Ponerinae). Mitochondrial DNA Part A DNA Mapping, Seq. Anal. 30: 296–306.

Mill, A. E. 1984. Predation by the ponerine ant Pachycondyla commutata on termites of the genus Syntermes in Amazonian rain forest. J. Nat. Hist. 18: 405–410.

Minh, B. Q., M. A. T. Nguyen, and A. Von Haeseler. **2013**. Ultrafast approximation for phylogenetic bootstrap. Mol. Biol. Evol. 30: 1188–1195.

Nguyen, L. T., H. A. Schmidt, A. Von Haeseler, and B. Q. Minh. **2015**. IQ-TREE: A fast and

effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol. Biol. Evol. 32: 268–274.

Oster, G. F., and E. O. Wilson. **1978**. Caste and ecology in the social insects. Princeton University Press, Princeton.

Paez, A. 2017. Gray literature: An important resource in systematic reviews. J. Evid. Based. Med. 10: 233–240.

Pollard, D. A., V. N. Iyer, A. M. Moses, and M. B. Eisen. **2006**. Widespread Discordance of Gene Trees with Species Tree in Drosophila: Evidence for Incomplete Lineage Sorting. PLOS Genet. 2: e173.

Price, S. L., S. Powell, D. J. C. Kronauer, L. A. P. Tran, N. E. Pierce, and R. K. Wayne. **2014**. Renewed diversification is associated with new ecological opportunity in the Neotropical turtle ants. J. Evol. Biol. 27: 242–258.

Rohland, N., and D. Reich. **2012**. Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. Genome Res. 22: 939–946.

Schmidt, C. 2013. Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). 3647: 201–250.

Schmidt, C. A., and S. O. Shattuck. **2014**. The Higher Classification of the Ant Subfamily Ponerinae (Hymenoptera: Formicidae), with a Review of Ponerine Ecology and Behavior.

Schonberg, L. A., J. T. Longino, N. M. Nadkarni, S. P. Yanoviak, and J. C. Gering. **2004**. Arboreal ant species richness in primary forest, secondary forest, and pasture habitats of a tropical montane landscape. Biotropica. 36: 402–409.

Schwartz, R. S., and R. L. Mueller. **2010**. Branch length estimation and divergence dating: Estimates of error in Bayesian and maximum likelihood frameworks. BMC Evol. Biol. 10.

Schwarz, G. 1978. Estimating the Dimension of a Model. Ann. Stat. 6: 461–464.

Seyfullah, L. J., C. Beimforde, J. Dal Corso, V. Perrichot, J. Rikkinen, and A. R. Schmidt. **2018**. Production and preservation of resins – past and present. Biol. Rev. 93: 1684–1714.

Swofford, D. L., P. J. Waddell, J. P. Huelsenbeck, P. G. Foster, P. O. Lewis, and J. S. Rogers. **2001**. Bias in phylogenetic estimation and its relevance to the choice between parsimony and

likelihood methods. Syst. Biol. 50: 525–539.

Talavera, G., and J. Castresana. **2007**. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst. Biol. 56: 564–577.

Tamura, K., F. U. Battistuzzi, P. Billing-Ross, O. Murillo, A. Filipski, and S. Kumar. **2012**. Estimating divergence times in large molecular phylogenies. Proc. Natl. Acad. Sci. U. S. A. 109: 19333–19338.

Tamura, K., G. Stecher, and S. Kumar. **2021**. MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Mol. Biol. Evol. 38: 3022–3027.

To, T. H., M. Jung, S. Lycett, and O. Gascuel. **2016**. Fast Dating Using Least-Squares Criteria and Algorithms. Syst. Biol. 65: 82–97.

Troya, A., and J. Lattke. **2022**. Neoponera Emery, 1901 (Hymenoptera: Formicidae) revisited: 1. The N. laevigata species-group. Insect Syst. Evol. 1901: 1–76.

Tschinkel, W. R. 1988. Colony growth and the ontogeny of worker polymorphism in the fire ant, Solenopsis invicta. Behav. Ecol. Sociobiol. 22: 103–115.

Ward, P. S., B. B. Blaimer, and B. L. Fisher. **2016**. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera Colobopsis and Dinomyrmex. Zootaxa. 4072: 343–357.

Ward, P. S., and B. E. Boudinot. **2021**. Grappling with homoplasy: taxonomic refinements and reassignments in the ant genera Camponotus and Colobopsis (Hymenoptera: Formicidae). Arthropod Syst. Phylogeny. 79: 37–56.

Ward, P. S., S. G. Brady, B. L. Fisher, and T. R. Schultz. **2015**. The evolution of myrmicine ants: Phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Syst. Entomol. 40: 61–81.

Wheeler, D. E. 1991. The developmental basis of worker caste polymor- phism in ants. Am. Nat. 138: 1218–1238.

Wheeler, W. 1936. Ecological relations of ponerine and other ants to termites. Proc. Am. Acad. Arts Sci. 71: 158–243.

Wiley, E. O., and B. S. Lieberman. **2011**. Phylogenetics: Theory and practice of phylogenetic

systematics, Second edi. ed. Wiley-Blackwell.

Wills, B. D., S. Powell, M. D. Rivera, and A. V. Suarez. **2018**. Correlates and Consequences of Worker Polymorphism in Ants. Annu. Rev. Entomol. 63: 575–598.

Yagound, B., R. Gouttefarde, C. Leroy, R. Belibel, C. Barbaud, D. Fresneau, S. Chameron, C. Poteaux, and N. Châline. **2015**. Fertility Signaling and Partitioning of Reproduction in the Ant Neoponera apicalis. J. Chem. Ecol. 41: 557–566.

CHAPTER II

SUBCHAPTER I

Neoponera Emery, 1901 (Hymenoptera: Formicidae) revisited: 1. The *N. laevigata* species-group

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***Neoponera* Emery, 1901 (Hymenoptera: Formicidae) revisited: 1. The *N. Laevigata* species–group**

ABSTRACT

The Neotropical *Neoponera laevigata* species–group is revised. This group can be separated from others in the genus by means of a new key to *Neoponera* species–groups. We propose two new species, *N. gojira* sp. nov., and *N. mashpi* sp. nov., the latter being usually confused with its putative sister species, *N. laevigata* (Smith). This small, termite–feeding species–group now contains five taxa. We provide comprehensive redescriptions for the known castes of the three previously known species, together with images and notes about intraspecific morphological variation, biology, and distribution of the taxa here treated. We reveal the external morphological features of the genitalia of the known males. This is the first contribution en route to a better understanding of the systematics of this charismatic ponerine genus.

Keywords: Neotropical Region, polymorphism, Ponerinae, termite–hunting, Termitopone.

ZooBank: https://zoobank.org/490A02AE-77DC-435E-A673-E87C2C288A7A

INTRODUCTION

Neoponera Emery is a behaviorally and morphologically diverse group of ground and mostly arboreal, solitary hunting ants which inhabit exclusively tropical and sub–temperate regions of the Americas (Schmidt & Shattuck 2014). A few species, like *N. apicalis* (Latreille) and *N. villosa* (Fabricius) are recognizable at a glance, whereas most of the remaining taxa require detailed examination, and little is known about the natural history of most species. Schmidt & Shattuck (2014) provide a good primer about various aspects of their social and reproductive behavior, nesting ecology, chemical communication, and some other details on the biology of a few well–studied *Neoponera*.

Neoponera is closely related to *Pachycondyla* Smith, with which it shares numerous morphological features (Schmidt & Shattuck 2014). Emery (1901) erected *Neoponera*, and in his work he described the genus as "the American *Pachycondyla* with keeled cheeks" (p. 43), i.e. with malar carina, which separated them from the true *Pachycondyla* and other related Neotropical forms, like *Mayaponera* Schmidt and Shattuck. Although this character probably proved useful for earlier researchers distinguishing *Neoponera* species from similar ponerines, a number of taxonomic issues emerged as the material increased in collections. The apparent lack of synapomorphies among several *Pachycondyla*–related groups probably led Brown (1973) to synonymize all of them under *Pachycondyla*. Prior to Schmidt (2013), who provided a phylogenetic classification framework for the whole subfamily Ponerinae based on molecular data, *Pachycondyla*, as formerly considered, remained broadly accepted (Bolton 1995, Mackay & Mackay 2010, Fernandes et al. 2014).

Schmidt and Shattuck (2014) revived *Neoponera* from synonymy and transferred to it some species previously considered in *Eumecopone*, *Mesoponera, Pachycondyla*, and *Termitopone*. This latter is composed of termite feeding specialists which is considered a unique behavioral trait within the genus. Mackay & Mackay (2010) assigned them to the *N. laevigata* species–complex, but here we treat it as a species–group. Despite being revised twice (see details below), in the last years, as part of a complete revision of the genus which is currently ongoing, we have found new information about this small, but certainly iconic clade. In addition, we detected that most of the material which is frequently assigned to the commonly collected *N. laevigata* (Smith), in fact belongs to a new species which we describe here. Also, based on new

morphological information we provide detailed descriptions for all known castes, along with notes, in most cases, about intra– and interspecific morphological variation, biology and distribution.

MATERIALS AND METHODS

Repositories of examined material

Morphological observations are based on close to 400 specimens which are deposited in the following institutions. Within that number, 16 specimens were examined through high quality images available online on AntWeb (www.antweb.org). Museum abbreviations are based on Arnett et al (2019).

ALWC	Alex L. Wild Collection, TX, USA.
BMNH	The British Museum of Natural History, London, U.K.
CASC	California Academy of Sciences, San Francisco, CA, USA.
CPDC	Coleção do Laboratório de Mirmecologia, Centro de Pesquisas do Cacau, Ilhéus, Bahia, Brazil.
DZUP	Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil.
ECOFOG	EcoFoG–Joint Research Unit Ecology of Guianan Forests, Kourou, French Guiana.
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia.
INBC	Instituto Nacional de Biodiversidad, Heredia, Costa Rica.
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil.
JTLC	John T. Longino Collection, University of Utah, Salt Lake City,

	UT, USA.
LACM	Los Angeles County Museum, LA, USA.
MECN	Museo Ecuatoriano de Ciencias Naturales, Instituto Nacional de Biodiversidad, Quito, Ecuador.
MPEG	Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.
MEPN	Museo de Historia Natural "Gustavo Orcés V.", Escuela Politécnica Nacional, Quito, Ecuador.
MIZA	Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
MUCR	Colección de Insectos, Universidad de Costa Rica, San Pedro, Costa Rica.
MUSENUV	Museo de Entomología de la Universidad del Valle, Cali, Colombia.
PSWC	Philip S. Ward Collection, University of California, Davis, CA, USA.
QCAZ	Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
UFVLABECOL	Laboratório de Ecologia de Comunidades, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

Imaging

Images were taken using a Canon® EOS DSLR 70D with a Laowa® 25mm F2.8, 2.5X – 5.0X macro lens, coupled to a Cognisys StackShot® macro rail system which enabled depth–focus shooting through Helicon Remote v. 3.9.9, and posterior stacking in Helicon Focus v. 7.5.6 (Helicon Soft Ltd.). A dome–shaped, cold–light (LED) source was used for illumination. Images

of type material and some non–type specimens, as well as collection data of all examined specimens with a unique specimen identifier (a unique code) in this work are available online on AntWeb (but see further below in “Material examined”).

Images and illustrations by A. Troya, except those in Figures: 5b (by Júlio Chaul), 8a (by April Nobile), and 20a, b, c, f (by Will Ericson), available on AntWeb.org. SEM images in Figures 14a, b and 18b by Paula Carolina Ferreira, Centro de Microscopia Eletrônica, Universidade Federal do Paraná.

Morphometric variables

All observations and measurements of the following morphological variables [Figure 1, and Supplementary Material 1 (available online)] were taken using a pin–holding stage, allowing rotations around the X, Y, and Z axes at magnifications from 8X to 50X with an ocular micrometer incorporated to a Zeiss® Stemi SV6 stereo microscope.

Measurements are presented in mm with an accuracy of two decimal places, minimum and maximum values are indicated when more than one specimen was measured. Most of our measurements are in line with those previously used in other ponerine taxonomic studies, e.g., Lattke (2012), Rakotonirina and Fisher (2013), Fernandes et al. (2014), Longino and Branstetter (2020). Other measurements, e.g., length of gastral sclerites, are less common in Formicidae taxonomy and its use is intended to support the body of typically used morphological variables in discriminating difficult–to–discern variations across populations in a given species. Criteria for selecting specimens for measurement follow each species' known distribution, by picking up a number of differently sized specimens per collection site, when available. Morphometric variables facilitate, to a certain degree, examining across the morphospace the intra– and inter–population variability in the set of treated species. This is also useful as another line of evidence for testing and/or supporting species hypotheses.

HL Head length. In frontal view, maximum distance from the posterior margin of head to the anterior margin of clypeus.

HW Head width. In frontal view, maximum width of head, excluding the eyes.

EL Eye length. In lateral view, measured along its maximum length.

SL Scape length. In frontal view, maximum length of scape excluding its basal condyle and neck.

PrW Pronotum width. In dorsal view, maximum width of pronotum.

WL Weber's length. In lateral view, distance between the anterior margin of pronotum, excluding collar, to the posteroventral margin of metapleuron.

MsW Mesonotum width. In dorsal view, maximum width of mesonotum.

MsL Mesonotum length. In a dorsal view, the maximum distance from the anterior margin of the mesonotum to its posterior margin.

PW Petiolar width. In dorsal view, maximum width of the petiolar node.

PH Petiolar height. In lateral view, the perpendicular distance from the posteroventral lobe of the petiolar tergite to its maximum dorsal margin.

PL Petiolar length. In a lateral view, the distance between the anteriormost margin of petiole to its posterior margin, excluding the posteroventral ridge.

GL Gaster length. In lateral view, the oblique distance between the anterior margin of abdominal segment III to the posterior margin of the pygidium, excluding the sting. This is a relative measure since it can vary in relation to the extension or contraction of abdominal segments IV to VII.

A3L Abdominal segment III length. In dorsal view, the distance between the anterior and posterior margin of abdominal tergite III.

A3W Abdominal segment III width. In dorsal view, maximum width of tergite of abdominal segment III.

A4L Abdominal segment IV length. In dorsal view, the distance between the anterior and posterior margins of abdominal tergite IV.

A4W Abdominal segment IV width. In dorsal view, maximum width of tergite of abdominal segment IV.

TLa Total accurate length of body: HL + WL + PL + A3L + A4L

TLr Total relative length of body: HL + WL + PL + GL

Indices

The following ratios were multiplied by 100:

CI Cephalic index: HW/HL

OI Ocular index: EL/HW

SI Scape index: SL/HW

MsI Mesonotum index: MsW/MsL

LPI Lateral petiolar index: PL/PH

DPI Dorsal petiolar index: PW/PL

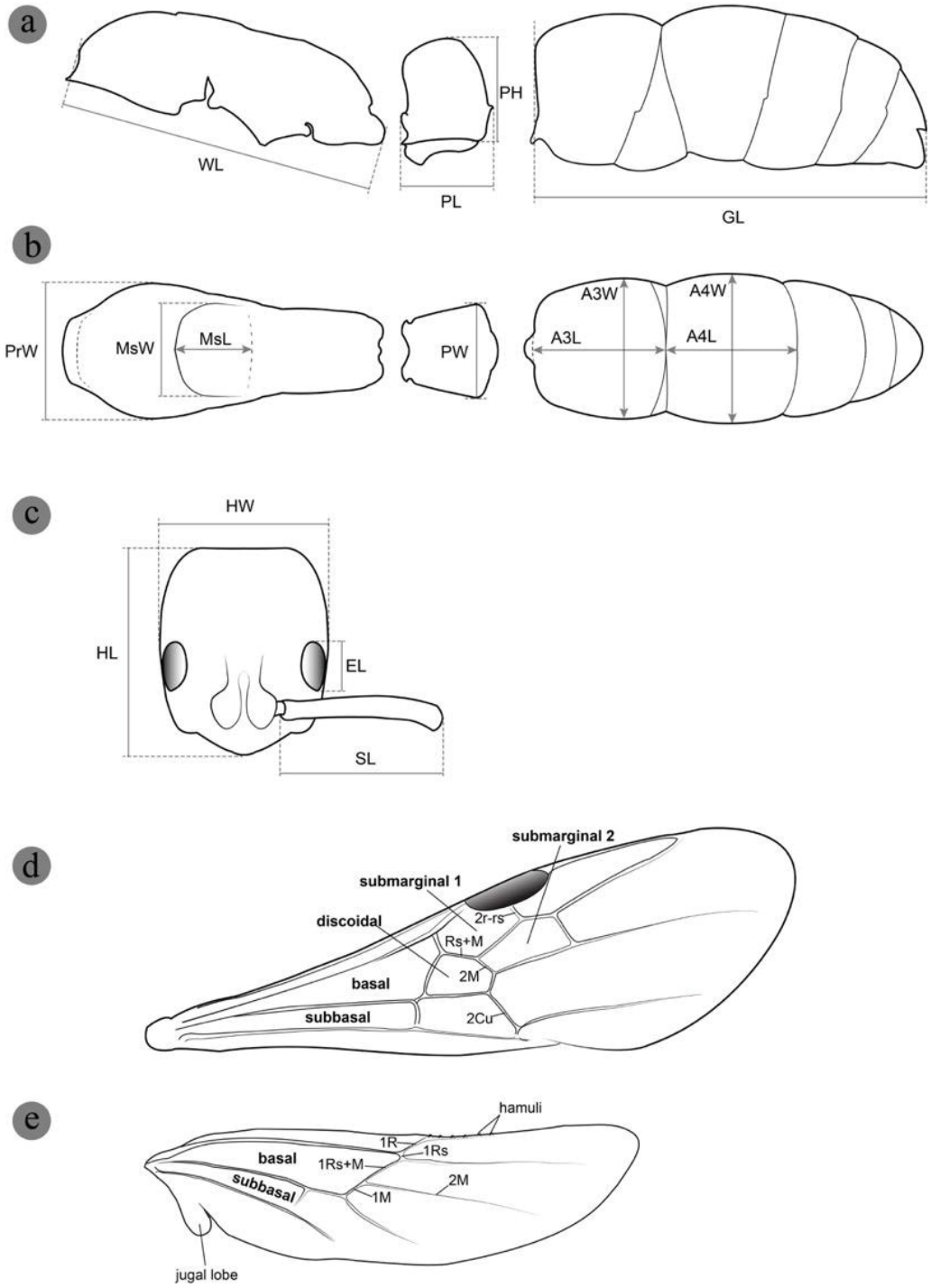


Fig. 1. Morphometric variables and wing venation (valid for male & female). **a.** GL: gaster length, PH: petiolar height, PL: petiolar length, WL: Weber's length; **b.** A3L: Abdominal segment III length, A3W: Abdominal segment III width, A4L: Abdominal segment IV length, A4W: Abdominal segment IV width, MsL: mesonotum length, MsW: mesonotum width, PW: petiolar width, PrW: pronotum width; **c.** EL: eye length, HL: head length, HW: head width, SL: scape length; **d.** Fore wing; **e.** Hind wing. Only some cells (in bold) and veins are shown since these are cited in the species descriptions.

Distribution maps

We used the open–source package Quantum GIS 2.18 to generate maps of distribution, based on coordinates written on specimen labels and from notes recorded in field books from the authors. All localities were transformed to decimal degrees. Google Earth (Google.com 2021), and the online conversion tool NCAT (National Geodetic Survey 2021) were used as information sources to check and confirm locality names. In regards to unusual records without specific localities which were below the administrative circumscription of state, province, or similar, the center of the next most specific site was georeferenced. We also included in the maps, appropriately labeled AntWeb records of *N. commutata* Roger and *N. marginata* Roger for which we were confident on their taxonomic and geographic information. Selected AntWeb records belonging to these two common taxa were identified by ant taxonomists, for example, Alex Wild, Bryan Fisher, Flavia Esteves, Jack Longino. Due to their unique morphology within *Neoponera* these are easily identifiable species, showing low morphological variation across their range of distribution, thus making misidentifications unlikely.

Jack Longino (lead researcher in several Central American ant survey campaigns) aided in examining diagnostic characters from representative AntWeb records of *N. laevigata* from Costa Rica and Panama. This was required since we believe most *N. laevigata* specimens from these countries are confused with *N. mashpi* **sp. nov.** (see below under each species treatment).

Morphometric analysis

Due to imbalance among the number of measured specimens per caste, namely 59 workers vs 15 reproductives, we chose only the former caste for creating the data matrix which incorporates 24 morphological variables.

Using the package vegan v2.5–7 (Oksanen et al. 2015) implemented in R (R Core Team 2021), we first analyzed the data using principal components analysis (PCA) to visually explore the relative quality of each morphometric variable as shown in the factor map of a circular correlation plot (Figure 1, Supplementary material 3, available online). We also calculated the amount of retained variance by each of the 10 dimensions in the PCA by means of the eigenvalues (Figure 2, Supplementary material 3, available online). The eigenvalues are useful for determining the number of principal components to retain in a PCA (Kaiser 1961). Since our main goal for using ordination techniques is to statistically discern differences among our species set,

particularly between the highly similar *N. mashpi* **sp. nov.** and *N. laevigata* with respect to the morphometric variables, we chose to use non–metric multidimensional scaling (NMDS) for representing the final plot due to its robustness in handling non–parametric data, as well as its versatility in allowing the use of a range of dissimilarity indices. We used the following basic parameters for generating the NMDS ordination: No. of dimensions (*K*): 2 – 4 (though, the final result is represented in dimensions 1 & 2, since dimensions 3 & 4 returned unrealistic results); method for calculating the dissimilarity matrix (*distance*): *euclidean*; No. of permutations (*trymax*) set to 1000. In order to examine potential global differences among the whole set of species we ran a permutational multivariate analysis of variance (PERMANOVA), using the *adonis* function, with 1000 permutations, and the *gower* method (Gower 1971) for calculating *pairwise distances*. Finally, for examining statistical differences between each species pair, we ran a pairwise contrast analysis using the function *pairwise.adonis* (Pedro Martinez Arbizu, unpublished) with a *Bonferroni* adjustment. The user can find the annotated script containing the full commands for performing and plotting the statistical analyses in the Supplementary Material 4 (available online).

Morphological terms

General morphological terminology follows mainly Bolton (1994), Keller (2011), Boudinot (2015), Silva & Feitosa (2019), and the Hymenoptera Anatomy Ontology – HAO (Yoder et al. 2010). Surface sculpture is based mainly on Harris (1979). Male and female forewing venation on Ogata (1991), and Cantone (2017); hind wing venation on Cantone & Von Zuben (2019). Degree of pilosity inclination follows Wilson (1955), Serna & Mackay (2010): 0°– 5°for appressed hairs running parallel or nearly parallel to body surface; 10°– 20° for decumbent hairs slightly standing from surface; 20°– 40° for subdecumbent hairs; 40°– 70° for suberect hairs; and more than 70° for erect hairs when these stand vertical or nearly vertical. For male genitalia we followed Boudinot (2013) and Tozetto & Lattke (2020). Palp formula is denoted by "PF" followed by the number of maxillary and labial segments, for example, PF: 4, 4, which means that both appendices have four segments. Tibial spur formula is denoted by "s" – simple, and "p" – pectinate, for example, 2(1s, 1p) which means that two spurs are present, one simple, and 1 pectinate.

Descriptions and material examined

We used the computer package DELTA (Dallwitz 1980) for encoding the attributes of species (character states) and subsequently translating them into natural language (RTF–rich text

files) taxonomic descriptions, requiring only posterior final editing from the user. Transcription of the collection information of examined specimens, from a spreadsheet data matrix to correspondent RTF file, was mostly done using AUTOMATEX (Brown 2013).

Under "status as species" in the taxonomic history of each species, only their first appearance in the taxonomic literature is cited, as well as relevant redescriptions which are usually part of revisionary studies. The user can access the complete history of literature mentions for each species on the Online Catalogue of the Ants of the World – AntCat (AntCat by B. Bolton 2022).

Although the "material examined" section represents the complete set of recorded localities in this work, it does not contain the whole list of specimens/locality. We have included, however, at the beginning of each section the total number of specimens/caste/species examined. The reader can freely download from the Supplementary Material 2 (available online) the full list of specimen records containing collection and geographic information, most of which have unique specimen identifiers.

The format of type material follows: [# specimens examined], [country], [first administrative region], [second administrative region or, if known, specific locality], [coordinates in decimal degrees], [elevation in meters], [collection date in format yyyy–mm–dd], [collector], [method of collection (if known)], [habitat (if known)], and [institution where the material is located, usually represented by a unique specimen identifier composed of capitalized letters and numbers]. The format for "Other material examined" is essentially equal except that unique specimen identifiers are not shown, but museum acronyms are.

Relationships among taxa

In this work we have chosen to add brief comments about the relationships between species within the *N. laevigata* group, and also between *Neoponera* and a newly recognized clade (see further below). Our statements are grounded on prior studies by Schmidt (2013) and Branstetter & Longino (2022), as well as on molecular-based preliminary results (A. Troya, J. Longino, M. Branstetter et al. unpublished) which are part of a larger ongoing collaborative study about the phylogeny of the genus *Neoponera* which will be published separately. This additional information is not to be treated as conclusive, nevertheless we think it adds support to our morphology–based arguments around the species hypotheses shown here.

Species delimitation

We follow the biological species concept *sensu* Mayr (1942) by considering species as population assemblages which are under presumed continuous gene flow. Since we did not directly assess this process, our criterion for species delimitation was to detect a continuum of expected character gradations lacking discontinuities among distinctive populations. In sympatry, interspecific gene flow can obscure populational distinctness (Arnold 1992, Field et al. 2011). In such case species can be detected by consistently grouping morphologically similar individuals assumed to belong to structured populations, which is a proxy for gene flow (Wild 2005).

The species hypotheses presently proposed, especially the newly described taxa, should be evaluated in further studies using additional information criteria, e.g., population genetics, natural history observations. These will add more objective evidence aiding in the discrimination of species boundaries among cryptic populations which may potentially be under differing selective pressures that are suspected, yet untested in this study.

RESULTS

Morphology

The following few terms are defined in detail to aid in the comprehension of this treatment. In regards to the comparatively complex male external morphological terminology the user can consult Boudinot (2013, 2015), and HAO.

Mesosternal (msp) and metasternal (mtp) processes (Figures: 16d, 19f, 20e, 22f, 25e): also called articular coxal processes of the meso– and metapectus (see HAO): in ants, especially in the Ponerinae, a pair of ventrally directed extensions of the cuticle, usually with acute or blunt apices, emerge medially from the meso– and metasternon. Each of these emerge either immediately posterior– or just around the mesosternal and metasternal pits, respectively, approximately in between the coxal cavities. When present, these structures may vary considerably in size, external shape and orientation, though probably the most generalized is the triangular–shaped form with acute apices, easily discernible in posteroventral view when the posterior coxae are oriented laterally (not posterad as is usual). In *Neoponera*, their presence/absence, as well as their size and shape, are considered useful character–states aiding in species and species-groups

distinction.

Pheromone venting canal (fvc) at the metapleural gland opening (Figure 2): a depression of the cuticle located just anteriorly and below the orifice of the metapleural gland. This structure is present in virtually all Ponerinae and is located at the posteroventral margin of the propodeum. It varies in depth, being clearly concave, e.g., *Neoponera commutata*, to shallowly concave, e.g., *Megaponera analis* (Latreille). In most *Neoponera* it is flanged posteriorly by a cuticular flap, and dorsally by an excavated edge of the propodeum.

Anteroventral petiolar carina: a transverse ridge located near the ventral part of the anterior face of tergite of A2 (petiolar node), relatively close to the petiolar condyle which articulates with the propodeal foramen, as seen in dorsal view. In Ponerinae, when well–developed, this carina usually extends anterolaterad forming salient, either acute or blunt projections ("spiracular horns" in Mackay and Mackay 2010). Two variations are recognized: complete and incomplete carina. In the first state, the carina runs horizontally uninterrupted connecting both anterolateral nodal projections, e.g., *Leptogenys luederwalti* Forel, *Loboponera nasica* (Santschi). When it is incomplete, it disappears medially on the petiolar tergite, leaving the nodal projections virtually unconnected, in which case these usually are notoriously salient. An incomplete carina is the norm in *Neoponera*, e.g., *Neoponera verenae* Forel, *N. commutata*, *N. villosa*, as well as in most ponerines. Within *Neoponera*, a complete carina is found for example, in *N. apicalis*, *N. rostrata* (Emery).

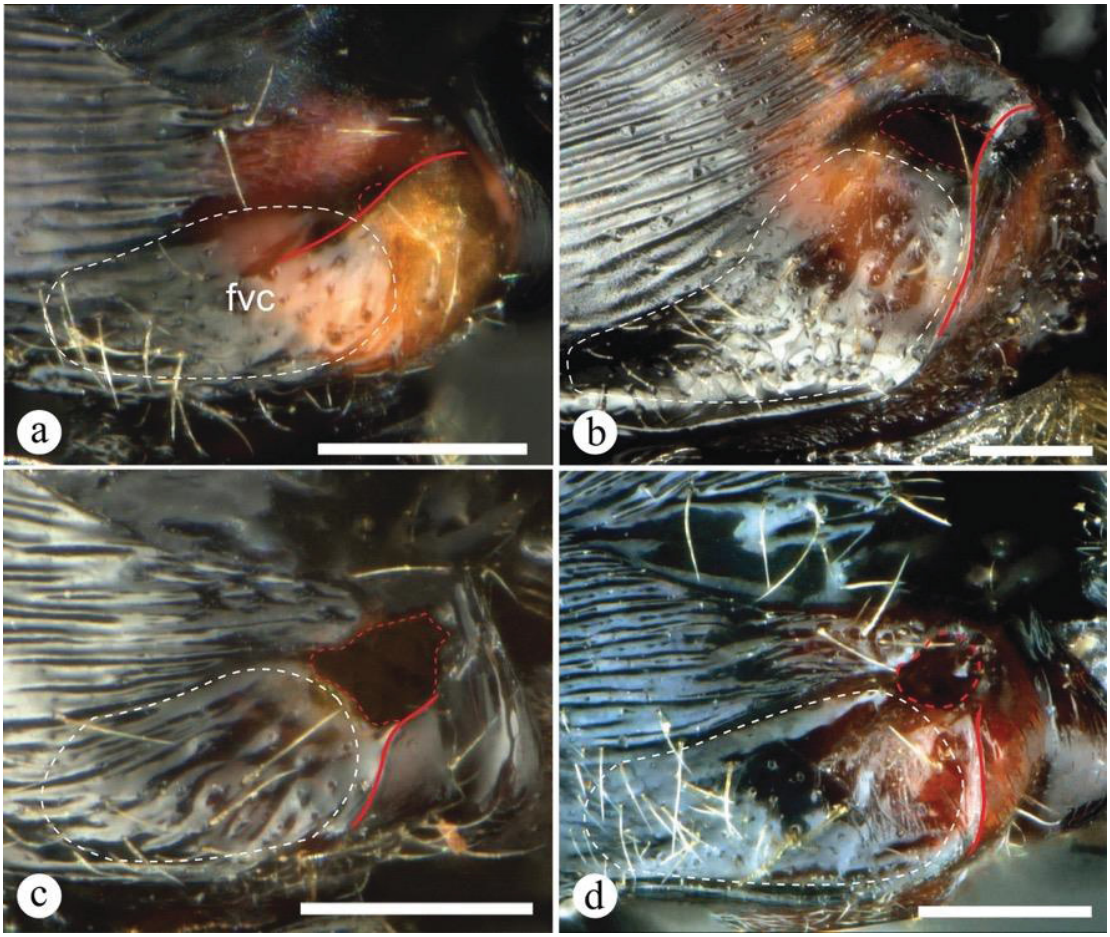


Fig. 2. Cuticular flap variations (solid red line) at the orifice of metapleural gland (dashed red line) in queens and workers of the *N. laevigata* species–group, as seen in lateral view. **a**. *Neoponera mashpi* **sp. nov.** (CPDC: ATPFOR2054–2), the flap is well–developed, strongly curved anterad so that it conceals most of the gland opening, this variation is almost identical to that present in *N. laevigata*; **b**. *Neoponera commutata* (DZUP: DZUP549422), the flap is well–developed, barely curved anterad and slightly hides the orifice of the gland; **c**. *Neoponera marginata* (MEPN: ATPFOR1988), the flap is present but is less developed than in *N. commutata*, the orifice of the gland is almost entirely visible; **d**. *Neoponera gojira* **sp. nov.** (DZUP: DZUP549444), the flap is strongly reduced and modified into a carina, the orifice of the gland is completely visible. Dashed white lines represent the approximate area of the pheromone venting canal (fvc). Scale bars: 0.2 mm.

Morphometrics

The PCA circular plot (Figure 1, Supplementary material 3, available online) shows that most variables are positively correlated and also most of them are well–represented in the factor map (= they are close to the circumference margin), which means they are important in explaining the total morphometric variance (ca. 92%) represented in the first two dimensions of the ordination. The quality of representation of the variables is calculated using the square cosine and expressed through the eigenvalues as shown in Figure 1 for dimensions 1 and 2 (Supplementary

material 2, available online). On the other hand, the NMDS ordination was supported by a robust stress value of 0.01826, which according to the criteria of Kruskal (1964), indicates a strong correlation between ranked observed dissimilarities and ordinated distances. This value also suggests that our observations, i.e. measured specimens, are not grouped randomly. The graph shows a small cluster of convergent observations representing most taxa, except *N. commutata*, which is suggestive of morphometric similarity as these share a significant fraction of their morphospace. As expected, this is evident between *N. mashpi* **sp. nov.** and *N. laevigata* since their measured characters are more similar in size between each other than with the remaining species (Figure 3). The PERMANOVA, however, rejected the null hypothesis that all the observations are equal ($p < 0.000999$; 85% of variance explained, see the full output statistics in Supplementary material 3, available online), and the pairwise contrast test was significant for some species pairs, including *N. mashpi* **sp. nov.** and *N. laevigata* (p adjusted = 0.03), thus supporting our hypothesis that these belong to distinct, though phylogenetically close lineages (Troya et al. unpublished). Except for the dorsal petiolar index (DPI), which is shown in the ordination plot relatively distanced apart from all the species groupings, the remaining indices are comparatively important in explaining the morphometric differences between *N. mashpi* **sp. nov.** and the rest of related taxa. Whereas, most of the other variables are important for distinguishing between *N. commutata* and its congeners. In regards to *N. gojira* **sp. nov**., for which a single individual was identified, the ordination shows that it is more similar to *N. laevigata* than to *N. marginata* and *N. mashpi* **sp. nov.** The morphospecies *Neoponera* nr. *gojira*, which is supposed to be closer (or perhaps conspecific) to *N. gojira* **sp. nov.**, is placed within the morphospace of *N. laevigata*, *N. marginata*, and *N. mashpi* **sp. nov.** Since the sample size of both *N. gojira* **sp. nov.** and *Neoponera* nr. *gojira* is currently insufficient for making solid conclusions about the potential place occupied by them in the morphospace of the *N. laevigata* group, further specimens are required to confirm current assumptions. However, as detailed in its corresponding species treatment, we do have valid reasons to treat *N. gojira* **sp. nov.** as a good species.

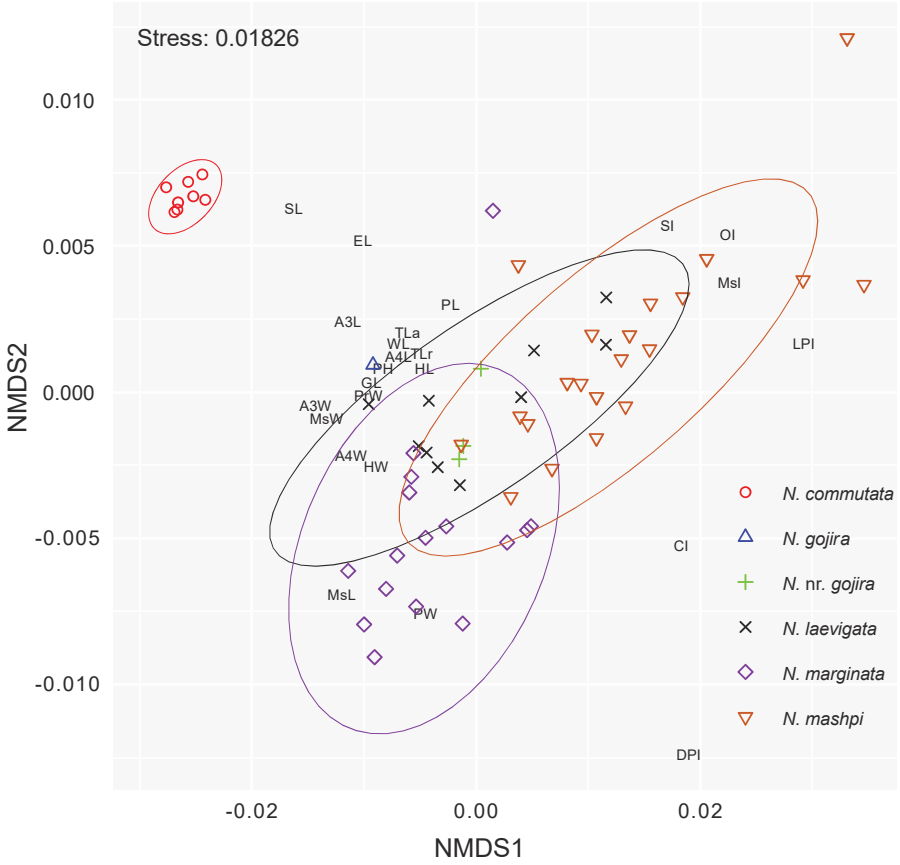


Fig. 3. Non–metric multidimensional scaling (NMDS) plot depicting the 24 morphometric variables shown in abbreviated letters (see materials and methods) which best contribute to explain the morphological variance among the observations (N= 59 workers) across the morphospace which is composed of five species and one morphospecies in the *N. laevigata* group. The ellipses margins represent the 95% confidence intervals. See extended explanation under results.

Worker– and queen–based key to Neoponera species–groups

The following key allows distinguishing species–groups within *Neoponera*, as well as a newly recognized genus lineage which is apparently sister to *Neoponera* (Troya et al. unpublished). For practical reasons only we here refer to this new genus as "*N. emiliae* 2", since the three species composing this clade, *Neoponera concava* Mackay & Mackay, *N. schultzi* Mackay & Mackay, and *N. venusta* Forel, are currently assigned to the *Neoponera emiliae* group *sensu* Mackay & Mackay (2010). In addition, we have evidence that *N. bucki* Borgmeier does not belong to *Neoponera* but it is distantly related to it, probably another new genus lineage. Nevertheless, as we are not proposing new nomenclatural acts in this regard, we have included

both *N. bucki* and the "*N. emiliae* 2" group in the present key until formalizing their new status in a coming contribution.

Character states in each statement appear in relative order of importance for the identification of a given group.

1. Propodeal spiracle circular (Figure. 4a); malar carina present, running over anterointernal eye region, in lateral view (Figure 4d); body black, while legs usually yellowish to brownish; workers comparatively small (WL = 1.4 – 2.1 mm); ground living; eastern Brazil (mostly Atlantic Forest), Southern Colombia (?), Rondônia (?), Pará (?) ……..……. ……..…….**"*N. emiliae* 2"**

   Propodeal spiracle either oval (Figure 4b) or slit-shaped (Figure 4c); malar) carina present or absent, when present never running over anterointernal eye region but in front of it, in lateral view (Figure 4e); body (including legs) varying in color from black, to brownish, to yellowish, to iridescent bluish-greenish; size of workers may vary greatly, but in general, significantly larger than in previous statement (WL usually > 2 mm up to about 6 mm); Neotropical Region: southern United States to central – northern Argentina ……..…… **2 *Neoponera***

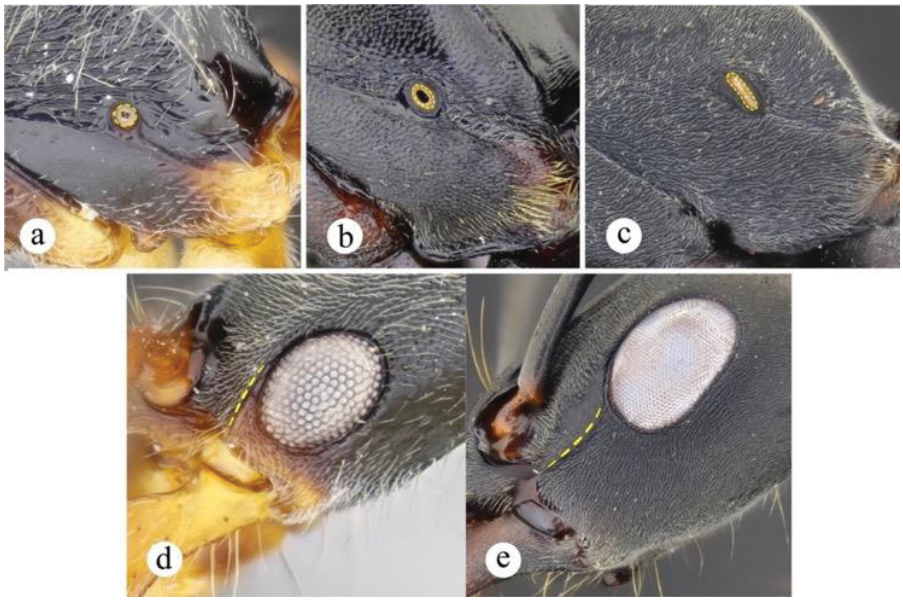


Fig. 4. Propodeal spiracle (**a** – **c**). **a**. Circular (*Neoponera schultzi*, MEPN: ATPFOR2024); **b.** Oval (*N. metanotalis*, CPDC: ATPFOR1997); **c.** Slit–shaped (*N.verenae*, DZUP: DZUP549670). Malar carina (**d**, **e**, highlighted by yellow dashed line). **d**. Running over anterointernal eye region (*N. schultzi*, MEPN: ATPFOR2024); **e**. Placed in front of anterointernal eye margin (*N.verenae*, DZUP: DZUP549670).

2(1). Ventrolateral pronotal margin with well-impressed, usually cross ribbed groove (Figure 5f); propodeal spiracle oval to suboval (Figure 4b) and, in only two species (*N. magnifica* Borgmeier and the undescribed "*N. magnifica*-5" DZUP549389, image on AntWeb.org) this spiracle is slit-shaped; mesonotum and propodeum divided by feeble notopropodeal suture which **never** forms a groove (Figure 5c); malar carina present or absent, when present always tenuously impressed and hard to discern at first sight; ground living; northern Venezuela, eastern Colombia (Amazonia), and eastern Brazil (Amazonia and Atlantic Forest) …… ***N. emiliae* group**

Ventrolateral pronotal margin without well-impressed groove, if a groove if present, then always shallow and never sculpted (Figure 5e); propodeal spiracle always slit-shaped (Figure 4c); mesonotum and propodeum either fused, although a vestigial line can be present (Figure 5a, b), or divided by notopropodeal groove (Figure 5d); malar carina either present or absent ……**3**

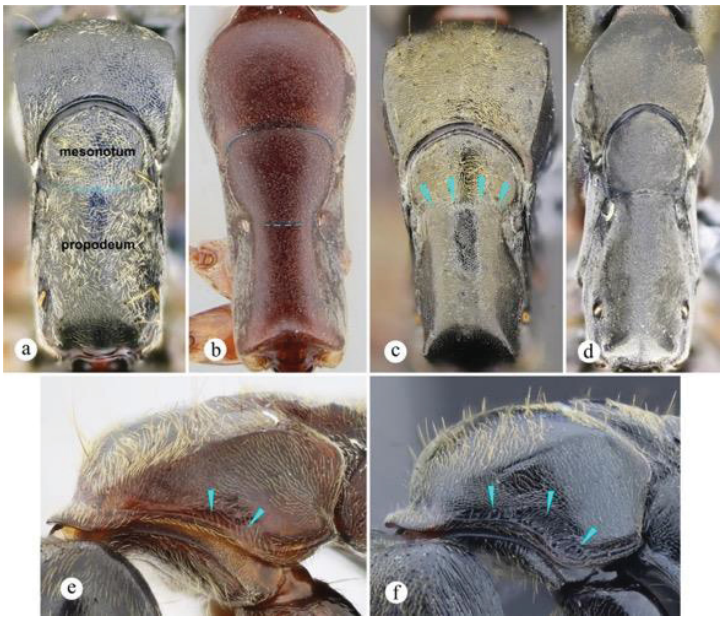


Fig. 5. Notopropodeal suture (**a** – **d**). In **a** and **b**, dashed, cyan lines demarcate the approximate region where the mesonotum and propodeum converge, in these cases the suture is either vestigial or tenuously impressed and the mesonotum and propodeum are fused; in **c**, the suture (as pointed by cyan arrowheads) is more discernible than in **a** and **b**, so that mesonotum and propodeum appear slightly separated; while in **d**, the suture is clearly visible, forming a shallow groove, so that mesonotum and propodeum are clearly separated. Ventrolateral pronotal margin (**e**, **f**). In **e**, with a shallow groove (as pointed by cyan arrowheads), while in **f**, the groove is strongly impressed and cross ribbed. **a**. *Neoponera carinulata* Roger (DZUP: DZUP549576), **b.** *N. bucki* (UFV: UFV-LABECOL007493), **c.** *N. metanotalis* (CPDC: ATPFOR1997), **d.** *N. verenae* (DZUP: DZUP549670), **e.** *N. goeldii* (MEPN: MEPNINV37890), **f.** *N. metanotalis* (UFV: UFVLABECOL000625).

3(2). Body integument jet-black and polished, with scarce appressed hairs (Figure 6a); anterior mandibular region strongly bent ventrad in lateral view (Figure 6c); ground (and arboreal?) living; Central America to Northern Argentina ……..…… ***N. laevigata* group**

Body integument varying in color and surface sculpture, but never jet-black, usually with abundant appressed hairs which may vary in size and thickness (Figure 6b); anterior mandibular region not strongly bent ventrad in lateral view (Figure 6d)…… **4**

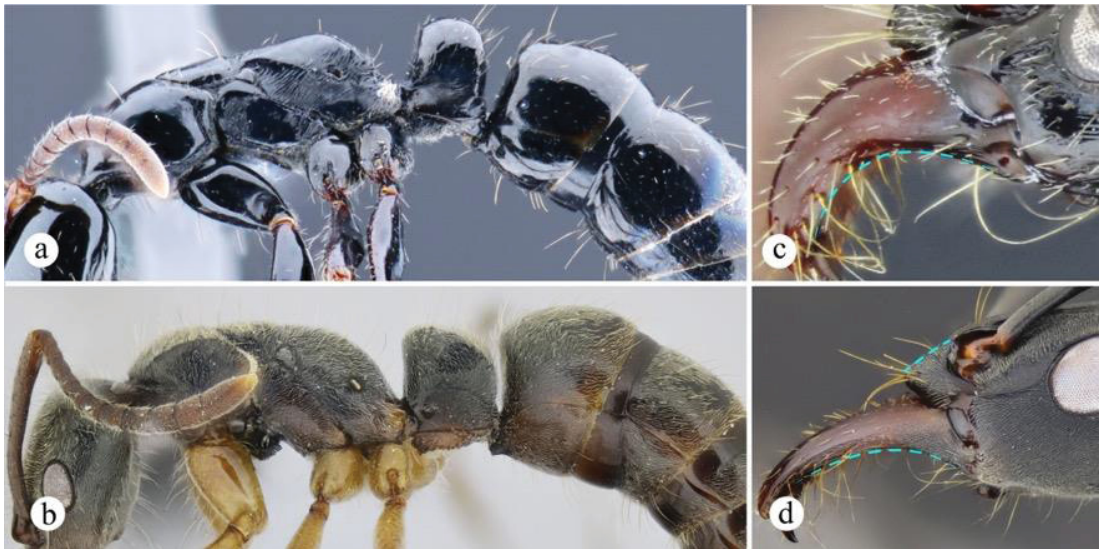


Fig. 6. Overall integument (**a**, **b**) and mandible curvature (**c**, **d**). **a.** Body with scarce appressed hairs (*Neoponera marginata*, MEPN: CASENT0649897); **b.** Body with abundant appressed hairs (*N. unidentata* Mayr, DZUP: DZUP549462); **c.** Mandible strongly curved ventrad (*N. laevigata*, CPDC: ATPFOR2040); **d.** Mandible not strongly curved ventrad (*N. verenae*, DZUP: DZUP549670).

4(3). Clypeus, in lateral view, with convex, longitudinal carina medially, tip of carina acute (Figure 7a, b); eye relatively flat, not surpassing lateral head margin, in frontal view (Figure 7b); body with pruinose pilosity (tiny appressed hairs forming a dusty-looking coat) and completely devoid of erect hairs on dorsum (Figure 5b, d); mesonotum and propodeum fused, but usually a vestigial line is discernible dorsally (Figure 5a, b); ground living; eastern Brazil (mostly Atlantic Forest) and eastern Venezuela …….…….……..…….. ***N. bucki***

Clypeus, in lateral view, without convex longitudinal carina medially (shown in dashed cyan line, Figure 6d); eye convex to globose, surpassing lateral head margin, in frontal view (Figure 7c); body either with pruinose pilosity (few species) or with moderate to abundant appressed hairs (most species) (Figure 6b); mesonotum and propodeum either fused (though a vestigial line can be discernible) or separated by notopropodeal groove…… **5**

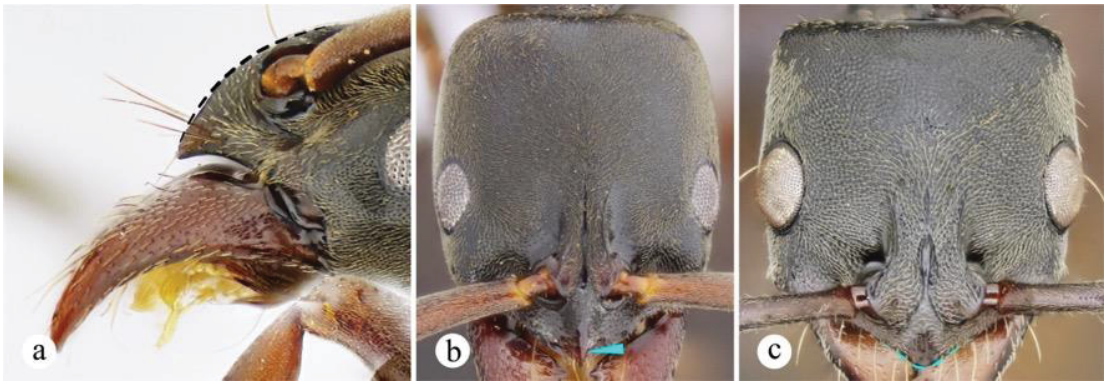


Fig. 7. Clypeus (**a**) and eye format (**b**, **c**). **a.** Clypeus with convex longitudinal carina medially (dashed black line) (*Neoponera bucki*, DZUP: DZUP549473); **b.** Eyes relatively flat, not surpassing lateral head margins; the yellow arrowhead points to the clypeal carina (*N. bucki*, DZUP: DZUP549473); **c.** Eyes convex, surpassing lateral head margins (*N. carinulata*, DZUP: DZUP549576).

5(4). Mesonotum and propodeum fused, and in many species a vestigial line is present (Figure 5a, b); anterior mid clypeal region with usually blunt, subtriangular cuticular extension (dashed cyan line, Figure 7c); arboreal living; southern Mexico to central – northern Argentina……..……. ***N. crenata*** **group**

Mesonotum and propodeum separated by shallow, but distinct notopropodeal groove (Figure 5 d); anterior mid clypeal region without subtriangular cuticular extension, it may be convex, flat or concave but never as described above (Figure 8a, b); ground and arboreal species…….…... **6**

6(5). Mandible narrow at base, very long, usually three fourths or slightly more of head length, armed with 18–19 teeth alternating with 8–10 denticles (Figure 8a); arboreal living mostly; South America: northwestern Venezuela to northwestern Argentina …. ***N. rostrata*** **group**

Mandible relatively wide at base, always shorter than three fourths of head length, armed with 10–13 teeth alternating with denticles (Figure 8b)……..**7**

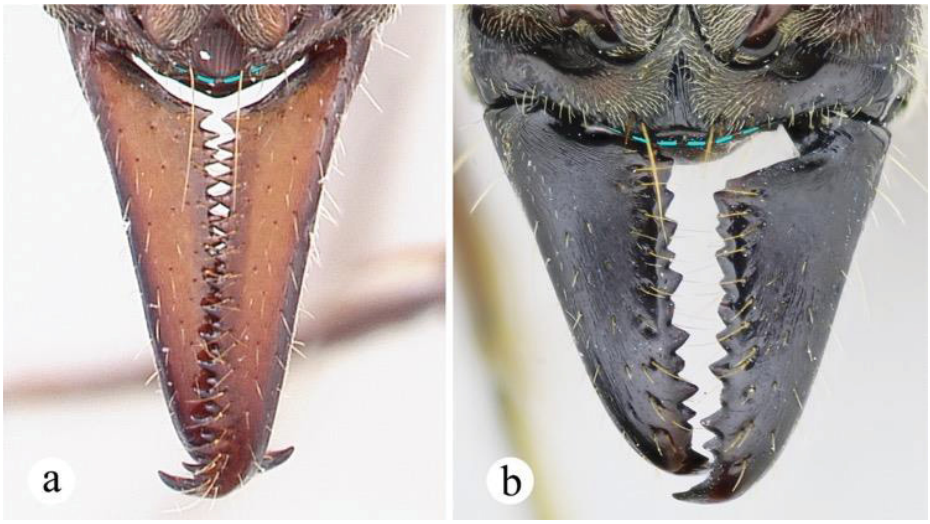


Fig. 8. Mandible. **a.** Very long, bearing about 18-19 teeth, alternating with denticles (*Neoponera rostrata*, MIZA: CASENT0178713); **b.** Bearing about 10-13 teeth alternating with denticles (*N. villosa*, MEPN: MEPN2930).

7(6). Body with white, pruinose pilosity, combined with scattered erect hairs (except *N. cooki* Mackay & Mackay, which bears abundant, black erect hairs); integument always black and in most species opaque (Figure 9a); ground living; northern Mexico to northern Argentina ……..…….***N. apicalis* group**

Body without pruinose pilosity, but bearing abundant appressed hairs, and usually abundant erect hairs (Figure 9b); integument varying in color from black, to brownish black, to iridescent bluish-greenish……...…. **8**

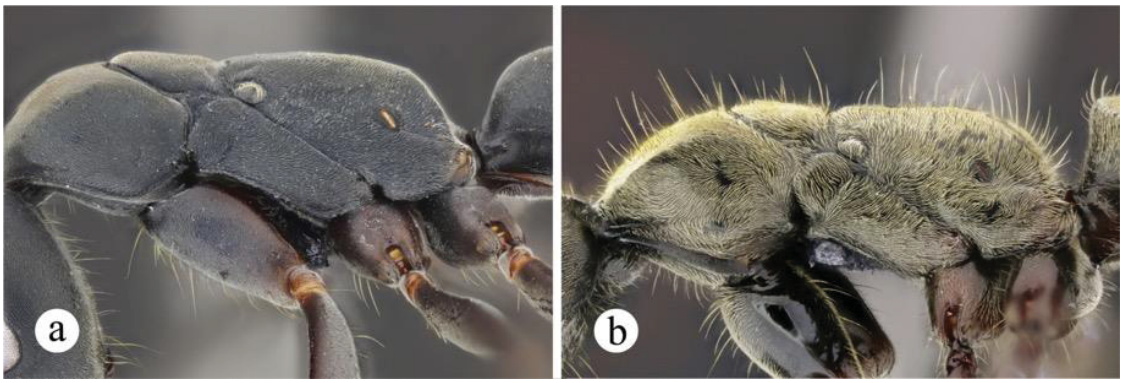


Fig. 9. Pilosity. **a.** Body surface pruinose with scattered erect hairs mostly ventrally (*Neoponera verenae*, DZUP: DZUP549670); **b.** Body surface with abundant appressed and erect hairs (*N. villosa*, DZUP: DZUP549448).

8(7). Malar carina absent (Figure 10a); ground living; some species with iridescent, bluish-greenish integument; Central America to Northwest Argentina…..... ***N. aenescens* group**

Malar carina present (Figure 10b); body integument black to brownish black, but never iridescent bluish-greenish; arboreal living mostly; southern United States to northern Argentina ……..... ***N. foetida* group**

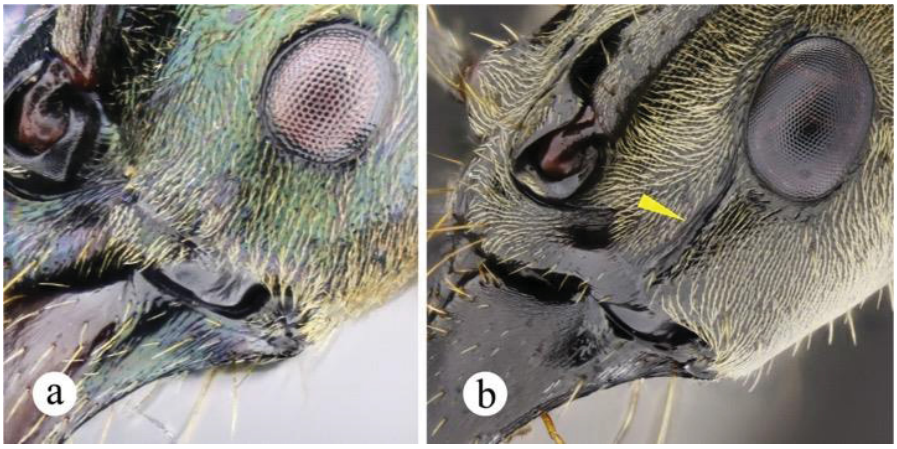


Fig. 10. Malar carina. a. Absent (*Neoponera carbonaria* Smith, MEPN: CASENT0649889); b. Well-developed (pointed by yellow arrowhead), usually reaching anterointernal eye margin (*N. villosa*, DZUP: DZUP549448).

Taxonomy

Neoponera laevigata species–group brief taxonomic notes

Probably based mainly on the presence of the malar carina of *Neoponera commutata* Roger, Emery (1911) created the "*Commutata* group" and placed it within *Neoponera*. Later, Wheeler (1936) in a treatment of the ecological relations of ants and termites, with a focus on ponerines, created *Termitopone* to accommodate *N. commutata*, *N. laevigata*, and *N. marginata* Roger. This author based his decision on morphological and ecological observations related to specialized termite predation which is common to all three species. Wheeler's *Termitopone* remained valid for a relatively long time until its synonymy under *Pachycondyla* by Brown (1973). Mackay & Mackay (2010) included these three termitophagous species, again under *Pachycondyla* within the "*P. laevigata* species–complex", providing a new key to its species, distribution, and brief field and literature notes on their biology and ecology. Schmidt and Shattuck (2014) included these taxa in *Neoponera*, and according to their molecular phylogeny the *N. laevigata* group is sister to the *N. aenescens* group.

We found the following combination of morphological and behavioral characters useful for diagnosing this clade of above–ground termite–raiding species. In addition to the strongly ventrally bent mandibles, we consider such behavioral traits as being synapomorphic for the species here treated. The sole exception to confirmed termite–raiding is *N. gojira* **sp. nov.**, for which we found a single worker and information about its natural history is unknown. Most of the following character states will not be repeated in the general synoptic description, nor in the diagnoses and descriptions of individual species, and apply to all castes except where otherwise stated.

***Neoponera laevigata* species–group differential diagnosis**

Known species in the *N. laevigata* group are easily recognized from other species in the genus by the following: 1) the integument of workers and queens is entirely black and exceptionally lustrous (reflecting objects very much like a mirror), bearing scant piligerous punctae, usually with whitish to pale yellowish tiny appressed pilosity, and erect golden hairs. Although the integument of the males is also black and lustrous, it shows significantly more piligerous punctae than in the other castes within this species–group. Workers and queens in some species of the *N. aenescens* group (for example, *N. carbonaria* Smith), *N. crenata* group (for example, *N. moesta* Mayr), and *N. emiliae* group (for example, *N. magnifica* Borgmeier) also show lustrous integuments but these are covered with abundant piligerous punctae, especially on the dorsum of head and mesosoma, and with the exception of *N. magnifica*, the body surface is on average dark brownish to bluish–greenish, never jet–black as in all species of the *N. laevigata* group. The integument of *N. magnifica* is also jet-black and the gaster is lustrous, without sculpture, but this species is easily distinguished from all species in the *N. laevigata* group since it bears costae on the dorsum of head, pronotum and mesonotum. 2) Except for *N. commutata*, the distal region of the mandibles in workers and queens is strongly bent ventrad, in lateral view, clearly more than in any other *Neoponera* species. Although the mandibles of workers and queens in *N. commutata* are similarly bent ventrad as in most *Neoponera*, the lustrous black integument of the body and their large size (maximum relative body length of workers: 19 mm, and queens: 20 mm, the largest species in the genus), are the easiest clues to separate it from all other *Neoponera* species. The male caste of *N. commutata* is the only case within the genus showing well–developed torular lobes (Figure 14a), and maxillary palps with segments 4 th to 6th fused (Figure 18b) (see extended details under this species' comments).

Following, is a set of traits which together provide a detailed characterization of the species of the *N. laevigata* group.

1. Compound eye relatively large, ca. one fourth of head length; in most species flat with its external margin not surpassing lateral margin of head in frontal view. In *Neoponera commutata* the eye is globose and surpasses the lateral head margin. In males the eye is slightly notched anterodorsally, globose, and occupies ca. two–fourths or more of head length; its external margin clearly surpasses the lateral head margin in frontal view.
2. Torular lobe subtriangular with rounded lateral margins, covering approximately 90% of acetabulum of antennal socket in frontal view. Known males of *N. mashpi* **sp. nov.** and *N. marginata* with strongly reduced torular lobe, while the male of *N. commutata* shows a small, but well–developed lobe covering approximately less than 10% of the antennal socket.
3. Frontal carina surpassing ocular mid–length in frontal view. In *N. commutata* this carina just reaches ocular mid–length.
4. Malar carina, absent in most species, instead a swelling is present and usually bears foveae and striae. Only *N. commutata* exhibits a strongly developed malar carina which reaches the anterior eye margin. Males lack this character.
5. Mandibles strongly bent ventrad in lateral view, with external margin weakly sinuous medially in full–face view. Males bear the typical Ponerini spatulate to semi–triangular, small, toothless mandibles, always bearing the oval–shaped groove dorsally near the mandibular base.
6. Pronotum lacking a distinct humeral carina, though a very tenuous, blunt, almost indistinguishable border may be present in workers and queens of all species, except for *N. commutata* and males of all species where the humerus is completely rounded.
7. Notauli absent on mesoscutum (males only).
8. Notopropodeal suture present, forming groove, not depressed though (*N. laevigata*, *N. mashpi* **sp. nov.**, and *N. gojira* **sp. nov.**), or slightly depressed (*N. commutata* and *N. marginata*) in dorsal view. This groove is usually cross ribbed. In males and queens the metanotum is clearly separated from the mesonotum anteriorly, and from the tergum of A1 posteriorly, by well–defined grooves.

9. Mesosternal and metasternal processes well–developed, fang–shaped, anteroposteriorly flattened.

10. Posteroventral cuticular flap at metapleural gland opening and its relative visibility in posterolateral view: strongly reduced, gland orifice entirely visible (worker of *N. gojira* **sp. nov.**); well–developed, strongly bent anterad, gland orifice barely visible (worker and queen of *N. laevigata* and *N. mashpi* **sp. nov.**); well–developed, bent dorsad nearly vertically straight, gland orifice almost entirely visible (worker and queen of *N. commutata*, *N. marginata*). In males of examined species this structure varies from well–developed, slightly bent dorsad, gland orifice clearly visible (*N. mashpi* **sp. nov.**, *N. marginata*), to absent, instead forming a vertically–oriented, salient carina, gland orifice completely visible (*N. commutata*).

11. Petiolar node cuboid, usually subquadrate in lateral view, or slightly tapering dorsad, the latter state only seen in *N. commutata*. In males of all examined species the petiolar node also tapers dorsad with both anterior and posterior margins relatively straight in lateral view.

12. Prora either well–developed, with a blunt tip projecting ventrad (*N. mashpi* **sp. nov**., *N. commutata*, *N. marginata*), or poorly developed with only a small cuticular lip that is usually hardly discernible laterally (*N. laevigata*, *N. gojira* **sp. nov.**).

13. Cinctus moderate (most species) to absent or barely distinguishable (only in *N. commutata*). All examined males showed a moderate cinctus.

14. Stridulitrum present on presclerite of A4, sometimes poorly developed, faint and narrow.

15. Arolium present, small, roughly half length or less of pretarsal claw. In males the arolium is slightly longer than half–length of pretarsal claw.

16. General body appearance jet–black, surface with sparse erect golden hairs interspersed with few scattered, piligerous punctures from which golden, appressed tiny hairs emerge, most of which do not touch each other. Queens show relatively more erect pilosity than workers, particularly ventrally on head and on abdominal segments 5 – 7. Males depart from this in showing a body surface with less erect hairs and significantly more piligerous punctures bearing appressed pale–yellowish pubescence.

17. All species show striae on the head, mesosoma and petiolar node, that varies interspecifically in abundance, thickness and complexity. The petiolar node of *N. gojira* **sp. nov.**, and that of

most populations of *N. mashpi* **sp. nov.** are almost devoid of striae. Subpetiolar process covered with transverse, strongly impressed, irregular striae. The head, petiole, and subpetiolar process in males are usually significantly less sculptured than in workers and queens.

18. Worker caste either monomorphic (only *N. commutata*), or polymorphic (*N. mashpi* **sp. nov.**, *N. laevigata*, *N. marginata*). Evidence is lacking for *N. gojira* **sp. nov.**, though probably also polymorphic.

19. This is the only clade within *Neoponera* with all constituent species being specialized in termite–raiding. The feeding biology of *N. gojira* **sp. nov.** is unknown, but probably it raids on termites too.

Synonymic list

In square brackets the known distribution by political and administrative regions, and in parentheses the studied castes: ☿ – worker; ♀ – queen; ♂ – male.

Neoponera commutata (Roger, 1860) [Colombia to southeast Brazil: São Paulo, to southern Paraguay] (☿, ♀, ♂)

Neoponera gojira Troya & Lattke, **sp. nov.** [Brazil: Minas Gerais] (☿)

Neoponera laevigata (Smith, 1858) [Northwestern Colombia to Brazil: São Paulo] (☿, ♀)

= *Neoponera gagatina* (Emery, 1890: 75) (synonymy by Emery 1892: 9)

= *Neoponera laevigata whelpleyi* (Wheeler, 1922: 3) (synonymy by Wheeler 1936: 164)

Neoponera marginata (Roger, 1861) [Trinidad & Tobago to eastern Ecuador, to southern Brazil: Rio Grande do Sul] (☿, ♀, ♂)

Neoponera mashpi Troya & Lattke, **sp. nov.** [Costa Rica to Brazil: Bahia] (☿, ♀, ♂)

Worker– and queen–based key to species of the *Neoponera laevigata* species–group

1. Eye globose, surpassing lateral margin of head, and placed approximately at cephalic mid–length in frontal view (Figure 11b)…….…….. ***Neoponera commutata***

   Eye relatively flattened, not surpassing lateral margin of head, and placed anterior to cephalic mid–length in frontal view (Figure11a)…….**2**

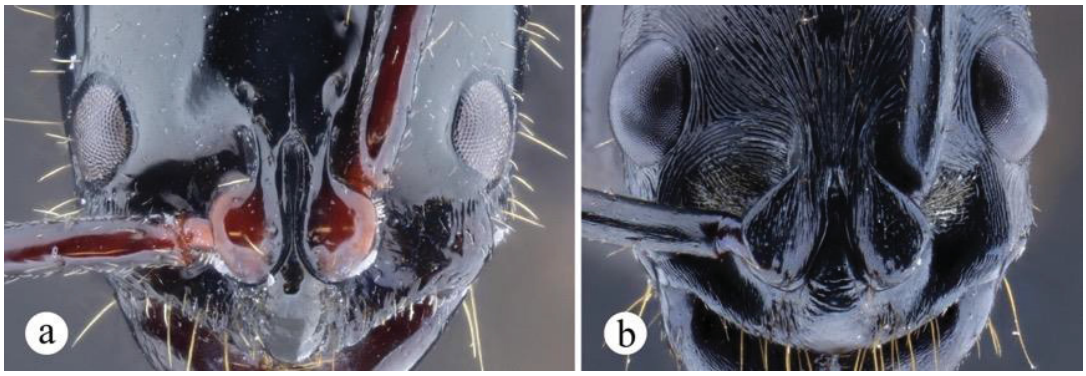


Fig. 11. Eyes. **a.** Flattened, not surpassing lateral margin of head (*Neoponera. marginata* MEPN: CASENT0649897); **b.** Globose, surpassing lateral margin of head (*N. commutata* DZUP: DZUP549422).

2. Mandibular dorsum, near masticatory margin with a strongly carved longitudinal groove in frontal view (Figure 12a); posterior flap at metapleural gland orifice well–developed, the gland orifice is almost completely visible in posterolateral view (Figure 2c) ……... ***Neoponera marginata***

   Mandibular dorsum, near masticatory margin with shallow, somewhat irregular, longitudinal rim in frontal view (Figure 12b); posterior flap at metapleural gland orifice strongly reduced to a narrow carina, the gland orifice is completely visible in posterolateral view (Figure 2d) …….***Neoponera gojira* sp. nov.**

   Mandibular dorsum, near masticatory margin without the structures mentioned above, though hair–bearing small fossulae and punctae are present (Figure 12c); posterior flap at metapleural gland orifice well–developed though strongly curved anterad so that it conceals most of the gland orifice in posterolateral view (Figure 2a) ……. **3**

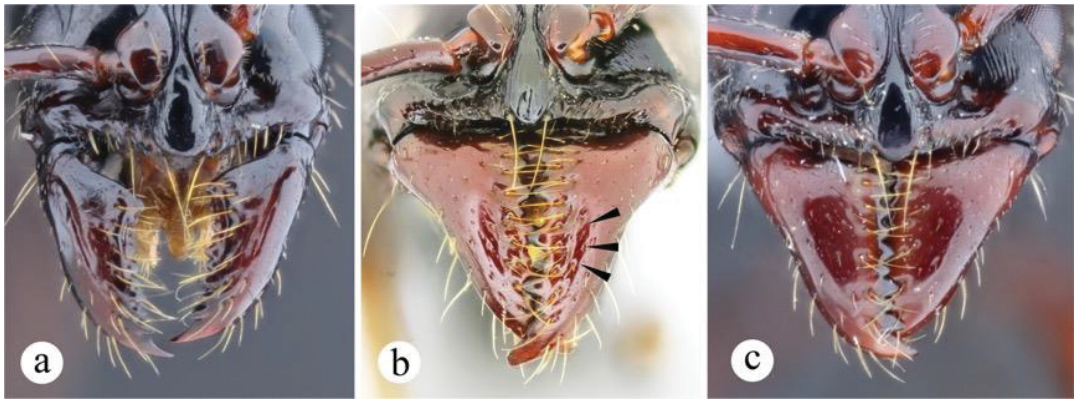


Fig. 12. Mandibular dorsum **a.** Strongly carved longitudinal groove (*Neoponera marginata*, MEPN: ATPFOR1988), **b.** Shallow longitudinal rim (black arrowheads show part of the structure) (*N. gojira* **sp. nov.**, DZUP: DZUP549444); **c.** Even surface, without groove or rim (*N. laevigata*, CPDC: ATPFOR2054-2).

3. Scape fails to reach posterior head margin (smallest workers and queen, Figure 13a), or barely reaches it (largest workers) in frontal view; prora well–developed, keel–shaped, clearly discernible in lateral view (Figure 13c); subpetiolar process **usually** with a straight, robust, ca. 45° posterior slope in lateral view (Figure 13c)…… ***Neoponera mashpi* sp. nov.**

   Scape surpassing posterior margin of head by approximately one apical scape width (sometimes slightly less) in frontal view (Figure 13b); prora very small, lip–shaped, not easily discernible in lateral view (Figure 13d); subpetiolar process **usually** with a relatively concave to flattened, less robust, posterior slope in lateral view (Figure 13d) ……..***Neoponera laevigata***

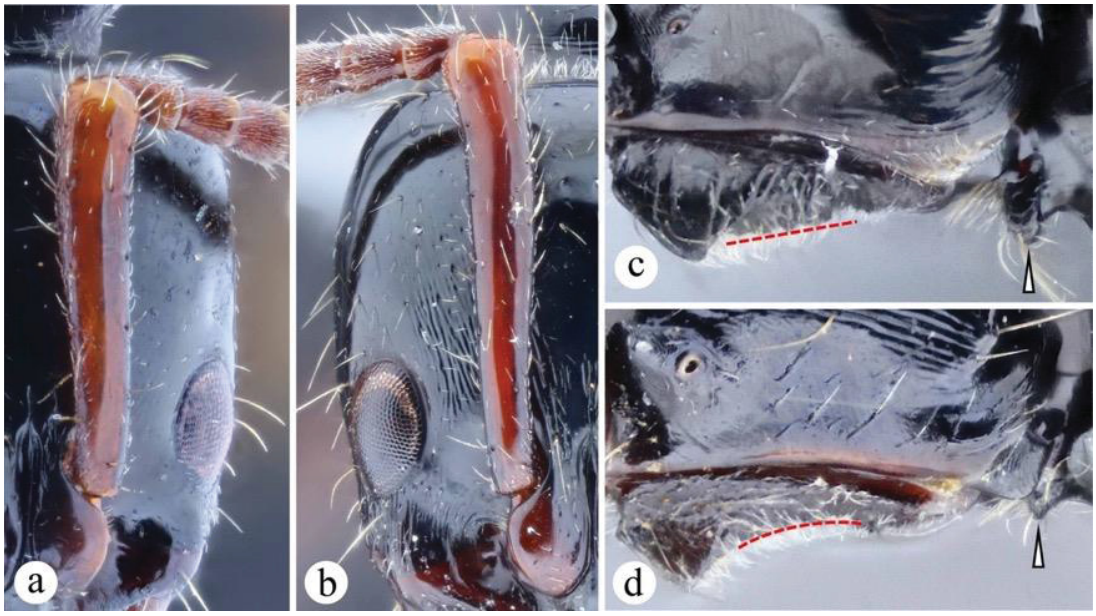


Fig. 13. Scape length, subpetiolar process and prora. **a.** Scape not surpassing posterior margin of head (*Neoponera mashpi* **sp. nov**., CPDC: ATPFOR2054-2); **b.** Scape surpassing posterior margin of head (*N. laevigata*, MPEG: ATPFOR2027); **c.** Subpetiolar process subtriangular, robust with a straight slope (dashed line); prora well–developed (white arrowhead), keel–shaped (*N. mashpi* **sp. nov.**, CPDC: ATPFOR2054-2); **d.** Subpetiolar process subtriangular, less robust than in Figure 13c, with relatively concave to flattened slope (dashed line); prora very small (white arrowhead), lip–shaped (*N. laevigata*, MPEG: ATPFOR2027).

Male–based key to known species of the *Neoponera laevigata* species–group

1. Torular lobe comparatively small but well–developed, covering ca. less than 10% of antennal socket acetabulum in frontal view (Figure 14a); posterior face of propodeum weakly concave in lateral view, bearing strong rugae and striae, outline carinate and usually salient (Figures 18a, c) ……..……***Neoponera commutata***

   Torular lobe strongly reduced, almost vestigial, cuticle not extending over antennal socket acetabulum (frontal view) (Figure 14b); posterior face of propodeum straight in lateral view (Figures 24a, c, 27a, b), sculpture present or absent but never strongly impressed, outline not carinate…….……**2**

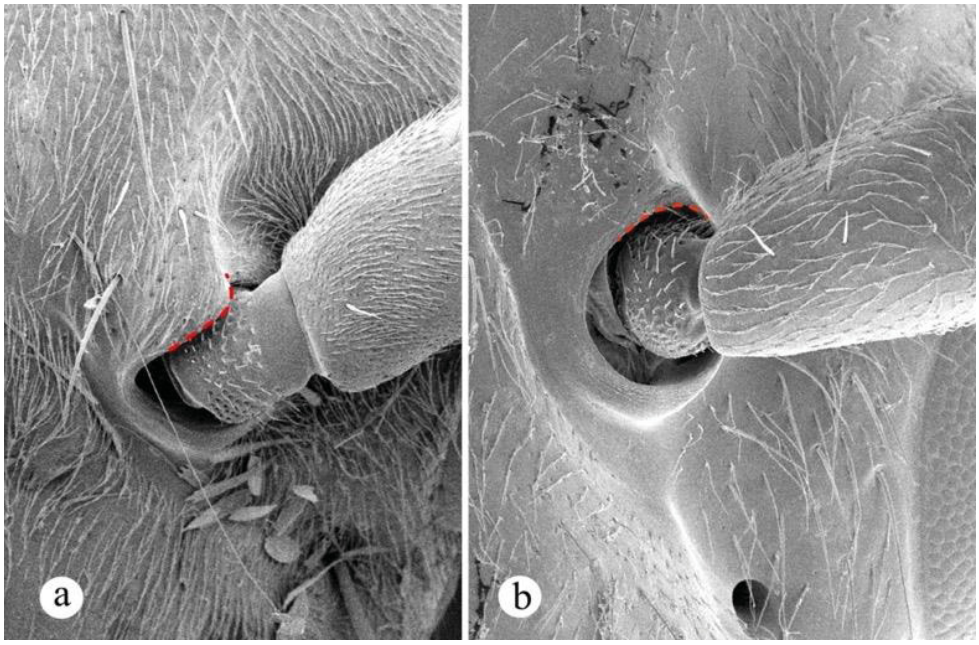


Fig. 14. Torular lobes (demarcated by red dashed lines). **a.** Well–developed though comparatively small, covering ca. less than 10% of antennal socket acetabulum (*Neoponera commutata*, DZUP: DZUP549398); **b.** Strongly reduced, not extending over antennal socket acetabulum (*N. marginata*, CPDC: ATPFOR2011).

2. Pretarsal claw armed with well–developed median tooth; mesoscutum with weakly impressed, median longitudinal line in dorsal view (Figure 15a); spine at sternum of A8 dorsoventrally depressed with round tip……..…….. ***Neoponera marginata***

   Pretarsal claw unarmed, without any accessory tooth; mesoscutum smooth, without median longitudinal line in dorsal view (Figure 15b); spine at sternum of A8 subconical, not dorsoventrally depressed, with acute tip……..***Neoponera mashpi* sp. nov.**

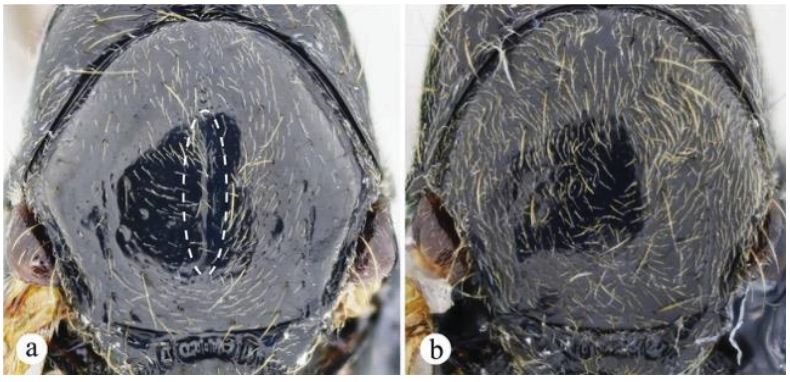


Fig. 15. Male mesoscutum in dorsal view. **a.** Weakly impressed longitudinal line (marked by dashed white ellipse), or shallow groove (*Neoponera marginata*, UFVLABECOL: UFV–LABECOL010414) present in the center of the sclerite; **b.** Mid surface of mesoscutum devoid of grooves and/or striae (*N. mashpi* **sp. nov.,** CPDC: ATPFOR2054–2).

***Neoponera laevigata* species–group description**

The following describes the morphological traits shared by all examined species in each caste: worker, queen and male. Species–specific traits are shown under each species description in the "Species accounts" section. The male of *N. laevigata*, and the queen and male of *N. gojira* **sp. nov.** are unknown.

Worker

Head. Frontal view: Mandible triangular, longer than wide, strongly bent ventrad, dorsolateral margin weakly sinuous medially. PF: 4,4. Stipes mostly smooth with strong longitudinal internal groove. Clypeus anteromedially convex, slightly projecting over base of mandibles when closed. Posterior margin of frontoclypeal sulcus just reaching ocular mid–length (except *N. commutata* where the sulcus barely reaches anterior horizontal ocular length). Frontal carina surpassing ocular mid–length. Eye suboval, maximum length ca. one–fourth of head length, in workers placed anterior to cephalic mid–length while in males is slightly anterior to it (except *N. commutata* where the eye is placed at cephalic mid–length). **Mesosoma**. Lateral view: Dorsal margin straight. Propodeal spiracle slit–shaped. Ventral view: probasisternum shield–shaped, strongly grooved. Meso– and metasternal processes well–developed, fang–shaped, relatively flattened anteroposteriorly, with internal margins running parallel; space between apices approximately equal to– or shorter than width of each apex. Metasternal process inclined posterad 20°–30° in lateral view (except for *N. commutata* where the process is inclined ca. 45°). Apices of metasternal processes slightly higher than half height of metacoxal internal margin. Lateral view: Pheromone venting canal at metapleural gland opening usually well–developed with few interspecific variations. **Petiole**. Lateral view: Subpetiolar process covered with transverse, usually well–impressed, irregular striae. Dorsal view: anteroventral nodal carina incomplete, with feeble concavity medially. **Gaster**. Lateral view: Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 nearly as high as maximum height of petiolar node margin. **Legs**. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Internal mid tibial spur half length of external spur. Internal hind tibial spur close to one–third length of external spur. Arolium present, roughly 0.5 times the length of pretarsal claw. Pretarsal claw arched, unarmed (without accessory teeth on its surface). Metabasitarsal gland present on basalanterior face. **Pilosity**. Body with sparse, flexuous, golden, erect and suberect hairs; appressed pubescence almost absent on entire body (only smallest

workers of *N. laevigata*, and *N. mashpi* **sp. nov.**) to slightly more abundant (remaining workers of all species); subpetiolar process always with a combination of fine, relatively abundant whitish (all species except *N. commutata*) to light golden (only *N. commutata*) appressed and suberect hairs. Scape hairs mostly erect and suberect with sparse appressed pubescence. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing flexuous hairs. **Sculpture**. Integument polished, mostly smooth.

Queen

Head. Morphology as in worker except for: Frontal view: Ocelli approximately equidistant to each other. Ocellar area not protruding from cuticle. **Mesosoma**. Morphology as in worker except for: Dorsal margin convex in lateral view. Dorsal view: Parapsidal lines weakly impressed, slightly divergent; scutoscutellar sulcus present, slightly arched posterad, not separating mesoscutum from mesoscutellum. Anterior subalar area shorter than tegular maximum width in lateral view. Metanotum well–developed, clearly discernible dorsally, surface even, slightly flat. Lateral view: Metanotal trough deeply impressed; anapleural sulcus present, almost completely dividing anepisternum from katepisternum; metapleural sulcus present. Metapleuropropodeal groove vestigial in dorsal view. **Wings**. Hyaline, weakly infuscated, moderately setose. Forewing venation: Ogata type Ia: submarginal cells 1 and 2, and discoidal cell present, vein 2M present, 2r–rs offset from 2rs–m. Hindwing venation: Cantone Type I: basal and subbasal cells, and vein 2M present, 1R well–developed. Jugal lobe present. **Petiole**. Morphology as in worker except for: Dorsal view: Node of petiole proportionally shorter and wider than in worker. **Gaster and legs.** Morphology as in worker. **Pilosity and sculpture.** As in worker.

Male

Head. Frontal and/or lateral view: Subrhomboid. Mandible spatulate, longer than wide, blunt apically, close to 1.5 oval pits (maximum diameter) fit on mandibular dorsum. Stipes mostly smooth with feeble longitudinal internal groove. Malar carina absent. Eye convex, globose. Ocellar area not protruding from cuticle. Anterior ocellus maximum diameter subequal to posterior ocelli. Ocelli approximately equidistant. Occipital carina reduced. Length of first flagellomere subequal to second flagellomere. **Mesosoma**. Morphology as in queen except for: Lateral and/or dorsal view: Pronotum lacking humeral carina, completely rounded. Mesoscutum about as long as broad. Notauli absent. Transscutal line well–developed. Scutoscutellar sulcus present, strongly

impressed, cross ribbed. Mesoscutellum subtrapezoidal, convex. Anapleural sulcus present in just a short pleural portion, not reaching midpleural region. Metapleural sulcus present. Anterolateral propodeal corner rounded. Propodeal lateral margins subparallel in posterodorsal view. The morphology of probasisternum and metasternal process is almost identical to that of the worker and queen. Posteroventral cuticular flap at propodeal posterolateral corner present, though reduced and not bent dorsad. **Wings**. Morphology as in queen. **Petiole**. Lateral view: subtriangular, shorter than that of worker and queen, and with rounded nodal dorsum (except for *N. commutata* worker and queen which show relatively round node, dorsally). Lateral and/or posterolateral carinae absent on node. **Gaster**. Morphology as in worker and queen except for: Lateral and/or ventral view: Prora well–developed, with blunt tip projecting ventrad. Spine at posterior margin of tergum of A8 well–developed, usually surpassing length of sternum of A9. Posterior margin of sternum of A9 convex. Pygostyles present. **Legs**. Morphology as in worker and queen except for the presence of medial tooth (only *N. commutata* and *N. marginata*) on pretarsal claw, which is absent in *N. mashpi* **sp. nov. Genitalia**. Dorsointernal margins of basimeres slightly touching each other. Basivolsella setose. Internal and external margins of cuspis nearly straight, its apex very close to posterior margin of digitus. Penial scleritess dorsomedially fused up to approximately one–half or less their length. **Pilosity and sculpture**. As in worker and queen except for: Appressed pubescence abundant mostly on body dorsum. Erect hairs smaller than maximum eye length. Scape hairs mostly with abundant appressed pubescence, mostly shorter than apical scape width. Meso– and metatarsi bearing abundant stiff setae interspersed with abundant suberect and appressed hairs.

Species accounts

***Neoponera commutata* (Roger, 1860)**

Figures. 16: a – e (☿); 17: a – d (♀); 18: a – d (♂); 28: a – c, j (♂ genitalia); 29: b (distribution)

Ponera commutata Roger, 1860: 311 (☿). South America. Unconfirmed type locality [but *sensu* Smith, 1858, possibly Brazil (Pará), and Guyana)]. Type material (syntypes): 1 ☿, 1 ♀ (MNHN) [not examined]. Combinations. In *Pachycondyla*: Emery, 1890: 72; Brown in Bolton, 1995: 304. In *Termitopone* (*Syntermitopone*): Wheeler, 1936: 169. In *Neoponera*: Emery, 1901a: 47; Schmidt & Shattuck, 2014: 151.

Status as species. Mayr, 1863: 447; Wheeler, 1936: 169 (redescription); Mackay & Mackay, 2010: 257 (redescription).

Worker and queen diagnosis. Head with strong, concentric striae ventrally; eye globose, surpassing lateral margin of head in frontal view (Figure 11b); scape sub–triangular in transverse plane (Figure 17c); malar carina distinctive (Figures 11b, 16c); occipital (nuchal) carina present, though feebly developed (Figures 16c, 17c); posterolateral margin of propodeal declivity with blunt, salient, slightly crenulated carina (Figures 16 a, b, 17d); petiolar node slightly tapering at top, posterolaterally bearing convex carina, in lateral view (Figures 16e, 17d); largest workers (WL $\bar{X}$ = 5.64 mm) and queens (WL $\bar{X}$ = 6.31 mm) of the *N. laevigata* group.

Worker description. Measurements (n=8): HW: 2.97–3.18; HL: 3.56–3.73; EL: 0.93–1.02; SL: 3.39–3.73; WL: 5.59–5.68; PrW: 2.29–2.46; MsW: 1.53–1.74; MsL: 1.14–1.27; PW: 1.27–1.36; PH: 1.78–1.95; PL: 1.36–1.48; GL: 5.25–8.48; A3L: 2.2–2.46; A4L: 2.2–2.29; A3W: 2.58–2.88; A4W: 2.71–2.88; TLa: 15–15.51; TLr: 15.85–19.24. **Indices**. CI: 81.82–86.9; OI: 29.49–30.26; SI: 85.9–86.84; MsI: 79.55–84.15; LPI: 64.15–76; DPI: 131.58–155.88.

Head. Frontal view: Subquadrate. Masticatory margin of mandible with six to seven large teeth interspersed with five to nine denticles, basal margin edentate. Labrum dorsum mostly smooth, rugose basally. Posterolateral margin of torular lobe straight. Malar carina usually reaching anterior eye margin. Eye convex, relatively globose, placed at cephalic mid–length. Posterior margin of head straight to slightly concave. Scape when pulled back, surpasses posterior margin of head by close to three times apical scape width. Ventral view: Prementum with strong transverse carina. **Mesosoma**. Lateral view: Pronotum lacking humeral carina, completely rounded. Metanotal groove present, slightly depressed, mesonotum and propodeum clearly separated. Anapleural sulcus present, though usually merged with surrounding striae. Posterior face of propodeal declivity mostly flat. Propodeal lateral margins convergent dorsally in posterodorsal view. Pheromone venting canal at metapleural gland opening, well–developed, mostly smooth. Ventrolateral propodeal declivity without deep transverse groove. Ventral view: Probasisternal posterior projection with spine. Metasternal process inclined posterad, ca. 45° in lateral view. **Petiole**. Lateral view: anterior and posterior margins of node nearly straight at base and slightly tapering dorsad; dorsal margin convex, highest point posterior to nodal longitudinal midline. Lateral projection of anteroventral nodal carina well–developed, with stout acute tip moderately bent dorsad. Dorsal view: Anterior margin of petiolar node slightly shorter than width of posterior margin. Anteroventral nodal carina incomplete, feebly concave medially. Lateral view: Subpetiolar process subtriangular, with rounded anterior cusp, followed by posterior slightly

concave slope (ca. 30°). **Gaster**. Lateral view: Prora well–developed, with blunt tip projecting ventrad. Meeting of anterior margin of abdominal tergum 3 with its dorsal margin rounded. Cinctus weak. Dorsal view: Tergum of A3 slightly longer than A4. Posterior dorsum of epipygium completely smooth. **Legs**. Mesofemur roughly equally thick as metafemur, in dorsal or ventral view. Ventral surface of meso– and metafemora almost entirely flattened from base to apex, without longitudinal groove. **Color**. Appendages including antennae and mandibles black to ferruginous black, mandibles feebly lighter than remaining integument of body. **Pilosity**. Erect hairs on body dorsum mostly shorter than maximum eye length. Scape hairs mostly shorter than apical scape width. Meso– and metatarsi bearing abundant spines interspersed with few suberect hairs. Posterior dorsum of epipygium surrounded by sparse, ca. 10, long flexuous hairs. **Sculpture**. Striae on head strongly impressed both dorsally and ventrally, covering most surface, longitudinal and slightly divergent on dorsum, roughly concentric ventrally; strong striae posterolaterally on pronotal margin, usually anepisternum and part of katepisternum, axillula, metapectus, and lateral side of propodeum; striae on petiolar node mostly absent.

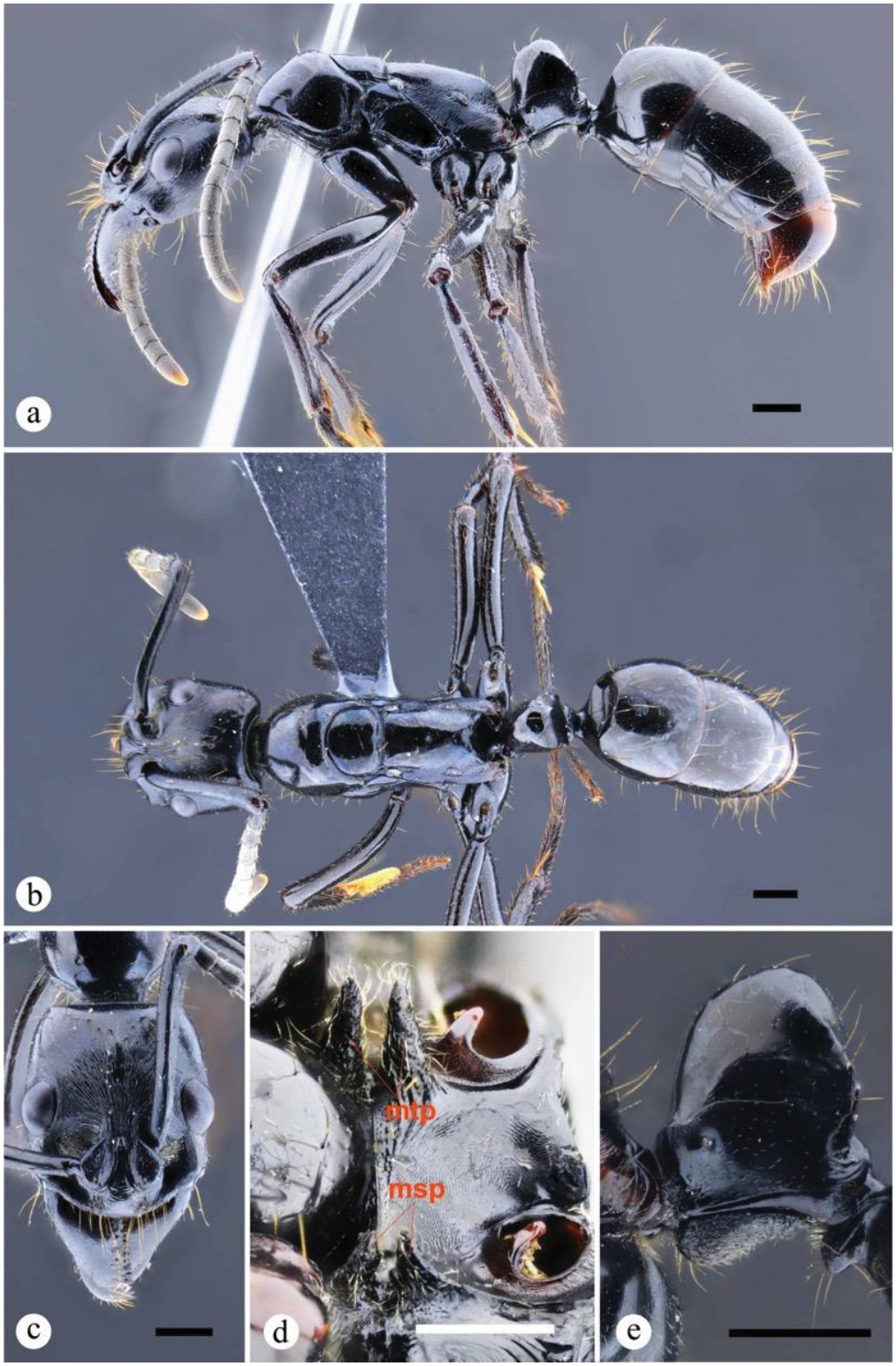


Fig. 16. *Neoponera commutata*. ☿ (DZUP: DZUP549422), Brazil, Acre. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Mesosternal (msp) and metasternal (mtp) processes in anteroventral view; **e.** Petiole in lateral view. Scale bars: 1 mm (**a** – **c**, **e**); 0.5 mm (**d**).

Queen description. Measurements (n=2). HW: 3.39; HL: 3.94–3.9; EL: 1.1–1.02; SL: 3.81–3.73; WL: 6.78–5.85; PrW: 2.92–2.67; MsW: 2.71–2.2; MsL: 3.39–2.8; PW: 1.61–1.44; PH: 2.29–1.95; PL: 1.53–1.53; GL: 7.8–5.85; A3L: 2.8–2.5; A4L: 2.88–2.46; A3W: 3.56–3.09; A4W: 3.52–3.05; TLa: 17.92–16.23; TLr: 20.04–17.12. **Indices**. CI: 86.02–86.96; OI: 30–32.5; SI: 110–112.5; MsI: 78.79–80; LPI: 66.67–78.26; DPI: 94.44–105.56.

Morphology mostly as in worker except for: **Head**. Frontal view: anterior ocellus maximum diameter subequal to that of posterior ocelli, though sometimes larger. Distance from posterior ocellar margin to posterior margin of head close to twice apical scape width. Distance between anterior and posterior ocellus approximately 1.8 times anterior ocellus diameter. **Mesosoma**. Dorsal view: Mesoscutum broader than long, close to twice as long as mesoscutellum. Transscutal line well–developed. Scutoscutellar sulcus strongly impressed, cross–ribbed. Mesoscutellum subtrapezoidal, slightly flat dorsally. Anterodorsal median propodeal sulcus vestigial. Lateral view: Posterior face of propodeal declivity slightly concave. Posterolateral margin of propodeal declivity very similar as in worker though usually less salient and sometimes with crenulae. Ventral view: Mesosternal process with internal margins slightly divergent. **Wings**. Forewing venation: Rs–M one–third much longer than 2M. Forewing evenly covered by fine setose layer, except for subbasal and basal cells which are almost completely devoid of pilosity. Hindwing venation: 1Rs absent or highly reduced. Hindwing bearing 10–14 hamuli. **Petiole.** Lateral view: anterior nodal margin shows a more pronounced slope than posterior margin. **Color, pilosity and sculpture**. Mostly as in worker (but see general synoptic description).

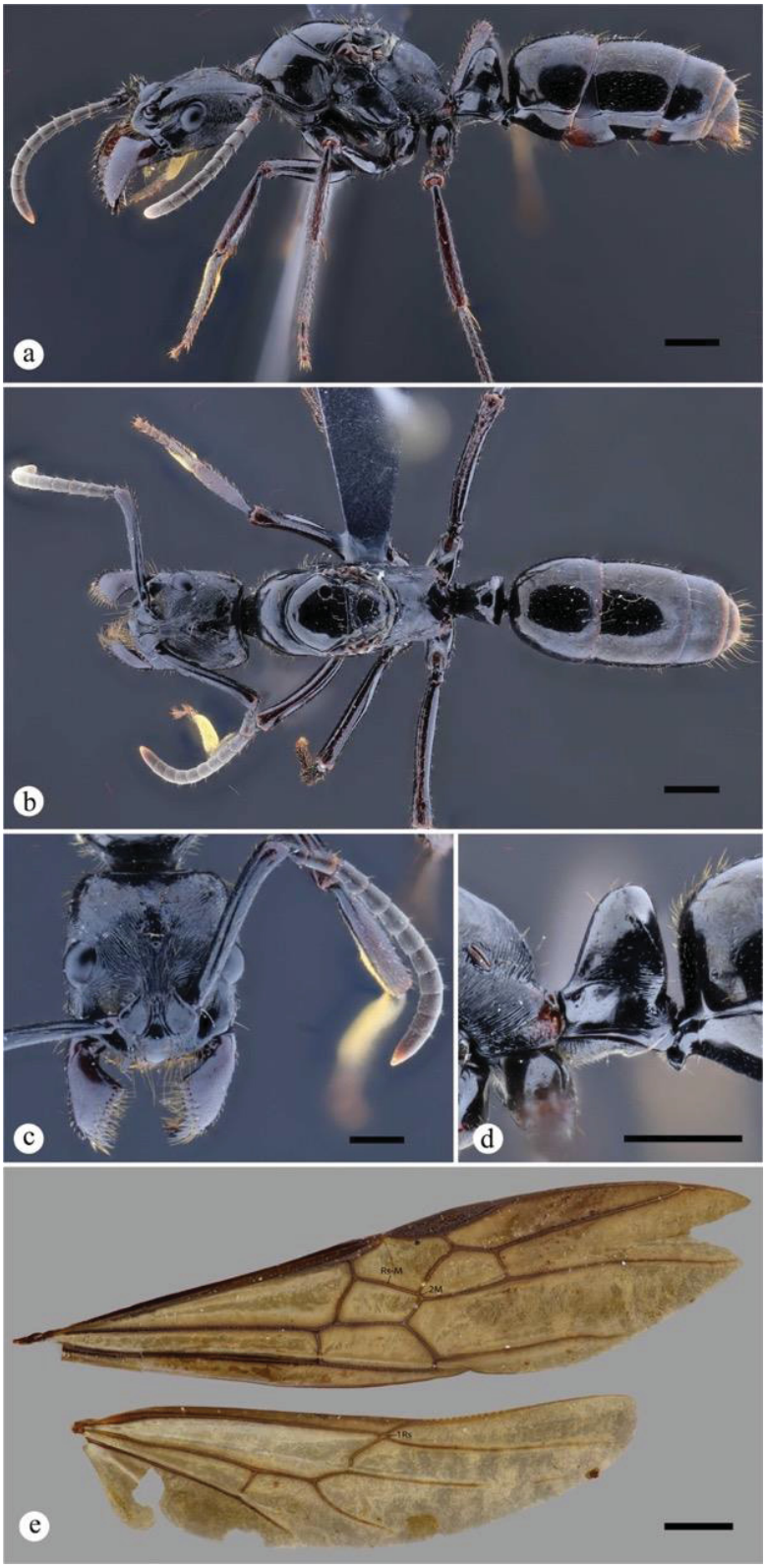


Fig. 17. *Neoponera commutata*. ♀ (INPA), Brazil, Amazonas. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Petiole in lateral view; **e.** Fore and hind wings. Scale bars: 1 mm.

Male diagnosis. Maxillary palpomeres 4 to 6 fused (Figure 18b); posterior supraclypeal area round, followed by carinate swelling (Figure 18e); torular lobe present, well–developed, small though compared to that of the worker and queen, covering ca. less than 10% of antennal socket acetabulum (Figure 14a, 18d); posterior face of propodeal declivity concave, its margin bearing relatively sharp carina (Figure. 18a); posteroventral cuticular flap at metapleural gland opening absent, replaced by strong vertical carina; pheromone venting canal absent at metapleural gland opening; forewing subbasal and basal cells almost completely devoid of pilosity (Figure 18f).

Male description. Measurements (n=3). HW: 1.94–2.04; HL: 2.04–2.19; EL: 1.02–1.08; SL: 0.44–0.48; WL: 4.95–5.14; PrW: 2.03–2.16; MsW: 2.29–2.3; MsL: 2.96–3.05; PW: 1.08–1.11; PH: 1.4–1.46; PL: 1.07–1.14; GL: 5.52–6.98; A3L: 1.84–2.14; A4L: 1.9–1.94; A3W: 2.04–2.16; A4W: 2.19–2.29; TLa: 12–12.35; TLr: 13.78–15.46. **Indices**. CI: 88.41–100; OI: 50–55.74; SI: 22.58–23.75; MsI: 75–77.59; LPI: 75–81.82; DPI: 94.44–102.38.

Head. Frontal view: Mandibular apex, when closed, slightly surpasses lateral margin of labrum. PF: pseudo 4, 4. Labral dorsum mostly rugose. Clypeus anteromedially straight to slightly concave. Area between posterior margin of clypeus and supraclypeal area without depression. Posterior supraclypeal area rounded, slightly protruding from cuticle, followed posteriorly by carinate swelling. Distance between internal margins of antennal sockets 1.5 times socket diameter. Ocellar area positioned slightly posterad to vertex. Distance from posterior ocellar margin to posterior margin of head equal to twice apical scape width. Distance between anterior and posterior ocelli close to one anterior ocellus diameter. Scape cylindrical, twice as long as pedicel. Ventral view: Prementum with strong transverse carina. Lateral view: Dorsal surface of clypeus relatively straight to slightly convex, not inflated as in remaining known males of the *N. laevigata* group, always covering anterior clypeal margin. Eye suboval, located at cephalic mid–length, slightly notched in the dorsal third, maximum length slightly shorter than half head length. **Mesosoma**. Dorsal view: Mesoscutum close to twice as long as mesoscutellum, anterior triangular impression weakly impressed, lacking median longitudinal line. Parapsidal lines strongly impressed, slightly divergent. Scutoscutellar sulcus straight. Anterior subalar area approximately as broad as tegular maximum width. Metanotum surface even, slightly flat. Metapleuropropodeal groove deeply depressed. Anterodorsal median propodeal sulcus present, strongly impressed. Lateral view: Posterior face of propodeal declivity concave. Posterolateral margin of propodeal declivity with strong, sharp carina, running along the posterodorsal propodeal margin. Pheromone

venting canal at metapleural gland opening absent, replaced by circular groove surrounded by strong, salient carinae. Ventral view: Probasisternal posterior projection with minute spine. Mesosternal process well–developed, fang–shaped, with internal margins running parallel, relatively flattened anteroposteriorly, inclined posterad ca. 45° in lateral view, space between apices approximately equal to width of each apex. Metasternal process inclined posterad, ca. 45° in lateral view, space between apices wider than width of each apex. **Wings**. Forewing venation: Rs–M one–third longer than 2M. Forewing evenly covered by fine setose layer, except for subbasal and basal cells which are almost completely devoid of pilosity. Hindwing venation: as in queen. Hindwing bearing 10–14 hamuli. **Petiole**. Lateral view: anterior and posterior margins of node nearly straight at base and tapering at top. Lateral projection of anteroventral nodal carina well–developed, with acute tip strongly bent dorsad. Dorsal view: Anterior margin of petiolar node slightly shorter than width of posterior margin. Lateral view: Subpetiolar process subtriangular, with rounded anterior cusp, followed by posterior, slightly concave slope (ca. 20° or less), usually with two slightly divergent longitudinal carinae bearing groove in between. **Gaster**. Lateral view: Meeting of anterior margin of abdominal tergum 3 with its dorsal margin rounded. Cinctus weak. Spine at posterior margin of tergum of A8 strongly acute, slightly flattened laterally, with sharp dorsal carina posteriorly. Abdominal sternum 9 longer than broad. Pygostyles close to four times longer than broad. Dorsal view: Tergum of A3 slightly shorter than A4. Ventral view: Abdominal sternum 7 showing uneven surface, with strong ditch initiating on second third, most surface bearing abundant erect and suberect hairs, ventrolaterally with long barbiculate hairs. **Legs**. Mesofemur roughly equally thick as metafemur, in dorsal view. Ventral surface of meso– and metafemora almost entirely flattened from base to apex, without longitudinal groove. Arolium roughly 0.7 times (two–thirds) the length of pretarsal claw. Pretarsal claw with tiny, barely distinguishable median tooth. **Color**. Appendages, including antennae and mandibles, black to slightly yellowish black. **Genitalia**. Dorsal view: Cupula: posterior margin of medial invagination relatively broad. Lobular process well–developed. Gonopod dorsally elongated, with approximately subequal margins from base to apex, elongated in lateral view, with dorsal and ventral margins subparallel along its length, dorsolateral margin rounded medially, smooth surface. Gonostylus subrounded apically, dorsointernal margin mostly evenly continuous. Basivolsella externally convex. Digitus subrectangular, with outer margin nearly straight in ventral view. Penial sclerites, overall outline, subrectangular, dorsal surface mostly flat, though slightly

convex posteriorly. Dorsoapical third of penial sclerite surface continuous, not modified. **Sculpture**. Head feebly rugulose mostly on dorsum; posterolateral pronotal margin slightly striated; axillula, metapleuron, and most of propodeum rugose; striae on petiolar node almost absent.

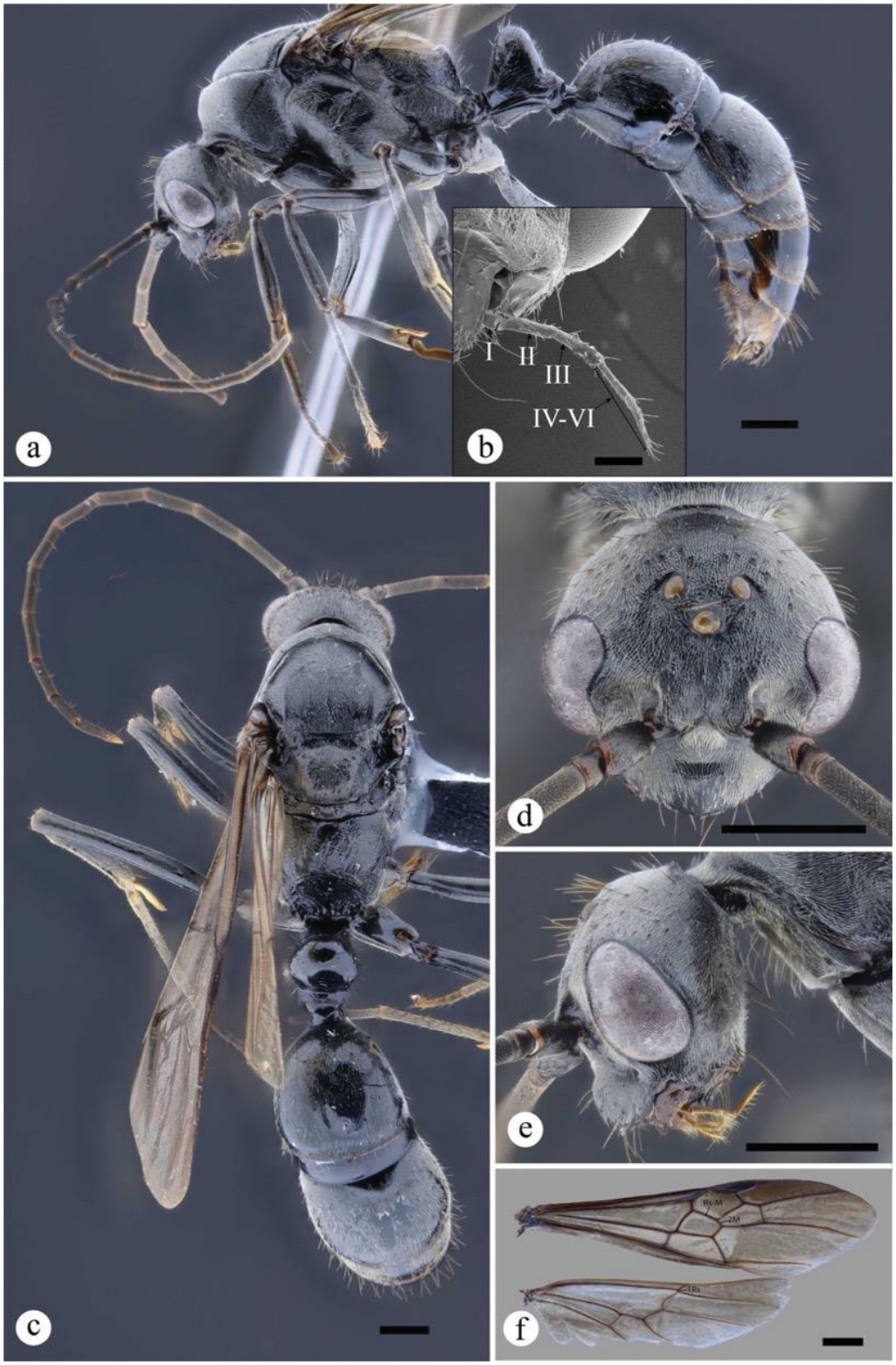


Fig. 18. *Neoponera commutata*. ♂ (MEPN: ATPFOR2051), Colombia, Chocó. **a.** Lateral view; **b.** Left maxillary palp showing fused IV-VI palpomeres; **c.** Dorsal view; **d.** Head in dorsal view; **e.** Head in lateral view; **f.** Fore and hind wings. Scale bars: 1 mm (**a**, **c** – **f**); 0.2 mm (**b**).

Natural history notes. This is a relatively common ground surface dweller, found mostly in a variety of habitats from the Amazon–Orinoco watershed, where the majority of the records are known, and have been examined in this study. Individuals of all castes have been collected throughout the year, however, research is still pending in regards to colony life cycle and production of alate forms (but see Schmidt and Overal 2009). Nothing is known in regards to its flight phenology. Several techniques have been used to collect this species including (from the most to the least effective) ground surface pitfall traps, hand collections, Malaise (mostly males), litter sifting and Winkler, and very unusually with canopy fogging. *Neoponera commutata* nests underground (Wheeler 1936, Mill 1984, Schmidt & Overal 2009, A. Troya pers. obs.) with colonies varying in population size from approximately 400–1000 individuals (Mill 1984; Schmidt & Overal 2009). Adrian Troya observed various individuals of *N. commutata* coming in and out from an (apparently) empty, ca. 1m diameter, dome–shaped, termite nest. The structure was attached to a live tree trunk in a lowland Amazonian forest in Ecuador, and seemed to host an ant colony. After ca. 15 minutes of observation no prey of any kind was seen in the mandibles of the workers. Although no guarding behavior was recognized at what would be their nest entrance located laterally on the dome, the hypothesis of reutilization of termite nests by *N. commutata* needs further confirmation.

Mill (1982a, 1984), as part of his research on termites, registered the group recruitment, predatory behavior of *N. commutata* on several termite groups, including the genus *Syntermes* Holmgren, some of the species of which are considered exclusive prey of these ants, for example *S. calvus* Emerson, *S. molestus* (Burmeister), *S. spinosus* (Latreille) [=*S. solidus* Emerson] (Wheeler 1936, Hermann 1968?, Mill 1984), all of them broadly distributed in Amazonia, except for *S. calvus* which has only been found in Brazil, French Guiana, and Guyana (Constantino 2020). Most of this data was recorded in a few sites, such as Kartabo and Kaieteur in Guyana, and Vista Alegre, state of Amazonas and Ilha de Maracá state of Roraima, in Brazil. John Lattke observed nocturnal hunting of *Syntermes* in forests of Cerro Los Pijiguaos, southern Venezuela. A loose column of 6–8 workers making their way through the litter was seen, and a little over an hour later, presumably the same column was seen returning, each worker carrying 2–3 termites in their mandibles. Based on this pattern of specific predatory behavior Wheeler (1936) proposed that the distribution of *N. commutata* should follow that of their prey. Thus far, this hypothesis has not been challenged, nor tested. *N. commutata* is an efficient predator, according to Mill (1984)

estimations, only three colonies can consume as much as three times the worker and soldier populations of the above–mentioned termite species per hectare, annually. Mill (1982b) also informed on the nest migration strategy of *N. commutata* in an Amazonian rain forest.

The venom of *N. commutata* contains antimicrobial, insecticidal and haemolytic peptides, according to Aili et al. (2016). These proteins are known as ponericins and it is assumed these help prevent diseases originated from the prey organisms brought by the ants inside their colonies (Orivel et al. 2001). Aili et al. (2016) also found in the venom of *N. commutata* the highest number of proteins as compared to the venoms of the ants *Ectatomma brunneum* Smith, *Myrmecia gulosa* (Fabricius), *Neoponera apicalis*, and *Odontomachus hastatus* (Fabricius). Schmidt & Overal (2009) found that raiders and nest defenders are equipped with more amounts of venom and that also this is more lethal than in other worker nest mates who do not get involved in foraging activities and colony defense.

Comments. Current morphological evidence allows an unequivocal evolutionary relatedness of *N. commutata* to the remaining species in the *N. laevigata* group. However, despite showing some apomorphies with other members in this clade, for example, the mandibles strongly bent ventrad in workers and queens, mesoscutum lacking notauli in males (Figure 17b), specialized termite–feeding, this lineage is an outlier from a morphological perspective. Traits like the subtriangular antennal scapes (transverse plane), the occipital and malar carinae in workers and queens, the presence of well–developed torular lobes in males, all of which are absent in the remaining species within the clade, provide signs of an evident separation of this lineage with respect to its more derived clade partners which thus far appear to form a closely related group (Troya et al. unpublished). This is also clearly depicted by the multivariate analysis in Figure 3. In addition, we consider a striking feature in this species the (secondary?) fusion of the male maxillary palpomeres 4–6 (Figure 18b), which is evidenced by the absence of a complete joint between the 4^{th} and 5^{th}, and the 5^{th} and 6^{th} segments. Thus far, this is the only known case in *Neoponera*, and to our knowledge unknown in ponerine males. Why and when this loss of segmentation occurred during the course of evolution in this caste, remain open questions.

Distribution notes. Based on our records and the literature, the populations of *N. commutata* are exclusively South American (Figure 29b). The elevational range of the species extends from nearly the sea level up to approximately 1300 m. The northern geographic range reaches the Serranía de la Macarena, a Colombian mountainous region lying just at the transition

zone between the Amazonian lowlands and the pre–mountainous Andean forests, in the center of that country. The southernmost distribution of *N. commutata* appear to be marked by the Humid Chaco and the Atlantic Forest in Paraguay, whereas its eastern limit is the state of Paraíba in northeast Brazil, where we examined a single worker from a heavily anthropized zone with remains of stepic savannas, some of which are part of the threatened Caatinga biome. In northwestern South America the Andean Cordilleras may act as the ultimate barrier for *N. commutata* entering Mesoamerica. Except for an isolated record from the Department of Bolívar in northern Colombia (mined from Antmaps.org, Janicki et al. 2016), no other sightings or collections have been reported from the northern region of that country, nor in Atlantic or Pacific regions in Central America. The Costa Rican record in San José, reported by Mackay & Mackay (2010), is a possible interception of South American origin, as no individuals have been found so far after years of sampling in the region (J. Longino, pers. comm.).

Material examined. 117☿, 9♀, 12♂: **BRAZIL**: **Acre**: 24 km SE Río Branco, Fazenda Experimental Catuaba– UFAC, 10.0667°S, 67.6167°W, 214m, 2016–11–07, Lattke, J., hand collected (DZUP), 35 km NW of Plácido de Castro, 10.3333°S, 67.4833°W, 203m, 2014–08, Rufino, C. P. B.; Souza, C. S. (CPDC), Rio Branco–Res, 9.97454°S, 68.4299°W, 219m, 2007–01–07, Oliveira, M. A. (CPDC), Villa Thaumaturgo, 10.3188°S, 67.1813°W, 130m, 1962–02, Herbst, P. (MPEG); **Amapá**: Parque Nacional Montanhas do Tumucumaque , 1.61667°N, 52.4833°W, 150m, 2017–07–25, Feitosa, R.; et al. (DZUP); **Amazonas**: 1 Km W Taruma falls, 3.00809°S, 60.07°W, 44m, 1981–03–02, Young, C. (MPEG), 30 Km N Manaus, CEPLAC, 2.83065°S, 60.0201°W, 49m, 1976–11–26 (INPA), Conjunto Villar Câmara, 3.03154°S, 59.9267°W, 65m, 1987–09–22, Daniel, P.; Diniz, L (DZUP), Instituto Nacional de Pesquisas da Amazôna (INPA), BR 174, KM 70, 3.09424°S, 59.9893°W, 100m, 1977–12–21, Soares, A. (INPA), Instituto Nacional de Pesquisas da Amazônia (INPA), Est. Aleixo Campus I, 3.09393°S, 59.9888°W, 82m, 1973–06–07, Castriloh, A. (MPEG), Manaus, 3.11863°S, 60.0217°W, 56m, , Roger (DZUP), Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA), 2.93333°S, 59.9667°W, 106m, 1982–08–27, Rafael, J., Malaise (INPA), São Francisco, 3.12267°S, 58.433°W, 17m, 2009–10–02, Fernandes, I. (INPA), Tapurucuara, 0.4°S, 65.0333°W, 64m, 1962–07–01, Oliveira, F. M. (DZUP), UFAM, 3.1°S, 59.9667°W, 80m, 2008–07–28, Oliveira, C. S. N. (DZUP); **Ceará**: Reserva Particular do Patrimônio Nacional Serra das Almas, 5.14141°S, 40.916°W, 624m, 2011–06–05, Nunes, F. A., pitfall (DZUP); **Goiás**: 20 km S of Padre

Benardo, Fazenda Lagoa Santa, 15.3918°S, 48.3156°W, 881m, 1976–12–30, Kunze (DZUP); **Mato Grosso**: 85km W of Alta Floresta, rio dos Apiacás, 9.9°S, 56.9°W, 209m, 2017–11, Lopes, F. J. A.; Araujo, C. B. (DZUP), Chapada dos Guimarães, 15.45°S, 55.7333°W, 726m, 1983–11–18 (DZUP), Fontes e Lacerda, 15.3167°S, 59.2333°W, 295m, 2014–01–03, Queiroz–Santos, L. (DZUP), Nossa Senhora do Libramento, 15.7714°S, 56.3443°W, 224m, 2015–07, Thomas, E. O., pitfall (CPDC), Pantanal de Cáceres, 16.08°S, 57.6778°W, 100m, 1984–11, Elias, C., Malaise (DZUP), Parque Estadual Cristalino (PPBio), 9.53333°S, 55.5333°W, 272m, 2013–05–01, Vicente, R. E. , pitfall (DZUP), Vila Bela da Santíssima Trinidade, 15.05°S, 59.7667°W, 216m, 2014–02–06, Maravalhas, J.; Vasconcelos, H. (DZUP); **Mato Grosso do Sul**: Fazenda Retiro Conc., 21.6833°S, 57.7667°W, 93m, 2012–08, De Souza, B., pitfall (DZUP); **Pará**: 54 km W Oeiras do Pará, 2.1°S, 50.35°W, 31m, 2015–06–22, Raveta, A. (MPEG), 65 km W Oeiras do Pará, 2.08333°S, 50.4667°W, 17m, 2015–06–16, Silva, R.; Siqueira, E. (MPEG), Alter do Chão, 2.5°S, 54.95°W, 85m, 2009–01–23, Ulyssea, M. A. (DZUP), Buena Vista, Ilha Arapiranga, 1.33319°S, 48.5669°W, 15m, 1992–11–21, Dias, J., arboreal Malaise (MPEG), Curionopolis, 6.2°S, 49.75°W, 343m, 2017–08–07, Tavares, M., pitfall (MPEG), Fazenda Florentino, 7.11667°S, 55.3833°W, 226m, 2010–12–12, Krinsk, D., pitfall (DZUP), Floresta Nacional Caxiuanã, 1.73333°S, 51.45°W, 21m, 2012–01, Cunha, D. et al., pitfall (MPEG), Floresta Nacional Caxiuanã, Estação Científica Ferreira Pennna – ECFPn, 1.75°S, 51.5167°W, 44m, 2003–10–28, Souza, J.; Moura, C., pitfall (INPA), Floresta Nacional de Carajas, Mina do Arenito, 6.08563°S, 50.2313°W, 653m, 2017–10–14, Albuquerque, E.; Monteiro, M., hand collected (MPEG), Floresta Nacional de Saracá–Taquera, 1.85°S, 56.45°W, 70m, 2016–08–25, Feitosa, R. M.; et al. (DZUP), Ilha Taboca, 2.88548°S, 52.0126°W, 16m, 2000–11–21, Santos, R.; Dias, J., hand collected (MPEG), Jarí–Amazônia, 0.88333°S, 52.6°W, 18m, 2011, Silva, E. A. (DZUP), Mina do Palito, 6.31667°S, 55.7833°W, 224m, 2018–02–02, Silva, R.; Prado, L., hand collected (MPEG), Serra das Andorinhas, 6.23333°S, 48.4667°W, 271m, 2000–07–23, Mascarenhas, B. (MPEG); **Paraíba**: Rio Tinto, 6.8083°S, 35.0775°W, 17m, 1999–03, Henriques, A., hand collected (DZUP); **Piauí**: Estação Ecológica Uruçuí–Una, 8.85996°S, 45.2001°W, 570m, 1980–12–02, Almeida, A. J. F. (DZUP); **Rondônia**: 16 km SE de Vilhena, 12.8333°S, 60.0333°W, 580m, 2012–08–14, Cavichioli, R.; et al. (DZUP), Área de Mata, quadrante 1, 11.45°S, 61.4333°W, 182m, 2013–07–01, Silva, L. S., hand collected (DZUP), Área de Mata, quadrante 8, 11.4167°S, 61.4333°W, 196m, 2013–08–01, Silva, L. S., hand collected (DZUP), Flona do Jamarí,

9.13333°S, 63°W, 114m, 2013–06–07, Bueno, L.; Williams (DZUP), Floresta Nacional de Jamari, 9.21225°S, 62.9406°W, 111m, 2017–12–19, Aurea; et al., hand collected (INPA), Jaci Paraná, Rio Madeira, 9.54037°S, 64.3728°W, 85m, 2011–10–03, Santana, F. D. (CPDC), Jaci Paraná, Três Praias, 9.54037°S, 64.3728°W, 85m, 2011–10–07, Santana, F. D. (CPDC), Parque Estadual do Guajara–Mirim, 18 km SW of Nova Dimensão, 10.3167°S, 64.55°W, 152m, 1998–02–20, Santos, J. R. M. , hand collected (DZUP), Reserva Biológica de Ouro Preto do Oeste, 10.7°S, 62.2333°W, 287m, 2009–07–13, Fernandes, I. (INPA); **Roraima**: Estação Ecológica de Maracá, 3.41667°N, 61.65°W, 127m, 1981–05–27 (MPEG); **São Paulo**: Rio Claro, 22.4°S, 47.55°W, 615m, 2004–12–10, Bacau, L. S. R. (DZUP). **COLOMBIA**: **Amazonas**: 11 km Via Tarapacá, 4.10068°S, 69.9292°W, 90m, 2002–04–27 (ICN), Amancayu, 1989–07, Castillo, R. (MUSENUV); **Meta**: Parque Nacional Natural Serranía de La Macarena, 8 SW San Juan de Arama, 2.96922°N, 73.9004°W, 1257m, 1986–12–01, Fernández, F. (ICN), Parque Nacional Natural Serranía de La Macarena, Vereda Caño Curia, 3.40672°N, 73.9537°W, 520m, 2004–03–05, Villalba, W., Malaise (MEPN), San Juan de Arama, 3.34643°N, 73.8894°W, 430m, 1986, Fernández, F. (MUSENUV). **ECUADOR: Orellana**: Estación Chiruisla, 0.61389°S, 75.8761°W, 200m, 2005–12–05, Donoso, D., fogging (QCAZ); **Pastaza**: Montalvo, 2.04987°S, 77.0072°W, 314m, 1985–07–16 (MECN); **Sucumbíos**: Limoncocha, 0.39983°S, 76.6002°W, 280m, 1967–11–17, Rettenmeyer, G. W. (QCAZ), Reserva de Producción Faunística Cuyabeno, Cooperativa Flor de Oro, 0.08667°S, 76.7147°W, 227m, 2010–04–20, Guerra, P., pitfall (MECN). **FRENCH GUIANA**: **Cayenne**: 1km E Nouragues Station, Grand Plateau, Nouragues Natural Reserve, 4.08885°N, 52.6749°W, 120m, 2009–09, Groc, S. , pitfall (CPDC), 9km W of Kaw Camp Patawa, Kaw Mountains, 4.53419°N, 52.1516°W, 284m, 2008–09, Groc, S.; Dejean, J., Winkler (CPDC), CSG, P62, 5.24142°N, 52.8386°W, 28m, 2015–04–20, Orivel, J.; Fichaux, M.; Petitclerc, F.;, Pitfall72h (EcoFoG), Petit Saut, 5.06667°N, 53.0333°W, 75m, 2002–11–01, Orivel, J. (DZUP); **Saint–Laurent–du–Maroni**: Belvedere de Saul, 3.61667°N, 53.2°W, 326m, 2010–07, SEAC (DZUP), Itoupe, P1, 3.26391°N, 53.7616°W, 800m, 9/11/14, Orivel, J.; Fichaux, M., Pitfall72h (EcoFoG), Itoupe, P5, 3.22583°N, 53.9692°W, 600m, 2014–11–11, Orivel, J.; Fichaux, M., Pitfall72h (EcoFoG), Itoupe, P6, 3.12221°N, 53.9932°W, 600m, 11/15/14, Orivel, J.; Fichaux, M., Pitfall72h (EcoFoG), Laussat, P6, 5.4683°N, 53.5809°W, 50m, 2015–08–28, Orivel, J.; Fichaux, M.; Jackie; N. Milhom, Winkler48h (EcoFoG), Mitaraka, P1, 2.24362°N, 54.4588°W, 385m, 2015–03–03, Orivel, J.; Petitclerc, F., Winkler48h (EcoFoG), Mitaraka, P10, 2.21636°N, 54.457°W, 392m,

2015–02–28, Orivel, J.; Petitclerc, F., Pitfall72h (EcoFoG). **PERU**: **Cusco**: Estación Biológica Villa Carmen, 1.5 Km N Pillcopata, 12.8833°S, 71.4°W, 521m, 2013–08–05, Ant course 2013 (DZUP); **Loreto**: 3 km NE of Genato Herraro, Estación Genaro Herrera, 4.83333°S, 73.65°W, 121m, 2011–01–13 (ICN); **Madre de Dios**: Greenhouse at the Universidad Nacional Amazónica , 12.5833°S, 69.2°W, 207m, 2011–04–14, Salcedo, J. M. C. (DZUP), Reserva Nacional Tambopata, Sachavacayoc, Condenado I trail, 12.85°S, 69.3663°W, 186m, 2012–07–20, Fernandes, I., Winkler (INPA), Sachavacayoc Centre, 12.85°S, 49.3667°W, 209m, 2012–07–19, Feitosa, R. M.; Probst, R. S. (DZUP). **VENEZUELA**: **Amazonas**: Caño Panaben, Marurucu, 4.5 Km NE Santa Bárbara, 3.965°N, 67.024°W, 110m, 2000–10, García, D. (MIZA), Parque Nacional Parima Tapirapecó, Cerro Delgado Chalbaud, 2.277°N, 63.362°W, 1000m, 11/2/92, Clavijo, J.; Chacón, A. (MIZA), Yutajé, 5.611°N, 66.118°W, 120m, 10/19/88, Chacón, A. (MIZA); **Bolívar**: 40 Km E La Paragua, 6.826°N, 62.986°W, 290m, 6/11/83, Bordón, C. (MIZA), Alto Caura region, Cuchime, 5.8°N, 64.66°W, 280m, 4/7/63, La Salle expedition (MIZA), Amarawai Tepuy, Talud Norte, 6.083°N, 62.25°W, 500m, 5/1/86, Lattke, J. (MIZA), Canaima, 6.239°N, 62.852°W, 390m, 10/17/88, Mackay, W. (MIZA), Caura river, 7.611°N, 64.9118°W, 18m, 1899–02–11, Klages, E. (MPEG), El Dorado a Santa Elena de Uairen, Km. 17, 6.715°N, 61.637°W, 120m, 6/28/84, Lattke, J. (MIZA), El Dorado a Santa Elena de Uairen, Km. 88, 6.148°N, 61.431°W, 150m, 1998–11–10, Chacón, A. (MIZA), El Hormiguero, Altiplanicie de Nuria, 7.666°N, 61.333°W, 190m, 1974–12–03 (MIZA), El Playón, Caura river, 6.3151°N, 64.4899°W, 250m, 1980–09–08, Osuna, E.; Clavijo, J. (MIZA), Gran Sabana, San Ignacio, 5.033°N, 60.95°W, 1100m, 1993–03–01, Osborn, F. et al. (MIZA), Guri, 7.779°N, 63.026°W, 200m, 1988–06–27, Joly, L.; et al. (MIZA), Hato El Amparo, Cachipo river, 8.203°N, 63.31°W, 20m, 1984–04–15, Chacón, M. (MIZA), Icabarú, 4.3332°N, 61.7413°W, 500m, 1957–06–18, Bernardi, J. (MIZA), Las Bonitas, Caroní river, 7.866°N, 61.661°W, 34m, 1984–12–18, Osuna, E. (MIZA), Los Pijiguaos, 6.572°N, 66.811°W, 87m, 1987–03–23, Lan, D. (MIZA), Los Pijiguaos, Bauxilum mine, 6.483°N, 66.766°W, 690m, 2004–11–02, Lattke, J. (MIZA), Mantecal, Cuchivero river, 6.866°N, 65.633°W, 150m, 1970–03–23, Fernández, F.; Rosales, C. J. (MIZA), Mariposa, camp. Corocate, between Caura river and Sipao river, 7.5703°N, 65.2782°W, 50m, 1990–08–12, Alemán, M. (MIZA), Paragua river, E Chiguao river, 6.8478°N, 63.0475°W, 425m, 1983–04–02 (MIZA), Paraitepuy, Vía Roraima, 5.055°N, 60.934°W, 1200m, 1978–02–25, Escobar, A. (MIZA), Parque Nacional El Caura, 6.108°N, 64.716°W, 340m, 1986–08–28, Ayala, J. (MIZA), Quebrada Jaspe, 4.907°N, 61.092°W,

920m, 1986–08–19, Gill, B. (MIZA), Salto Las Babas, Caroní river, 6.519°N, 62.877°W, 425m, 1983–04–08 (MIZA), San Ignacio de Yuruaní, Gran Sabana, 4.984°N, 61.15°W, 910m, 1986–12–30, Hernández, J. (MIZA), San Juan de Manapiare, carretera Caicara, Suapure river, 6.027°N, 66.2549°W, 400m, 1971–12–27, García, J. (MIZA), San Juan de Manapiare, km. 170, carretera Caicara, 6.3091°N, 66.1882°W, 300m, 1973–12–21, García, J. (MIZA), Santa Elena, 4.59503°N, 61.1094°W, 1000m, 1975–03–01, Ross, E. S. (CASC), Santa Elena de Uairén, 4.606°N, 61.105°W, 1000m, , Revelo (MIZA), Santa María de Erebato, 5.15°N, 64.833°W, 330m, 1963–04–09, La Salle expedition (MIZA); **Monagas**: Caripito, 10.107°N, 63.103°W, 36m, 1963–07–17, Rosales, C.; Requena, J. (MIZA).

Geographic range.: Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, Venezuela.

***Neoponera gojira* sp. nov.**

ZooBank: https://zoobank.org/D146DCC3-6FE5-4BEF-9E2A-009BAAD12740

Figures. 19: a – g (☿); 29: a (distribution)

Type material. ***Holotype*.** 1☿; **BRAZIL**: **Minas Gerais**: Pandeiros, Efeito antropização no Cerrado APA REVISE (Project), 511m (alt.), 15°29’58.15”S, 44°45’39.94’O, 07.i.2016, Santiago, et al. (leg.), Area 9, Local APA, pitfall epigéico (col. method), ponto 1, repetição D, quadrante 1. (DZUP: DZUP549444).

Etymology. The specific name honors the French metal band Gojira, in recognition of their altruistic activism for the conservation of nature, as well as for supporting the rights of ancestral indigenous peoples living across Amazonia. Through their lyrics the band promotes an increasing awareness of our paramount, nonetheless usually neglected, biological diversity. The name is a noun in apposition, thus invariable.

Worker diagnosis. Antennal scape surpassing posterior margin of head by ca. one apical scape width; head in frontal view trapezoid, slightly wider posteriorly than anteriorly (Figure 19d); dorsal masticatory margin of mandible uneven, with shallow, irregular rim (Figure 19b); masticatory margin of mandible with three comparatively large blunt teeth alternating with blunt denticles (Figures 19b); posteroventral cuticular flap at metapleural gland opening reduced to

narrow carina, orifice of gland completely visible in posterolateral view (Figure 2d); petiolar node laterally lacking striae, though very tenuous lines are present near its ventral margin (Figure 19e); prora tiny, barely discernible laterally (Figure 19e); posterior region of abdominal sternites 5 – 7 showing significantly more piligerous punctures compared to the rest of species in the *N. laevigata* group.

Worker description. Measurements (n=1): HW: 2.19; HL: 2.5; EL: 0.66; SL: 1.94; WL: 3.72; PrW: 1.63; MsW: 0.97; MsL: 0.87; PW: 1.17; PH: 1.28; PL: 1.12; GL: 5.1; A3L: 1.43; A4L: 1.48; A3W: 1.73; A4W: 1.89; TLa: 10.26; TLr: 12.45; **Indices**. CI: 87.76; OI: 30.23; SI: 88.37; MsI: 111.76; LPI: 88; DPI: 104.55.

Head. *Frontal view*: trapezoidal, with posterior margin wider than anterior margin. Masticatory margin of mandible with four large, blunt teeth interspersed with four denticles, basal margin edentate. Prementum with clear transverse dome. Labral dorsum mostly smooth. Posterolateral margin of torular lobe rounded. Malar carina absent, though swelling is present. Eye convex, relatively flat, not surpassing lateral margin of head, placed anterior to cephalic mid–length. Posterior margin of head concave. Occipital carina absent. *Lateral and/or frontal view*: Scape when pulled back, surpasses posterior margin of head by close to one apical scape width. **Mesosoma**. *Lateral view*: Pronotum with weak, blunt, barely distinguishable humeral carina. Metanotal groove present, though not depressed, usually clearly separating mesonotum and propodeum. Anapleural sulcus present, completely merged with surrounding striae. Posterior face of propodeal declivity flat. Posterolateral margin of propodeal declivity with feeble, blunt carina, almost devoid of crenulae. Pheromone venting canal at metapleural gland opening well–developed, smooth. Propodeal lateral margins subparallel in posterodorsal view. Ventrolateral propodeal declivity with deep transverse groove just dorsad to metapleural gland opening. *Ventral view*: Probasisternal posterior projection acute. Space between apices of mesosternal process wider than width of each apex. **Petiole**. *Lateral view*: Anterior and posterior margins of node nearly straight and semi–parallel, posterior margin slightly convex; posterodorsal margin slightly higher than anterodorsal margin; mid–dorsal margin mostly flat. Lateral projection of anteroventral nodal carina well–developed, with slightly blunt tip moderately bent dorsad. *Dorsal view*: Anterior margin of petiolar node roughly as broad as width of posterior margin. Anteroventral nodal carina incomplete, feebly concave medially. *Lateral view*: Subpetiolar process subtriangular, with acute anterior cusp, keel–shaped, followed by posterior relatively straight slope (ca. 30°). **Gaster**.

Lateral view: Prora present, though poorly developed, similar to a cuticular lip, usually hardly discernible. Meeting of anterior margin of abdominal tergum 3 with its dorsal margin relatively angled. Cinctus moderate. *Dorsal view*: Tergum of A3 slightly shorter than A4. Posterior dorsum of epipygium smooth, feeble striations and punctae present but hardly discernible and requires rotation of specimen to get better angle of observation. **Legs**. Mesofemur thickened medially, thicker than metafemur, in dorsal or ventral view. Ventral surface of meso– and metafemora flattened roughly on distal two–thirds, bearing longitudinal shallow groove. **Color**. Appendages including antennae and mandibles black to ferruginous black, mandibles feebly lighter than remaining integument of body. **Pilosity**. Erect hairs on body dorsum about as long as maximum eye length. Posterior dorsum of epipygium surrounded by ca. 20, long flexuous hairs. **Sculpture**. Striae on head present, only dorsally, covering most of surface except posterior third, anepisternum, katepisternum, metapleuron and lateral side of propodeum bearing strong striae; striae on petiolar node almost absent.

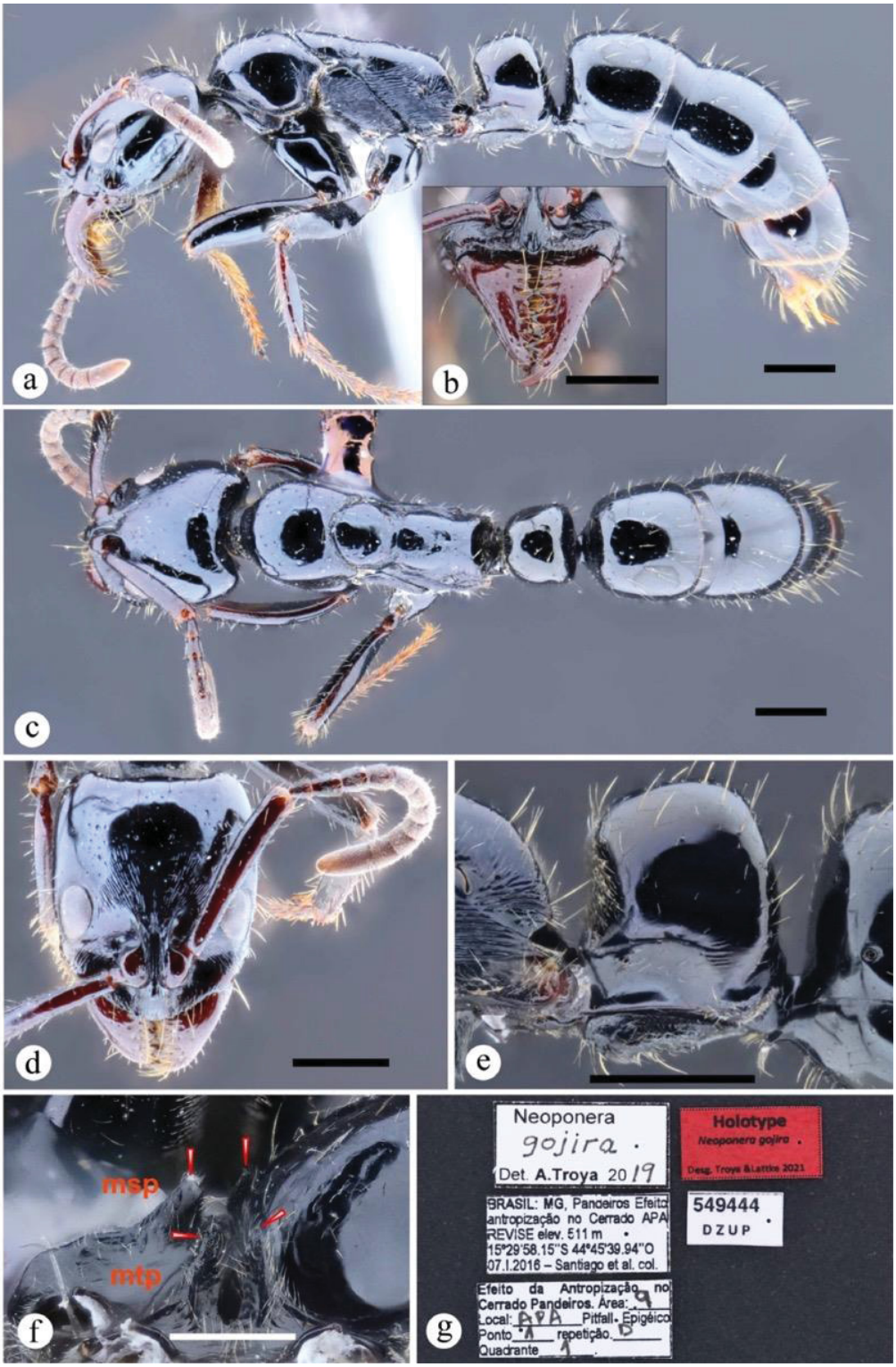


Fig. 19. *Neoponera gojira* **sp. nov.** Holotype ☿ (DZUP: DZUP549444), Brazil, Minas Gerais. **a.** Lateral view; **b.** Mandibles in frontal view; **c.** Head in frontal view; **e.** Petiole in lateral view; **f.** Meso– and metasternal processes (red arrowheads) in posteroventral view; **g.** Collection labels. Scales bars: 1 mm (**a** – **e**); 0.25 mm (**f**).

Queen and male. Unknown.

Natural history notes. Unknown. The holotype was collected in January 2016 in a project aiming to analyze anthropogenic disturbance in the Brazilian Cerrado. The ecosystem where this species was found is composed of tropical savannas, deciduous and semi–deciduous forests, and highly disturbed areas used mostly for agriculture (IBGE 2004, Soterroni et al. 2019, García et al. 2021)

Comments. *Neoponera. gojira* **sp. nov.** is currently known from a single specimen, nonetheless, various morphological features clearly separate it from its potential closest species: *N. laevigata* and *N. mashpi* **sp. nov.** The following characters are useful for separating the workers: the dorsal masticatory mandibular region shows a depressed rim (Figure 19b) which is absent in *N. laevigata* and *N. mashpi* **sp. nov.**, this feature is not to be confused with the strongly excavated mandibular groove of *N. marginata*, which runs uninterrupted posterad along the entire mandibular base (Figure 12a); posterior margin of head in full–face view clearly concave, with relatively salient posterolateral corners (Figure 19d), while in *N. laevigata* this margin is straight or feebly concave (Figure 20c, 21d), and straight or slightly convex in *N. mashpi* **sp. nov.** (Figure 25c); flap at metapleural gland opening strongly reduced to a narrow, but sharply delineated carina, in posterolateral view, while in both *N. laevigata* and *N. mashpi* **sp. nov.** this flap is well–developed and runs uninterrupted along the ventrolateral margin of the metapleuron until reaching its anterior lobe (Figure 2d); clypeus and internal side of frontal lobes heavily sculpted with foveae and striae (Figure 12b), in *N. laevigata* and *N. mashpi* **sp. nov.**, on the other hand, the clypeus is feebly striated, and the frontal lobes almost always lack sculpture, except for two shallow foveae on the internal side. Heavily impressed clypeal sculpture is also typical in *N. marginata*, and to a lesser degree in *N. commutata*. However, impressed sculpture (foveae and striae) on the frontal lobe area has only been seen in *N. gojira* **sp. nov.** Compared to the workers of similarly sized species, e.g., *N. laevigata* (WL= 2.45 – 3.57 mm; TLa= 7.88 – 10.03 mm) and *N. marginata* (WL= 2.75 – 3.59 mm; TLa= 7.41 –10 mm), the holotype of *N. gojira* **sp. nov.** is thus far the second largest worker caste found (WL= 3.72 mm; TLa= 10.26 mm), only oversized by workers of *N. commutata* in this species–group. It is assumed that the still unknown conspecifics (but see below) may have a similar size showing the characteristic continuous polymorphic size variation that is present in its closest lineages.

Geographic range. Eastern Brazil.

Phenotypic variant of *N. gojira* sp. nov.

In the northeastern Brazilian states of Piauí and Bahia we found ten workers morphologically similar to *N. gojira* **sp. nov.** and *N. laevigata*. This variant shares morphospace with these two species, but also with *N. marginata* (Figure. 3). Until additional material is discovered we leave this morphotype as *Neoponera* nr. *gojira* which shows the following diagnostic traits: dorsal margin of mandibles, near the masticatory region, with shallow fossulae; antennal scape surpassing posterior

margin of head by approximately one apical scape width (Figure 13b); flap at metapleural gland orifice present, though not strongly curved anterad, so that the orifice is easily visible in posterolateral view (Figure 2b); petiolar node mostly smooth, though with feebly impressed striae laterally (Figure 22b); prora tiny (Figure 13d, 19e).

Neoponera nr. *gojira* differs from *N. gojira* **sp. nov.** in the following: relatively smaller (WL= 3.24 – 3.32 mm; TLa= 8.78 – 8.93 mm); four to five teeth on mid masticatory margin of mandibles clearly smaller and more acute (*N. gojira* **sp. nov.** bears three relatively large, blunt teeth, Figure 19b); posterior margin of head less concave than in Figure 19d). *Neoponera* nr. *gojira* differs from *N. laevigata* in the following: dorsal mandibular surface, near masticatory margin, bearing fused, shallow fossulae (we saw these fossulae in some workers of *N. laevigata,* though clearly less impressed); petiolar node with tenuously impressed striae (node strongly striated laterally in *N. laevigata,* especially specimens from Amazonian populations); flap at metapleural gland orifice well–developed but not strongly curved anterad (this flap is also well–developed in *N. laevigata* but is strongly curved anterad, partially hiding the gland orifice, Figure 2a).

Measurements (n=3) of *Neoponera* nr. *gojira*: HW: 1.73–1.84; HL: 2.09–2.19; EL: 0.56–0.56; SL: 1.58–1.73; WL: 3.24–3.32; PrW: 1.3–1.33; MsW: 0.84–0.92; MsL: 0.69–0.77; PW: 1.02–1.07; PH: 1.07–1.07; PL: 0.82–0.97; GL: 2.91–4.13; A3L: 1.1–1.22; A4L: 1.33–1.43; A3W: 1.53–1.58; A4W: 1.68–1.71; TLa: 8.78–8.93; TLr: 9.26–10.46. **Indices**. CI: 79.07–87.8; OI: 30.56–32.35; SI: 88.57–100; MsI: 116.67–122.22; LPI: 76.19–90.48; DPI: 105.26–128.13.

Material examined for *Neoponera* nr. *gojira*: 10☿: **BRAZIL**: **Bahia**: Barreiras, 12.1333°S, 45.1333°W, 527m, 2011–05–15, Carvalho, K. S. (DZUP); **Piauí**: Ribeiro Gonçalves, 8.85996°S, 45.2001°W, 570m, 1980–12–10, Almeida, A. J. F. (DZUP), 1980–12–13, Almeida, A.

J. F. (DZUP), 1980–12–16, Almeida, A. J. F. (DZUP), 1980–12–12, Almeida, A. J. F. (DZUP), 1980–12–15, Almeida, A. J. F. (DZUP), 1980–12–18, Almeida, A. J. F. (MPEG), 1980–12–11, Almeida, A. J. F. (DZUP), 1980–12–14, Almeida, A. J. F. (DZUP), 1980–12–17, Almeida, A. J. F. (MPEG).

***Neoponera laevigata* (Smith, 1858)**

Figures. 20: a – f (☿); 21: a – f (♀); 29: a (distribution)

Ponera laevigata Smith, 1858: 98. BRAZIL (Amazonas), Ega (currently Tefé), (3.3°S, 64.7°W, 57m), (*Bates, H. W.*). Type material: 1 ☿ syntype (BMNH) (not examined), and 1 ☿, **lectotype** (present designation), BMNH(E)1015554, AntWeb CASENT0902510 (image examined).

Combinations. In *Euponera* (*Mesoponera*): Emery, 1901: 47. In *Termitopone*: Wheeler, 1936: 159. In *Pachycondyla*: Mayr, 1886: 358; Brown, 1995: 306; In *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species. Mayr, 1863: 448; Wheeler, 1936: 161 (redescription); Mackay & Mackay, 2010: 414 (redescription).

Senior synonyms. *Neoponera gagatina* (Emery): Emery, 1892: 167; *Neoponera laevigata* var. *whelpleyi* (Wheeler): Wheeler, 1936: 164 [type material: 1 ☿ **paralectotype** (present designation), Trinidad & Tobago, Caparo, 1910-02-12, Whelpley, P.B., MCZENT20454. (image examined)].

Worker and queen diagnosis. Antennal scape, when pulled back, surpasses posterior head margin by about one apical scape width (Figure 13b); longitudinal striae present around internal margin of eye and between frontal carinae, diverging posterad and usually vanishing at vertex, but reaching lateral head margin just posterior to eyes (Figures 13b, 21d); dorsum of head in smaller workers significantly less sculpted than larger workers to almost devoid of striae; lateral face of petiolar node always with oblique, usually strongly impressed striae (Figure 20d); subpetiolar process, in lateral view, subtriangular, with acute anterior cusp, usually followed by relatively flat surface posterad (Figure 13d, 20d); prora absent or very small, lip–shaped (Figure 13d).

Worker description. Measurements (n=10): HW: 1.43–2.12; HL: 1.71–2.45; EL: 0.41–0.61; SL: 1.35–1.94; WL: 2.45–3.57; PrW: 0.94–1.53; MsW: 0.69–1.04; MsL: 0.55–0.97; PW: 0.69–1.07; PH: 0.78–1.25; PL: 0.73–1.05; GL: 2.61–4.34; A3L: 0.98–1.48; A4L: 0.98–1.48;

A3W: 1.06–1.76; A4W: 1.1–1.69; TLa: 6.9–10.03; TLr: 7.55–11.4. **Indices**. CI: 79.18–90.57; OI: 28.13–31.17; SI: 88.89–101.3; MsI: 105.26–126.47; LPI: 76.92–94.74; DPI: 94.44–117.65.

Head. *Frontal view*: subrectangular. Masticatory margin of mandible with four to five teeth interspersed with three to six denticles, basal margin edentate. Prementum with clear transverse dome. Labral dorsum mostly smooth, posterolateral margin rounded. Malar carina absent, though swelling present. Eye convex, relatively flat, not surpassing lateral margin of head, placed anterior to cephalic mid–length. Posterior margin of head straight to slightly concave. Occipital carina absent. Scape when pulled back, surpasses posterior margin of head by close to one apical scape width. **Mesosoma**. *Lateral view*: Pronotum with weak, blunt, barely distinguishable humeral carina. Metanotal groove present, though not depressed, usually clearly separating mesonotum and propodeum. Anapleural sulcus present, though usually merged with surrounding striae. Posterior face of propodeal declivity mostly flat. Posterolateral margin of propodeal declivity with feeble, blunt carina, sometimes with crenulae. Pheromone venting canal at metapleural gland opening well–developed, smooth. Propodeal lateral margins subparallel in posterodorsal view. Ventrolateral propodeal declivity with deep transverse groove just dorsad to metapleural gland opening, in posterolateral view. *Ventral view*: Probasisternal posterior projection acute. Space between mesosternal process lobes approximately equal to width of each. Metasternal process inclined posterad 20°–30° in lateral view. **Petiole**. *Lateral view*: anterior and posterior margins of node usually nearly straight and semi–parallel, sometimes posterior margin slightly convex; posterodorsal margin slightly higher than anterodorsal margin; mid–dorsal margin mostly flat. Lateral projection of anteroventral nodal carina well–developed, with acute or slightly blunt tip moderately bent dorsad. *Dorsal view*: Anterior margin of petiolar node slightly shorter than width of posterior margin. Anteroventral nodal carina incomplete, with feeble concavity medially. *Lateral view*: Subpetiolar process subtriangular, usually with keel–shaped, acute anterior cusp, followed by posterior straight slope (ca. 20° or less). **Gaster**. *Lateral view*: Prora present, though poorly developed, similar to a cuticular lip, usually hardly discernible. Meeting of anterior margin of abdominal tergum 3 with its dorsal margin relatively angled. Cinctus moderate. *Dorsal view*: Tergum of A3 slightly shorter than A4. *Posterior view*: Posterior dorsum of epipygium smooth, though feeble striations and punctae may be present. **Legs**. Mesofemur thickened medially, thicker than metafemur, in dorsal or ventral view. Ventral surface of meso– and metafemora flattened roughly on distad two thirds, usually bearing longitudinal shallow groove.

Color. Appendages including antennae and mandibles brown to ferruginous brown, occasionally legs yellowish and mandibles lighter than remaining integument of body. **Pilosity**. Most erect hairs on body dorsum approximately as long as maximum eye length. Scape hairs about as long as apical scape width. Posterior dorsum of epipygium surrounded by ca. 20, long flexuous hairs. **Sculpture**. Striae on head present, only dorsally, covering most of surface except posterior third, anepisternum, usually part of katepisternum, metapleuron, lateral and part of dorsal side of propodeum with strong striae, on petiolar node always present, oblique and strongly impressed.

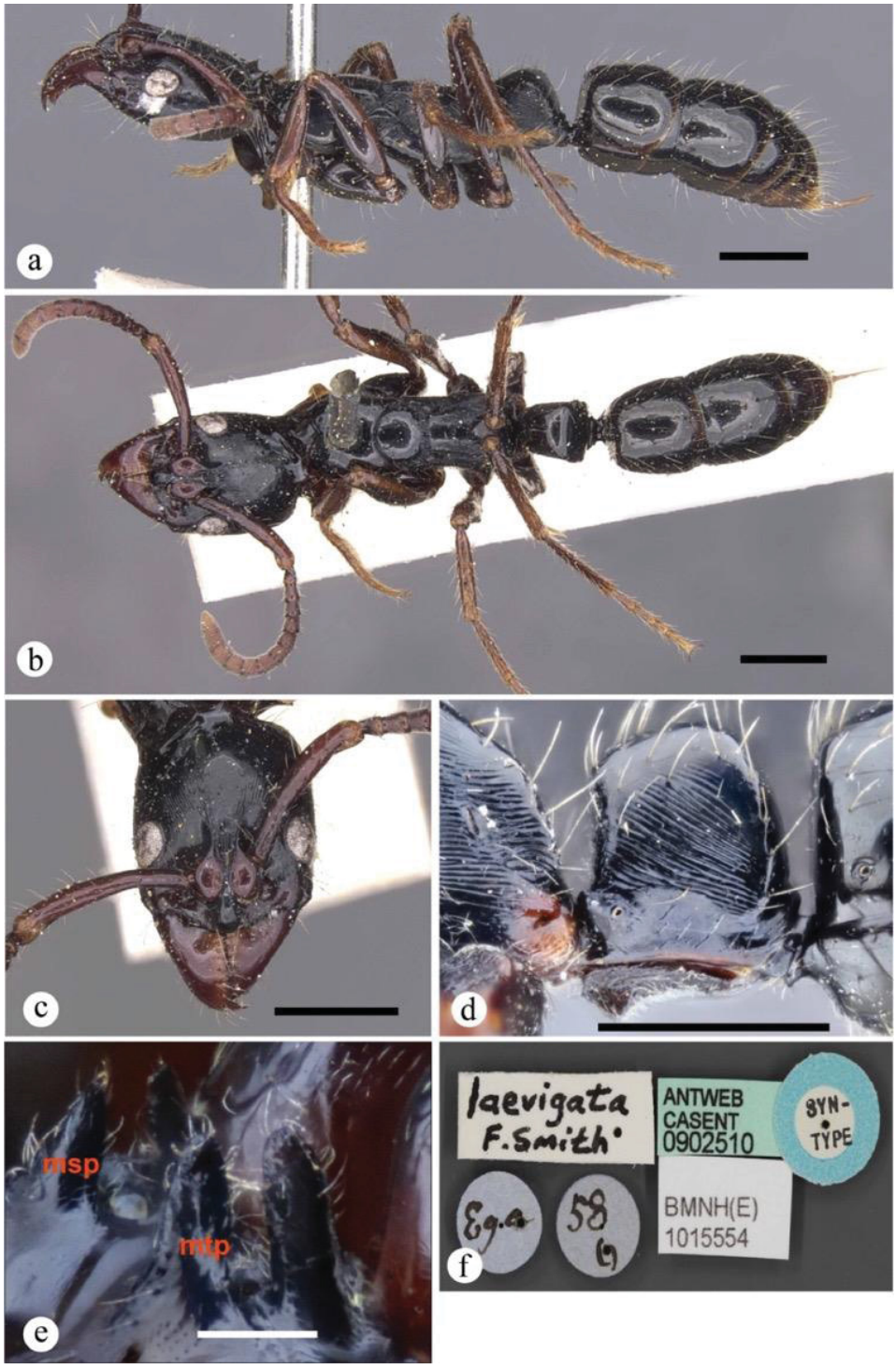


Fig. 20. *Neoponera laevigata*. Lectotype ☿ (BMNH: BMNH(E)1015554), Brazil, Amazonas. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **f.** Collection labels. Images **d, e**: non-type ☿ (MPEG: ATPFOR2027), Brazil, Roraima. **d.** Petiole in lateral view; **e.** Mesosternal (msp) and metasternal (mtp) processes in posteroventral view. Scale bars: 1 mm (**a** – **d**); 0.2 mm (**e**).

Queen description. Measurements (n=2). HW: 2.48–2.41; HL: 2.79–2.73; EL: 0.73–0.73; SL: 2.13–2.1; WL: 4.95–4.7; PrW: 2.29–2.1; MsW: 2.22–2.19; MsL: 2.79–2.6; PW: 1.59–1.68; PH: 1.59–1.68; PL: 1.21–1.08; GL: 6.6–6.1; A3L: 1.97–2.1; A4L: 1.97–1.97; A3W: 2.6–2.54; A4W: 2.73–2.7; TLa: 12.89–12.57; TLr: 15.56–14.6. **Indices**. CI: 88.37–88.64; OI: 29.49–30.26; SI: 85.9–86.84; MsI: 79.55–84.15; LPI: 64.15–76; DPI: 131.58–155.88.

Morphology as in worker except for: **Head**. *Frontal view*: Anterior ocellus maximum diameter subequal to that of posterior ocelli. Distance from posterior ocellar margin to posterior margin of head close to twice apical scape width. Distance between anterior and posterior ocelli approximately 1.5 times anterior ocellus diameter. Posterior margin of head straight to slightly concave. **Mesosoma**. *Dorsal view*: Mesoscutum about as long as broad, close to 2.5 times as long as mesoscutellum. Transscutal line feebly developed. Scutoscutellar sulcus shallowly impressed, formed by scrobiculate sculpture. Mesoscutellum subquadrate, slightly flat dorsally. Posterior face of propodeal declivity flat. Posterolateral margin of propodeal declivity slightly rounded to barely carinate, not forming crenulae. Anterodorsal median propodeal sulcus present, weakly impressed. Probasisternal posterior projection with spine. **Wings**. Forewing venation: Rs–M approximately one half larger than 2M. Forewing evenly covered by fine setose layer. Hindwing venation: 1Rs highly reduced. Hindwing bearing 10–13 hamuli. **Petiole**. *Lateral view*: anterior and posterior margins of node nearly straight at base and slightly tapering dorsad, with posterior margin slightly convex and with more pronounced slope than anterior margin which is almost perpendicular to horizontal body axis. **Gaster.** Prora absent. **Color**. Appendages, including antennae and mandibles, dark brown to black. **Pilosity**. Meso– and metatarsi bearing abundant spines and stiff setae interspersed with abundant suberect hairs. **Sculpture**. Striae on head present only dorsally, covering most of surface except posterior third; strong striae on posterolateral margin of pronotum, usually anepisternum and part of katepisternum, axillula, metapectus, and propodeum laterally; petiolar node always with oblique, strong striae laterally.

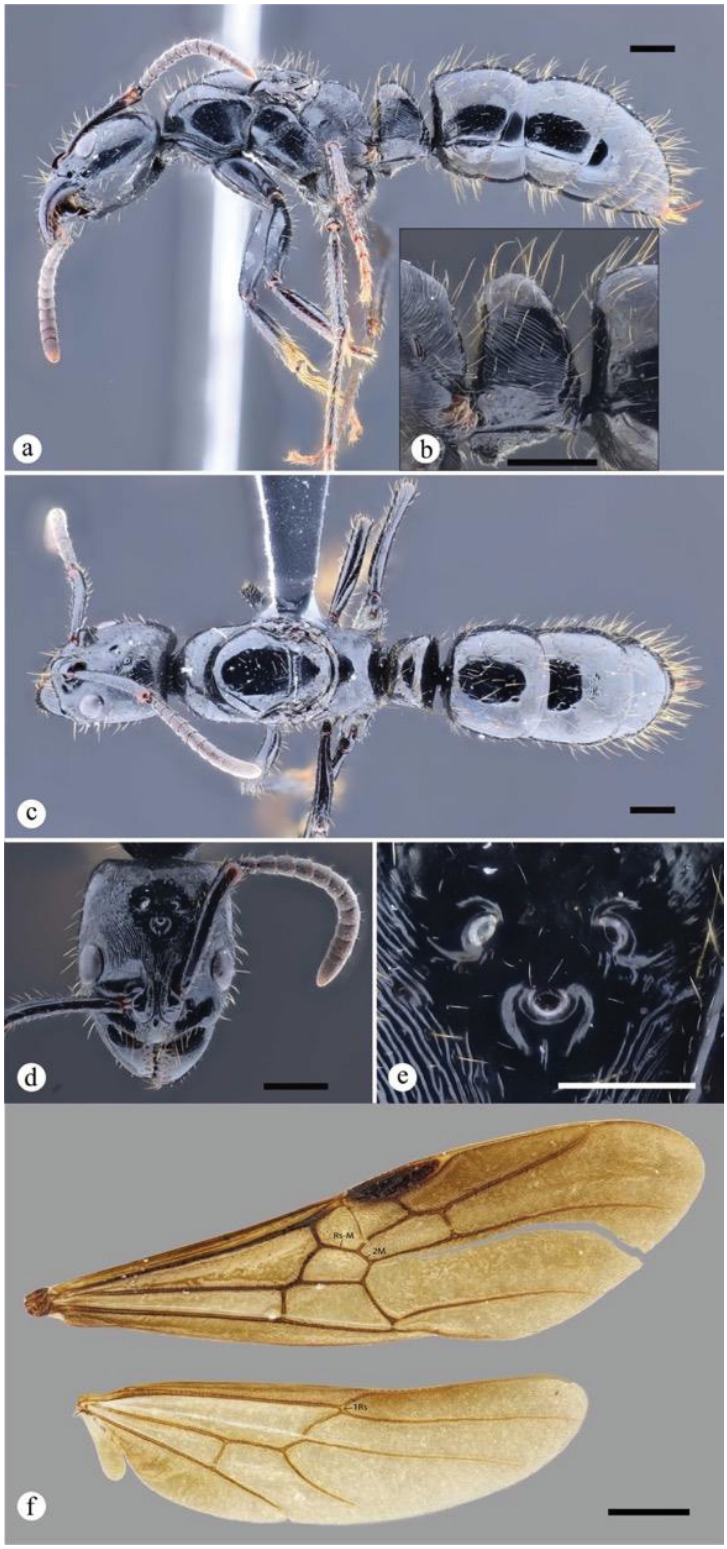


Fig. 21. *Neoponera laevigata*. ♀ (MPEG: ATPFOR2049), Brazil, Pará. **a.** Lateral view; **b.** Petiole in lateral view; **c.** Dorsal view; **d.** Head in frontal view; **e.** Ocelli in frontal view; Fore and hind wings. Scale bars: 1 mm (**a** – **d**, **f**); 0.5 mm (**e**).

Male description. Not available, but see Wheeler (1936), and Mackay & Mackay (2010). These authors possibly revised material of both *N. laevigata* and *N. mashpi* **sp. nov.** males. Since these two species are probably closely related, the male of *N. laevigata* might likely be very similar to that of *N. mashpi* **sp. nov.** If the male is finally found in the future we strongly recommend extracting and illustrating its genitalia, in particular the penisvalva, which shows interesting differing features among the species here examined (see Figure 28).

Natural history notes. Since *N. laevigata* is probably closely related to *N. mashpi* **sp. nov.** we consider the possibility that it could display a similar behavior, such as a diet based on termites. Borgmeier (1959) cites the observation "formando fila" [making a row] from P. Telles who collected specimens in Linhares, Espírito Santo, southeastern Brazil. Schmid–Hempel (1998) noted that the phorid fly *Ecitomyia juxtaposita* Borgmeier is associated with colonies of this species in Brazil. Mackay & Mackay (2010) collected winged gynes in March and October, also in Brazil. These are the only published sources which could potentially be associated with N. *laevigata*. However, since we could not find the vouchers of these studies no confirmation is currently possible. In regards to Baroni Urbani (1993) who includes this species in an overall analysis of the evolution of recruitment behavior in ants, it is uncertain whether this is in fact *N. laevigata* as no details about the voucher material is mentioned.

Comments. Workers of this species, which are much more commonly encountered in the field than other castes, are very similar to those of *N. mashpi* **sp. nov.** Even for a trained eye it is sometimes uneasy to differentiate both forms. However, upon recognizing the specific body features that vary between these two taxa, the task becomes easier. The queens of both species, however, are not so similar and proper examination allows separation without much trouble. We were fortunate in finding a nest series with close to 300 individuals from Pará, Monte Dourado (MPEG) which allowed us to associate workers with queens, but also to examine size polymorphism among workers, which is less variable than in its closest species *N. mashpi* **sp. nov.** (Figure 3). For instance, the difference in size observed mainly in the variables WL and HL is less extended in the morphospace than in *N. mashpi* **sp. nov.**

The morphological characters allowing a differentiation of the known castes of *N. mashpi* **sp. nov.** and *N. gojira* **sp. nov.** which, based on their examined morphology, we assume are the most closely related species to *N. laevigata*, are detailed in the 'comments' section of those species.

Wheeler (1922) in his work of "Ants of Trinidad", upon studying a specimen collected by P. Whelpley at Caparo, Trinidad and Tobago, mentions for the first time the lateral petiolar node striations and decides to erect *Neoponera* [=*Euponera* (*Mesoponera*)] *laevigata* var. *whelpleyi*. Later, in 1936, this author synonymizes it under *Termitopone laevigata*. We examined the image of Wheeler's (1922) syntype (MCZENT20454) and confirm this is *N. laevigata* since it matches the diagnostic traits specified in this study, whose populations are mostly distributed in Amazonian habitats. Together, with the record of *N. marginata* (voucher at American Museum of Natural History) by Mackay & Mackay (2010), these are the only records from the *N. laevigata* group for a Caribbean island. Although this specimen was collected more than a century ago, the forests of Trinidad and Tobago are relatively well–preserved (Baksh–Comeau et al. 2016) making it likely to find populations of this species in the present. Surprisingly, we could not find a single *N. laevigata* specimen from Venezuela, yet it is very likely that this species is also present in a number of habitats and regions in that country. AntWeb record CASENT0249152 identified as *N. laevigata* from the Venezuelan state of Bolívar, represents in fact *N. mashpi* **sp. nov.**

Distribution notes. This species is distributed only in South America, with most of the records coming from the Amazonian biome. The remaining scant records belong to the Caribbean forests of Trinidad, the tropical Andean forests of the Cordilleras Central and Occidental of Colombia, and the Pacific forests of the Chocó–Darien, also in Colombia. Although no records of this species were found for any bioregion in Bolivia, Ecuador and Peru, its populations are probably present there. For example, a *N. laevigata* record in the extremely isolated western Amazonian site of Estirão do Equador in Brazil, lies just at the political border with the northern Peruvian Amazon. Increasing sampling in these regions will likely unveil records for this species.

Material examined. 32 ☿, 7♀: **BRAZIL**: **Acre**: Parque Nacional da Serra do Divisor, Formosa, 7.43328°S, 73.65°W, 245m, 2016–11–15, Feitosa, R.; et al. (DZUP); **Amazonas**: Br. 174, Km 70, 2.46726°S, 60.0307°W, 123m, 1995–04–05, Matsuo, A.; Vasconcelos, H. (INPA), Estirão do Equador, 4.53583°S, 71.6236°W, 114m, 1979–10, Alvarenga, M. (MPEG), Presidente Figueiredo, 2.07361°S, 60.0148°W, 138m, 1994–02–25, Queiroz, hand collected (INPA), Reserva Florestal ZF3, Km 41, 2.41667°S, 59.8°W, 118m, 1996–09–20, Macedo, A. (INPA), ZF2, 2.6°S, 60.2°W, 89m, 1997–07–29, Cabini, G.; et al. (INPA); **Mato Grosso**: 65 Km S Sinop, 12.5167°S, 55.6167°W, 430m, 1974–10, Alvarenga, M. (MPEG); **Pará**: 30 Km E Belén, 1.27417°S, 48.2742°W, 30m, 2020–08–05, Oliveira, A. M.; Manne, W. S., hand collected

(DZUP), Conceição do Araguaia, 8.26187°S, 49.2696°W, 177m, 1979–11–07, Overal, W. (MPEG), Mina do Palito, 6.3°S, 55.8°W, 229m, 2018–01–31, Silva, R.; Prado, L., hand collected (MPEG), Monte Dourado, 0.867652°S, 52.5348°W, 76m, 1979–10–31, Overal, W.; Neto, R. (MPEG), Utinga, 1.42424°S, 48.4454°W, 18m, 1979–07–10, Overal, W. (MPEG); **Roraima**: Estação Ecológica de Maracá, 3.41667°N, 61.65°W, 127m, 1976–03, Negre, R. (DZUP). **COLOMBIA**: **Amazonas**: Parque Nacional Natural Amacayacu, Matamata, 3.68333°N, 70.25°W, 150m, 2000–05–18, Parente, A., Winkler (IAvH); **Boyacá**: San Luís de Gaceno, 4.81966°N, 73.1696°W, 400m, 2007–03–20, Campos, D. (ICN); **Chocó**: Parque Nacional Natural Utría, 6.01673°N, 77.3334°W, 390m, 1993, Baena, M., Malaise (IAvH); **Meta**: Parque Nacional Natural Serranía de La Macarena, Vereda Caño Curia, 3.40672°N, 73.9537°W, 520m, 2003–12–13, Villalba, W., Malaise (MEPN); **Valle del Cauca**: Campo–Tronco, 3.93333°N, 76.6667°W, 550m, 1994–04–01, Aldana, R. (IAvH), Parque Nacional Natural Farallones de Cali, Anchicaya, 3.43333°N, 76.8°W, 1455m, 2001–05–08, pitfall (IAvH). **FRENCH GUIANA**: **Cayenne**: Montagne des Singes, 5.07327°N, 52.7005°W, 127m, 2016–05–02, Petitclerc, F.; et al. (CPDC); **Saint–Laurent–du–Maroni**: Belvedere de Saul, 3.61667°N, 53.2°W, 326m, 2011–03–22, Team, S. E. A. G. (DZUP). **GUYANA**: **Upper Essequibo**: Parabara, 2.1819°N, 59.3371°W, 240m, 2013–11–05, Helms, J. A. (USNM). **TRINIDAD AND TOBAGO**: **Caroni**: Caparo, 10.4494°N, 61.3286°W, 90m, 1910–02–12, Whelpley, P. B. (MCZC).

Geographic range. Brazil, Colombia, French Guiana, Guyana, Peru, Trinidad and Tobago.

***Neoponera marginata* (Roger, 1861)**

Figures. 22: a – e (☿); 23: a – c (♀); 24: a – e (♂); 28: d – f, k (♂ genitalia); 29: b (distribution)

Ponera marginata Roger, 1861: 8. Brazil, (Minas Gerais), São Joao del Rey. Type material (syntypes): 1 ☿, 1 ♀(MNHU), 1 ☿, 1 ♂ (ZSBS) [not examined]. Combinations. In *Euponera* (*Mesoponera*): Emery, 1901: 47. In *Termitopone*: Wheeler, 1936: 166. In *Pachycondyla*: Roger, 1863: 18; Brown, 1995: 307; In *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species. Roger, 1863: 18; Gallardo, 1918: 67 (redescription); Wheeler, 1936: 166 (redescription); Mackay & Mackay, 2010: 455 (redescription).

Worker and queen diagnosis. Head rectangular (usually workers), and trapezoid or subquadrate (usually queens), when trapezoid the posterior margin is broader than anterior margin (Figure 23c); dorsal masticatory margin of mandible with deep longitudinal groove (Figure 22e); dorsoanterior clypeal margin usually strongly striated, sometimes bearing piligerous foveae (Figure 22e); scape, when pulled back, almost reaching posterior margin of head, space between tip of scape usually less than half apical scape width (Figures 22d, 23c); prora well–developed, directed ventrad (Figures 22b, 23d).

Worker description. Measurements (n=16): HW: 1.59–2.25; HL: 1.84–2.57; EL: 0.39–0.53; SL: 1.25–1.88; WL: 2.75–3.59; PrW: 1.12–1.65; MsW: 0.72–1.1; MsL: 0.63–0.98; PW: 0.78–1.12; PH: 0.86–1.2; PL: 0.72–0.94; GL: 2.9–5.1; A3L: 0.98–1.39; A4L: 1.06–1.51; A3W: 1.14–1.71; A4W: 1.22–1.88; TLa: 7.41–10; TLr: 8.53–12.21; **Indices**. CI: 79.63–97.03; OI: 22.73–30.23; SI: 71.15–95.35; MsI: 89.58–118.75; LPI: 71.43–92; DPI: 90.48–122.22.

Head. Frontal view: Rectangular. Masticatory margin of mandible with four to five large teeth interspersed with denticles, usually posterior half bearing only four to six tiny denticles, basal margin edentate. Prementum with clear transverse dome. Labral dorsum mostly smooth. Torular lobe posterolateral margin rounded. Malar carina absent, though a swelling is present. Eye convex, relatively flat, not surpassing lateral margin of head, placed anterior to cephalic mid–length. Posterior margin of head straight. Occipital carina absent. **Mesosoma**. Lateral view: Pronotum with weak, blunt, barely distinguishable humeral carina. Metanotal groove present, slightly depressed, mesonotum and propodeum clearly separated. Anapleural sulcus present, though usually merged with surrounding striae. Posterior face of propodeal declivity mostly flat. Posterolateral margin of propodeal declivity with feeble, blunt carina, sometimes with crenulae.

Propodeal lateral margins subparallel in posterodorsal view. Ventrolateral propodeal declivity with deep transverse groove just dorsad to metapleural gland opening. Pheromone venting canal at metapleural gland opening well–developed, slightly striated. Ventral view: Probasisternal posterior projection with spine. **Petiole**. Lateral view: anterior and posterior margins of node usually nearly straight and semi–parallel, sometimes posterior margin slightly convex. Petiolar node anterior and posterior dorsal margins equal in length vertically. Petiolar node dorsal margin mostly flat. Lateral projection of anteroventral nodal carina well–developed, with acute or slightly blunt tip moderately bent dorsad. Dorsal view: Anterior margin of petiolar node roughly as broad as width of posterior margin. Anteroventral nodal carina incomplete, with feeble concavity medially. Lateral view: Subpetiolar process subtriangular, with acute anterior cusp, sometimes keel–shaped, followed by posterior straight slope (ca. 30°). **Gaster**. Lateral view: Prora well–developed, with blunt tip projecting ventrad. Meeting of anterior margin of abdominal tergum 3 with its dorsal margin relatively angled. Cinctus moderate. Dorsal view: Tergum of A3 slightly shorter than A4. Posterior dorsum of epipygium smooth, though feeble striations and punctae may be present. **Legs**. Mesofemur thickened medially, thicker than metafemur, in dorsal or ventral view. Ventral surface of meso– and metafemora flattened roughly on distad two–thirds, usually bearing longitudinal shallow groove. Arolium roughly 0.5 times the length of pretarsal claw. Pretarsal claw with strong, median tooth., **Color**. Appendages including antennae and mandibles black to ferruginous black, mandibles feebly lighter than remaining integument of body. **Pilosity**. Most erect hairs on body dorsum approximately same as long as maximum eye length. Scape hairs about as long as apical scape width. Meso– and metatarsi bearing abundant spines and stiff setae interspersed with abundant suberect hairs. Posterior dorsum of epipygium surrounded by ca. 20 long, flexuous hairs. **Sculpture**. Striae on head mostly absent, though when present only anteriorly on dorsum, laterally on clypeus, and malar area; anepisternum, usually part of katepisternum, metapleuron, lateral and posterior surface of propodeum strongly striated; sometimes propodeal dorsum with longitudinal, feeble, broken line of tiny foveae; striae on petiolar node usually weak and only posterolaterally.

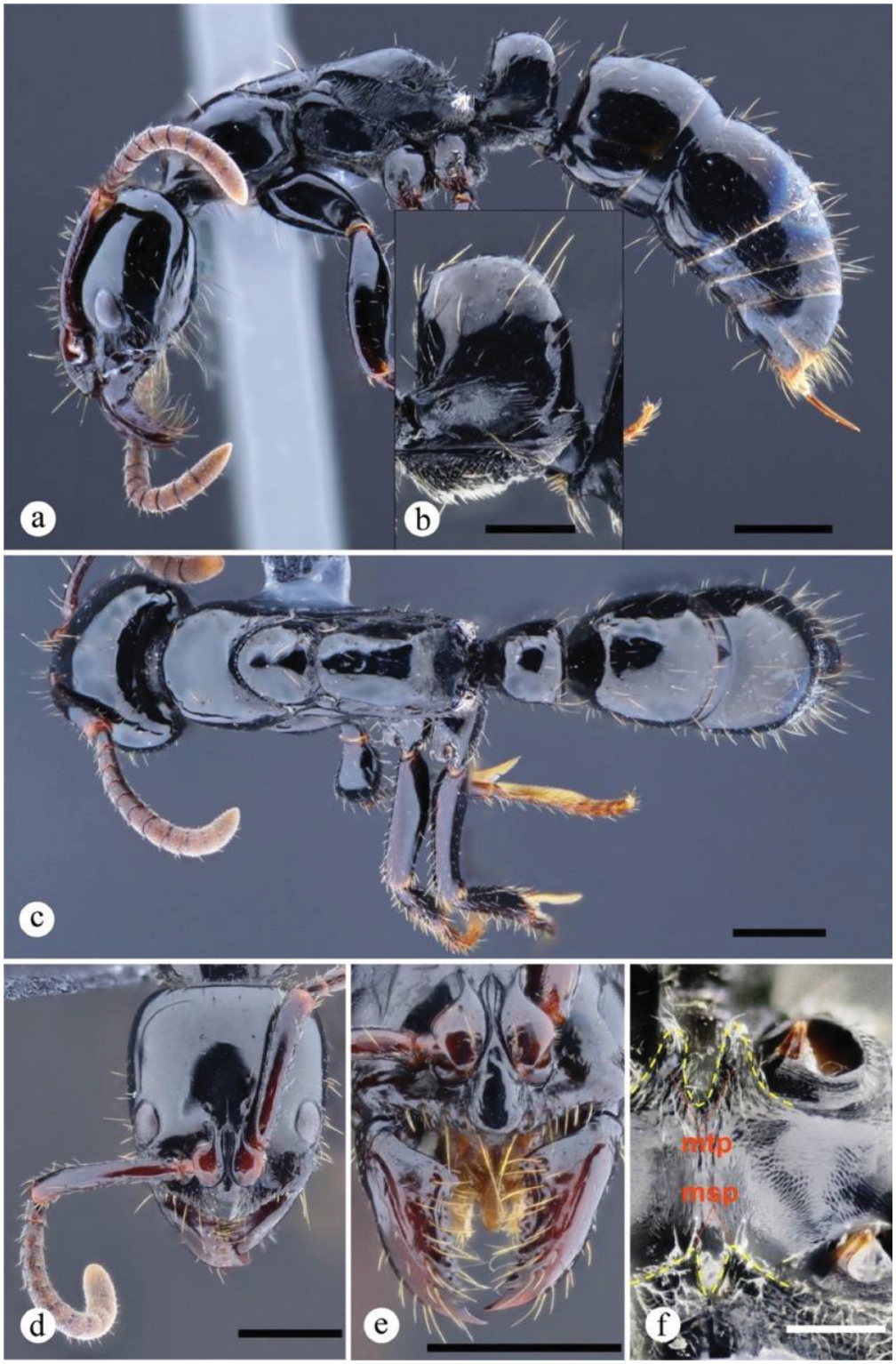


Fig. 22. *Neoponera marginata*. ☿ (MEPN: CASENT0649897), Brazil, Paraná. **a.** Lateral view; **b.** Petiole in lateral view; **c.** Dorsal view; **d.** Head in frontal view; **e.** Mandibles in frontal view; **f.** Mesosternal (msp) and metasternal (mtp) processes (dashed red line) in anteroventral view. Scale bars: 1 mm (**a** – **d**); 0.5 mm (**e**); 0.25 mm (**f**).

Queen description. Measurements (n=5). HW: 2.54–2.79; HL: 2.79–2.92; EL: 0.63–0.73; SL: 1.95–2.1; WL: 4.25–4.75; PrW: 1.97–2.2; MsW: 1.78–1.95; MsL: 2.48–2.63; PW: 1.33–1.46; PH: 1.4–1.52; PL: 0.95–1.11; GL: 4.51–6.03; A3L: 1.78–1.91; A4L: 1.84–2.03; A3W: 2.29–2.37; A4W: 2.35–2.54; TLa: 11.84–12.67; TLr: 12.7–14.63; **Indices**. CI: 90.91–97.78; OI: 23.86–26.74; SI: 70.45–77.5; MsI: 71.79–75.41; LPI: 66.67–76.47; DPI: 130.77–143.75.

Morphology as in worker except for: **Head**. Frontal view: Head usually trapezoidal. Anterior ocellus maximum diameter subequal to that of posterior ocelli. Distance from posterior ocellar margin to posterior margin of head close to 2.5 times apical scape width. Distance between anterior and posterior ocelli close to 2.5 times anterior ocellus diameter. **Mesosoma.** Dorsal view: Mesoscutum about as long as broad, 2.5 times as long as mesoscutellum. Transscutal line well–developed. Scutoscutellar sulcus shallowly impressed, formed by scrobiculate sculpture. Mesoscutellum sub–trapezoid, flat dorsally. Posterior face of propodeal declivity flat. Posterolateral margin of propodeal declivity slightly round to barely carinate, not forming crenulae. Anterodorsal median propodeal sulcus present, weakly impressed. **Wings**. Forewing venation: Rs–M approximately one fifth longer than 2M. Forewing evenly covered by fine setose layer. Hindwing venation: 1Rs highly reduced. Hindwing bearing 10–14 hamuli. **Petiole**. Lateral view: anterior and posterior margins of node nearly straight at base and slightly tapering at top. **Gaster.** Dorsoposterior view: Posterior dorsum of epipygium with feeble striations and punctae. **Color**. Appendages, including antennae and mandibles, mostly black. **Pilosity and sculpture**. Mostly as in worker (but see general synoptic description).

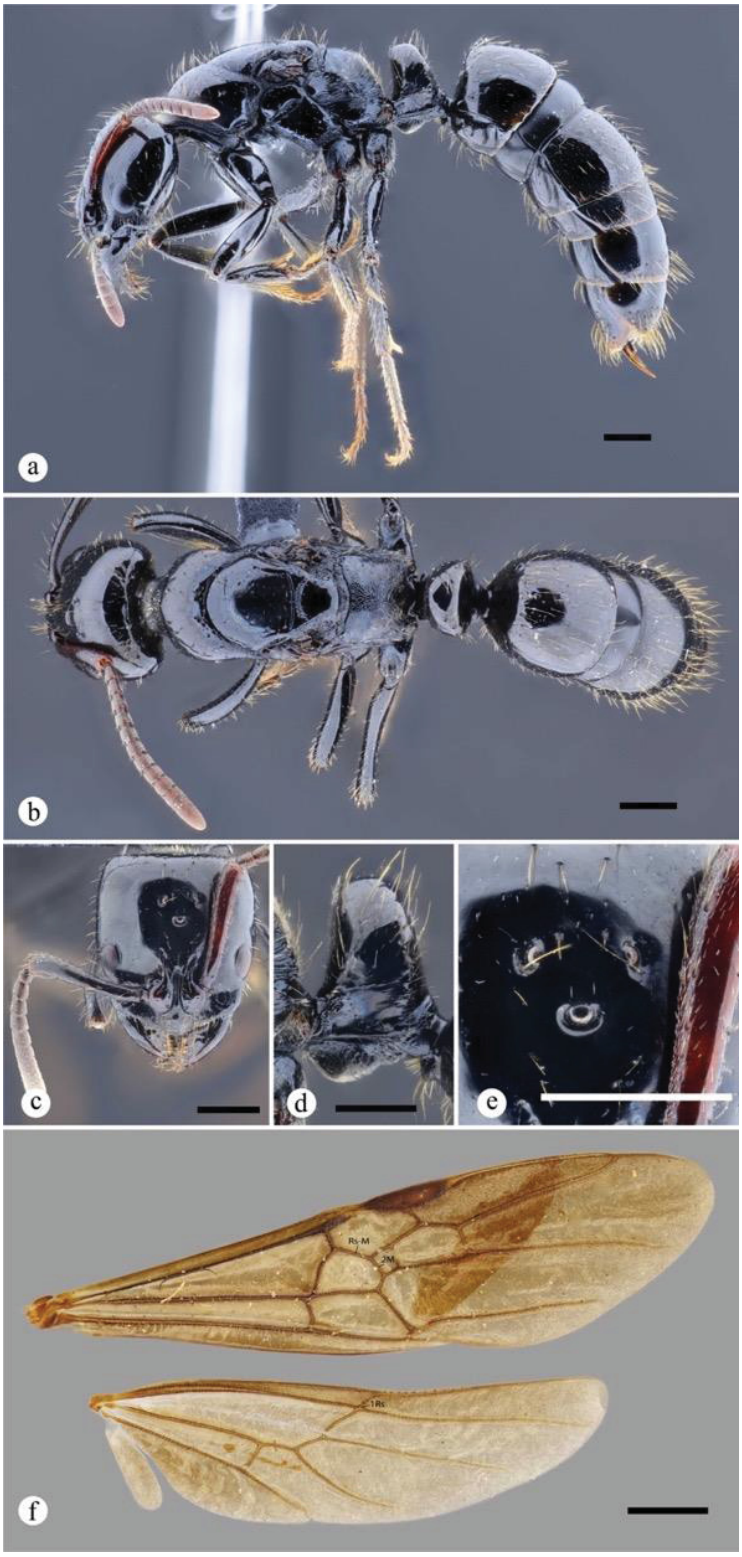


Fig. 23. *Neoponera marginata*. ♀ (MPEG: ATPFOR2028), Brazil, Espírito Santo. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Petiole in lateral view; **e.** Ocelli in frontal view; **f.** Fore and hind wings. Scale bars: 1 mm (**a** – **d**, **f**); 0.5 mm (**e**).

Neoponera marginata **male diagnosis.** Antennal scape trapezoidal (Figure 24e); mesoscutum dorsally with weakly impressed, median longitudinal line (Figure 15a); median tooth on pretarsal claw well–developed; sternum of A8 with dorsoventrally depressed spine, with blunt (somewhat round) posterior tip.

Male description. Measurements (n=2). HW: 1.51–1.75; HL: 1.73–1.9; EL: 0.69–0.76; SL: 0.35–0.38; WL: 3.52–4; PrW: 1.95–2.16; MsW: 1.7–1.9; MsL: 2.23–2.54; PW: 0.91–1.08; PH: 1.13–1.33; PL: 0.82–0.89; GL: 5.08–5.91; A3L: 1.26–1.46; A4L: 1.42–1.59; A3W: 1.57–1.9; A4W: 1.82–2.16; TLa: 8.74–9.84; TLr: 11.87–11.98; **Indices**. CI: 87.27–91.67; OI: 43.64–45.83; SI: 20–25; MsI: 75–76.06; LPI: 66.67–72.22; DPI: 111.54–121.43.

Head. Frontal view: Mandibular apex, when closed, barely touches lateral margin of labrum. PF: 6,4. Clypeus anteromedially straight to slightly concave, dorsally inflated, with somewhat globular–shaped dome, always covering anterior clypeal margin. Area between posterior margin of clypeus and supraclypeal area with evident depression. Posterior supraclypeal area acute. Supraclypeal area slightly protruding from cuticle, followed posteriorly by tenuously impressed longitudinal carina. Distance between internal margins of antennal sockets approximately one socket diameter. Torular lobe strongly reduced. Eye suboval, slightly notched medially, maximum diameter ca. one–third of head length, placed slightly anterior to cephalic mid–length. Ocellar area positioned at vertex. Distance from posterior ocellar margin to posterior margin of head close to two–thirds apical scape width. Distance between anterior and posterior ocelli approximately equal to 1.5 times anterior ocellus diameter. Scape trapezoidal, twice as long as pedicel. **Mesosoma**. As in queen with the following differences: Dorsal view: Mesoscutum close to 2.5 times as long as mesoscutellum, anterior triangular impression vestigial, with faint median longitudinal line. Parapsidal lines weakly impressed, slightly divergent. Scutoscutellar sulcus slightly arched posterad. Dorsolateral view: Anterior subalar area shorter than tegular maximum width. Metanotum surface even, convex. Pheromone venting canal at metapleural gland opening poorly developed, striated. Dorsoposterior view: Metapleuropropodeal groove relatively shallow. Posterolateral margin of propodeal declivity slightly rounded, rugose midventrally. Ventral view: Probasisternal posterior projection round. Mesosternal process vestigial or absent. **Wings**. As in queen, except for Rs–M approximately as long as 2M. **Petiole.** Lateral view: anterior and posterior margins of node nearly straight at base and slightly tapering at top. Lateral projection of anteroventral nodal carina well–developed, with acute or slightly blunt tip moderately bent

dorsad. Dorsal view: Anterior margin of petiolar node approximately four–fifths (0.8 times) shorter than width of posterior margin. Lateral view: Subpetiolar process subtriangular, with rounded cusp at middle of process, mostly smooth, though few striae may be present. **Gaster**. Morphology mostly as in worker and queen with the following differences: Lateral view: Abdominal sternum 7 showing even surface with no sulci, anterior half glabrous, posterior half with semicircular patch bearing abundant, appressed, stout hairs. Spine at posterior margin abdominal tergum 8 blunt, slightly flattened dorsoventrally. Pygostyles close to three times longer than broad. Ventral view: Abdominal sternum 9 roughly as long as broad. **Color**. Appendages, including antennae and mandibles, dark brown to black with slightly light brown tarsi. **Genitalia**. Ventral view: Cupula: posterior margin of medial invagination narrow. Lobular process vestigial. Basivolsella externally nearly straight. Lateral view: Gonopod subtriangular posterior half strongly directed ventrad, dorsolateral margin relatively straight medially, with medial, oblique, weak incision. Dorsal view: Gonopod subtriangular (subrectangular in lateral view). Gonostylus subacute apically, dorsointernal margin with rounded, tooth–shaped, swelling. Digitus spatulate, with outer margin round in ventral view. Penial sclerites overall outline axe–shaped, dorsal surface convex anteriorly, with an abrupt slope posteriorly. Dorsoapical third of penial sclerite surface with strong flap. **Sculpture**. Striae absent on head; axillula, metapleuron and lateral propodeal surface rugose; posterior and dorsopropodeal surface strongly striated; striae on petiolar node usually feeble and only posterolaterally.

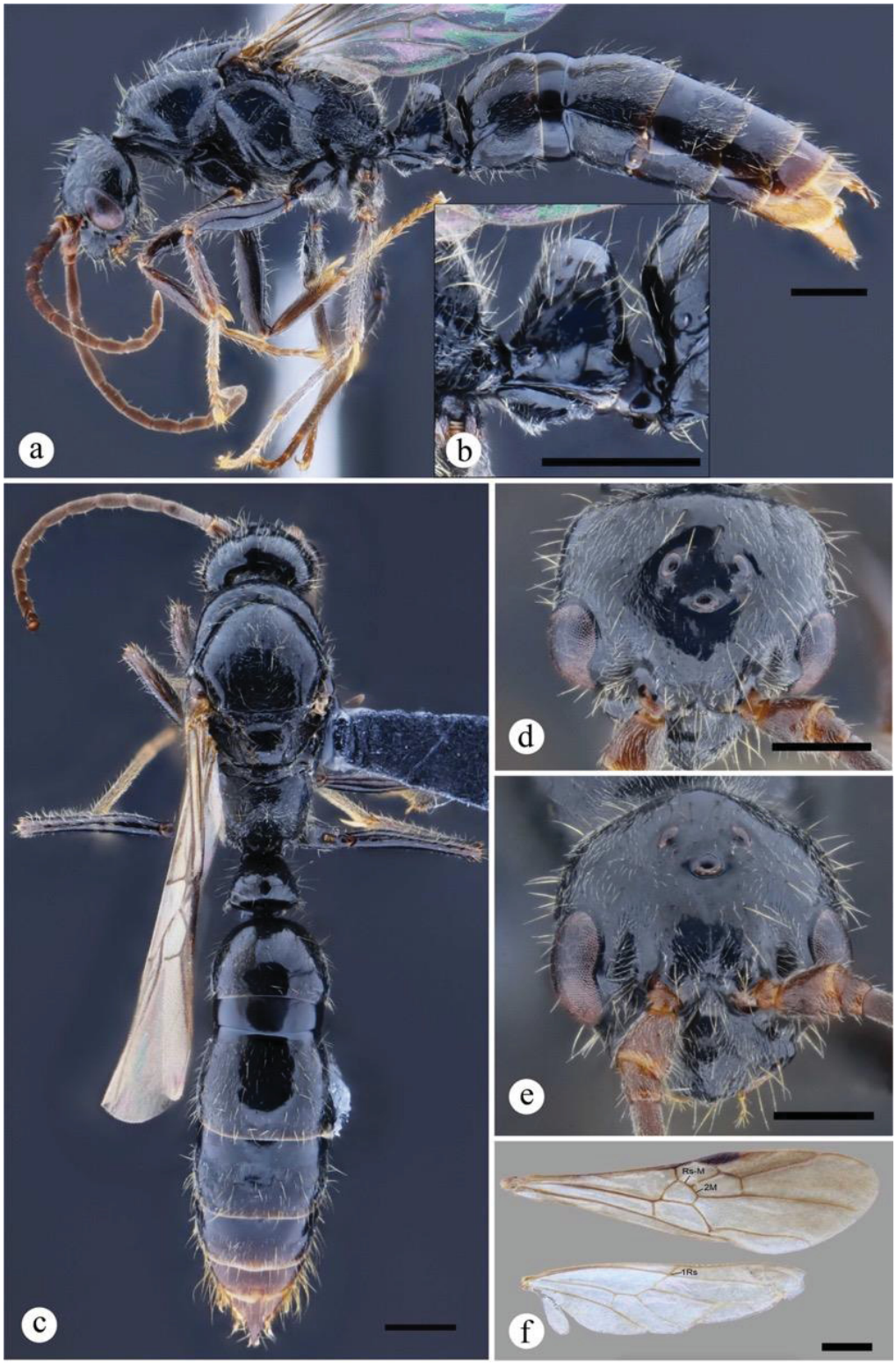


Fig. 24. *Neoponera marginata*. ♂ (DZUP: UFVLABECOL010414), Brazil, Minas Gerais. **a.** Lateral view; **b.** Petiole in lateral view; **c.** Dorsal view; **d.** Had in dorsal view; **e.** Head in frontal view; **f.** Fore and hind wings. Scale bars: 1 mm (**a** – **c**, **f**); 0.5 mm (**d**, **e**).

Natural history notes. This is a relatively common, surface ground forager, termite feeding species (Wheeler 1936, Leal & Oliveira 1995, Hölldobler et al. 1996). The workers are usually collected through pitfall traps or by hand. Alate females and queens are much less commonly captured, unless searching for underground colonies. Males are quite rare, though they might be present in bulk Malaise samples. Due to their similarity to males of *N. mashpi* **sp. nov.**, and likely also to males of *N. laevigata* (which were not examined here), they can be misidentified as such. In warm morning hours the workers can be quite active around the nest entrance on the ground surface: while taking photos of them at a tourist trail, in Reserva Guartelá, southern Brazil, AT observed ca. 10–20 workers removing soil particles from underground and piling them some 30 cm near the entrance. None of the ants showed aggressiveness when clearing part of the surrounding grass in order to get a clearer view, nor even when collecting some specimens.

Despite being comparatively easy to identify, and commonly collected in the field, most of what is known about the behavioral biology of *N. marginata* is basically summarized in three studies. In the first, Leal & Oliveira (1995) provided a comprehensive account on the group–raiding and migratory habits of this species in a semi–deciduous region of the state of São Paulo in southeastern Brazil. The authors recorded more than 200 raids, all of them directed against the termite species *Neocapritermes opacus* (Hagen). Within the *N. laevigata* group this "extreme diet specialization" has been documented only in this species, so far (but see Krishna & Araujo 1968, Mill 1982b). Leal & Oliveira (1995) also concluded that *N. marginata* shows a rudimentary form of the "army ant syndrome", with colonies relocating their nests less frequently than other group–raiding taxa, as for example, some Dorylinae. On the other hand, in regards to the communication system, Hölldobler et al. (1996) found that the pygidial gland of *N. marginata* produces Citronelal, the main monoterpenoid responsible for triggering trail–recruitment in ants. The third main contribution came from Acosta–Avalos et al. (1999) who found magnetic iron oxides in the head and gaster of *N. marginata* (but see also Wajnberg et al. 2017). Based on this result, they proposed that colonies of this species use the geomagnetic field during migrations, i.e., nest relocations. Two years later, Acosta–Avalos et al. (2001) linked that hypothesis to their observations of *N. marginata* colonies displaying a preferred directional migration which is deviated ca. 12° from the magnetic North–South axis.

Comments. Workers and queens of *N. marginata* are morphologically similar only to those of *N. gojira* **sp. nov.**, *N. mashpi* **sp. nov.**, and *N. laevigata*. These four lineages share traits

like, for example, the relatively flattened eyes placed anterior to cephalic mid–length (Figures 20c, 21d, 22d, 23f, 25c, 26d); absence of malar carina; pronotal humerus feebly angled (not completely rounded as in *N. commutata*); a cuboid petiolar node, in lateral view; polymorphic workers, and presumably so in *N. gojira* **sp. nov.** for whom a single individual is known. However, *N. marginata* workers and queens are unique among these other lineages in showing a strongly carved, longitudinal groove on the inner side of the mandibular surface (absent in *N. mashpi* **sp. nov.** and *N. laevigata*, while *N. gojira* **sp. nov.** shows a shallow rim). Another useful feature, which helps identify queens of *N. marginata*, is its trapezoidal head which is broader posteriorly than anteriorly, in frontal view, though this character is more evident in the queens. The head in queens of *N. mashpi* **sp. nov.** and *N. laevigata* is subquadrate. In regards to known males, those of *N. marginata* could only be confused with those of *N. mashpi* **sp. nov.** The easiest way to distinguish both forms is using the following combination of traits: a feebly impressed, longitudinal line present medially on the mesoscutal dorsum (Figure 15a), while in *N. mashpi* **sp. nov.** such line is absent; scape trapezoidal (Figure 24e), whereas in in *N. mashpi* ***sp. nov.*** it is cylindrical; pretarsal claws bearing subapical teeth, while those of *N. mashpi* **sp. nov.** lack teeth; blunt tipped spine on posterior margin of tergum of A8, while in *N. mashpi* **sp. nov.** the spine tip is acute. The male caste of *N. commutata* is quite dissimilar to that of *N. marginata* and *N. mashpi* **sp. nov.** Some unique features of the males in the *N. laevigata* group were already discussed under the treatment for that species, however, the user may also find the following useful: a roughly round head in frontal view (subquadrate in remaining species); dorsoposterior propodeal margin strongly carinate (carina lacking in remaining species); forewing with glabrous subbasal and basal cells (setose in remaining species).

Distribution notes. Our records confirm an exclusively South American distribution for *N. marginata*, with an elevational range varying between 10 m to around 1700 m. Most of these records lie in the southern limit of its range represented mainly by three biomes: the southern Humid Chaco in Paraguay; the Atlantic Forest in Argentina (Misiones), northern Paraguay, and Brazil (Paraná and São Paulo); and the Cerrado in Brazil (Goias, Mato Grosso do Sul, São Paulo, Minas Gerais). Although highly anthropized (Ribeiro et al. 2009, Da Ponte et al. 2017) the remaining vegetation cover in these regions is mostly represented by ombrophyllous dense and open broadleaf forests, and tropical and subtropical grasslands, savannas, and shrublands (Sena–Souza et al. 2020). We found scant records of *N. marginata* in Amazonian regions, namely in

northwestern Bolivia, western Brazil (Rondônia), and eastern Ecuador. The latter is the northwestern limit range for this species in the continent. However, as there are no large geographic barriers, e.g., mountain ranges, separating Amazonian regions between northern Ecuador and southern Colombia, we might expect *N. marginata* populations to be present at least in Colombian southern lowland rain forests. Mackay & Mackay (2010) list a record from the northeastern side of the continent, at Arima Reserve (voucher at the American Museum of Natural History), from the island of Trinidad, Trinidad and Tobago. The record of Wheeler (1936) from Churubamba (not 'Charubamba'), a Bolivian region in the Department of La Paz, is possibly wrong since its elevation surpasses 3400 m. This record is probably related to that from the same author (1925) from Ixiamas at 260 m (voucher at Natural History Museum Sweden), located in the same Bolivian Department.

As in *N. mashpi* **sp. nov.** and *N. laevigata*, *N. marginata* workers show gradual size polymorphism, though less marked than in the former two. Across its distribution range we did not notice major morphological variations in size, nor in coloration departing from the average ground plan of this species, as diagnosed here. Specimens from Bolivian Amazonian habitats were virtually identical to those examined from wet broadleaf forests in the Atlantic, and from the semi–dry grasslands and savannas in Paraná, southeast Brazil.

Material examined. 99☿, 5♀, 2♂: **ARGENTINA**: **Misiones**: Parque Nacional Iguazú, 25.6801°S, 54.4528°W, 180m, 2018–11–01, Troya, A., hand collected (MEPN), Parque Provincial Teyú Cuaré, 27.284°S, 55.594°W, 140m, 2015–01–20, Hanisch, P. (MACN), Reserva Natural Osonunu, 27.2797°S, 55.5702°W, 92m, 2015–01–19, Hanisch, P. (MACN). **BOLIVIA**: **Santa Cruz**: Las Gamas, P. N. Noel Kempff Mercado, 14.8°S, 60.3833°W, 700m, 1993–12–02, Ward, P. (PSWC). **BRAZIL**: **Distrito Federal**: IBGE Ecological Reserve, 15.932°S, 47.8997°W, 1031m, 2013–11–14, Rabeling, C. (MEPN); **Espirito Santo**: Reserva Biológica Santa Lucia, 19.95°S, 40.5333°W, 600m, 2018–11–18, Formigas do Brasil, hand collected (MPEG); **Goiás**: Br–364,Km 192 , 17.9242°S, 51.7171°W, 673m, 1997–09–29, Diniz, J., light trap (DZUP), Serranópolis, 18.3064°S, 51.9577°W, 743m, 2003–10–12, Diniz, J. (DZUP); **Mato Grosso**: Pontes e Lacerda, 15.2333°S, 59.3167°W, 292m, 2013–07–28, Queiroz–Santos, L. (DZUP), Universidade Federal de Mato Grosso, 15.9167°S, 52.2667°W, 352m, 2011–07–19, Oliveira, C. X., pitfall (DZUP), Utiarití, 13.0167°S, 58.2667°W, 325m, 1966–11–06, Lenko, K.; Pereira (MPEG); **Mato Grosso do Sul**: Fazenda Retiro Conc., 21.6833°S, 57.7667°W, 93m, 2012–03–

08, Souza, P. R.; Morais, E., pitfall (DZUP), Parque Nacional da Serra da Bodoquena, 21.1°S, 56.6333°W, 556m, , Silvestre, R. et al. (CPDC); **Minas Gerais**: Araxa, 19.5833°S, 46.9333°W, 979m, 1965–11–14, Elias, C. (DZUP), Betim, 19.9668°S, 44.201°W, 845m, 1980–06–18 (DZUP), Caraça, 20.1333°S, 43.4833°W, 1674m, 1965–07–11, Moure, J. S. (DZUP), Convento Santa Isabel, 19.9565°S, 44.1615°W, 840m, 1981–01–10 (DZUP), Estação ao Buriti, 19.3386°S, 48.0332°W, 940m, 1983–11–21, Binda, hand collected (INPA), Mina Tamanduá, 20.0667°S, 43.9333°W, 1254m, 2012–07–12, Queiroz, et al., pitfall (DZUP), Ouro Preto, 20.3333°S, 43.75°W, 981m, , Moura, M. N.; et al. (DZUP), Santuário de Caraça, 20.0982°S, 43.488°W, 1287m, 2000–12–22, Frey, M (CPDC), Universidade Federal de Viçosa, 20.7623°S, 42.8605°W, 708m, , Noqueira, S. B. (DZUP), Universidade Federal de Viçosa, forest at the faculty of Biology, 20.7572°S, 42.8608°W, 706m, 2012–11–30, Chaul, J. (DZUP), Viçosa, 20.8167°S, 42.8833°W, 760m, 1995–10–19, Frenéav, D. (CPDC), 1994–02, Sperber, et al. (DZUP), Viçosa, 20.7474°S, 42.8833°W, 648m, 1995–10–19, Frenéav, D. (CPDC), 1994–02, Sperber, et al. (DZUP); **Paraná**: Jardim das Américas, 25.4333°S, 49.2333°W, 933m, 2016–04–01, Escárraga, M., hand collected (DZUP), Palmeira, 25.4167°S, 50°W, 865m, 2015–09–15, Franco, W. (DZUP), Parque Estadual do Cerrado , 24.1667°S, 49.6667°W, 780m, 2017–03–31, Ferreira, C.; et al. (DZUP), Parque Estadual do Guartelá, 30 Km W Piraí do Sul, 24.5667°S, 50.25°W, 981m, 2018–10, Troya, A., hand collected (MEPN), 2015–09–20, Franco et al., pitfall (DZUP), Parque Estadual do Guartelá, 30 Km W Piraí do Sul, 24.55°S, 50.25°W, 985m, 2018–10, Troya, A., hand collected (MEPN), 2015–09–20, Franco et al., pitfall (DZUP), São José dos Pinhais, 25.6°S, 49.1833°W, 880m, 2016–07–09, Domahovski, A. C. , Malaise (DZUP), Universidade Federal do Paraná, Centro Politécnico, 25.4333°S, 49.2333°W, 916m, 2007–07–09, Ribeiro, A., hand collected (DZUP); **Rondônia**: Jaci Paraná, Rio Madeira, 9.54037°S, 64.3728°W, 85m, 2011–10–10, Santana, F. D. (CPDC); **São Paulo**: Bálsamo, 20.7341°S, 49.5836°W, 547m, 2003–02–04 (DZUP), Campus da USP, 21.1667°S, 47.8°W, 517m, 1998–09–10, Melo (DZUP), Guarulhos, 23.4532°S, 46.5337°W, 763m, (DZUP), Mirassol, 20.8161°S, 49.5042°W, 572m, 1977–12–12, Diniz, J. (DZUP), Reserva Santa Ginebra, 22.8275°S, 47.105°W, 623m, 1993–05, hand collected Rio Claro, 22.4145°S, 47.565°W, 615m, 2013–06–05, Melo, A. (CPDC). **PARAGUAY**: **Cordillera**: Caacupé, Jack Norment camp, 25.38°S, 57.15°W, 190m.

Geographic range. Argentina, Bolivia, Brazil , Ecuador, Paraguay, Trinidad and Tobago.

***Neoponera mashpi* sp. nov.**

ZooBank: https://zoobank.org/956C245D-24BB-46CE-865D-621CC07C009D

Figures. 25: a – f (☿); 26: a – e (♀); 27: a – e (♂); genitalia 28: g – i, l (♂); 29: a (distribution).

Type material. ***Holotype*.** 1☿; **FRENCH GUIANA**: (**Sinnamary)**: Paracou, PS-02-3, (12km East from the village of Sinnamary), (5.2666°N, 52.9166°W), Abril–2002, J. Orivel (leg.), CPDC ant collection: ATPFOR2054–2. ***Paratypes***. 12☿, 2♀, 2♂; **BRAZIL**: **Amazonas**: Reserva Florestal Adolpho Ducke, INPA, 2.93333°S, 59.96666°W, 106m, 1999–07–29, Melo, G. (BMNH: 1☿, ATPFOR1985); 2.96304°S, 59.92286°W, 111m, 1987–09–14, fotoeclector, Souza, J. (INPA: 1☿, INPAHYM033803); **Bahia**: Porto Seguro, 16.44545°S, 39.06579°W, 3m, 1997–09–23, Malaise, Santos, J. R. M (CPDC: 1♂, ATPFOR2077); Refugio da Vida Silvestre do Una, 15.2323°S, 39.1151°W, 70m, 1999–10–04, Santos, J. R. S. (DZUP: 2☿, DZUP549512; **Pará**: Fazenda Vitoria, 2.98345°S, 47.34994°W, 82m, 1991–12–21, Moutinho, P. (ICN: 1☿, ATPFOR2029); Floresta Nacional Caxiuana, 1.716667°S, 51.45000°W, 32m, 1998–03–24, Malaise, Silveira, O., Pena, J. (MPEG: 1☿, MPEG03006223); 1.73333°S, 51.45000°W, 21m, 2012–09, ex pitfall, Cunha, D. et al. (CASC: 1 ☿, MPEG03020126); **Rio Grande do Norte**: Tabatinga 6.06753°S, 35.10311°W, 12m, 2005–09, Martins, J. (MHNG: 1☿, ATPFOR2010); **Rondônia**: Area Caiçara, 9.433110°S, 64.80237°W, 103m, 2011–01–04, winkler, Silva, R., Probst, R. (MPEG: 1☿, AT2206). **COLOMBIA**: **Putumayo**: Parque Nacional Natural La Playa, 0.11667°S, –74.93333°W, 320m, 2001–05–14, Cobete, R. (IAvH: 1☿, IAVH–E–49610). **ECUADOR**: **Orellana**: Tiputini Biodiversity Station, 0.63333°S, 76.15°W, 236m, 2011–12–11, Donnell, S. O. (MCZC: 1☿, DZUP549443), **Pichincha**: Reserva de Biodiversidad Mashpi, 50 Km NW Quito, 0.1544°N, 78.8905°W, 746m, 2017–04, hand collected, Troya, A. (MEPN: 1☿, MEPNINV38315). **FRENCH GUIANA**: **Cayenne**: Nouragues Natural Reserve, 1km E of Nouragues Station, Grand Plateau, 4.0889°N, 52.6749°W, 120m, 2018–08–21, (USNM: 1☿, ATPFOR1976); Sinnamary, 12km East from the village of Sinnamary, Paracou Station, 5.26667°N, 52.91667°W, 50m, 2002–04, Orivel, J. (CPDC: 1♀, ATPFOR2054; MZSP: 1☿, ATPFOR2054–1). **PERU**: **Madre de Dios**: Sachavacayoc camp, 12.81667°S, 69.36667°W, 229m, 2012–07–26, Fernandes, I. (INPA:1♀, INPAHYM033802).

Etymology. The name is derived from the Kichwa word ‘mash’ meaning ‘friend’, and ‘pi’, from the ancient Yumbo people, meaning ‘water’. We thus acknowledge the Reserva de Biodiversidad Mashpi, as well as its supporters, in northwestern Ecuador (where one of the paratypes was found), for their efforts in the preservation of one of the last remnants of a highly threatened and diverse tropical Andean forest in the Chocó–Darien Global Ecoregion. The species name is a noun in apposition, thus invariable.

Worker and queen diagnosis. Antennal scape, in smallest workers (WL= 1.66 mm) and queens, when pulled back, fails to reach posterior margin of head by about one apical scape width (Figures 13a, 25c, 26d), whereas the scape of largest workers (WL= 3.31 mm) usually reaches such head margin, but never surpasses it; head mostly smooth in workers only (Figure 25c), while in queens the head dorsum shows feeble, divergent striae at posterior limits of frontal carina and posteriorly to eye, these striae vanish before reaching lateral head margin (Figure 26d); anterior margin of petiole usually narrower than posterior margin in dorsal view (Figures 25b, 26c); lateral face of petiolar node completely lacking striae (Figures 25d, 26b), this is mostly seen in South American and Pacific Central American populations, while in Atlantic Central American populations the node bears slight striae laterally; subpetiolar process subtriangular with anterior acute cusp, in lateral view (Figure 25d); prora with blunt, well–developed tip projecting ventrad (Figures 25d, 26b); workers of this species are the smallest within the *N. laevigata* group (WL = 1.66 – 3.31 mm), and among the smallest in *Neoponera*.

Worker description. Measurements (n=21; holotype in parenthesis): HW: 0.88–1.84 (1.43); HL: 1.19–2.2 (1.8); EL: 0.25–0.53 (0.41); SL: 0.75–1.71 (1.22); WL: 1.66–3.31 (2.57); PrW: 0.66–1.22 (1.1); MsW: 0.38–0.88 (0.65); MsL: 0.3–0.78 (0.57); PW: 0.31–1.04 (0.73); PH: 0.53–1.03 (0.82); PL: 0.5–0.92 (0.73); GL: 1.72–3.76 (2.78); A3L: 0.56–1.22 (0.98); A4L: 0.69–1.39 (1.1); A3W: 0.59–1.57 (1.1); A4W: 0.67–1.71 (1.18); TLa: 4.67–9.02 (7.18); TLr: 5.2–9.84 (7.88). **Indices.** CI: 72.22–83.7 (79.55); OI: 27.78–30.77 (28.57); SI: 84.21–94.51 (85.71); MsI: 104.35–133.33 (114.29); LPI: 69.7–105.88 (90); DPI: 59.39–117.95 (100).

Head. Frontal view: Subrectangular. Masticatory margin of mandible with four to five large teeth interspersed with three to four denticles, basal margin edentate. Prementum with clear transverse dome. Labral dorsum mostly smooth. Torular lobe posterolateral margin rounded. Malar carina absent, though swelling is present. Eye convex, relatively flat, not surpassing lateral

margin of head, placed anterior to cephalic mid–length. Posterior margin of head straight to slightly convex. Occipital carina absent. **Mesosoma**. Lateral view: Pronotum with weak, blunt, barely distinguishable humeral carina. Metanotal groove present, though not depressed, usually clearly separating mesonotum and propodeum. Anapleural sulcus present, though usually merged with surrounding striae. Posterior face of propodeal declivity mostly flat. Posterolateral margin of propodeal declivity with feeble, blunt carina, sometimes with crenulae. Propodeal lateral margins subparallel in posterodorsal view. Ventrolateral propodeal declivity with deep transverse groove just dorsad to metapleural gland opening. Probasisternal posterior projection acute. Metasternal process inclined posterad, 20°– 30° in lateral view. **Petiole**. Lateral view: anterior and posterior margins of node usually nearly straight and semiparallel, sometimes posterior margin slightly convex; posterodorsal margin slightly higher than anterodorsal margin; mid–dorsal margin mostly flat. Lateral projection of anteroventral nodal carina well–developed, with acute or slightly blunt tip usually projecting anterad. Dorsal view: Anterior margin of petiolar node slightly shorter than width of posterior margin. Anteroventral nodal carina complete. Lateral view: Subpetiolar process subtriangular, with acute anterior cusp, sometimes keel–shaped, followed by posterior straight slope (ca. 30°). **Gaster**. Lateral view: Prora well–developed, with blunt tip projecting ventrad. Meeting of anterior margin of A3 tergum with its dorsal margin relatively angled. Cinctus moderate. Dorsal view: Tergum of A3 slightly shorter than A4. Posterior dorsum of epipygium smooth, though feeble striations and punctae may be present. **Legs**. Mesofemur thickened medially, thicker than metafemur, in dorsal or ventral view. Ventral surface of meso– and metafemora flattened roughly on distal two–thirds, usually bearing longitudinal shallow groove. **Color**. Appendages including antennae and mandibles brown to ferruginous brown, occasionally legs yellowish and mandibles lighter than remaining integument of body. **Pilosity**. Most erect hairs approximately same length as eye maximum length. Scape hairs about as long as apical scape width. Posterior dorsum of epipygium surrounded by ca. 20, long flexuous hairs. Meso– and metatarsi bearing abundant spines and stiff setae interspersed with abundant suberect hairs. **Sculpture**. Striae on head generally absent, though when present, very feeble and on dorsum only, laterally on clypeus, around frontal carinae, and malar area; anepisternum, metapleuron and lateral side of propodeum with strong striae; petiolar node usually devoid of striae, though when present feebly impressed on lateral face (but see diagnosis and comments).

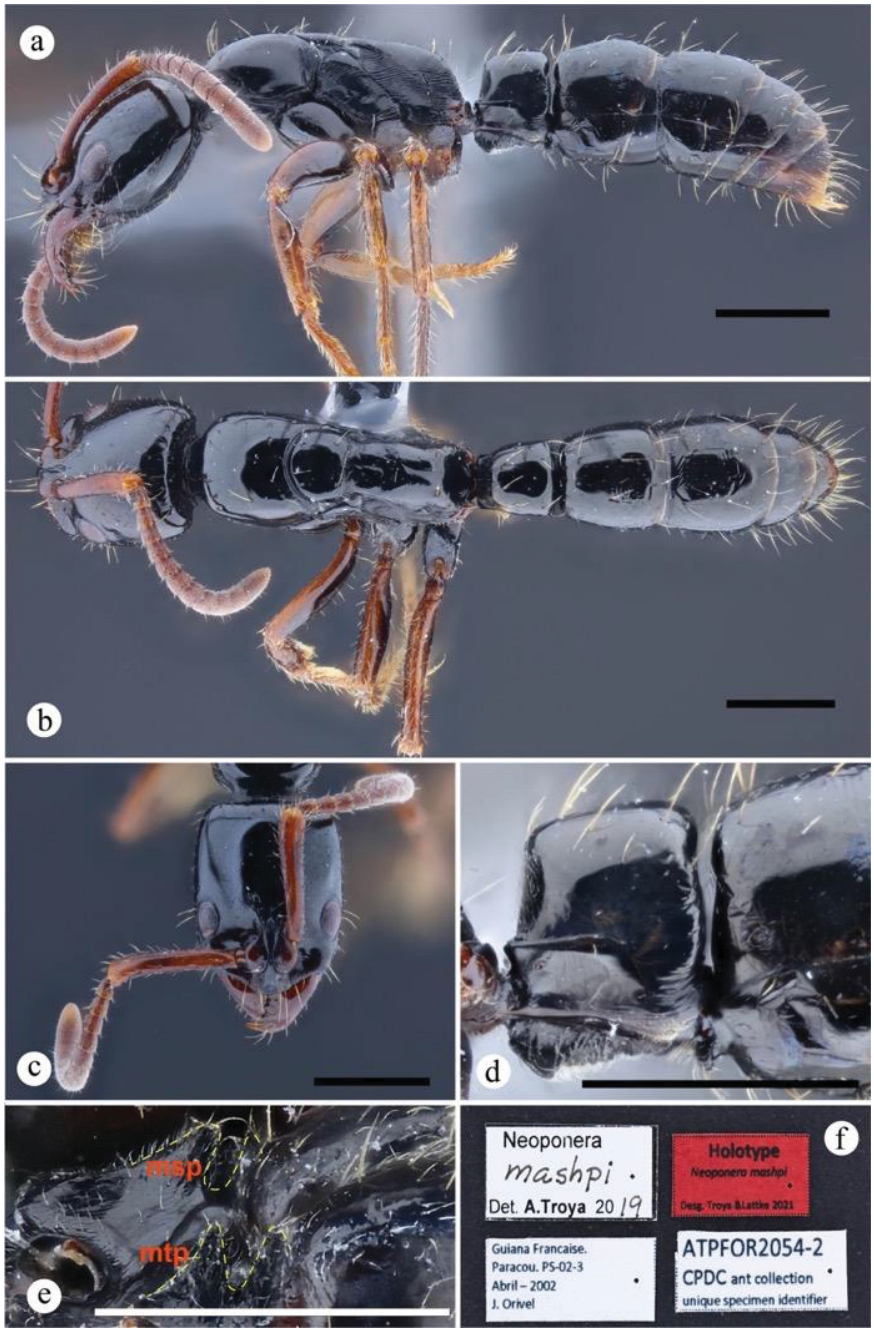


Fig. 25. *Neoponera mashpi* **sp. nov.** Holotype ☿ (CPDC: ATPFOR2054–2), French Guiana, Paracou. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Petiole in lateral view; **e.** Mesosternal (msp) and metasternal (mtp) processes (dashed yellow line) in posteroventral view. Scales bars: 1 mm (**a** – **d**); 0.6 mm (**e**).

Queen description. Measurements (n=2): HW: 1.96–2.14; HL: 2.29–2.55; EL: 0.61–0.64; SL: 1.47–1.73; WL: 3.67–4.08; PrW: 1.63–1.84; MsW: 1.22–1.63; MsL: 1.98–2.22; PW: 1.17–1.18; PH: 1.43–1.48; PL: 0.98–1.07; GL: 4.29–4.34; A3L: 1.31–1.79; A4L: 1.39–1.73; A3W: 1.47–2.04; A4W: 1.55–2.14; TLa: 9.63–11.22; TLr: 11.23–12.04. **Indices.** CI: 84–85.71; OI: 29.76–31.25; SI: 75–80.95; MsI: 61.86–73.56; LPI: 68.57–72.41; DPI: 109.52–120.83.

Morphology as in worker except for: **Head**. Frontal view: Anterior ocellus maximum diameter subequal to that of posterior ocelli. Distance from posterior ocellar margin to posterior margin of head close to twice apical scape width. Distance between anterior and posterior ocelli close to 2.5 times anterior ocellus diameter. **Mesosoma**. Dorsal view: Mesoscutum about as long as broad, close to 2.5 times as long as mesoscutellum. Transscutal line well–developed. Scutoscutellar sulcus shallowly impressed, formed by scrobiculate sculpture. Mesoscutellum subquadrate, flat dorsally. Posterior face of propodeal declivity flat. Posterolateral margin of propodeal declivity slightly rounded to barely carinate, not forming crenulae. Anterodorsal median propodeal sulcus present, weakly impressed. Ventral view: Mesosternal process with internal margins slightly divergent. **Wings**. Unknown. **Petiole**. Lateral view: anterior and posterior margins of node nearly straight at base and slightly tapering dorsad. Lateral projection of anteroventral nodal carina slightly acute and moderately bent dorsad. **Color**. Appendages, including antennae and mandibles, dark brown to black. **Sculpture**. Striae on head present only dorsally, covering most of surface except posterior third; strong striae on posterolateral margin of pronotum, usually anepisternum and part of katepisternum, axillula, metapectus, and laterally on propodeum; petiolar node lacking striae, (see also general synoptic description).

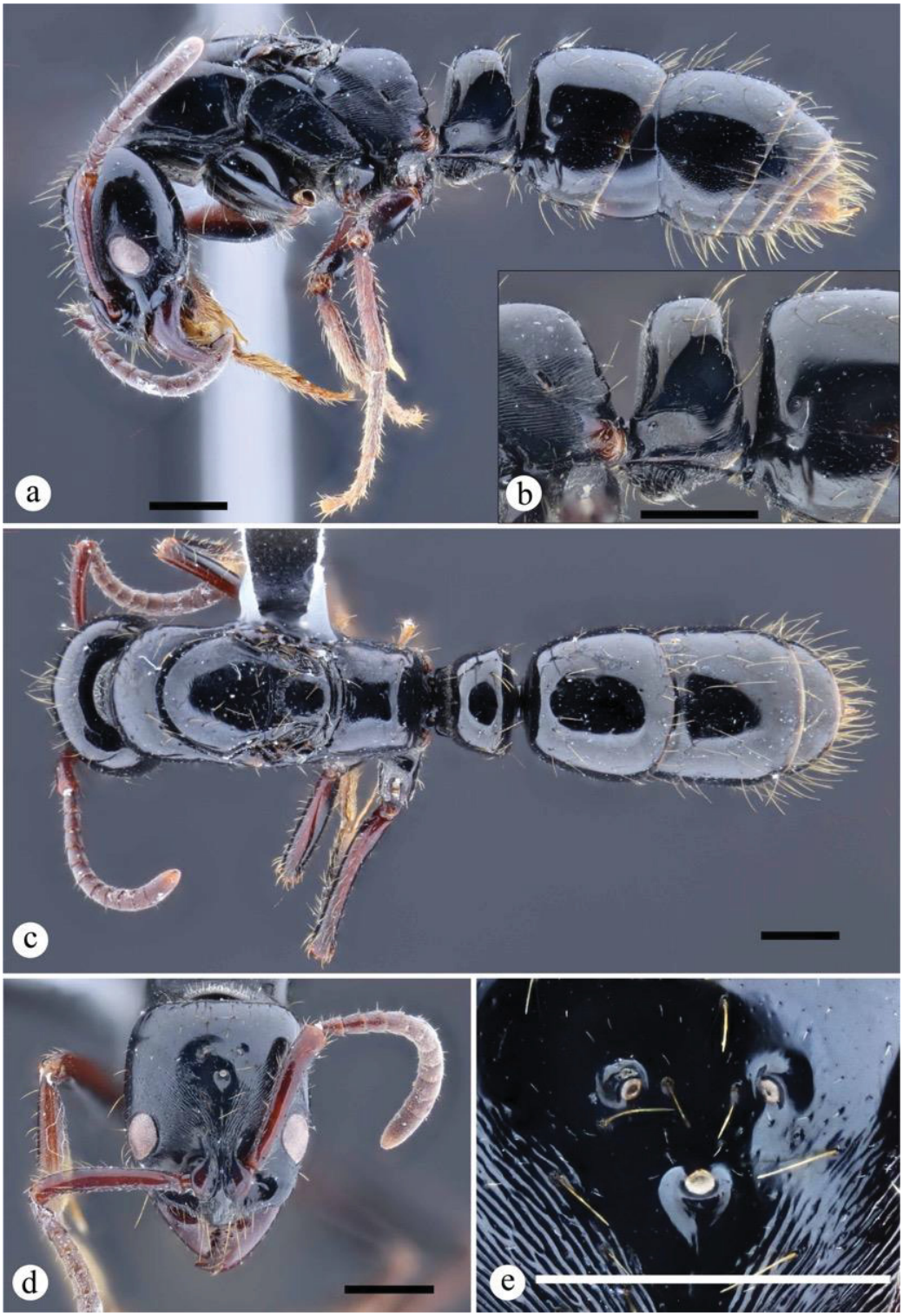


Fig. 26. *Neoponera mashpi* **sp. nov.** Paratype ♀ (CPDC: ATPFOR2054), French Guiana, Paracou. **a.** Lateral view; **b.** Petiole in lateral view; **c.** Lateral view; **d.** Head in frontal view; **e.** Ocelli in frontal view. Scale bars: 1 mm (**a** – **d**); 0.5 mm (**e**).

Male diagnosis. Antennal scape cylindrical (Figure 27d); mesoscutum lacking median longitudinal line (Figure 15b); mesosternal process absent; forewing vein Rs–M feebly longer than 2M (Figure 27f); hindwing with vein 1Rs incomplete or poorly developed (Figure 27f); pretarsal claw arched, unarmed (without accessory teeth).

Male description. Measurements (n=2): HW: 1.13–1.16; HL: 1.32–1.38; EL: 0.63–0.63; SL: 0.22–0.25; WL: 2.89–2.89; PrW: 1.26–1.45; MsW: 1.2–1.26; MsL: 1.76–1.76; PW: 0.75–0.75; PH: 0.88–0.94; PL: 0.69–0.75; GL: 4.4–4.53; A3L: 0.94–1.01; A4L: 1.2–1.29; A3W: 1.13–1.2; A4W: 1.32–1.42; TLa: 7.04–7.33; TLr: 9.31–9.56; **Indices**. CI: 81.82–88.1; OI: 54.05–55.56; SI: 18.92–22.22; MsI: 67.86–71.43; LPI: 78.57–80; DPI: 100–109.09.

Head. Frontal view: Mandibular apex, when closed, barely touches lateral margin of labrum. Prementum with clear transverse dome. PF: 6,4. Labral dorsum mostly smooth. Clypeus anteromedially straight to slightly concave, with weak dorsal dome, feebly swelling from cuticle and covering anterior clypeal margin. Area between posterior margin of clypeus and supraclypeal area with evident depression. Posterior supraclypeal area acute. Supraclypeal area slightly protruding from cuticule, followed posteriorly by tenuously impressed longitudinal carina. Distance between internal margins of antennal sockets less than one socket diameter. Torular lobe strongly reduced. Eye suboval, slightly notched medially, maximum diameter slightly less than half head length, placed slightly anterior to cephalic mid–length. Ocellar area positioned at vertex. Distance from posterior ocellar margin to posterior margin of head close to twice apical scape width. Distance between anterior and posterior ocelli varying between 1–1.5 times anterior ocellus diameter. Scape cylindrical, one third longer than pedicel. **Mesosoma**. Dorsal view: Mesoscutum close to 3 times as long as mesoscutellum, anterior triangular impression weakly impressed, median longitudinal line absent. Parapsidal lines weakly impressed, slightly divergent. Scutoscutellar sulcus straight. Anterior subalar area shorter than tegular maximum width. Metanotum surface even, slightly flat. Metapleuropropodeal groove relatively shallow. Posterior face of propodeal declivity mostly flat. Anterodorsal median propodeal sulcus present, weakly impressed. Lateral view: Posterolateral margin of propodeal declivity slightly rounded to barely carinate, not forming crenulae. Pheromone venting canal at metapleural gland opening poorly developed, sightly striated. Ventral view: Probasisternal posterior projection acute. Mesosternal process vestigial. Metasternal process as in worker and queen. **Wings**. Forewing venation: Rs–M slightly longer than 2M. Forewing evenly covered by fine setose layer. Hindwing venation: 1Rs

present, very short though. Hindwing bearing 8–10 hamuli.. **Petiole**. Lateral view: anterior and posterior margins of node nearly straight at base and slightly tapering dorsad; dorsal margin convex. Lateral projection of anteroventral nodal carina well–developed, with acute or slightly blunt tip feebly projecting anterodorsad. Dorsal view: Anterior margin of petiolar node approximately two–thirds shorter than width of posterior margin. Lateral view: Subpetiolar process subtriangular, with rounded anterior cusp, followed by posterior straight slope (ca. 30°), with two slightly divergent longitudinal carinae separated by groove. **Gaster**. Lateral view: Meeting of anterior A3 margin with dorsal margin relatively angled. Cinctus moderate. Pygostyles close to three times longer than broad. Dorsal view: Tergum of A3 shorter than A4. Ventral view: Abdominal sternum 7 showing even surface with no ditches, anterior half glabrous, posterior half with semicircular patch bearing abundant, appressed, stout hairs. Spine at posterior margin of tergum of A8 acute, semitubular (not dorsoventrally flattened). Abdominal sternum 9 roughly as long as broad. **Legs**. Mesofemur thickened medially, thicker than metafemur, in dorsal or ventral view. Ventral surface of meso– and metafemora flattened roughly on distal two–thirds, surface even, without groove. **Genitalia**. Ventral view: Cupula: posterior margin of medial invagination narrow. Lobular process vestigial. Gonopod dorsally subtriangular, subrectangular in lateral view, with subtriangular posterior half strongly directed ventrad, dorsolateral margin relatively straight medially, with medial, oblique, weak incision. Gonostylus subacute apically, dorsointernal margin with rounded, tooth–shaped, swelling. Basivolsella externally nearly straight. Digitus spatulate, with outer margin round in ventral view. Penial sclerites overall outline axe–shaped, dorsally broadly round. Dorsoapical third of penial sclerite surface with strong flap. **Color**. Appendages including antennae and mandibles brown to ferruginous brown, occasionally legs yellowish and mandibles lighter than remaining integument of body. **Sculpture**. Striae absent on head, axillula, metapleuron and lateral propodeal surface slightly rugose, on petiolar node usually absent, though when present, feebly impressed on lateral face.

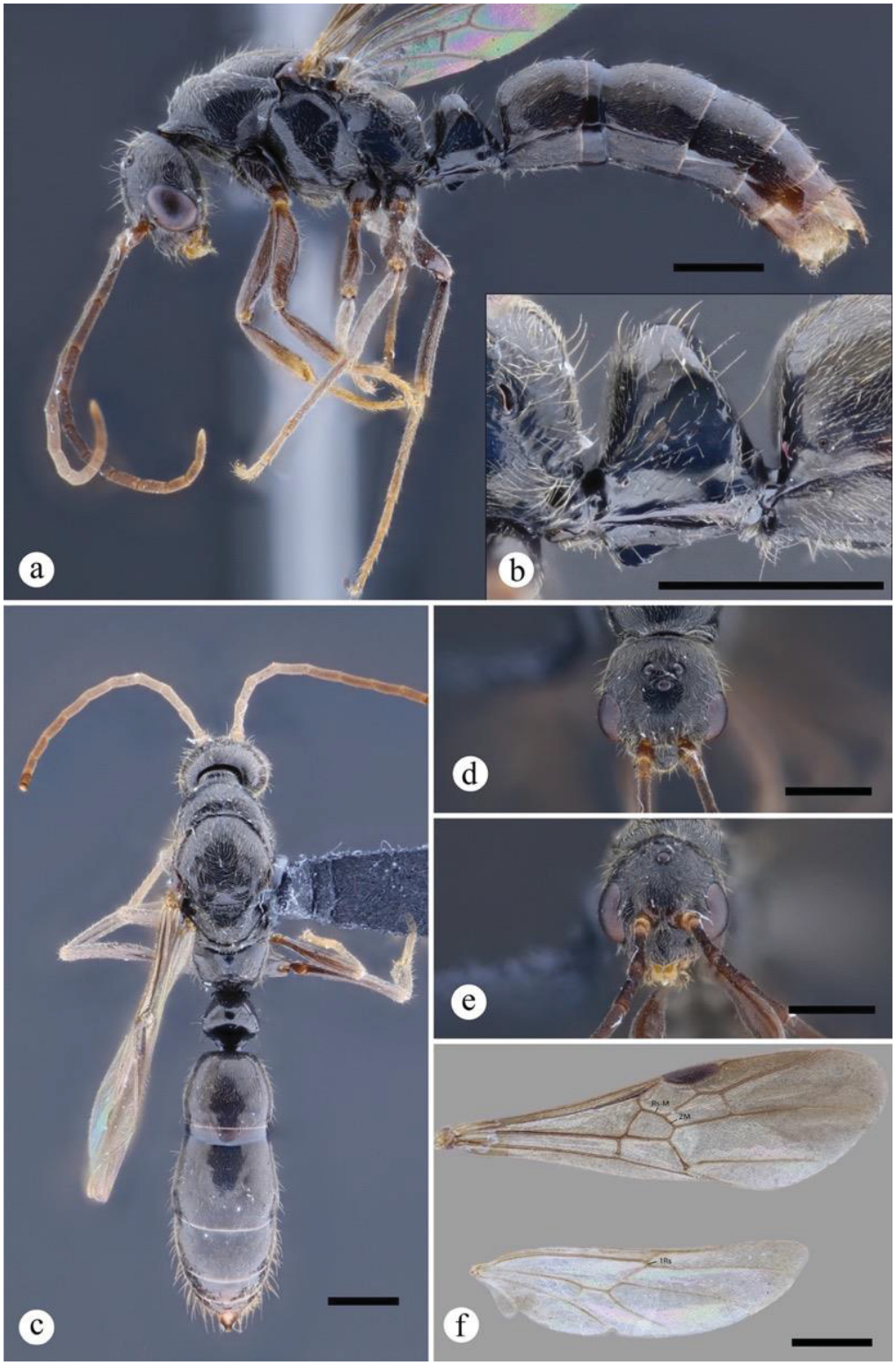


Fig. 27. *Neoponera mashpi* **sp. nov.** Paratype ♂ (CPDC: ATPFOR2077), Brazil, Bahia. **a.** Lateral view; **b.** Petiole in lateral view; **c.** Dorsal view; **d.** Head in dorsal view; **e.** Head in frontal view; **e.** Fore and hind wings. Scale bars: 1 mm.

Natural history notes. *Neoponera mashpi* **sp. nov.** has been collected mostly by hand and Malaise trapping. The elevation records vary from 3 to 746 m, being this species mostly found in preserved mature habitats from lowland and pre–montane rain forests in Central America, to Andean mountainous and Pacific lowland forests from the Chocó–Darien, to dense and open Amazonian and Atlantic ombrophyllous forests in South America. J. Longino (1999) observed this species raiding on unidentified termites in Costa Rica; he also briefly described a possible colony relocation of about 1400 to 1800 workers moving out from an underground nest into the remains of a termite nest, and over its entrance he noted a hovering cloud of unidentified fungus gnats. Adrian Troya observed a few foraging individuals approaching an unidentified termite nest built inside a fallen log in a tropical Andean cloud forest (Reserva de Biodiversidad Mashpi), northwestern Ecuador, the ant colony was located near their potential prey source some 5 m away.

Virtually all published observations on behavioral biology made by previous authors in the island of Barro Colorado (BCI), Panama, which have been attributed to *N. laevigata*, probably correspond to *N. mashpi* **sp. nov.**: Wheeler (1936): colony activity and diet (termite predation); Borgmeier (1959): diet (termite predation); Downing (1978): foraging and migratory behavior; Hölldobler & Traniello (1980): pheromone recruitment communication; Traniello (1981): behavior against termite deterrence; Longino (1999): foraging and migratory behavior; Mackay & Mackay (2010): sporadic gyne and male collections. Although we could not find vouchers from that specific Central American site, we did examine specimens of *N. mashpi* **sp. nov.** from the Panamanian regions of Coclé and Colón, which are in relative proximity to BCI.

Comments. *Neoponera mashpi* ***sp. nov.*** can only be confused with two species in the *N. laevigata* group: *N. laevigata* and *N. gojira* **sp. nov.** The remaining species, *N. commutata* and *N. marginata* are clearly different, with the worker caste in the former being much larger (WL= 5.59–5.68 mm), whereas the latter shows a strongly excavated dorsal groove on the mandible, in frontal view (Figure 12a), this groove is absent in *N. mashpi* **sp. nov.** The following features facilitate separating *N. mashpi* **sp. nov.** from *N. laevigata* and *N. gojira* **sp. nov.** in the worker caste: when compared to the first, the scape is smaller, when pulled back it does not reach the posterior head margin by at least one apical scape width, this is usual in the smallest workers and queens, but see also diagnosis (Figure 6a), while in *N. laevigata* the scape always surpasses said margin by close to one apical scape width (Figure 6b); the lateral nodal face is smooth (Figures 25d, 26b), while that of *N. laevigata* always bears oblique striae. However, *N. mashpi* **sp. nov.** populations from

Central American Atlantic forests may also show nodal striations laterally (see distribution notes below), though less strongly impressed than in *N. laevigata*. The subpetiolar process is subtriangular with an acute anterior cusp, in lateral view (Figure 25d), in *N. laevigata* the subpetiolar process is also subtriangular but with an anterior keel–shaped cusp, followed posteriorly by a relatively flat or slightly concave surface (Figure 13d); prora well–developed (Figure 15d), while in *N. laevigata* the prora is either absent or shaped as a tiny cuticular lip (Figure 13d). Workers of *N. mashpi* **sp. nov.** differ from *N. gojira* **sp. nov.** in the following features: dorsal masticatory mandibular surface smooth, with few shallow piligerous fossulae medially (Figure 12c), in *N. gojira* **sp. nov.** this region has a distinct longitudinal rim with piligerous foveae and longitudinal striae medially, Figure 12b); flap at metapleural gland opening well–developed and strongly curved anterad so that the orifice of the gland is barely visible in posterolateral view (Figure 2a), while in *N. gojira* **sp. nov.** the flap is reduced to a narrow, poorly discernible, blunt carina, leaving the gland orifice completely visible in posterolateral view, Figure 2d; prora well–developed, while in *N. gojira* **sp. nov.** the prora is tiny and lip– shaped, Figure 19e); clearly smaller (WL = 1.66 – 3.31 mm), whereas the holotype of *N. gojira* **sp. nov.** is the largest worker of the *N. laevigata* group (WL= 3.72 mm); the area of the pheromone venting canal at the metapleural gland opening in lateral view (Figure 2a) is clearly less impressed than in *N. gojira* **sp. nov.** (Figure 2d).

The queen: in *N. mashpi* **sp. nov.** the queen is smaller (WL= 3.67 – 4.08 mm) than that of *N. laevigata* (WL = 4.70 – 4.95), the ocelli are also smaller: ca. 0.085 mm vs ca. 0.14 mm. The scape in *N. mashpi* **sp. nov.**, when pulled back, fails to reach posterior head margin, whereas in *N. laevigata* the scape always surpasses said margin by approximately one apical scape width. The petiolar node of the currently known queens of *N. mashpi* **sp. nov.** is completely devoid of striae, while in *N. laevigata* those striae are always strongly impressed and present laterally on the nodal face. The queen of *N. gojira* **sp. nov.** is unknown.

The male: we only found two specimens of *N. mashpi* **sp. nov.** from the Brazilian Amazon, both bearing a well–developed prora which is one of the diagnostic features for the worker, and according to our observations of the current set of specimens in the *N. laevigata* group, the form and size of this structure is relatively conserved among all castes in each species. These males are virtually identical to the specimen identified as "*Pachycondyla" laevigata* by W. Mackay from the Pacific side of Costa Rica, Estación Pitilla (AntWeb record:

INBIOCRI001099170, image examined). The Brazilian specimens slightly differ from this Costa Rican specimen in the following: outline of head feebly straight posterad to eyes (rounded in INBIOCRI001099170), and propodeal posterolateral surface more striated than in INBIOCRI001099170. Populations of *N. mashpi* **sp. nov.** from the Pacific regions of Central America do not show lateral nodal striae as is the case for INBIOCRI001099170. Thus, we can assign (for now) this Costa Rican male to *N. mashpi* **sp. nov.** Since the males of *N. commutata* greatly differ from the other known males examined in this study, e.g., in bearing torular lobes (absent in remaining known species), those of *N. mashpi* **sp. nov.** can only be confused with the males of *N. marginata*. Among other features, these two species can be distinguished mainly by the presence of a median longitudinal line (but can also be seen as a shallow groove) on the mesoscutum of *N. marginata* (absent in *N. mashpi* **sp. nov.**), and by the spine on the tergum of A8 being dorsoventrally depressed and with blunt posterior tip in *N. marginata* (conical and acute posteriorly in *N. mashpi* **sp. nov.**).

Neoponera mashpi **sp. nov.** is very similar to *N. laevigata* and since both occur in sympatry in several ecoregions, mostly in South America (Figure 29a), they could well be sister lineages as suggested by preliminary molecular analyses (Troya et al, unpublished). Additional insights from future studies, for example through population genetics, may potentially evidence a recent divergence. Some of the differential characters presented above, for example, the shape of the subpetiolar process in workers and queens, show certain degree of continuous variation in some examined populations (see distribution notes below). This may cause difficulty in its separation from correspondent castes of *N. laevigata*, however we consider these variations within the taxonomic limits of *N. mashpi* **sp. nov.** In prior treatments of the *N. laevigata* group, Wheeler (1936) and Mackay & Mackay (2010), these two forms were treated as a single species. The work of Wheeler partially depicts our definition of *N. laevigata*, nevertheless, the two workers illustrated in his plates (pg. 161) show a developed, ventrally directed prora which we consider diagnostic for *N. mashpi* **sp. nov.** We assume that the specimens on which Wheeler (1936) based his descriptions were a mixture of both *N. mashpi* **sp. nov.** and *N. laevigata*. Mackay & Mackay (2010), on the other hand, represent in their descriptions mostly the morphology of *N. mashpi* **sp. nov.**, although without providing details on the prora, subpetiolar process, and the flap of the metapleural gland opening, the first two being key diagnostic characters.

Distribution notes. Populations of the Atlantic forests of Central America: Panama, Costa Rica, up to southern Nicaragua, show very tenuous to clear petiolar node striae, though not as strongly impressed as in the Amazonian populations of its known closest species, *N. laevigata*. The remaining examined populations of *N. mashpi* **sp. nov.**, including those from the Pacific forests of Costa Rica, south to Amazonia and the Atlantic forests of Brazil (Bahia), lack these striae. This gradual variation in sculpture, i.e., well–impressed striae turning into smooth surfaces, from South American regions north to Central America, has been observed in other ant groups as well (J. Longino, per. com.). Despite that, our observations on this trait do not support or suggest a lineage split between Central American and South American populations, though they could represent ongoing hybridization between both species.

Populations of *N. mashpi* **sp. nov.** and *N. laevigata*, are distributed in sympatry in several Amazonian and Chocó–Darien sites. Our current specimen set supports a Central American distribution up to northern Costa Rica only for *N. mashpi* **sp. nov.**, whereas *N. laevigata* populations reach up to the mid–western tropical regions of the Cordillera Occidental, up to approximately the Golfo de Cupica in the Chocó–Darien of Colombia. *N. mashpi* **sp. nov.** shows a broader range in South America, reaching the Atlantic Forest in northeast Brazil (Rio Grande do Norte and Minas Gerais), to the southern Peruvian Amazon.

Except for the petiolar node striae present in Central American *N. mashpi* **sp. nov.**, the diagnostic traits of this species are relatively stable across examined specimens from Amazonian and Atlantic forests. Costa Rican records from Guanacaste, to the northwestern Pacific, represent the northernmost distribution range of this species. Thus far no records of any species in the *N. laevigata* group have been found north of southern Nicaragua (J. Longino, per. com.), with the Hess Escarpment potentially acting as a biogeographic barrier not only for this group but for other biota as well (see Mendoza et al. 2019).

Other material examined. 67☿, 9♀, 4♂: **BRAZIL**: **Amapá**: Parque Nacional Montanhas do Tumucumaque , 1.61667°N, 52.4833°W, 150m, 2017–07–25, Feitosa, R.; et al. (DZUP); **Amazonas**: Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA), 2.96304°S, 59.9229°W, 111m, 1987–09–14, Souza, J., fotoecletor (INPA), 1999–07–29, Melo, G. (DZUP), Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA), 2.93333°S, 59.9667°W, 106m, 1987–09–14, Souza, J.,

fotoecletor (INPA), 1999–07–29, Melo, G. (DZUP), Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA), 2.93333°S, 59.9667°W, 106m, 1987–09–14, Souza, J., fotoecletor (INPA), 1999–07–29, Melo, G. (DZUP), Reserva Florestal ZF3, Km 27, 2.41667°S, 59.8°W, 118m, 1981–08–08, Harada, A. (INPA); **Bahia**: Itororó, 15.1158°S, 40.0646°W, 600m, 2001–10–04, Santos, J. R. M (CPDC), Japu, Fazenda Duas Barras, 14.8832°S, 39.1933°W, 130m, 1988–11–27, hand collected (DZUP), Porto Seguro, 16.4455°S, 39.0658°W, 3m, 1997–09–23, Santos, J. R. M, Malaise (CPDC), Refugio da Vida Silvestre do Una, 15.2323°S, 39.1151°W, 70m, 1999–10–04, Santos, J. R. S. (DZUP); **Pará**: Fazenda Vitória, 2.98345°S, 47.3499°W, 82m, 1991–12–21, Moutinho, P. (ICN), Floresta Nacional Caxiuanã, 1.73333°S, 51.45°W, 21m, 1998–03–24, Silveira, O.; Pena, J., Malaise (MPEG), 2012–09, Cunha, D. et al., pitfall (MPEG), Floresta Nacional Caxiuanã, 1.71667°S, 51.45°W, 32m, 1998–03–24, Silveira, O.; Pena, J., Malaise (MPEG), 2012–09, Cunha, D. et al., pitfall (MPEG); **Rio Grande do Norte**: Tabatinga, 6.06753°S, 35.1031°W, 12m, 2005–09, Martins, J. (DZUP); **Rondônia**: Area Caiçara, 9.43311°S, 64.8024°W, 103m, 2011–01–04, Silva, R.; Probst, R., Winkler (MPEG). **COLOMBIA**: **Chocó**: Aruzi, 5.56668°N, 77.4667°W, 49m, 1998–11–25, Jimenez, E., hand collected (MUSENUV); **Putumayo**: Parque Nacional Natural La Playa, Cabaña Viviano, 0.116667°N, 74.9333°W, 320m, 2002–05–14, Cobete, R., pitfall (IAvH); **Valle del Cauca**: Darien, 3.93371°N, 76.6833°W, 545m, 1994–07–15, Aldana, R., Winkler (MUSENUV). **COSTA RICA**: **Guanacaste**: Estación Pitilla, 9 Km S Santa Cecilia., 10.9926°N, 85.4295°W, 700m, 1989–12–01, C. Moraga & P. Rios (INBio); **Heredia**: 11km SE La Virgen, 10.3333°N, 84.0667°W, 500m, 2003–02–12, ALAS, Malaise (INBC); **Limón**: Reserva Biológica Hitoy Cerere, 9.65724°N, 83.0259°W, 530m, 2015–06–11, J. Longino, search (MUCR), 2015–06–11, ADMAC, maxiWinkler (MUCR), Reserva Biológica Hitoy Cerere, 9.65727°N, 83.026°W, 530m, 2015–06–11, J. Longino, search (MUCR), 2015–06–11, ADMAC, maxiWinkler (MUCR); **Puntarenas**: Cerro Rincon, Corcovado National Park, 8.55°N, 83.4833°W, 700m, 1981–02–27, J. Longino (JTLC), San Pedrillo, Corcovado National Park, 8.61667°N, 83.7333°W, 5m, 1980–06–14, J. Longino, hand collected (JTLC). **ECUADOR**: **Orellana**: Parque Nacional Yasuní, Tiputini Biodiversity Station, 288 km SE Quito, 0.633333°S, 76.15°W, 236m, 2011–12–11, Donnell, S. O. (DZUP); **Pastaza**: Parque Nacional Yasuní, Bameno, sendero Curaray 2, 1.301°S, 76.143°W, 240m, 2014–01–31, Troya, A.; Duque, P., fogging (MEPN); **Pichincha**: Reserva de Biodiversidad Mashpi, 50 Km NW Quito, 0.1544°N, 78.8905°W, 746m, 2017–04,

Troya, A., hand collected (JTLC); **Sucumbíos**: Reserva de Producción Faunística Cuyabeno, Trocha Zábalo–Güepi, 0.25°S, 75.6833°W, 270m, 2000–08–08, Araujo, P., fogging (MEPN). **FRENCH GUIANA**: **Cayenne**: 12km East from the village of Sinnamary. Paracou Station, 5.26667°N, 52.9167°W, 50m, 2002–04 , Orivel, J. (CPDC), 1km E Nouragues Station, Grand Plateau, Nouragues Natural Reserve, 4.08885°N, 52.6749°W, 120m, 2018–08–21 (DZUP); **Saint–Laurent–du–Maroni**: Mitaraka, 2.22755°N, 54.4537°W, 335m, 2015–03–01, pitfall (EcoFoG). **PANAMA**: **Coclé**: 8 km NNW El Copé, Parque Nacional Omar Torrijos, 8.68543°N, 80.5989°W, 710m, 2015–01–22, hand collected (JTLC); **Colón**: Parque Nacional Soberanía, Pipeline road, La Seda, 9.15622°N, 79.7344°W, 60m, 2015–05–07, Schar, S., hand collected (MEPN). **PERU**: **Madre de Dios**: Reserva Nacional Tambopata, Sachavacayoc , 12.8167°S, 69.3667°W, 229m, 2012–07–26, Fernandes, I. (INPA). **VENEZUELA**: **Bolívar**: Nichare Field Station, Río Tawadu, 200m, 6.4333°N, 64.8833°W, 200m, 1996–02–10 (PSWC).

***Neoponera mashpi* sp. nov. geographic range.** Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Panama, Peru, Suriname, Venezuela.

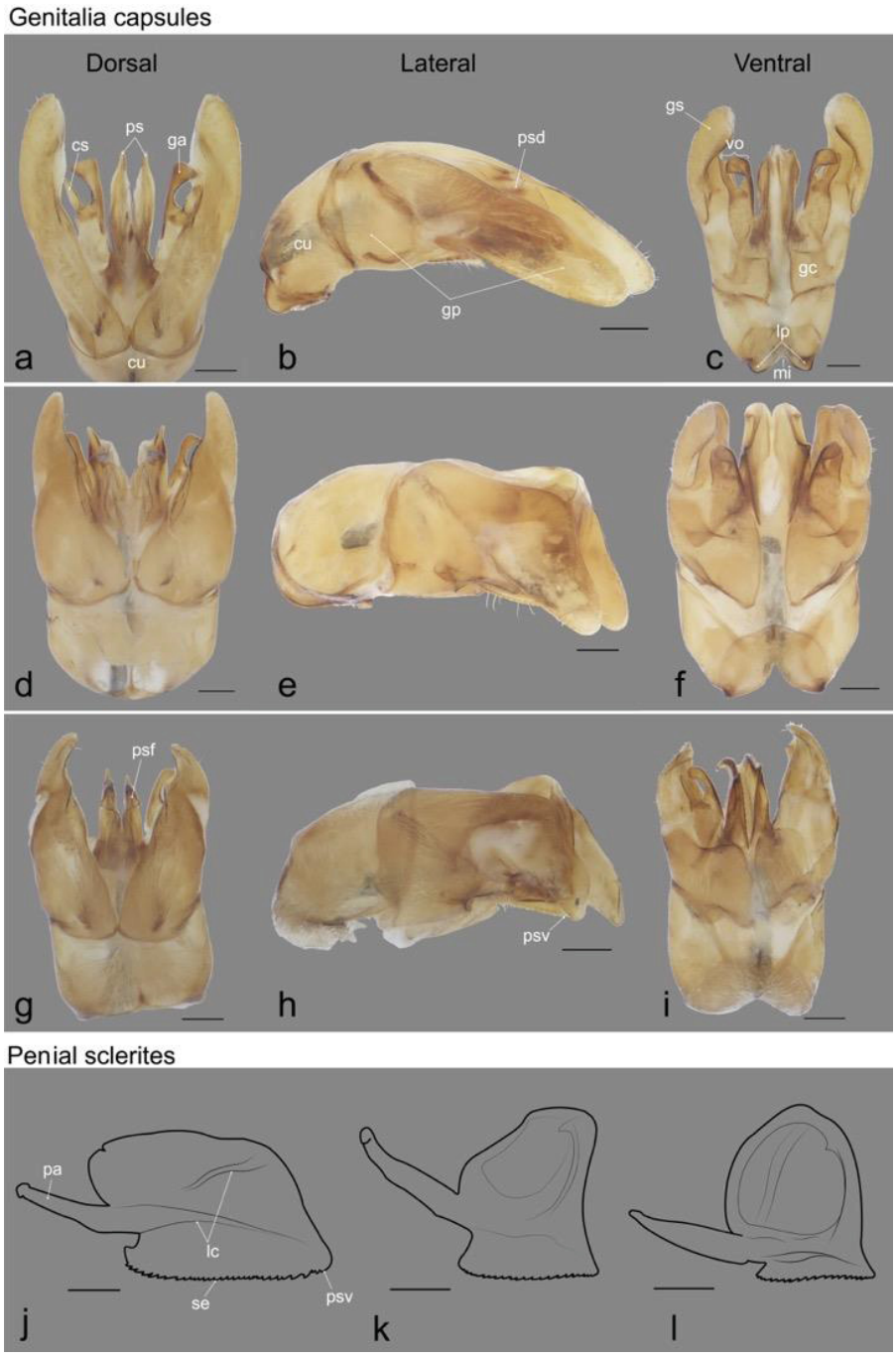


Fig. 28. *Neoponera laevigata* species–group, male genitalia capsules and right penial sclerites. *Neoponera commutata*, MEPN: ATPFOR2051 (**a–c**, **j**); *N. marginata*, UFVLABECOL: UFV–LABECOL010414 (**d–f**, **k**); *N. mashpi* **sp. nov.,** CPDC: ATPFOR2054–2 (**g–i**, **l**). Abbreviations: **cs** Cuspis; **cu** Cupula; **ga** Gonapophysis; **gc** Gonocoxa; **gp** Gonopod; **gs** Gonostylus; **lc** Lateral carina; **lp** Lobular process; **mi** Medial invagination; **pa** Penial apodeme; **ps** Penial sclerites; **psd** Penial sclerite dorsal apex; **psf** Penial sclerite flap; **psv** Penial sclerite ventral apex; **se** Serrated edge; **vo** Volsella. Scale bars = 0.2 mm.

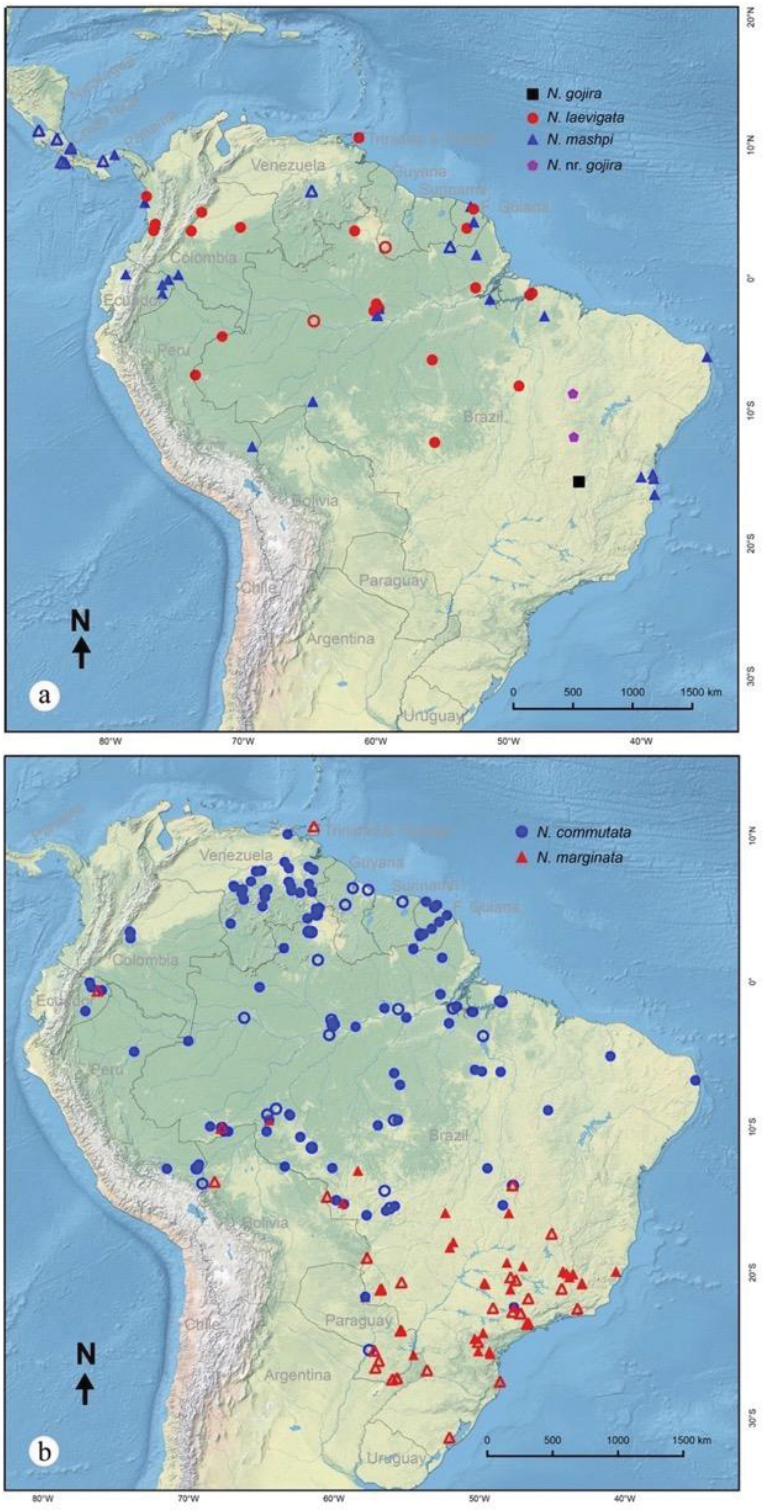


Fig. 29. Distribution of species in the *Neoponera laevigata* group. **a.** *Neoponera gojira* **sp. nov.**, *Neoponera* nr. *gojira*, *N. mashpi* **sp. nov.**, *N. laevigata*; **b.** *Neoponera commutata*, *N. marginata*. Empty icons (circles and triangles) belong to the same species as those with filled icons in each Figure, but these represent records obtained from the literature and AntWeb (see references below).

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REFERENCES

Acosta–Avalos, D., Wajnberg, E., Oliveira, P.S, Leal, I., Farina, M. & Esquivel, D.M.S. (1999) Isolation of magnetic nanoparticles from *Pachycondyla* marginata ants. *Journal of Experimental Biology* 202: 2687–2692. https://doi.org/10.1242/jeb.202.19.2687

Acosta–Avalos, D., Esquivel, D.M., Wajnberg. E., Lins de Barros, H.G., Oliveira, P.S. & Leal, I. (2001) Seasonal patterns in the orientation system of the migratory ant *Pachycondyla marginata*. *Naturwissenschaften* 88: 343–346. https://doi.org/10.1007/s001140100245

Aili, S.R., Touchard, A., Koh, J.M.S., Dejean, A., Orivel, J., Padula, M.P., Escoubas, P. & Nicholson, G.M. (2016) Comparisons of Protein and Peptide Complexity in Poneroid and Formicoid Ant Venoms. *Journal of Proteome Research* 15: 3039–3054. https://doi.org/10.1021/acs.jproteome.6b00182

AntCat (2022) An online catalogue of the ants of the world by Barry Bolton. Available from: https://www.antcat.org. (accessed on Mar 2022).

AntWeb (2021) AntWeb. Available from: https://www.antweb.org. (accessed on Mar 2022).

Arnett, R., Samuelson, A.G. & Nishida, G.M. (2019) The Insect & Spider Collections of the World. CRC Press, Boca Ratón: 316 pp.

Arnold, M.L. (1992) Natural hybridization as an evolutionary process. *Annual review of Ecology and Systematics* 23 (1): 237–261. https://doi.org/10.1146/annurev.es.23.110192.001321

Baksh–Comeau, Y.S., Maharaj, S.S., Adams, C.D., Harris, S.A., Filer, D.L. & Hawthorne, W.D. (2016). An annotated checklist of the vascular plants of Trinidad and Tobago with analysis of vegetation types and botanical 'hotspots'. *Phytotaxa* 250 (1): 1–431. https://doi.org/10.11646/phytotaxa.250.1.1

Baroni Urbani, C. (1993) The diversity and evolution of recruitment behaviour in ants, with a discussion of the usefulness of parsimony criteria in the reconstruction of evolutionary histories. *Insectes Sociaux* 40: 233–260. https://doi.org/10.1007/BF01242361

Bolton, B. (1994) Identification guide to the ant genera of the world. Harvard University Press, Cambridge, Mass., United States: 232 pp.

Bolton, B. (1995) A new general catalogue of the ants of the world. Harvard University Press, Cambridge, Mass., United States: 504 pp. https://www.antcat.org/references/122860

Borgmeier, T. (1959) Myrmecologische Studien. II. *Anais da Academia Brasileira de Ciencias* 31: 309–319. https://antcat.org/references/122939

Boudinot, B.E. (2013) The male genitalia of ants: Musculature, homology, and functional morphology (Hymenoptera, Aculeata, Formicidae). *Journal of Hymenoptera Research* 30: 29–49. https://doi.org/10.3897/jhr.30.3535

Boudinot, B.E. (2015) Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata): a new diagnosis of the family, the first global male–based key to subfamilies, and a treatment of early branching lineages. *European Journal of Taxonomy* 120: 1–62. https://doi.org/10.5852/ejt.2015.120

Branstetter, M.G., & Longino, J.T. (2022) UCE Phylogenomics of New World *Cryptopone*

(Hymenoptera: Formicidae) elucidates genus boundaries, species boundaries, and the vicariant history of a temperate–tropical disjunction. *Insect Systematics and Diversity* 6 (1): 6. https://doi.org/10.1093/isd/ixab031

Brown, B.V. (2013) Automating the "Material examined" section of taxonomic papers to speed up species descriptions. *Zootaxa* 3683: 297–299. https://doi.org/10.11646/zootaxa.3683.3.8

Brown, W. (1973) A comparison of the Hylean and Congo–west African rain forest ants faunas. In: Meggers, B.J., Ayensu, E.S. & Duckworth, W.D. (Eds.), Tropical forest ecosystems in Africa and South America: a comparative review. Smithsonian Institution Press, Washington, D.C, pp. 350. https://www.antcat.org/references/search?reference_q=Brown%2C+W.+%281973%29

Brown, W.L. (1995) [Untitled. Taxonomic changes in *Pachycondyla* and *Neoponera* attributed to William L. Brown]. In: Bolton, B. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, pp. 504.

Cantone, S. (2017) Winged ants – The male. Dichotomous key to genera of winged male ants in the world. Behavioral ecology of mating flight. Autopubblicato, São Paulo, Brazil: 318 pp. https://antcat.org/references/143115

Cantone, S., Von Zuben, C.J. (2019) The Hindwings of Ants: A Phylogenetic Analysis. *Psyche* 2019: 1–11. https://doi.org/10.1155/2019/7929717

Constantino, R. 2020. Termite Database. Brasília, University of Brasília. Available from: http://termitologia.net. (version Dec 2020).

Dallwitz, M. (1980) A general system for coding taxonomic descriptions. *Taxon* 29: 41–46. https://doi.org/10.2307/1219595

Da Ponte, E., Mack, B., Wohlfart, C., Rodas, O., Fleckenstein, M., Oppelt, N., ... & Kuenzer, C. (2017) Assessing forest cover dynamics and forest perception in the Atlantic Forest of Paraguay, combining remote sensing and household level data. *Forests* 8 (10), 389. https://doi.org/10.3390/f8100389

Downing, H. (1978) Foraging and migratory behavior of the ponerine ant *Termitopone laevigata*. Smith College. Doctoral dissertation, Smith College, Northampton, Mass.

Emery, C. (1890) Voyage de M. E. Simon au Venezuela (Décembre 1887 - Avril 1888). Formicides. *Annales de la Société Entomologique de France* 10: 55–76. https://www.antcat.org/references/124550

Emery, C. (1892) ["1891"]. Note sinonimiche sulle formiche. *Bullettino della Società Entomologica Italiana* 23: 159-167. https://antcat.org/references/124557

Emery, C. (1901) Notes sur les sous–familles des dorylines et ponérines (famille des Formicides): 32–54. https://www.antcat.org/references/124641

Emery, C. (1911) Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. Genera Insectorum 118: 1–25. https://www.antcat.org/references/124702

Fernandes, I.O., De Oliveira, M.L & Delabie, J.H.C. (2014) Description of two new species in the Neotropical *Pachycondyla foetida* complex (Hymenoptera: Formicidae: Ponerinae) and taxonomic notes on the genus. *Myrmecological News* 19: 133–163. https://www.antcat.org/references/142549

Field, D.L., Ayre, D.J., Whelan, R.J., & Young, A. G. (2011) Patterns of hybridization and asymmetrical gene flow in hybrid zones of the rare *Eucalyptus aggregata* and common *E. rubida*. *Heredity*, 106 (5): 841–853. https://doi.org/10.1038/hdy.2010.127

Gallardo, A. (1918) Las hormigas de la República Argentina. Subfamilia Ponerinas. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 30: 1–112. https://antcat.org/references/125422

García, M., Rijk, G. & Piotrowski., M. (2021) Key Cerrado Deforesters in 2020 Linked to the Clearing of More Than 110,000 Hectares. *Chain Reaction Research*: 1–16. https://chainreactionresearch.com/wp-content/uploads/2021/03/Key-Cerrado-Deforesters-Linked-to-the-Clearing-of-More-than-110000-Hectares-2.pdf

Google Maps (2021). Google. https://earth.google.com.

Gower, J. C. (1971) A general coefficient of similarity and some of its properties. *Biometrics* 27 (4): 857–871 https://doi.org/10.2307/2528823

Harris, R.A. (1979) Glossary of surface sculpturing. *Occasional Papers in Entomology*: 32. http://bioguid.osu.edu/xbiod_pubs/4823

Hermann, H.R. (1968) Group raiding in *Termitopone commutata* (Roger) (Hymenoptera: Formicidae). *Journal of the Georgia Entomological Society* 3: 23–24. https://www.antcat.org/references/125869

Hölldobler, B., Traniello, J.F.A. (1980) The pygidial gland and chemical recruitment communication in *Pachycondyla* (=*Termitopone*) *laevigata*. *Journal of Chemical Ecology* 6: 883–893. https://doi.org/10.1007/BF00990472

Hölldobler, B., Janssen, E., Bestmann, H.J., Leal, I.R., Oliveira, P.S., Kern, F. & König, W.A. (1996) Communication in the migratory termite–hunting ant *Pachycondyla* (= *Termitopone*) *marginata* (Formicidae: Ponerinae). *Journal of Comparative Physiology A*: Sensory, Neural, and Behavioral Physiology 178: 47–53. https://antcat.org/references/131491

IBGE (2004) Mapa da vegetação do Brasil. Ministerio do Planejamento, Orçamento e Gestão. Available from: https://www.ibge.gov.br/geociencias/informacoes–ambientais/vegetacao/15842–biomas.html?edicao=16060&t=acesso–ao–produto. (accessed on Oct 2020).

Janicki, J., Narula, N., Ziegler, M., Guénard, B. & Economo, E.P. (2016) Visualizing and interacting with large–volume biodiversity data using client–server web–mapping applications: The design and implementation of antmaps.org. *Ecological Informatics* 32: 185–193. https://doi.org/10.1016/j.ecoinf.2016.02.006l

Kaiser, H.F. (1961) A Note on Guttman'S Lower Bound for the Number of Common Factors. *British Journal of Statistical Psychology* 14: 1–2. https://doi.org/10.1111/j.2044-8317.1961.tb00061.x

Keller, R.A. (2011) A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. *Bulletin of the American Museum of Natural History* 2011: 1–90. https://doi.org/10.1206/355.1

Krishna, K., Araujo, R.L. (1968) A revision of the neotropical termite genus *Neocapritermes* (Isoptera: Termitidae: Termitinae). *Bulletin of the AMNH* 138. http://hdl.handle.net/2246/1107

Kruskal, J.B. (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1–27. https://doi.org/10.1007/BF02289565

Lattke, J.E. (2012) Revision of the new world species of the genus *Leptogenys* Roger Insecta: Hymenoptera: Formicidae: Ponerinae. *Arthropod Systematics and Phylogeny* 70: 71. https://www.antcat.org/references/132941

Leal, I.R. & Oliveira, P.S. (1995) Behavioral ecology of the neotropical termite–hunting ant *Pachycondyla* (= *Termitopone*) *marginata*: colony founding, group–raiding and migratory patterns. *Behavioral Ecology and Sociobiology* 37: 373–383. https://doi.org/10.1007/BF00170584

Longino, J. (1999) Ants of Costa Rica. https://ants.biology.utah.edu/AntsofCostaRica.html (accessed on Aug 2021).

Longino, J.T. & Branstetter, M.G. (2020) Phylogenomic species delimitation, taxonomy, and 'bird guide' identification for the Neotropical ant genus *Rasopone* (Hymenoptera: Formicidae). Insect Systematics and Diversity 4 (2): 1–33. https://doi.org/10.1093/isd/ixaa004

Mackay, E. & Mackay, W. (2010) The systematics and biology of the New World ants of the genus *Pachycondyla* (Hymenoptera: Formicidae). Edwin Mellen Press, Unites States: 642 pp. https://www.antcat.org/references/131785

Mayr, E. (1942) Systematics and the Origin of Species. Columbia University Press, New York: 334 pp.

Mayr, G. (1863) Formicidarum index synonymicus. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 13: 385–460. https://antcat.org/references/127213

Mayr, G. 1886. Notizen über die Formiciden-Sammlung des British Museum in London. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 36:353-368. https://antcat.org/references/127239

Mendoza, A.M., Bolívar–García, W., Vázquez–Domínguez, E., Ibáñez, R. & Parra Olea, G. (2019) The role of Central American barriers in shaping the evolutionary history of the northernmost glassfrog, *Hyalinobatrachium fleischmanni* (Anura: Centrolenidae). *PeerJ* 2019: 1–28. https://doi.org/10.7717/peerj.6115

Mill, A.E. (1982a) Emigration of a colony of the giant termite hunter, *Pachycondyla commutata*

(Roger) (Hymenoptera: Formicidae). *Entomologist's Monthly Magazine* 118: 243–245. https://agris.fao.org/agris-search/search.do?recordID=US201302602888

Mill, A.E. (1982b) Faunal studies on termites (Isoptera) and observations on their ant predators (Hymenoptera: Formicidae) in the Amazon Basin. *Revista Brasilera de Entomologia* 26: 253–260.

Mill, A.E. (1984) Predation by the ponerine ant *Pachycondyla commutata* on termites of the genus *Syntermes* in Amazonian rain forest. *Journal of natural History* 18: 405–410. https://doi.org/10.1080/00222938400770341

National Geodetic Survey (2021) NGS Coordinate Conversion and Transformation Tool (NCAT). https://www.ngs.noaa.gov/NCAT/. (accessed on Jan 2021).

Ogata, K. (1991) A generic synopsis of the poneroid complex of the family Formicidae (Hymenoptera). Part II. Subfamily Myrmicinae. *Bulletin of the Institute of Tropical Agriculture*. Kyushu Univ. 14: 61–149.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R. & O' Hara, R.B. (2015) Vegan community ecology package: ordination methods, diversity analysis and other functions for community and vegetation ecologists. R package version 2.5–7. https://github.com/vegandevs/vegan

Orivel, J., Redeker, V., Le Caer, J.P., Krier, K., Revol–Junelles, A.M., Longeon, A., Chaffotte, A., Dejean, A. & Rossier, J. (2001) Ponericins, new antibacterial and insecticidal peptides from the venom of the ant *Pachycondyla goeldii*. *Journal of Biological Chemistry* 276: 17823–17829. https://doi.org/10.1074/jbc.M100216200

Rakotonirina, J.C. & Fisher, B.L. (2013) Revision of the *Pachycondyla sikorae* species–group (Hymenoptera: Formicidae) in Madagascar. *Zootaxa* 3683: 447–485. https://doi.org/10.11646/zootaxa.3683.4.8

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142: 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Roger, J. (1860) Die *Ponera*–artigen Ameisen. Berliner *Entomologische Zeitschrift* 4: 278–312.

https://www.antcat.org/references/128087

Roger, J. (1861) Die *Ponera*–artigen Ameisen (Schluss). *Berliner Entomologische Zeitschrift* 5:1–54. https://antcat.org/references/128088

Roger, J. (1863) Verzeichniss der Formiciden-Gattungen und Arten. *Berliner Entomologische Zeitschrift* 7: 1-65. https://antcat.org/references/128094

Schmid–Hempel, P. (1998) Parasites in social insects. Princeton University Press: 393 pp. ISBN:9780691059242

Schmidt, C. (2013) Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). *Zootaxa* 3647: 201–250. https://www.antcat.org/references/142356

Schmidt, C.A. & Shattuck, S.O. (2014) The Higher Classification of the Ant Subfamily Ponerinae (Hymenoptera: Formicidae), with a Review of Ponerine Ecology and Behavior. Zootaxa 3817: 1–242. https://doi.org/10.11646/zootaxa.3817.1.1

Schmidt, J.O. & Overal, W.L. (2009) Venom and task specialization in *Termitopone commutata* (Hymenoptera: Formicidae). *Journal of Hymenoptera Research* 18: 361–367. https://antcat.org/references/132225

Sena–Souza, J.P., Houlton, B.Z., Martinelli, L.A. & Bielefeld Nardoto, G (2020) Reconstructing continental–scale variation in soil δ15N: a machine learning approach in South America. *Ecosphere* 11 (8): e03223. https://doi.org/10.1002/ecs2.3223

Serna, F. & Mackay, W. (2010) A descriptive morphology of the ant genus *Procryptocerus* (Hymenoptera: Formicidae). *Journal of Insect Science* 10 (1). https://doi.org/10.1673/031.010.11101

Silva, T.S.R. & Feitosa, R.M. (2019) Using controlled vocabularies in anatomical terminology: A case study with *Strumigenys* (Hymenoptera: Formicidae). *Arthropod Structure and Development* 52: 100877. https://doi.org/10.1016/j.asd.2019.100877

Smith, F. (1858) Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. London: British Museum, 216 pp. https://www.antcat.org/references/128685file:///Users/adrian/Documents/UFPR/Tesis/Manuscripts/Dissertation complete/10.1016/j.asd.2019.100877

Soterroni, A.C., Ramos, F.M., Mosnier, A., Fargione, J., Andrade, P.R., Baumgarten, L., Pirker, J., Obersteiner, M., Kraxner, F., Câmara, G., Carvalho, A.X.Y. & Polasky S (2019) Expanding the soy moratorium to Brazil's Cerrado. *Science Advances* 5. DOI: 10.1126/sciadv.aav7336

Tozetto, L., Lattke, J.E. (2020) Revealing male genital morphology in the giant ant genus *Dinoponera* with geometric morphometrics. *Arthropod Structure and Development* 57: 100943. https://doi.org/10.1016/j.asd.2020.100943

Traniello, J.F.A. (1981) Enemy deterrence in the recruitment strategy of a termite: Soldier–organized foraging in *Nasutitermes costalis*. *Proceedings of the National Academy of Sciences* 78: 1976–1979. https://doi.org/10.1073%2Fpnas.78.3.1976

Wajnberg, E, Rossi, A.L. & Esquivel, D.M.S. (2017) Titanium and iron titanium oxide nanoparticles in antennae of the migratory ant *Pachycondyla marginata*: an alternative magnetic sensor for magnetoreception? *BioMetals* 30: 541–548. https://doi.org/10.1007/s10534-017-0024-z

Wheeler, W.M. (1922) The ants of Trinidad. American Museum Novitates 45:1–16. https://antcat.org/references/130152

Wheeler, W.M. (1936) Ecological relations of ponerine and other ants to termites. *Proceedings of the American Academy of Arts and Sciences* 71: 158–243. https://www.antcat.org/references/130270

Wild, A.L. (2005) Taxonomic revision of the Pachycondyla apicalis species complex (Hymenoptera: Formicidae). *Zootaxa* 834: 1-25. https://doi.org/10.11646/zootaxa.834.1.1

Wilson, E.O. (1955) A Monographic Revision of the Ant Genus Lasius. *Bulletin of the Museum of Comparative Zoology at Harvard College* 113: 59–77. https://doi.org/10.5281/zenodo.25290

Yoder, M.J., Mikó, I., Seltmann, K.C., Bertone, M.A. & Deans, A.R. (2010) A gross anatomy ontology for Hymenoptera. *PLoS ONE* 5: e15991. https://doi.org/10.1371/journal.pone.0015991

References for non–examined material included in the distribution maps

Demétrio, M.F., Silvestre, R., de Souza, P. R. & Aoki, C. (2017) Inventário da fauna de formigas

(Hymenoptera, Formicidae) no Mato Grosso do Sul, Brasil. *Iheringia. Série Zoologia* 107. https://doi.org/10.1590/1678-4766e2017126

Emery, C. (1894) [Untitled.]. Pp. 373-401 in: von Jhering, H. 1894. Die ameisen von Rio Grande do Sul. Berliner Entomologische Zeitschrift 39: 321-447. https://www.antcat.org/references/124581

Fowler, H. G. (1981) Nuevos registros de hormigas para el Paraguay (Hymenoptera Formicidae). *Neotropica* 26: 183–186. https://www.antcat.org/references/125297

Harada, A.Y. (2016). State of art of ants (Hymenoptera: Formicidae) at Caxiuanã, Melgaco, Pará, Brazil. *Advances in Entomology* 4: 115–132. http://dx.doi.org/10.4236/ae.2016.43013

Hölldobler, B., Janssen, E., Bestmann, H. J., Kern, F., Leal, I. R., Oliveira, P. S., & König, W. A. (1996) Communication in the migratory termite–hunting ant *Pachycondyla* (= *Termitopone*) *marginata* (Formicidae, Ponerinae). *Journal of Comparative Physiology A* 178 (1): 47–53. https://antcat.org/references/131491

Lutinski, J.A., Lopes, B.C. & de Morais A.B.B. (2013) Diversidade de formigas urbanas (Hymenoptera: Formicidae) de dez cidades do sul do Brasil. *Biota Neotropica* 13: 332–342. https://doi.org/10.1590/S1676-06032013000300033

Mackay, E. & Mackay, W. (2010) The systematics and biology of the New World ants of the genus *Pachycondyla* (Hymenoptera: Formicidae). Edwin Mellen Press, Unites States: 642 pp. https://www.antcat.org/references/131785

Oliveira, M.A., Della Lucia, T.M.C., Marinho, C.G.S., Delabie, J.H.C., & Morato, F.F. (2009) Ant (Hymenoptera: Formicidae) diversity in an area of the Amazon forest in Acre, Brazil. Sociobiology 54 (1): 243–267.

Rosumek, F.B., Ulysséa, M.A., Lopes, B.C., Steiner, J., & Zillikens, A. (2008) Formigas de solo e de bromélias em uma área de Mata Atlântica, Ilha de Santa Catarina, sul do Brasil: Levantamento de espécies e novos registros. *Biotemas*, 21 (4): 81–89. https://doi.org/10.5007/2175-7925.2008v21n4p81

Santos–Silva, L., Vicente, R. E. & Feitosa, R.M. (2016) Ant species (Hymenoptera, Formicidae) of forest fragments and urban areas in a Meridional Amazonian landscape. *Check List* 12: 1885. https://doi.org/10.15560/12.3.1885

Souza, J.L.P., Baccaro, F.B., Landeiro, V.L., Franklin, E., Magnusson, W.E.L., Pequeno, P.A.C. & Fernandes, I.O. (2016) Taxonomic sufficiency and indicator taxa reduce sampling costs and increase monitoring effectiveness for ants. *Diversity and Distributions* 22: 111–122. https://repositorio.inpa.gov.br/handle/1/17405

Vicente, R.E., Prado, L.P. & Izzo, T.J. (2016) Amazon Rainforest Ant–Fauna of Parque Estadual do Cristalino: Understory and Ground–Dwelling Ants. *Sociobiology* 63: 894. https://doi.org/10.13102/sociobiology.v63i3.1043

Wheeler, W.M. (1936) Ecological relations of ponerine and other ants to termites. *Proceedings of the American Academy of Arts and Sciences* 71 (3): 159–243. https://www.antcat.org/references/130270

Wheeler, W.M. (1925) Neotropical ants in the collections of the Royal Museum of Stockholm. *Arkiv för Zoologi* 17: 1–55. https://www.antcat.org/references/130175

Wilkie, K.T.R., Mertl, A.L. & Traniello, J.F. (2010) Species diversity and distribution patterns of the ants of Amazonian Ecuador. *PLoS One* 5 (10): e13146. https://doi.org/10.1371/journal.pone.0013146

SUBCHAPTER II

Neoponera Emery, 1901 (Hymenoptera, Formicidae) revisited: 2. The arboreal *N. crenata* species-group

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Neoponera **Emery,1901 (Hymenoptera, Formicidae) revisited: 2. The arboreal *N. crenata* species-group**

ABSTRACT

We revised the *Neoponera crenata* species-group which is the largest (19 taxa) and most taxonomically complex group in the genus. Except for the commonly collected and broadly distributed *N. unidentata* Mayr, the species of this group are biologically poorly known due to the complexity in accessing the canopy strata where these species inhabit. The *N. crenata* group is distinguished from others in the genus mainly by the combination of the following traits – the latter two considered apomorphic: 1) Notopropodeal suture vestigial or completely absent in almost all species; 2) Mid clypeal region with blunt, subtriangular extension of the cuticle; and 3) Fang-shaped metasternal process with narrow, closely-approximated lobes. Except for the cecropia ant, *N. luteola* Roger, all species are morphologically very similar with extremes like *N. crenata* and *N. moesta*, that are almost indistinguishable. The shape of the petiolar node, and in few cases the mesosomal sculpture, are crucial for species delimitation. Three new species are proposed, *N. cylindrinodis* **sp. nov.** (southern Brazil), *N. dejeani* **sp. nov.** (French Guiana), and *N. yasuni* **sp. nov.** (Amazonian Ecuador), together with a worker & queen- based identification key to the species of this group. A general group diagnosis for all castes is provided, as well as revised diagnostic traits for all taxa, and descriptions for previously unknown castes, all of which are complemented with notes about comparative morphology, biology and distribution. The following names are synonymized under *N. crenata* Roger: *N. crenata confusa* Santschi (**syn. nov.**), *N. mesonotalis* Santschi (**syn. nov.**), and *N. crenata moesta subcarinata* Santschi (**syn. nov.**); and the following under *N. fiebrigi* Forel: *N. crenata confusa lata* Santschi (**syn. nov.**), and *N. latinoda* Mackay & Mackay (**syn. nov.**). We designate a **neotype** for *N. crenata*, thus clarifying a century-long taxonomic uncertainty.

Keywords: Canopy, cryptic species, mutualism, Neotropical region, neotype, sympatry.

INTRODUCTION

Neoponera Emery, 1901, conforms a group of morphologically and ecologically diverse, predominantly predatory tropical ants whose distribution is restricted to the Neotropics (Wheeler 1936, Wild 2005, Mackay, E., Mackay 2010, Fernandes et al. 2014, Schmidt and Shattuck 2014, Troya and Lattke 2022). In the subfamily Ponerinae this is a relatively large group with 58 valid species (AntCat.org), which display a spectrum of behavioral strategies ranging from ground solitary foraging (Fresneau 1985), to group raiding of termites (Mill 1982, 1984), to symbioses with plants (Gutiérrez-Valencia et al. 2017), to fast arboreal hunting (Orivel et al. 2000). Current knowledge about the ecology and biology of this genus is based on few commonly collected species, like *N. apicalis*, *N. commutata*, *N. villosa*. Whereas, the natural history of the majority is known from scant contributions (see Schmidt and Shattuck 2014) and random field observations, see for example, Longino (2010).

Neoponera taxonomy, on the other hand, is overall much better known. Out of the seven recognized species-groups *sensu* (Troya and Lattke 2022), two have been revised: the *N. apicalis* group (Wild 2005), and the *N. laevigata* group (Troya and Lattke 2022). Fernandes et al. (2014) contributed with a partial treatment of the *N. foetida* group and proposed two new taxa. MacKay and Mackay (2010) revised the entire genus, though as part of *Pachycondyla* Smith, proposed a number of new synonyms and erected 17 new species. More recently, new discoveries have been made as part of a comprehensive treatment with the goal of tracing the evolution of *Neoponera* through its first phylogenetic hypothesis.

In this context, we provide in this study new and revised insights about the taxonomy, distribution, and biology of the arboreal-adapted species belonging to the *N. crenata* group, which is currently the largest and, in our view, the most taxonomically complex of the genus. This latter is due to the high similarity of most of its component lineages, which according to recent phylogenomic evidence based on ultraconserved elements (Troya et al. unpublished), experienced a comparatively recent divergence, with most of these species majorly distributed in South America. This is the second contribution toward an updated view into the systematics of *Neoponera* in line to modern evidence stemming from phylogenomic methods.

MATERIALS AND METHODS

Repositories of examined material

Examined specimens, either physical and/or through images, are deposited in the below institutions. Part of this material is represented through images of the types available on the database of the MCZC, and AntWeb.org. We also identified image records from The Barcode of Life Systems – BOLD (Ratnasingham and Hebert 2007). Most museum abbreviations are based on Arnett et al (2019).

ALWC	Alexander L. Wild Collection, TX, USA.
BMNH	The British Museum of Natural History, London, U.K.
CBG	Centre for Biodiversity Genomics, Canada.
CASC	California Academy of Sciences, San Francisco, CA, USA.
CPDC	Coleção do Laboratório de Mirmecologia, Centro de Pesquisas do Cacau, Ilhéus, Bahia, Brazil.
CUIC	Cornell University Insect Collection, NYC, USA.
CWEM	William and Emma Mackay Collection, TX, USA.
DZUP	Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
ECOFOG	EcoFoG–Joint Research Unit Ecology of Guianan Forests, Kourou, French Guiana.
IAVH	Instituto Alexander von Humboldt, Colombia.
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia.
INBC	Instituto Nacional de Biodiversidad, Heredia, Costa Rica.

INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil.
JTLC	John T. Longino Collection, University of Utah, Salt Lake City, UT, USA.
LACM	Los Angeles County Museum, LA, USA.
MACN	Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, Argentina.
MCZC	Museum of Comparative Zoology, Harvard University, MA, USA
MECN	Museo Ecuatoriano de Ciencias Naturales, Instituto Nacional de Biodiversidad, Quito, Ecuador.
MEPN	Museo de Historia Natural “Gustavo Orcés V.”, Escuela Politécnica Nacional, Quito, Ecuador.
MGBPC	Michael G. Branstetter Collection, USA.
MHNG	Muséum d'histoire naturelle Genève, Switzerland.
MIZA	Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MPEG	Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.
MSNG	Museo Civico di Storia Naturale di Genova "Giacomo Doria", Genova, Italy
MUCR	Colección de Insectos, Universidad de Costa Rica, San Pedro, Costa Rica.
MUSENUV	Museo de Entomología de la Universidad del Valle, Cali, Colombia.
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
NHMB	Naturhistorisches Museum Basel, Switzerland.

NHMW	Naturhistorisches Museum Wien, Austria.
PSWC	Philip S. Ward Collection, University of California, CA, USA.
QCAZ	Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
UFVLABECOL	Laboratório de Ecologia de Comunidades, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.
UNMSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
USNM	United States National Museum of Natural History, Washington D.C., USA

Imaging

Images were taken using a Canon® EOS DSLR 70D with a Laowa® 25mm F2.8, 2.5X – 5.0X macro lens, coupled to a Cognisys StackShot® macro rail system which enabled depth–focus shooting through Helicon Remote v. 3.9.9, and posterior stacking in Helicon Focus v. 7.5.6 (Helicon Soft Ltd.). A dome–shaped, cold–light (LED) source was used for illumination. Images of type material and some non–type specimens, as well as collection data of all examined specimens with a unique specimen identifier (a unique code) in this work are available online on AntWeb.org (but see further below in "Material examined").

Images and illustrations by A. Troya, except that in Figure 2b by Ryan Perry, available on AntWeb.org. In this work we only provide images for the newly described taxa, as well as for the castes of certain species, morphospecies and/or variants for which no high-resolution digital images are available thus far on the internet. In specific cases like *N. fiebrigi*, we provide images of two differently sized specimens so as to support our arguments shown in the respective comments section. As for the rest of known, described species we provide an internet link to access the image of the respective type at its original source, in this case, AntWeb.org or the MCZC collections database.

Morphometric variables

All observations and measurements of the following morphological variables (Figure 1) were taken using a pin–holding stage, allowing rotations around the X, Y, and Z axes at magnifications from 8X to 50X with an ocular micrometer incorporated to a Zeiss® Stemi SV6 stereo microscope.

Measurements are presented in mm with an accuracy of two decimal places, minimum and maximum values are indicated when more than one specimen was measured. Most of these measurements are in line with those previously used in other ponerine taxonomic studies, e.g., Rakotonirina and Fisher (2013), Fernandes et al. (2014), Longino and Branstetter (2020), and Troya and Lattke (2022).

We selected specimens for measurement based on the distribution of each species by picking up a number of differently sized specimens per collection site, when available.

HL Head length. In frontal view, maximum distance from the posterior margin of head to the anterior margin of clypeus.

HW Head width. In frontal view, maximum width of head, excluding the eyes.

EL Eye length. In lateral view, measured along its maximum length.

SL Scape length. In frontal view, maximum length of scape excluding its basal condyle and neck.

PrW Pronotum width. In dorsal view, maximum width of pronotum.

WL Weber's length. In lateral view, distance between the anterior margin of pronotum, excluding collar, to the posteroventral margin of metapleuron.

MsW Mesonotum width. In dorsal view, maximum width of mesonotum.

MsL Mesonotum length. In a dorsal view, the maximum distance from the anterior margin of the mesonotum to its posterior margin.

PW Petiolar width. In dorsal view, maximum width of the petiolar node.

PH Petiolar height. In lateral view, the perpendicular distance from the posteroventral lobe of the petiolar tergite to its maximum dorsal margin.

PL Petiolar length. In a lateral view, the distance between the anteriormost margin of petiole to its posterior margin, excluding the posteroventral ridge.

GL Gaster length. In lateral view, the oblique distance between the anterior margin of abdominal segment III to the posterior margin of the pygidium, excluding the sting. This is a relative measure since it can vary in relation to the extension or contraction of abdominal segments IV to VII.

A3L Abdominal segment III length. In dorsal view, the distance between the anterior and posterior margin of abdominal tergite III.

A3W Abdominal segment III width. In dorsal view, maximum width of tergite of abdominal segment III.

A4L Abdominal segment IV length. In dorsal view, the distance between the anterior and posterior margins of abdominal tergite IV.

A4W Abdominal segment IV width. In dorsal view, maximum width of tergite of abdominal segment IV.

TLa Total accurate length of body: HL + WL + PL + A3L + A4L

TLr Total relative length of body: HL + WL + PL + GL

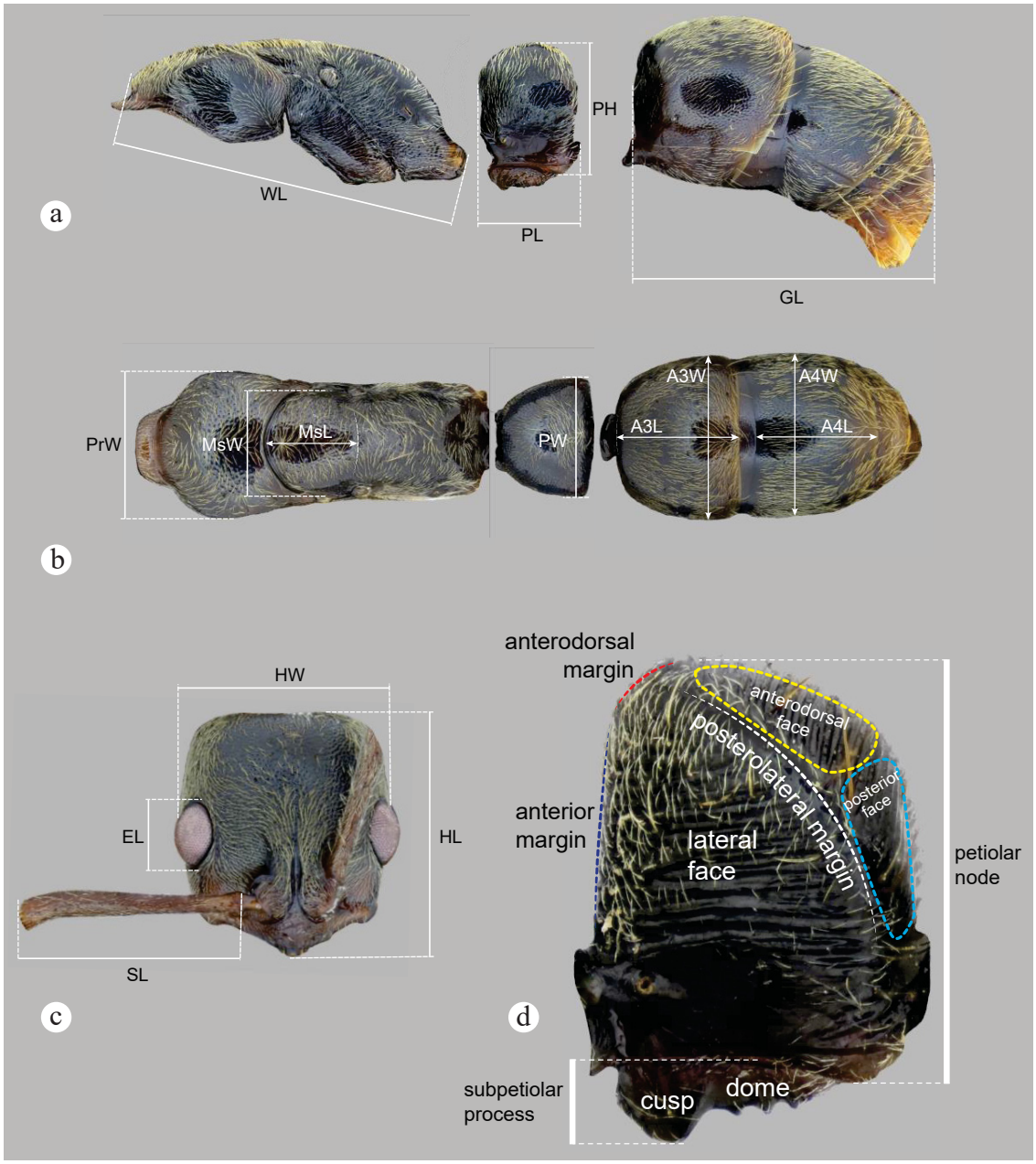


Fig. 1. Morphometric variables and petiolar node characters. a. Body in lateral view. GL: gaster length, PH: petiolar height, PL: petiolar length, WL: Weber's length; b. Body in dorsal view. A3L: abdominal segment III length, A3W: abdominal segment III width, A4L: abdominal segment IV length, A4W: abdominal segment IV width, MsL: mesonotum length, MsW: mesonotum width, PW: petiolar width, PrW: pronotum width; c. Head in frontal view. EL: eye length, HL: head length, HW: head width, SL: scape length; d. Petiole in lateral view.

Indices

The following ratios were multiplied by 100:

CI	Cephalic index: HW/HL
OI	Ocular index: EL/HW
SI	Scape index: SL/HW
MsI	Mesonotum index: MsW/MsL
LPI	Lateral petiolar index: PL/PH
DPI	Dorsal petiolar index: PW/PL

Distribution maps

We used the open–source package Quantum GIS 2.18 to generate maps of distribution, based on coordinates written on specimen labels. All localities were transformed to decimal degrees. We used Google Earth (Google 2022) as information source to check and confirm locality names. In regards to unusual records without specific localities, this is, below the administrative circumscription of state, province, or similar, the center of the next most specific site was georeferenced. In addition, we included in the maps selected literature records, mostly belonging from prior taxonomic treatments, for example from Mackay and Mackay (2010).

Morphological terms

General morphological terminology follows mainly Bolton (1994), Keller (2011), Boudinot (2015), and the Hymenoptera Anatomy Ontology – HAO Yoder et al. (2010). Surface sculpture is based mainly on Harris (1979). Male and female forewing venation on Ogata (1991), and Cantone (2017); hind wing venation on Cantone and Von Zuben (2019). Degree of pilosity inclination follows Wilson (1955), Serna and MacKay (2010): 0°– 5°for appressed hairs running parallel or nearly parallel to body surface; 10°– 20° for decumbent hairs slightly standing from surface; 20°– 40° for subdecumbent hairs; 40°– 70° for suberect hairs; and more than 70° for erect hairs when these stand vertical or nearly vertical. For male genitalia we followed Boudinot (2013)

and Tozetto and Lattke (2020). Palp formula is denoted by "PF" followed by the number of maxillary and labial segments, for example, PF: 4, 4, which means that both appendices have four segments. Tibial spur formula is denoted by "s" – simple, and "p" – pectinate, for example, 2(1s, 1p) which means that two spurs are present, one simple, and 1 pectinate.

Descriptions and material examined

We used the computer package DELTA Dallwitz (1980) for encoding the character states of each newly described caste and/or taxon. This package allows subsequent translation of such encoding into natural language (rich text format – RTF) taxonomic descriptions, which requires further editing from the user. We used TAXOMATA (Ambrosio and Troya, unpublished) a python script which makes a fast conversion of spreadsheet data (e.g., XML, CSV formats) into RTF. In this case, our spreadsheet dataset contained the measured morphometric variables, and the collection information shown in the "Material examined" section.

In the first paragraph of the taxonomic history per species, i.e. the type material, we included inside [ ] our notes, and inside ( ) the repository Collections of such material. Under "status as species" only the first appearance of the species name in the taxonomic literature is cited, as well as relevant redescriptions which are usually part of revisionary studies. The user can access the full history of literature mentions for each species on the Online Catalogue of the Ants of the World – AntCat (AntCat by B. Bolton 2022).

The format of the type material follows: # specimens examined, country, first administrative region, second administrative region or, if known, specific locality, coordinates in decimal degrees, elevation in meters, collection date in format yyyy–mm–dd, collector followed by the word "leg.", method of collection (if known), habitat (if known), and institution where the material is located, usually represented by a unique specimen identifier composed of capitalized letters and numbers. The format for "Other material examined" is essentially equal except that unique specimen identifiers are not shown, but museum acronyms are.

The "Material examined" section contains the complete set of recorded localities and specimens revised in this work. The user, however, can freely download from the Supplementary Material XX (available online) this same information as CSV format, containing additional details, for example, unique specimen identifiers, notes on natural history.

Relationships among taxa

We provide brief comments about the relationships between species in the *N. crenata* group. Our statements are grounded on prior studies by Schmidt (2013) and Branstetter and Longino (2022), as well as on molecular-based preliminary results (A. Troya, J. Longino, M. Branstetter et al. unpublished) which are part of a larger ongoing collaborative study about the phylogeny of the genus *Neoponera* which will be published separately. This additional information is not to be treated as conclusive, nevertheless we think it adds support to our morphology–based arguments around the species hypotheses shown here.

Species delimitation

We follow the biological species concept *sensu* Mayr (1942) by considering species as population assemblages which are under presumed continuous gene flow. Since we did not directly assess this process, our criterion for species delimitation was to detect a continuum of expected character gradations lacking discontinuities among distinctive populations. In sympatry, interspecific gene flow can obscure populational distinctness (Arnold 1992, Field et al. 2011). In such case species can be detected by consistently grouping morphologically similar individuals assumed to belong to structured populations, which is a proxy for gene flow (Wild 2005).

Both new and currently known species hypotheses shown in our study should be further evaluated using additional lines of evidence. These will add objectivity and will aid in the discrimination of species boundaries among cryptic populations which may potentially be under differing selective pressures that are suspected, yet here untested.

RESULTS

Worker- and queen-based key to species of the *Neoponera crenata* species-group

1 Anterior mid clypeal margin straight to slightly convex, not projected anterad in frontal view (Fig. 2a); notopropodeal suture present, forming shallow groove……..…..…***Neoponera luteola***

– Anterior mid clypeal margin convex and projected anterad, usually as subtriangular cuticular extension (Fig. 2b); notopropodeal suture absent or vestigial (except for *N. donosoi* where the suture is present and weakly grooved)……2

2 (1) Dorsoposterior margin of petiolar node feebly pointed posterad, in lateral or dorsal view (Fig. 3a)…….……***Neoponera cavinodis***

– Dorsoposterior margin of petiolar node convex, not extending posterad (Fig. 3b, i) ..……..……...3

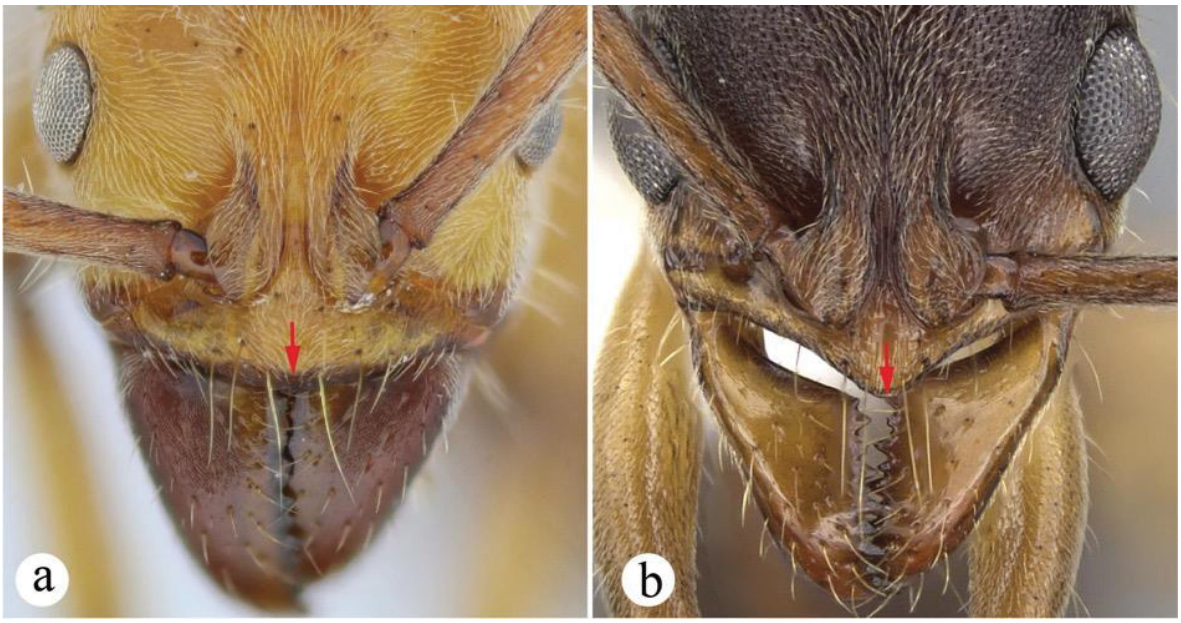


Fig. 2. Mid clypeal carina. **a.** Reduced to a tiny pointed structure below which is the straight to convex clypeus (*N. luteola*, DZUP: ATPFOR2102); **b.** Protruding (usually) as subtriangular extension of the cuticle (*N. moesta*, PSWC: CASENT0249139).

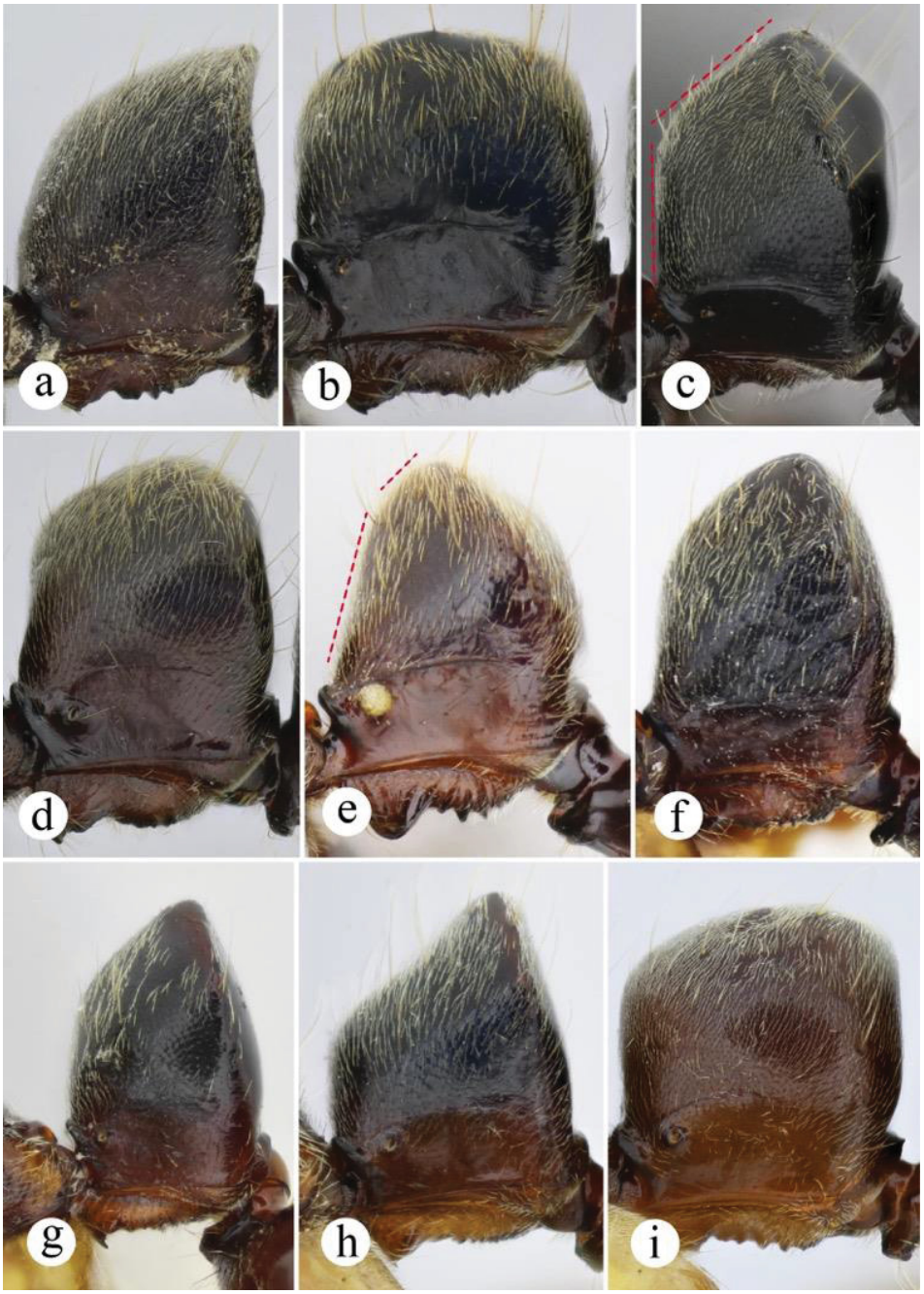


Fig. 3. Petiolar nodes in lateral view. **a.** *Neoponera cavinodis* (MEPN: ATPFOR0855); **b.** *Neoponera cylindrinodis* sp. nov. (DZUP: DZUP549367); **c.** *Neoponera carinulata* (DZUP: DZUP549406); **d.** *Neoponera fiebrigi* (CPDC: AT689); **e.** *Neoponera goeldii* (MEPN: MEPNINV37890); **f.** *Neoponera coveri* (DZUP: DZUP549599); **g.** *Neoponera oberthueri* (CPDC: ATPFOR2083); **h.** *Neoponera oberthueri* (MEPN: MEPN2944); **i.** *Neoponera globularia* (INB0003607588).

3 (2) Dorsal margin of petiolar node convex to relatively flat, with the nodal top placed at about nodal vertical mid line (Fig. 3b, i)…….……..……..….4

– Dorsal margin of petiolar node varying in shape, either convex to acute (e.g., Fig. 3c, 3d, 3g), if the margin is convex, however, the nodal top is placed posterior to nodal vertical mid line (Fig. 3d, only seen in *N. fiebrigi*)…….…..…….7

4 (3) Margin of petiolar node ovate (globular-shaped) in dorsal view (Fig. 8a) ……....***Neoponera globularia***

– Margin of petiolar node either subcylindrical (barrel-shaped) (Fig. 8b), subtriangular (Fig. 8c), or campanulate (Fig. 8d) in dorsal view……5

5 (4) Margin of petiolar node subcylindrical (barrel-shaped), slightly longer than broad in dorsal view (Fig. 8b); antennal scape long, exceeding posterior head margin by two times apical scape width, usually slightly more (Fig. 4c)…..***Neoponera cylindrinodis***

– Margin of petiolar node subtriangular, about as long as broad in dorsal view (Fig. 8c, 8d); antennal scape exceeding posterior head margin by one to 1.5 times apical scape width (Fig. 4d) …….……6

6 (5) Eye proportionally large (as compared to head length): distance from anterior eye margin to mandibular insertion about as long as **half** maximum eye length, in lateral view (Fig. 4a); posterior nodal face glabrous, this surface reaching posterodorsal face (Fig. 8c)……...……...***Neoponera moesta***

– Eye smaller: distance from anterior eye margin to mandibular insertion **always** longer than **half** maximum eye length, in lateral view (Fig. 4b); posterior nodal face with piligerous punctae (Fig. 8d)…….……..……..***Neoponera crenata***

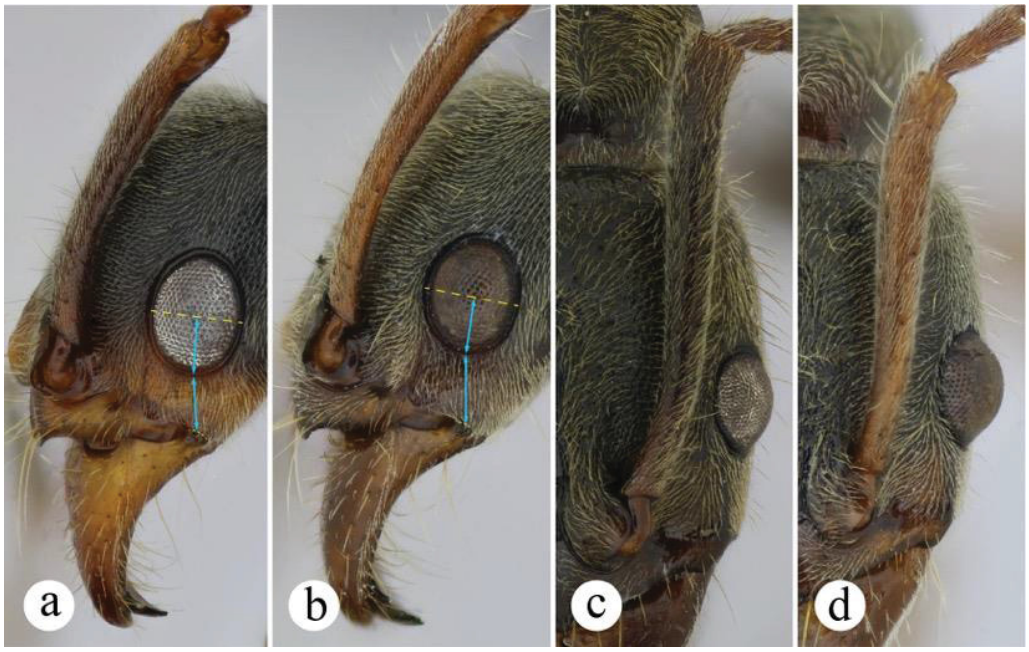


Fig. 4. Eye size and antennal scape length. **a.** Eye relatively large (proportional to head length), distance from its anterior margin to mandibular insertion about as long as half maximum eye length (*N. moesta*, JTLC: CASENT0631798); **b.** Eye smaller, distance from its anterior margin to mandibular insertion longer than half maximum eye length (*N. crenata*, MEPN: ATPFOR0059); **c.** Antennal scape relatively long, exceeding posterior head margin by two times apical scape width, usually slightly more (*N. cylindrinodis*, DZUP: DZUP549367); **d.** Antennal scape smaller, exceeding posterior head margin by about 1.5 times apical scape width (*N. crenata*, MEPN: ATPFOR0059).

7 (3) Anterodorsal margin of petiolar node equal to, or longer than anterior margin (e.g., Figs. 3c, d, f, g)…….…… 8

– Anterodorsal margin of petiolar node shorter than anterior margin (Figs. 3e, 6e, f). Note: in some species e.g., *N. striatinodis*, this region is angulate or blunt (Fig. 6b), so that a "true" anterodorsal margin is absent…….11

8 (7) Posterior face of petiolar node bearing piligerous punctae; node higher than long in lateral view, with strongly inclined anterodorsal margin (Fig. 3f)……... ……***Neoponera coveri***

– Posterior face of petiolar node glabrous and smooth (Figs. 8f, g); size of nodal margins (length vs high) variable, anterodorsal margin either strongly or feebly inclined……..……..…9

9 (8) Posterior **face** of petiolar node mostly flat (Fig. 3d); top of node convex, placed slightly posterior to nodal vertical midline (Fig. 3d); fore coxa with a well-impressed longitudinal carina laterally (Fig. 11)…….……***Neoponera fiebrigi***

– Posterior face of petiolar node convex, either with or without a truncate tumulus (Fig. 3c, 6e); top of node acute, placed either at about nodal vertical midline or posterior to it (Fig. 3c, g); fore coxa without a longitudinal carina laterally, if it is present, then weakly impressed, barely discernible……..…….……...…10

10 (9) Posterolateral head corner squared (Fig. 5a); head dorsum completely covered with dense, feebly raised piligerous punctae (Figs. 5a, 9b)……...…***Neoponera carinulata***

– Posterolateral head corner round (Fig. 5b); head dorsum bearing shallow, and less dense piligerous punctae, so that it seems smooth (Fig. 5b)…….....***Neoponera oberthueri***

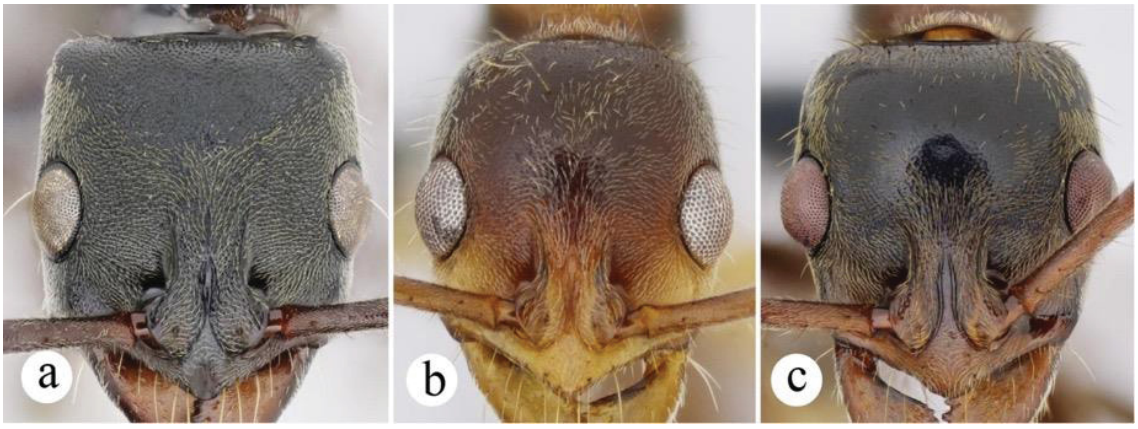


Fig. 5. Head shape and dorsal surface. **a.** Posterior head corner angulate, striate-rugose surface (*N. carinulata*, DZUP: DZUP549406); **b.** Posterior head corner round, smooth surface with shallow punctae (*N. oberthueri*, DZUP: DZUP549411); **c.** Posterior head corner less round than in b, and surface smother with micro, shallow punctae (*N. goeldii*, MEPN: MEPNINV37890).

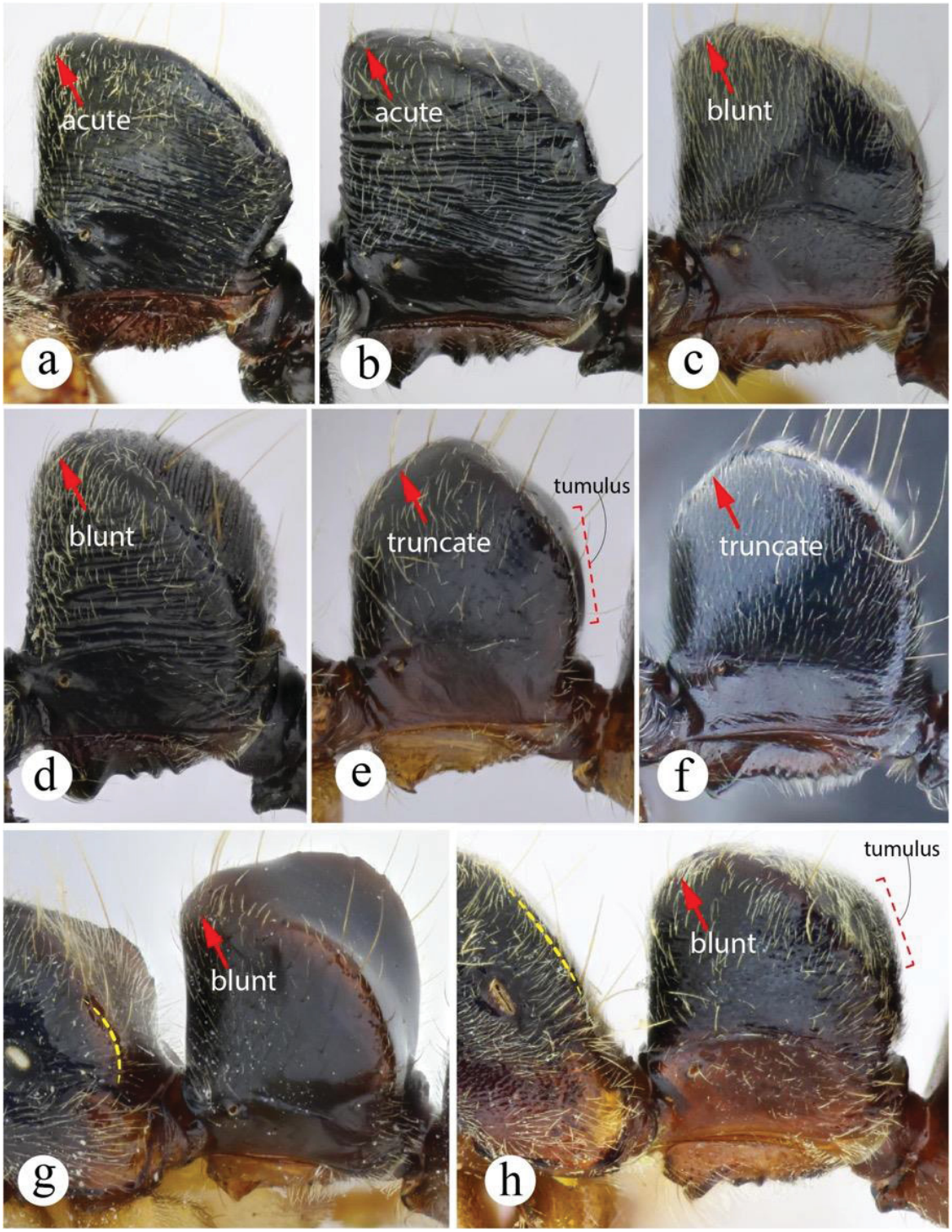


Fig. 6. Petiolar nodes in lateral view. **a.** *Neoponera rugosula* (DZUP: DZUP549517); **b.** *Neoponera striatinodis* (MEPN: GO-E-02-1-05); **c.** *Neoponera unidentata* (DZUP: DZUP549365); **d.** *Neoponera yasuni* (MEPN: MEPNINV28815), **e.** *Neoponera dejeani* sp. nov. (MPEG: ATPFOR1761); **f.** *Neoponera donosoi* (MEPN: CASENT0649894); **g.** *Neoponera recava* (UTIC: UTIC00212811). The yellow striped line on figures **g** and **h** shows variations of the propodeal carina.

11 (7) Anterior margin of petiolar node inclined posterad (Fig. 3e); head dorsum with shallow micro piligerous punctae giving the surface a smooth appearance (Fig. 5c)…… ***Neoponera goeldii***

– Anterior margin of petiolar node vertically straight (e.g., Figs. 6b, c, f); head dorsum **usually** densely covered with less shallow piligerous punctae (Fig. 5a)……12

12 (11) Meeting region of anterior and dorsal petiolar node margins relatively acute (Fig. 6, a, b)…….13

– Meeting region of anterior and anterodorsal petiolar node margins either blunt (Fig. 6c, d, g) or truncate (Fig. 6e, f)……..……14

13 (12) Posterolateral head corner striate (Fig. 7a); petiolar node almost completely covered with gross striae, its posterior margin crenulate (Fig. 6b)…….…***Neoponera striatinodis***

– Posterolateral head corner without striae (Fig. 7b); petiolar node usually bearing moderately impressed striae laterally only, its posterior margin without crenulae (Fig. 6a)……..…….……..……..***Neoponera rugosula***

14 (12) Posterior face of petiolar node concave, glabrous and smooth (Fig. 6g); posterolateral propodeal margin with salient, blunt carina (Fig. 6g)……..…….***Neoponera recava***

– Posterior face of petiolar node either convex or with a tumulus, glabrous and smooth or with piligerous punctae; posterolateral propodeal margin without carina, if this is present, not salient (Fig. 6h)……...…….....…15



Fig. 7. Posterolateral head corner. **a.** Striate (*N. striatinodis*, MEPN: GO-E-02-1-05); **b.** Smooth or punctate (*N. crenata*, MEPN: ATPFOR0059).

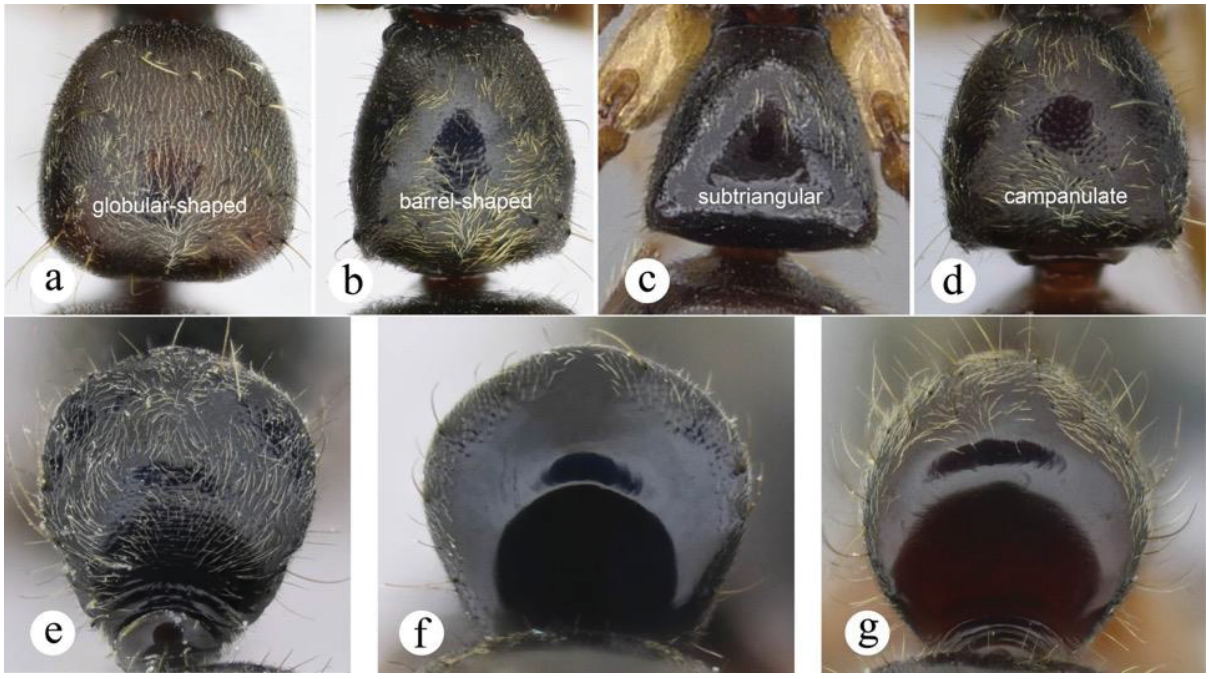


Fig. 8. Petiolar nodes in dorsal (a – d), and posterior (e – g) view. **a.** *Neoponera globularia* (MEPN: ATPFOR1967); **b.** *Neoponera cylindrinodis* (DZUP: DZUP549367); **c.** *Neoponera moesta* (PSWC: CASENT0249139); **d.** *Neoponera crenata* (MEPN: ATPFOR0059); **e.** *Neoponera antecurvata* (JTLC: JTL7095); **f.** *Neoponera carinulata* (MEPN: MEPN4296); *Neoponera fiebrigi* (UTIC: UTIC254630).

15 (14) Petiolar node completely covered with gross striae (Fig. 6d, 22d)……..... ……***Neoponera yasuni***

– Petiolar node lacking striae, if these are present, only feebly impressed and only on posterior face (Fig. 8e)……..…….16

16 (15) Posterior face of petiolar node clearly convex, with a tumulus (Fig. 6e, h)..…..…...17

– Posterior face of petiolar node weakly convex, without a tumulus……...…….18

17 (16) Posterior face of petiolar node with piligerous punctae and feebly impressed striae medially (Fig. 8e)……..……..…..***Neoponera antecurvata***

– Posterior face of petiolar node glabrous and smooth (Fig. 8f)……. ……..***Neoponera dejeani***

18 (16) Meeting region between anterior and anterodorsal margins of petiolar node truncate (Fig. 6f)……...……..……...***Neoponera donosoi***

– Meeting region between anterior and dorsal margins of petiolar node blunt (Fig. 6c)……...…….....***Neoponera unidentata***

Taxonomy

Synoptic list

In parentheses the known castes per species name: ☿ – worker; ♀ – queen; ♂ – male. The "?" indicates doubt about male-worker/queen association.

Neoponera antecurvata (Mackay & Mackay, 2010) (☿, ♀)

Neoponera carinulata (Roger, 1861) (☿, ♀)

= *N. carinulata azteca* Forel, 1899: 11 (♀) synonymy by Mackay and Mackay, 2010: 232)

= *N. carinulata gibbinota* Forel, 1909: 246 (♀) synonymy by Mackay and Mackay, 2010: 232

Neoponera cavinodis Mann, 1916 (☿, ♀, ♂)

Neoponera coveri (Mackay & Mackay, 2010) (☿)

Neoponera crenata (Roger, 1861) (☿, ♀, ♂)

= *N. pallipes* Smith, 1858: 98. (♀) homonym by same author & year

= *N. unidentata sulcatula* Santschi, 1919: 38. (☿) **syn. nov.**

= *N. crenata confusa* Santschi, 1921: 86. (☿) **syn. nov.**

= *N. mesonotalis* Santschi, 1923: 246. (☿) **syn. nov.**

= *N. crenata moesta subcarinata* Santschi, 1939: 313. (☿) **syn. nov.** (unavailable)

Neoponera donosoi (Mackay & Mackay, 2010) (☿, ♂)

Neoponera fiebrigi Forel, 1912 (☿, ♀, ♂)

= *N. crenata confusa lata* Santschi, 1921: 86. (☿) **syn. nov.**

= *N. latinoda* Mackay & Mackay, 2010: 468. (☿) **syn. nov.**

Neoponera globularia (Mackay & Mackay, 2010) (☿, ♀, ♂)

Neoponera goeldii Forel, 1912 (☿, ♀, ♂)

= *N. lydiae* Santschi, 1920: 361 (♀) synonymy by Mackay and Mackay, 2010: 362

Neoponera luteola (Roger, 1861) (☿, ♀)

Neoponera moesta (Mayr, 1870) (☿, ♀, ♂?)

= *N. stipitum* Forel, 1901: 348. (☿, ♀) synonymy by Mackay & Mackay, 2010: 468

Neoponera oberthueri (Emery, 1890) (☿, ♀, ♂)

Neoponera revaca (Mackay & Mackay, 2010) (☿, ♀)

Neoponera rugosula Emery, 1902 (☿, ♀, ♂)

= *N. laevinodis* André, 1902: 14. (☿, ♀) synonymy by Emery, 1911: 72

Neoponera striatinodis (Emery, 1890) (☿, ♀)

= *N. bakeri* Mann, 1916: 411 (☿, ♀) synonymy by Kempf, 1960: 391

= *N. rugosinodis* André, 1902: 15 (☿) synonymy by Mackay and Mackay, 2010: 533)

Neoponera unidentata (Mayr, 1862) (☿, ♀, ♂)

= *N. unidentata eburneipes* Wheeler & Bequaert, 1929: 29 (☿, ♀) synonymy by Brown, 1957: 232.

= *N. unidentata maya* Wheeler & Bequaert, 1929: 30 (☿) synonymy by Brown, 1957: 232.

= *N. unidentata trinidadensis* Wheeler & Bequaert, 1929: 30 (☿) synonymy by Brown, 1957: 232.

Neoponera cylindrinodis Troya **sp. nov.** (☿, ♀)

Neoponera dejeani Troya **sp. nov.** (☿, ♀, ♂)

Neoponera yasuni Troya **sp. nov.** (☿)

***Neoponera crenata* species-group differential diagnosis**

Worker and queen. Species in this group can be differentiated from other species-groups in *Neoponera* mainly by the combination of the following characters: 1) Notopropodeal suture vestigial or completely absent in almost all species, except for *N. donosoi* and *N. luteola* where the suture is weakly impressed (not grooved). This feature can also be nearly vestigial to weakly impressed in the *N. emiliae* group, like in *N. metanotalis* (Luederwaldt), but the petiolar node of these species is somewhat scale-shaped as seen in lateral view, while in species of the *N. crenata* group the node is highly variable departing from a block-shaped archetype, in lateral view. The notopropodeal suture in the remaining species of the genus is always moderately to well-impressed, usually forming a groove. 2) The mid clypeal region bears a usually blunt, subtriangular extension of the cuticle, sometimes feebly overhanging over the dorsointernal, proximal mandibular region (the edentate margin). Species in the *N. apicalis* group also have a similar structure, but the anterior margin is clearly less acute than that of species in the *N. crenata* group. The sole exception is *N. luteola* (Roger) where this structure is notably retracted posterad so that it does not overhang the mandibular dorsointernal margin, but it is discernible, however; 3) The mesosternal process may be somewhat stump-shaped to reduced, this is, significantly shorter than the metasternal process. A reduced to vestigial mesosternal process is also seen in most species of the *N. apicalis* group, except for *N. obscuricornis* (Emery) where it is well-developed, yet smaller than the metasternal process. In some species of the *N. aenescens* group, for example, in *N. carbonaria* (Smith), the mesosternal process is also quite reduced. This trait seems to show some level of plasticity among species-groups in *Neoponera*: sometimes vestigial and sometimes well-developed but always smaller than its homolog on the metasternum. In species of the *N. crenata* group, however, this process varies little, always from vestigial to reduced. This makes it a relatively good character for group diagnostics; 4) The metasternal process is fang-shaped, composed of acute-tipped, relatively narrow lobes with their internal margins running parallel or approximately so, and also usually quite flattened anteroposteriorly, especially on the distal half. Other species in the genus, like those in the *N. apicalis* and *N. foetida* groups also show a similar configuration of this structure, but never as described above. For example, the metasternal process of species in the *N. foetida* group is less flattened anteroposteriorly and the lobes are not as narrow as those in species of the *N. crenata* group. While in species of the *N. apicalis* group, although the metasternal lobes are flattened, the space between them is always broader than the width of each lobe, and the lobes themselves are not as spiny as those of the species in the *N. crenata* group.

Male. It is hard to diagnose the male caste of *Neoponera* species and *Neoponera* species-groups based only on external visible characters, i.e. without dissecting the genitalia. Despite the abundant body features which are predominantly represented by integumental sculpture variations, it is difficult to find a pattern characterizing populations of a given species because we noted variations in their morphology. With the exception of the genitalia, virtually all examined characters vary intraspecifically, which is not the case for the worker and queen castes whose morphology is significantly more stable. More male material will be needed in futures studies, not only of *Neoponera* but also of many other ponerine genera for which the male caste is scantly represented at the specific level. This will probably be of aid in finding a light out of the tunnel in the male taxonomy of ponerine ants.

This caste is known from nine species in the *N. crenata* group: *N. cavinodis*, *N. crenata*, *N. donosoi*, *N. fiebrigi*, *N. goeldii*, *N. moesta*, *N. oberthueri*, *N. rugosula*, and *N. unidentata*. We here examined male specimens of *N. fiebrigi*, *N. goeldii*, *N. globularia* (previously unknown), *N. unidentata*, and *N. dejeani* sp. nov. which we could confidently associate with their respective worker and queen castes as they belonged from the same nest series. We also found non-associated males in *N. crenata* and and *N. moesta*. Since these species are highly similar, however, as we describe under their respective species treatments, we cannot provide for now re-descriptions, nor diagnoses for them. Mackay and Mackay (2010) described and re-described the male caste for all the above species. Yet, those of *N. crenata* and *N. moesta* require further validation (see details under respective species treatment).

Although few males were identified in this species-group, we have managed to find the following features which can be used in combination to distinguish this caste from other castes in *Neoponera*: 1) Eyes relatively large, longer than half head length. This is similar only to known males in the *N. apicalis* group, for example, in *N. apicalis* (Latreille), and in *N. rostrata* Emery, where the eyes are also relatively large. In the remaining known *Neoponera* males, the eyes are either smaller than half head length or about as long as that distance; 2) In dorsal view, the propodeum always shows a well-developed, longitudinal groove anteromedially, sometimes bordered by two straight, well-developed carinae running posterad, parallel to each other (Fig. 12a). In examined males from six out of the seven *Neoponera* species-groups, a groove with differing depth degree is usually present at the anterior propodeal margin, but only on the known males of the *N. crenata* group the groove extends posterad, sometimes near the dorsal margin of

the posterior propodeal carina (next character); 3) The posterior face of the propodeum bears a usually feebly impressed carina, that runs uninterrupted and converges dorsally. This structure is also present in males of the *N. apicalis* group and in *N. commutata* (Roger) but in these taxa the carina is clearly more salient from the cuticle, and usually surrounded by rugae. Males of the *N. crenata* group lack rugae or strongly impressed striae laterally on the propodeum; 4) The structure of the mesosternal and metasternal processes is as described for the worker caste, but the lobes of each of these structures are almost touching each other; 5) Smooth subpetiolar process grooved, bounded by two external raised longitudinal carinae, and lacking a medial longitudinal carina. In all known males of the other species groups this groove is either present or absent, and the raised external carinae rarely form a deep groove as described here. If the groove is present, then the subpetiolar process has striae or rugae, or a medial longitudinal carina; 6) Discoidal cell of the forewing is rectangular-shaped, with veins M and 1m-cu straight and usually of about the same length; vein 2M is always reduced or very small, at least three times smaller than vein Rs+M; veins Cu and Rs+M horizontally straight and parallel (Fig. 12e). In all other known *Neoponera* males the discoidal cell is differently shaped. Only some examined species in the *N. foetida* group, like those of *N. villosa* (Fabricius) show a similarly shaped cell. However, in these species vein M is clearly longer than vein 1m-cu.

Species accounts

Following, we provide diagnoses and comments about the morphology of all known species including informative and relatively easy to discern traits so as to facilitate the distinction of a given taxon when compared to similar taxa within the *N. crenata* group. The reader can follow Troya and Lattke (2022) to identify *Neoponera* species-groups. All diagnoses contain some traits, or a combination of them, not previously found in the literature. Complete descriptions are provided only for the new taxa and previously unknown castes. The reader can follow Mackay and Mackay (2010) who described the male caste of *N. cavinodis*, *N. donosoi*, *N. fiebrigi*, *N. goeldii*, *N. moesta* (caution, see notes under that species), *N. oberthueri*, *N. rugosula*, and *N. unidentata*. M&M also redescribed the male of *N. crenata* (caution, see notes under that species), as well as the worker and queen castes of all previously known species.

Neoponera antecurvata (MacKay & MacKay, 2010)

Figs. 9: a – c (☿); 29: b (distribution).

Pachycondyla antecurvata MacKay & MacKay, 2010: 201. Figs. 331, 332. ☿ holotype, Costa Rica, Heredia, Est. Biol. La Selva, 5-150 m., 12°26'N, 84°01'W, INBio-OET, PROJECT ALAS, 3.xi.1994, FVK/32/01-40, canopy fogging sample, (INBC: INB0003207598) [not examined]; ☿ paratype, same data as for holotype, except: 19.x.1994, FOT/26/01-40, (CWEM: INB0003207503) [not examined]; "additional paratypes": Costa Rica, near Puerto Viejo, 19-26.vi.1995, D.R. Perry [leg.], 3 km S Puerto Viejo, 10°26'N, 84°01'W, 22.iii.1980, H.A. Hespenheide [leg.]; Puerto Viejo, 15 May 1974, R. L. Jeanne [leg.], (LACM) [not examined]. Note: AntWeb image (link) of non-type ☿ (UTEP: UTEPENTO3513), with same collection data as the paratype from "3 km S Puerto Viejo", identified by W. Mackay [examined].

Combinations. In *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species. Bezděčková et al., 2015: 123; Pazmiño-Palomino & Troya, 2022: 9.

Worker and queen diagnosis. Anterior margin of head straight, occipital corner relatively angulate (Fig. 9b); distance from anterior eye margin to mandibular insertion equal to, or slightly longer than maximum eye length (Fig. 9b, 4b); malar carina not reaching anterointernal eye margin; notopropodeal suture in workers faintly impressed, usually better discernible laterally; propodeum always bearing weakly to strongly impressed striae laterally (9a); petiolar node with carinate margin laterally, posterior face clearly convex, bearing a tumulus (Fig. 6h), and horizontal striae medially (Fig. 8e), this latter only seen in some Amazonian populations; in lateral view, anterodorsal petiolar node margin blunt or convex (Fig. 6a), never angulate or acute; prora keel-shaped in lateral view, laterally compressed, bunt tip directed anteroventrad (Fig. 6h).

Worker. Measurements (n= 12): HW: 1.38-1.59; HL: 1.53-1.76; EL: 0.39-0.47; SL: 1.44-1.67; WL: 2.19-2.65; PrW: 1.09-1.33; MsW: 0.65-0.86; MsL: 0.56-0.73; PW: 0.9-1.04; PH: 0.82-0.98; PL: 0.66-0.82; GL: 2.34-3.67; A3L: 1.03-1.27; A4L: 0.91-1.1; A3W: 1.34-1.59; A4W: 1.34-1.59; TLa: 6.34-7.55; TLr: 6.72-8.82. **Indices.** CI: 88.1-95.12; OI: 26.94-31.58; SI: 99.14-107.89; MsI: 105.0-133.33; LPI: 75.79-91.3; DPI: 112.5-147.06.

Queen (first description, AntWeb image CASENT0649083 link)**.** Measurements (n = 2): HW: 1.76-1.8; HL: 1.8-1.98; EL: 0.49-0.57; SL: 1.67-1.76; WL: 2.94-3.31; PrW: 1.55-1.59; MsW: 1.31-1.35; MsL: 1.55-1.59; PW: 1.22-1.22; PH: 1.1-1.14; PL: 0.9-0.9; GL: 3.35-3.43; A3L: 1.47-1.51; A4L: 1.27-1.43; A3W: 1.8-1.88; A4W: 1.8-1.84; TLa: 8.53-8.96; TLr: 8.98-9.61. **Indices.**

CI: 90.72-97.73; OI: 27.27-32.56; SI: 95.35-97.73; MsI: 84.21-84.62; LPI: 78.57-81.48; DPI: 136.36-136.36.

Head. Frontal view: subquadrate. Mandible triangular, longer than wide, distal region slightly bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with ten to twelve teeth, usually decreasing in size, sometimes interspersed with five to eight denticles, basal margin edentate. Prementum usually with well-developed transverse dome. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, with dorso-ventrally relatively flat, subtriangular-shaped, usually acute, extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina reaching, but not exceeding ocular mid-length. Torular lobe subtriangular, covering approximately 80% of acetabulum of antennal socket, posterolateral margin straight. Malar carina well-developed, not reaching anterointernal eye margin. Eye suboval, maximum length one-fourth to one third head length, convex, slightly globose, exceeding lateral margin of head, placed at cephalic mid-length. Anterior ocellus maximum length subequal to that of posterior ocelli. Ocelli approximately equidistant to each other. Distance from posterior ocellar margin to posterior margin of head roughly 1.5 times apical scape width. Distance between anterior and posterior ocelli approximately 3 times anterior ocellus maximum length. Posterior margin of head straight to slightly concave. Occipital carina reduced. Scape, when pulled posterad, exceeding posterior margin of head by approximately three times apical scape width. **Mesosoma**. Lateral view: Dorsal margin straight to slightly convex. Pronotum carinate, with carina slightly projecting from cuticle. Anterior subalar area approximately as broad as tegular maximum width. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum. Metanotal trough weakly impressed. Posterolateral margin of propodeal declivity slightly rounded to barely carinate, not forming crenulae. Propodeal spiracle slit shaped. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth but bearing micropunctae. Dorsal view: mesoscutum about as long as broad, close to twice length of mesoscutellum. Parapsidal lines weakly to well impressed, slightly divergent. Transscutal sulcus well-developed. Scutoscutellar sulcus present, slightly arched posterad, shallowly impressed, with scrobiculate sculpture, not separating mesoscutum from mesoscutellum.

Mesoscutellum subrectangular, flat dorsally. Metascutellum poorly developed, not clearly discernible dorsally, surface even, slightly flat. Posterior face of propodeal declivity mostly flat. Propodeal lateral margins parallel at base, convergent dorsad. Ventral view: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process poorly developed, tooth-shaped, internal margins of lobes slightly convergent, not parallel, relatively flattened anteroposteriorly, inclined posterad ca. 20–30 degrees in lateral view, space between lobes approximately equal to width of each. Metasternal process well-developed, inclined posterad, 20°-30° in lateral view, fang-shaped, flattened anteroposteriorly, apex slightly higher than half height of metacoxal internal margin, space between lobes approximately equal to- or shorter than width of each, internal margins running parallel. Metasternal process external margins usually convergent. **Legs**. Mesofemur thickened medially, feebly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora flattened roughly on distad half, surface even without groove. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about three times shorter than posterior spur. Pretarsal claw arched, unarmed (without accessory teeth on surface). Arolium present, roughly 0.5 times length of pretarsal claw. Wings. Unknown. **Petiole**. Lateral view: Petiolar node with straight anterior margin and convex posterior margin, anterior margin feebly higher than posterior margin, middorsal margin convex, highest point anterior to nodal longitudinal midline, anterodorsal margin slightly convex to feebly flattened, posterior face with feebly salient tumulus. Subpetiolar process subtriangular, with keel-shaped, grooved anterior cusp, followed by posterior slightly straight dome which bears transverse, usually three to four, strong striae, posterior region of dome bearing feebly impressed striae. Lateral projection of anteroventral nodal carina well-developed, with acute to slightly blunt tip moderately bent dorsad. Lateral nodal carina strongly impressed, slightly arched ventrad. Dorsal view: Anteroventral nodal carina incomplete, feebly concave medially. Node of petiole proportionally shorter and broader than in worker. **Gaster**. Lateral view: Prora well-developed, with blunt to acute tip projecting ventrad. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin relatively angled. Anterodorsal margin of tergum of A3 flat to slightly convex. Cinctus weak. Dorsal view: Tergum of A3 approximately equal in length to A4. Posterior dorsum of epipygium completely smooth. Color. Overall body black, mandibles, legs and antennae black to ferruginous black. **Pilosity**. Body with

moderately abundant, flexuous, whitish to golden, erect and suberect hairs. Appressed pubescence abundant, mostly composed of tiny hairs so that integument is easily discernible. Most erect hairs on body dorsum approximately equal to maximum eye length. Scape pilosity mostly composed of scattered erect hairs and appressed pubescence, erect hairs approximately equal in length to apical scape width. Meso- and metatarsi bearing stiff setae (ventrally only) interspersed with suberect and appressed fine setae. Posterior ventrolateral margin of hypopygium (just next to base of sting) bearing scattered flexuous hairs, usually longer than eye maximum length. Posterior dorsum of epipygium surrounded by 20–30 long flexuous hairs, longer than eye maximum length. **Sculpture**. Integument mostly polished, with abundant, shallowly impressed piligerous punctures, except for head dorsum where punctures are more densely and strongly impressed. Striae on head dorsum absent, sometimes finely striated ventrally, mandibles usually finely striate dorsally, mesosoma bearing shallow to strongly impressed striae laterally on metapleuron and propodeum, sometimes feebly impressed on anepisternum. Striae on petiolar node feebly impressed on median posterior face.

Male. Unknown.

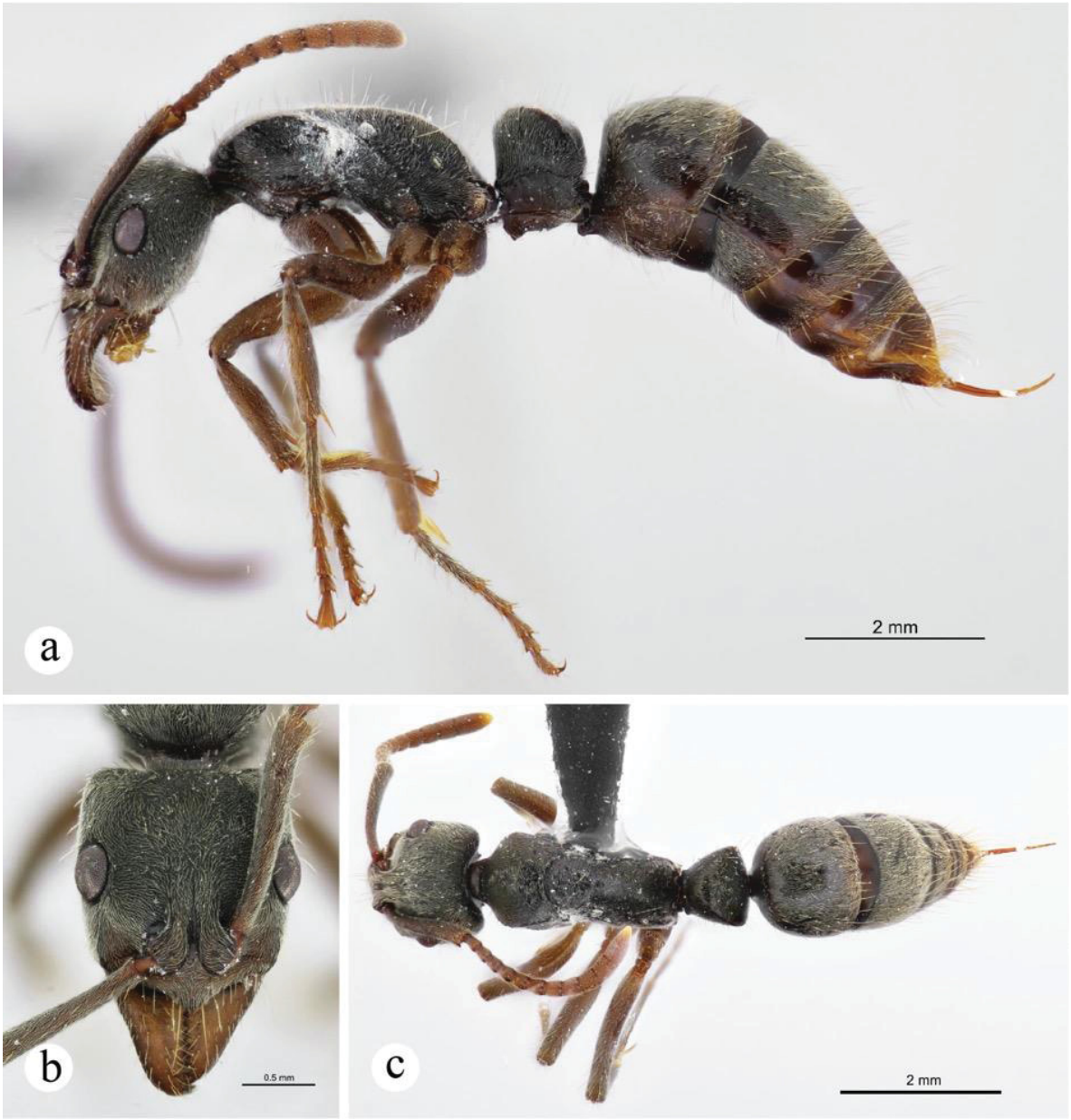


Fig. 9. *Neoponera antecurvata*. ☿ (JTLC: JTL7095), Honduras: Atlántida. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Comments. *Neoponera antecurvata* is a medium-sized species in the *N. crenata* group (Fig. 26; ☿: TLa = 6.34 – 7.55 mm; ♀: 8.53 – 8.96 mm). It shows a relatively homogeneous morphology across its distribution range, with no "extreme" forms departing from its morpho-ground plan. The material examined shows low size variation. Workers and queens of *N. antecurvata* can only be confused with three species within the *N. crenata* group: *N. unidentata*, *N. rugosula* and *N. yasuni* sp. nov. None of them, however, have the following traits combined: relatively angulate posterolateral head corners, a petiolar node with convex posterior face, and a truncate to convex anterodorsal nodal margin. Among them, *N. yasuni* sp. nov. is possibly most similar to *N. antecurvata* and maybe the closest phylogenetically. The easiest way to distinguish these two species is by examining their petiolar node which is completely striated in *N. yasuni* sp. nov., while in *N. antecurvata* only the mid region of the posterior face bears feebly impressed striae. This trait, however, has only been seen in Amazonian populations. Together these four species share a great portion of their morphospace which is presumably suggestive of recent lineage divergence. A fifth species, *N. carinulata*, could possibly be confused with *N. antecurvata*. These are easily distinguished from each other by examining the petiolar node: in *N. carinulata* the dorsalmost margin is convex, relatively acute, and is placed at- or posterior to nodal longitudinal midline, while the nodal dorsal margin in *N. antecurvata* is mostly flat.

N. antecurvata has been collected between an elevational range of 10 m to approximately 2300 m, this latter is very rare though. Records include tropical humid regions of the Atlantic forests of southern North America (Mexico: Veracruz), Central America, up to southeastern Amazonia of Peru, and southern Amazonia in Brazil (Fig. 26b). No records have been found for Venezuela, Bolivia and Colombia but it is likely it occurs there.

Natural history notes. Although not many specimens have been identified (see AntWeb, Antmaps, and material here examined), this is an apparently common arboreal form, usually collected through fogging, pitfall and arboreal Malaise, and prefers inhabiting mature, well-preserved areas. Before Mackay and Mackay (2010) recognition of its species status, *N. antecurvata* was probably confused with its similar form *N. unidentata*. Within the examined material we found a number of specimens identified as *N. unidentata* that actually represented *N. antecurvata*. J. Longino collected workers, queens and pupae of this species inside an *Erythrina* (Fabaceae) stem at a streamside of a mature wet forest in north eastern Honduras (AntWeb). The

type specimens were collected from a Malaise trap in *Dipteryx* (= *Coumarouna*) *oleifera* (Fabaceae) and on foliage of *Byttneria aculeata* (Malvaceae) (Mackay & Mackay 2010), commonly called choibá, a native tree from the wet forests of Nicaragua to Colombia (Gómez and Garcés 2013). A. Troya collected a worker at ca. 2300 m elevation from tepui-like forests at Cordillera del Cóndor, a mountain range extending from southern Ecuador to western Peru which is composed of mature forests lying amidst the tropical Andes and Amazonia. See additional notes on Longino (2010).

Material examined. 23☿, 4♀. **BRAZIL – Amazonas:** • 1☿; 14 Km W Eduardo Gómez International Airport, Manaus; -3.02, -60.17; alt. 20m; Adis, J. leg.; photo-eclector; (MEPN). • 1☿; Alvarães; -3.2278, -64.8014; alt. 65m; 1994-06-11; Gorayeb, I.; Silveira, O. leg.; arboreal Malaise; (MPEG). • 1♀; Coari; -3.8923, -63.4557; alt. 34m; 2003-09-24; Vasconcelos, H. leg.; beating; (INPA). • 1♀; Mamirauá; -3.0333, -64.85; alt. 51m; 1993-09-21; Gorayeb, I.; Silveira, O. leg.; Malaise; (MPEG). – **Mato Grosso:** • 1☿; 85km W of Alta Floresta, rio dos Apiacás; -9.9, -56.9; alt. 209m; 2017-09-01; Lopes, F. J. A.; Araujo, C. B. leg.; (DZUP). • 1☿; Sinop; -11.8592, -55.5103; alt. 382m; 1976-02-01; Roppa, O. leg.; (MZSP). • 1☿; Utiarití; -13.0167, -58.2667; alt. 377m; 1966-11-09; Lenko, K., Pereira leg.; (MZSP). – **Pará:** • 1☿; Tucuruí; -3.7655, -49.6702; alt. 35m; 1929-03-02; Overal, W. leg.; (MPEG). • 1☿; Xingu river, right shore; -3.8519, -51.8523; alt. 173m; 2001-03-05; Santos, R.; Dias, J. leg.; Malaise; (MPEG). **COSTA RICA – Guanacaste:** • 1☿; Area de Conservacion Guanacaste, Sector Pailas, Pailas Dos; 10.764, -85.335; alt. 828m; 2014-08-14; Janzen, D; Hallwachs, W. leg.; Malaise; (CBG). – **Heredia:** • 1☿; La Selva, 3 kilometers S of Puerto Viejo; 10.4333, -84.0167; alt. 56m; 1980-11-22; Hespenheide, H. A. leg.; (UTEP). – **Puntarenas:** • 1☿; Sirena, Corcovado National Park; 8.4833, -83.6; alt. 10m; 1982-09-07; Longino, J. leg.; hand collected; (JTLC). • 1☿; [no locality given]; 9.82, -83.7508; alt. 929m; Nevermann, F. leg.; (MZSP). **ECUADOR – Orellana:** • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-12; Erwin, T.; et al. leg.; fogging; (MEPN). • 1☿; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-07-03; Erwin, T.; et al. leg.; fogging; (MEPN). • 1☿; Parque Nacional Yasuní, Guiyero, 4 km W Comunidad de Guiyero; -0.6258, -76.495; alt. 207m; 2008-05-21; Troya, A. leg.; fogging; (MEPN). • 1☿; Parque Nacional

Yasuní, Guiyero, a 1.5 km del centro de la comunidad Waorani; -0.608, -76.456; alt. 186m; 2008-05-24; Troya, A. leg.; fogging; (MEPN). – **Zamora Chinchipe:** • 1☿; Paquisha alto, Hito 2, 15 Km SE Fruta del Norte, Cordillera del Cóndor; -3.9003, -78.4829; alt. 2325m; 2008-03-15; Troya, A. leg.; fogging; (MEPN). **HONDURAS – Atlántida:** • 5km S Tela; 15.7297, -87.4518; alt. 70m; 2010-06-16; Longino, J. leg.; hand collected; (JTLC). • 1♀; 5km S Tela; 15.7297, -87.4518; alt. 70m; 2010-06-16; J. Longino leg.; search; (JTLC). • 1☿; 5km S Tela; 15.7297, -87.4518; alt. 70m; 2010-06-16; Longino, J. leg.; hand collected; (JTLC). **MEXICO – Veracruz:** • 4☿; Las Hamacas, 17 Km N Santiago Tuxtla; 18.62, -95.3; alt. 200m; 1953-08-26; Wilson, E. O. leg.; (MZSP). • 1☿; Palma Sola; 19.769, -96.43; alt. 12m; Reyes, P. leg.; (MZSP). • 1☿; Pueblo Nuevo, near Tetzonapa; 18.6, -96.6; alt. 200m; Wilson, E. O. leg.; (MZSP). **PANAMA – Canal Zone:** • 1☿; Barro Colorado Island; 9.15, -79.8333; alt. 151m; Banks, N. leg.; (MZSP).

Geographic range. Mexico (Veracruz), Guatemala, Honduras, Costa Rica, Panama, Ecuador, Peru, Brazil (Amazonas, Minas Gerais, Mato Grosso).

Neoponera carinulata (Roger, 1861)

Fig. 27: a (distribution)

Ponera carinulata Roger, 1861: 4. ♀ holotype, Brazil, Minas Gerais, St [São] João del Rey, (MNHU) [not examined]; ☿ lectotype [of *N. carinulata gibbinota* Forel, by designation of Mackay and Mackay, 2010: 232], Guatemala, (AntWeb: CASENT0907243, link) [image examined].

Combinations. In *Pachycondyla*: Roger, 1863:18; Brown, 1995:303; In *Neoponera*: Emery, 1901:47

Status as species: Roger, 1863: 18; Mayr, 1863: 447; Mann, 1916: 412 (redescription); MacKay & MacKay, 2010: 232 (redescription)

Senior synonyms. *Neoponera carinulata Azteca*: Mackay & Mackay, 2010: 232; *Neoponera carinulata gibbinota*: Mackay & Mackay, 2010: 232.

Worker and queen diagnosis. Head quadrate, posterior head margin straight, and posterolateral head corner noticeably angulate, this is better discernible in posteroventral view; notopropodeal suture usually completely absent; anterior propodeal margin weakly raised dorsally; middorsal margin of petiolar node relatively acute and usually placed slightly posterad to nodal

longitudinal midline, sometimes at midline; posterior face of petiolar node usually truncate tumulus in lateral view, and always completely glabrous with polished surface, except marginally where piligerous punctae are present; prora subtriangular in ventral view, broadened basally and usually acute apically; dorsoanterior margin of tergite of A3 broadly convex.

Worker Measurements (*n* = 20): HW: 1.31-1.55; HL: 1.41-1.61; EL: 0.34-0.45; SL: 1.27-1.55; WL: 1.97-2.49; PrW: 0.98-1.2; MsW: 0.59-0.78; MsL: 0.45-0.78; PW: 0.84-1.2; PH: 0.91-1.12; PL: 0.66-0.82; GL: 2.03-3.27; A3L: 0.75-1.08; A4L: 0.72-0.94; A3W: 1.31-1.67; A4W: 1.31-1.59; TLa: 5.5-6.86; TLr: 6.31-8.02. **Indices.** CI: 86.08-97.44; OI: 25.88-31.43; SI: 94.52-111.76; MsI: 86.84-140.91; LPI: 68.0-83.33; DPI: 120.0-147.5.

Queen Measurements (*n* = 3): HW: 1.47-1.57; HL: 1.59-1.65; EL: 0.45-0.51; SL: 1.41-1.47; WL: 2.51-2.71; PrW: 1.25-1.31; MsW: 1.1-1.2; MsL: 1.37-1.47; PW: 1.02-1.18; PH: 1.08-1.22; PL: 0.73-0.86; GL: 2.73-3.71; A3L: 0.98-1.22; A4L: 0.95-1.04; A3W: 1.59-1.73; A4W: 1.55-1.67; TLa: 6.77-7.43; TLr: 7.57-8.88. **Indices.** CI: 92.31-95.06; OI: 30.56-32.47; SI: 93.51-95.95; MsI: 80.6-83.82; LPI: 65.0-72.41; DPI: 138.1-138.89.

Male. Unknown.

Comments. *Neoponera carinulata* is a medium-sized species in the *N. crenata* group (image, link); ☿: TLa = 5.5 – 6.86 mm; ♀: 6.77 – 7.43 mm). Its overall morphology is relatively homogeneous across its range. Slight variations are principally evidenced on the petiolar node, with some workers from Amazonian Ecuador and French Guiana showing a reduced to virtually absent tumulus on the posterior nodal face. In lateral view, the node in queens is always narrower and proportionally higher than in workers. The material we examined shows low size variation (see measurements).

Neoponera carinulata is easily identifiable among *Neoponera*, the combination of its cephalic features plus the nodal structure is normally enough to differentiate it from other taxa within the genus. Few species are very similar to *N. carinulata* (see comments under *N. antecurvata*), but probably the most similar is *N. oberthueri* which also has a very similar nodal shape, and whose populations are sympatric with *N. carinulata* in a number of regions in South America (Figs. 27 a, b). *Neoponera oberthueri*, however, is clearly smaller, and its head is rounded posterolaterally.

The elevational record of *N. carinulata* extends from 6 m to near 1200 m. Longino (2010) reports a record from Cordillera de Talamanca at 1300 m. This species has been collected mostly in mature, well-preserved lowland and mountainous, moist to wet tropical forests, but also in few occasions on agroforestry systems. A few records belong from dry to deciduous forests of the Pacific of Ecuador. This species is broadly distributed from southern Mexico (Veracruz), to Central America, to some regions of the Chocó-Darién at the Pacific side of South America, to a number of sites in the Brazilian Cerrado and Atlantic forest, as well as in numerous Amazonian regions (Fig. 24a). Interestingly, all the records either from examined material and from the literature illustrate a somewhat disjunct distributional pattern in South America, with few populations at some Atlantic Forest sites, and most populations ranging from a number of habitats including the Amazon, but no records thus far from the Brazilian states of Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Toncantins, Goiás, Matto Grosso do Sul, as well as no records from Paraguay. A large proportion of these political regions is composed of xerophilous, seasonally dry to semi-dry savannas, orchard-like, and gallery forests which comprise three major phytogeographical domains, the Chaco, Cerrado and Caatinga, together forming what is biogeographically known as the Eastern South American Dry Diagonal (Neves et al. 2015, Luebert 2021) which is usually acknowledged as of the main barriers structuring species distribution in South America, south of the equator (Luebert 2021).

Natural history notes. See Longino (2010) and Mackay and Mackay (2010). We coincide with Longino (1999) in describing *N. carinulata* as a common arboreal forager, which together with *N. unidentata* is among the commonest *Neoponera* obtained through canopy sampling methods. *N. carinulata* has been collected through the ADMAC, ALAS, and LLAMA projects led by J. Longino, in some Central American regions. Specimens and nests have been found inside live and/or death stems, logs, tree-trunks, shrubs, and epiphytes belonging to species like *Batocarpus* sp., *Brosimum* sp. ((Moraceae), *Licania* sp. (Chrysobalanaceae), *Myriocarpa* sp. (Urticaceae), *Passiflora pittieri* (Passifloraceae), *Stryphnodendron* sp. (Fabaceae), *Virola koschnyi* (Myristicaceae), among others.

Material examined. 69☿, 10♀. **BRAZIL – Acre:** • 1☿; Fazenda Experimental Catuaba; -10.0667, -67.6167; alt. 214m; 2016-12-07; (DZUP). • 2☿; Parque Nacional da Serra do Divisor; -7.4494, -73.6602; alt. 235m; 2016-11-15; Feitosa, R.; et al. leg.; (DZUP). – **Amazonas:** • 1☿;

Manaus; -3.1167, -60.0167; alt. 65m; (MZSP). • 1♂; Manaus ZF 3, Km Fazenda Estação Florestal; -3.1167, -60.0167; alt. 55m; 1983-03-23; Harada, A. leg.; hand collected; (MZSP). • 1♂; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9333, -59.9667; alt. 106m; 1982-08-04; Harada, A. leg.; (INPA). – **Bahia:** • 1♂; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1999-10-01; Delabie, J. H. C. leg.; (DZUP). • 1♂; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.7659, -39.2159; alt. 53m; 2002-08-01; Santos, J. R. M. leg.; (CPDC). • 1♂; Belmonte; -15.8, -38.8; alt. 6m; 1980-04-10; Benton, F. leg.; (CPDC). • 1♀; Camaçã; -15.4203, -39.4961; alt. 160m; 1991-03-15; (CPDC). • 1♂; Ilhéus, Cepec; -14.7979, -39.0375; alt. 8m; 1988-02-01; Majer, J. leg.; (CPDC). • 1♀; Ilhéus, Ceplac; -14.7979, -39.0375; alt. 8m; 1992-09-03; Casimiro, A. leg.; (CPDC). • 1♂; Ilhéus, Ceplac; -14.7979, -39.0375; alt. 8m; 1992-09-03; Casimiro, A. leg.; (CPDC). • 1♂; [no locality given]; -14.59, -39.28; alt. 102m; 1967-09-19; (CPDC). – **Mato Grosso:** • 1♂; Xingu river; -10.7774, -53.1017; alt. 271m; (MZSP). – **Minas Gerais:** • 1♂; Dionísio; -19.8134, -42.6881; alt. 324m; 2007-03-01; Sanchez; et al. leg.; (DZUP). – **Pará:** • 1♂; Cuiú-Cuiú; -5.9167, -56.5667; alt. 161m; 2018-06-18; Siqueira, E. leg.; arboreal pitfall; (MPEG). • 1♂; Floresta Nacional de Saracá-Taquera; -1.85, -56.45; alt. 70m; 2016-08-25; Feitosa, R. M.; et al. leg.; (DZUP). • 1♂; Parque Nacional Amazonia; -4.3799, -56.781; alt. 99m; 1978-11-13; Overal, W. leg.; (MPEG). • 1♂; Porto Trombetas; -1.46, -56.37; alt. 35m; 2004-08-03; Santos, J. leg.; (CPDC). • 1♂; Xingu river, right shore; -3.8519, -51.8523; alt. 173m; 2001-02-23; Santos, R.; Dias, J. leg.; Malaise; (MPEG). • 1♂; Área de Pesquisa Ecológica do Guamá; -1.4647, -48.4512; alt. 10m; 1969-12-05; Rosa, N. leg.; (MZSP). • 2♂; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; (MZSP). • 1♂; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-12-05; Rosa, N. leg.; (MPEG). – **Rio de Janeiro:** • 2♀; Corcovado; -22.95, -43.2; alt. 650m; 1958-09-08; Alvarenga, M. leg.; (MZSP). – **Rondônia:** • 1♂; Ouro Preto do Oeste; -10.7165, -62.2569; alt. 243m; 1985-03-25; Torres, M. leg.; Malaise; (MPEG). • 3♂; Área Abunã; -9.6333, -65.4333; alt. 96m; 2013-04-28; Mazão, G. R.; Mendoça R. T. leg.; (DZUP). • 1♂; Área Mutum; -9.5833, -65.0333; alt. 85m; 2010-02-27; Silva, R.; Feitosa, R. leg.; Winkler; (MPEG). – **Roraima:** • 1♂; Posto Xitei - Xidea, Area Indígena Yanomami; 2.6, -63.8667; alt.

783m; 1998-12-05; Torres, P. leg.; pitfall; (INPA). **COLOMBIA – Antioquia:** • 1♂; Reserva Cañón del Río Claro; 5.901, -74.8567; alt. 290m; 2006-10-30; Guerrero, R. leg.; (MEPN). **– Chocó:** • 1♂; Estación Silvicultura al Bajo Atrato; 7.0406, -77.3378; alt. 149m; 1992-07-01; Mendoza, L. leg.; (MEPN). **– Risaralda:** • 1♂; Puerto de Oro; 5.2995, -75.8869; alt. 1500m; 1991-09-01; Fernández, F. leg.; (ICN). **– Vaupes:** • 1♂; Estación Biológica Caparú; 1.0756, -69.5136; alt. 96m; 2003-04-25; Benavides, L. leg.; (ICN). **COSTA RICA – Cartago:** • 1♀; Centro Agronómico Tropical de Investigación y Enseñanza; 9.8904, -83.6557; alt. 614m; Novermann, F. leg.; (MZSP). • 5♂; Centro Agronómico Tropical de Investigación y Enseñanza; 9.8904, -83.6557; alt. 614m; Novermann, F. leg.; (MZSP). **– Cártago:** • 3♂; Centro Agronómico Tropical de Investigación y Enseñanza; 9.8904, -83.6557; alt. 614m; Novermann, F. leg.; (MZSP). **– Osa Peninsula:** • 1♂; Osa Península, 2.5 Mi SW Rincón; 8.6987, -83.4845; alt. 40m; 1967-03-06; Thomas, E. leg.; (QCAZ). **– San José:** • 3♂; San José; 9.9294, -84.0903; alt. 1171m; Schmidt, H. leg.; (MZSP). **ECUADOR – Guayas:** • 1♂; Reserva Manglares Churrute, Cerro Cimalón; -2.53, -79.71; alt. 80m; 2013-07-22; Troya, A. leg.; hand collected; (MEPN). **– Morona Santiago:** • 1♂; Reserva Wisui, Cordillera del Cutucú; -2.1, -77.7333; alt. 657m; 2008-02-28; Simbaña, M. A. leg.; Malaise; (MEPN). **– Orellana:** • 1♂; Parque Nacional Yasuní, Guiyero, a 1.5 km del centro de la comunidad Waorani, Bosque de Nambay; -0.608, -76.456; alt. 186m; 2008-05-24; Troya, A. leg.; fogging; (MEPN). **– Pichincha:** • 1♀; ENDESA Forest Reserve; 0.13, -79.05; alt. 600m; 2003-12-05; Wild, A. leg.; (UTIC). **FRENCH GUIANA – Cayenne:** • 1♀; Base Vie; 5.1667, -52.65; alt. 60m; 2000-06-01; Durou, S.; et al. leg.; (CPDC). • 1♂; Nouragues Natural Reserve; 4.0882, -52.6801; alt. 125m; 2006-03-01; Dejean, A. leg.; (CPDC). • 1♀; Petit Saut; 5.0667, -53.0333; alt. 67m; 2003-03-01; Orivel, J. leg.; (CPDC). **GUATEMALA – Suchitepéquez:** • 1♂; Finca Los Tarrales; 14.5167, -91.1333; alt. 760m; 2003-11-16; Wild, A. leg.; (UTIC). • 1♂; [no locality given]; 14.6211, -90.5269; (MHNG). **MEXICO – Veracruz:** • 1♂; Estación Biológica Los Tuxtlas; 18.5844, -95.0728; alt. 150m; 2016-05-31; ADMAC leg.; beating; (JTLC). • 1♂; Reserva de la Biosfera Los Tuxtlas; 18.4476, -95.2044; alt. 345m; (CPDC). **NICARAGUA – Matagalpa:** • 1♂; Reserva Natural Cerro Musún; 12.9586, -85.2272; alt. 580m; 2011-05-03; Prebus, M. leg.; (MEPN). **– Región Autónoma del Atlántico Norte:** • 1♂; PN Cerro Saslaya; 13.7704, -84.981;

alt. 320m; 2011-05-09; LLAMA leg.; baiting; (JTLC). **PANAMA – Barro Colorado:** • 1☿; Barro Colorado Island; 9.15, -79.8333; alt. 151m; 1960-01-01; Brown, W.; McCluskey, E. leg.; (MZSP). **– Colón:** • 1♀; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 18m; 2003-10-25; (CPDC). • 1♀; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 18m; 2003-10-25; IBISCA leg.; (CPDC). • 3☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 18m; 2004-05-05; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 18m; 2003-01-01; Dejean; Palmiers leg.; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 18m; 2003-10-14; IBISCA leg.; (CPDC). • 3☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 18m; 2004-05-05; IBISCA leg.; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 18m; 2004-05-15; Schmidt, J.; Bail, J. leg.; fogging; (CPDC). • 2☿; Bosque Protector San Lorenzo; 9.2522, -79.9894; alt. 96m; 2003-09-28; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2522, -79.9894; alt. 96m; 2004-11-02; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 18m; 2003-10-01; Palmiers; Dejean, A. leg.; (CPDC).

Geographic range. Southeastern Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Surinam*, French Guiana, Ecuador, Peru, Brazil (Acre, Amazonas, Bahia, Espirito Santo*, Minas Gerais, Mato Grosso, Mato Grosso do Sul, Rondônia, Pará, Rio De Janeiro, Roraima). *: record from literature (see distribution map).

Neoponera cavinodis *Mann, 1916*

Fig. 27: b (distribution)

Neoponera (Neoponera) cavinodis Mann, 1916: 414. ☿ holotype Brazil [Rondônia], 1911, W.M. Mann [leg.], MCZC [not examined]; ☿ syntype [same data as for Holotype], Mann & Baker [leg.], MCZC: MCZENT20436, link [image examined].

Combinations. In *Pachycondyla* Brown, 1995: 304; In *Neoponera* Schmidt & Shattuck, 2014: 151.

Status as species. Borgmeier, 1923: 65; Kempf, 1965: 275; MacKay & MacKay, 2010: 237 (redescription).

Worker and queen diagnosis. Eye broadly convex and slightly globose, clearly breaking lateral head margin in lateral view; malar carina relatively salient, usually reaching anterointernal

eye margin; posterolateral head corner round; posterior face of petiolar node almost completely devoid of piligerous punctae, concave, usually on dorsal half, while ventral half usually slightly convex; posterodorsal margin of node always feebly protruding posterad; anterodorsal margin of node either weakly convex or straight but always strongly inclined; body usually with relatively abundant erect long hairs, some as long as maximum eye length, particularly those on posterior gastral tergites.

Worker Measurements (*n* = 14): HW: 1.22-1.67; HL: 1.63-2.04; EL: 0.37-0.57; SL: 1.37-1.92; WL: 2.06-2.98; PrW: 0.9-1.47; MsW: 0.71-1.06; MsL: 0.61-0.86; PW: 0.99-1.37; PH: 0.94-1.31; PL: 0.73-1.02; GL: 2.65-4.04; A3L: 0.86-1.29; A4L: 1.06-1.39; A3W: 1.47-1.84; A4W: 1.45-1.84; TLa: 6.67-8.69; TLr: 7.2-10.05. **Indices.** CI: 75.0-88.64; OI: 30.0-35.77; SI: 103.85-123.68; MsI: 95.0-148.57; LPI: 70.0-83.33; DPI: 108.0-136.59.

Queen Measurements (*n* = 4): HW: 1.47-1.81; HL: 1.88-2.12; EL: 0.57-0.65; SL: 1.84-2.08; WL: 2.94-3.55; PrW: 1.27-1.51; MsW: 1.22-1.43; MsL: 1.53-1.8; PW: 1.22-1.39; PH: 1.27-1.43; PL: 0.92-1.14; GL: 3.27-4.33; A3L: 1.22-1.39; A4L: 1.27-1.45; A3W: 1.8-1.96; A4W: 1.71-1.92; TLa: 8.23-9.65; TLr: 9.82-10.78. **Indices.** CI: 78.26-85.19; OI: 33.86-38.89; SI: 109.52-125.0; MsI: 75.0-85.37; LPI: 72.58-80.0; DPI: 110.71-136.0.

Male. See Mackay and Mackay (2010).

Comments. *Neoponera cavinodis* is a medium-sized species in the *N. crenata* group (Fig. 26; ☿: TLa = 6.67 – 8.69 mm; ♀: 8.23 – 9.65 mm). Its morphology is remarkably homogeneous across its distribution range. Except for small variations in the degree of concavity and convexity posterolaterally and dorsoanteriorly on the petiolar node, the overall morphology of the body is basically identical in workers and queens. No extremes or anomalous forms were recorded, except for a worker from Sucumbíos, Ecuador (ATPFOR0894) which shows a strongly concave posterior nodal face, and a subpetiolar process with only two well-impressed striae on the dome, instead of more than four or five as usual in this species. We consider this, however, a not fully developed individual as its color is paler than the average examined specimens. The unusual strong nodal concavity is probably due to invagination of the cuticle, which is typically seen in underdeveloped specimens. The difference in number of striae on the subpetiolar process, although not common in this species, is still possible since its presence/absence, form and number are considered relatively plastic across the *Neoponera*.

Neoponera cavinodis shows the typical ground plan of the species belonging to the *N. crenata* species-group. Nevertheless, its petiole shape is unique not only among species of this group but among species in the genus, and this is the easiest way to distinguish it from any other *Neoponera*. The only species with which it could be misidentified is *N. oberthueri* since its petiolar node is somewhat similar. Nonetheless, the posterior nodal face of *N. oberthueri* is not concave but either convex or flat. In addition, *N. oberthueri* is significantly smaller (☿: TLa = 5.16 – 6.47) than *N. cavinodis*. The high similarity of these two species is probably due to its phylogenetic proximity (Troya et al. unpublished). Two other relatively similar species are *N. crenata* and *N. moesta*. These two species, however, have a block-shaped petiolar node in lateral view, with no concave posterior nodal face. Also, both are smaller than *N. cavinodis*, especially *N. crenata* which, together with *N. oberthueri*, and *N. dejeani* sp. nov., are the smallest taxa in *Neoponera*.

N. cavinodis has been recorded from 8 to 2230 m of elevation. The elevational range is significantly increased as compared to prior records (see Mackay and Mackay 2010 and AntWeb) because we found specimens from mountainous well-preserved forests at the western Amazonian cordilleras in southern Ecuador. Most of the examined material comprises sites at Amazonian lowland rain forests, with only one record from the Cordillera de la Costa, a montane region in northern Venezuela. Mackay and Mackay (2010) report a record from Canal Zone, in Panama. Thus, the northernmost limits for *N. cavinodis* appear to be the Panamanian Chocó-Darién forests, while the southernmost range reaches the Atlantic Forest of Mideastern Bahia, Brazil.

Natural history notes. See Mackay and Mackay (2010). According to the literature and AntWeb records, this is an uncommonly collected species, apparently. We have examined, however, close to 70 specimens, some of which were misidentified as *N. oberthueri*, *N. carinulata*, and *N. moesta*. Is possible then the real abundance of this taxon be higher than previously known. *N. cavinodis* inhabits mostly in well-preserved forests, though scant records belong from second growth, slightly disturbed areas. It has been collected with a number of methods but primarily using fogging, Malaise, and pitfall. Virtually nothing is known about its nesting habits and biology in general, but a single record of a worker obtained from a fallen *Cecropia* sp. (Urticaceae) stem in the state of Mato Grosso, Brazil.

Material examined. 64☿, 8♀. **BRAZIL – Amapá:** • 1☿; Oiapoque; 3.8441, -51.8323; alt. 18m; 1979-05-02; Overal, W. leg.; (MPEG). – **Amazonas:** • 1☿; Benjamin Constant; -4.376, -

70.0302; alt. 70m; (MZSP). – **Bahia:** • 1♀; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1994-11-05; Assis, J. leg.; (DZUP). • 1♀; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1994-11-05; Assis, J. leg.; pitfall; (DZUP). • 1♀; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1994-11-05; Assis, J. leg.; Winkler; (DZUP). • 1♀; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1994-11-05; Assis, J. leg.; hand collected; (DZUP). • 1♀; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; (CPDC). • 1♀; Canavieiras; -15.6, -38.9; alt. 8m; 1997-11-07; Santos, J. R. M. leg.; (CPDC). • 2♀; Lagoa Encantada; -14.6206, -39.1397; alt. 10m; 2000-11-09; Maia, R. J. leg.; (CPDC). • 1♀; Porto Seguro; -12.9, -39.85; 1998-05-08; Santos, J. R. M. leg.; Malaise; (CPDC). • 1♀; Reserva Biológica do Una; -15.1768, -39.1053; alt. 108m; 2005-10-01; Santos, J. R. M. leg.; (CPDC). • 1♀; Una; -15.2172, -39.1282; alt. 80m; 1996-08-29; Conceição, E. S. leg.; (CPDC). • 1♀; Una; -15.2172, -39.1282; alt. 80m; 1996-08-29; Conceição, E. S. leg.; (CPDC). – **Ceará:** • 1♀; 2km S of Pacoti; -4.25, -38.9167; alt. 700m; 2001-01-01; Hites, N. leg.; (CPDC). – **Goiás:** • 1♀; Jataí; -17.8667, -52.7167; alt. 737m; (MZSP). • 2♀; Parque Natural Municipal Mata Do Açude; -17.8605, -51.728; alt. 791m; 2001-05-12; Élio, A.,L.; Rone, S. G. F. leg.; (MZSP). • 2♀; Parque Natural Municipal Mata Do Açude; -17.8605, -51.728; alt. 791m; 2001-05-22; Diniz, J. leg.; (DZUP). – **Mato Grosso:** • 1♀; Barra do Tapirapé; -10.6457, -50.6131; alt. 189m; (MZSP). – **Mato Grosso do Sul:** • 1♀; Três Lagoas; -20.7, -51.7; alt. 300m; 2001-05-05; Flechtmann, C. A. leg.; (CPDC). – **Pará:** • Campus pesquisa MPEG; -1.45, -48.4667; alt. 23m; 2018-01-09; Almeida, R.; Alves, D. leg.; beating; (MPEG). • 1♀; Cuiú-Cuiú; -5.9167, -56.5167; alt. 162m; 2018-06-19; Siqueira, E. leg.; arboreal pitfall; (MPEG). • 4♀; Floresta Nacional Caxiuanã; -1.7333, -51.45; alt. 21m; 2016-09-29; Silva, R.; et al. leg.; pitfall; (MPEG). • Km 90, F. Candiru; -2.53, -50.78; alt. 14m; 1976-11-16; Pimentel , T. leg.; (MPEG). • 1♀; Mocambo Reserve; -1.4333, -48.4; alt. 29m; 1978-04-18; Torres, M. leg.; Malaise; (MPEG). • 2♀; Xingu river, right shore; -3.8519, -51.8523; alt. 173m; 2001-03-05; Santos, R.; Dias, J. leg.; Malaise; (MPEG). • 1♀; Área de Pesquisa Ecológica do Guamá-APEG; -1.4647, -48.4512; alt. 10m; 1969-11-01; Rosa, N. leg.; (DZUP). • 2♀; same data as preceding except: 1969-07-29; (MZSP). • 1♀;

same data as preceding except: 1969-11-11; (MZSP). • 15♂; same data as preceding except: 1969-07-29; (MZSP). • 1♂; same data as preceding except: 1969-11-11; (MZSP). • 2♂; same data as preceding except: 1969-12-17; (MZSP). – **Rondônia:** • 1♂; Porto Velho; -8.7612, -63.9004; alt. 88m; 1911-01-01; Mann, W.; Baker leg.; (MCZC). **ECUADOR – Morona Santiago:** • 1♂; Reserva Biológica El Quimi, Cordillera del Cóndor; -3.5167, -78.3833; alt. 2007m; 2017-07-01; Suárez, A. leg.; fogging; (MEPN). – **Napo:** • 1♂; 1km NNE Archidona; -0.8833, -77.8; alt. 600m; 2003-12-09; Wild, A. leg.; (UTIC). • 1♀; Reserva Jatun Sacha, 7 km ESE Puerto Misahualli; -1.05, -77.6; alt. 450m; 2008-12-05; Troya, A.; Vizuete, J. leg.; fogging; (MEPN). – **Pastaza:** • 1♂; Parque Nacional Yasuní, Bameno, sendero Curaray 1; -1.301, -76.138; alt. 207m; 2014-01-29; Troya, A.; Duque, P. leg.; fogging; (MEPN). • 1♂; Parque Nacional Yasuní, Lorocachi, Batallón de Selva 48 Sangay; -1.609, -75.968; alt. 172m; 2014-01-13; Chasiliquín, N.; Villacrés, E. leg.; fogging; (MEPN). – **Sucumbíos:** • 1♂; Limoncocha; -0.3998, -76.6001; alt. 280m; 1973-08-08; Morales, L. leg.; (MZSP). • 1♂; Limoncocha; -0.3998, -76.6001; alt. 280m; 1973-08-12; Chadab, R. leg.; (MZSP). • 1♂; Limoncocha; -0.3998, -76.6001; alt. 280m; 1973-08-09; Chadab, R. leg.; (MZSP). • 1♂; Reserva de Producción Faunística Cuyabeno, Trocha Zábalo-Güepi; -0.25, -75.6833; alt. 270m; 2000-08-08; Araujo, P. leg.; fogging; (MEPN). • 1♂; Reserva de Producción Faunística Cuyabeno, Trocha Zábalo-Güepi; -0.26, -75.69; alt. 270m; 2000-08-08; Araujo, P. leg.; fogging; (MEPN). **FRENCH GUIANA – Cayenne:** • 4♂; Base Vie; 5.1667, -52.65; alt. 60m; 1998-12-01; Dejan, A.; Orivel, J. leg.; (CPDC). • 1♀; Petit Saut; 5.0667, -53.0333; (CPDC). • 1♂; Petit Saut; 5.0667, -53.0333; (CPDC). **PERU** • 1♂; Zona Reservada Santiago de Comaina, 16 Km EES Fruta del Norte, Cordillera del Cóndor; -3.9, -78.4667; alt. 2230m; 2009-06-24; Troya, A. leg.; pitfall; (MEPN). – **Madre de Dios:** • 1♂; Los Amigos Biological Station; -12.5709, -70.0921; alt. 244m; 2012-07-25; Youngerman, E. leg.; search; (JTLC). **VENEZUELA – Aragua:** • 1♂; Henri Pittier National Park, Valle Santa Maria; 10.1076, -67.4495; alt. 650m; 2003-08-04; Rodriguez, E.; Grotto, A.; Lattke, J. E. leg.; (MIZA).

Geographic range. Panama, Colombia, Venezuela, Guyana*, French Guiana, Ecuador, Peru, Brazil (Amazonas, Bahia, Ceará, Goiás, Mato Grosso, Mato Grosso do Sul, Pará, Rondônia). *: record from literature (see distribution map).

***Neoponera coveri* (MacKay & MacKay, 2010)**

Figs. 10: a – c (☿); 27: b (distribution)

Pachycondyla coveri MacKay & MacKay, 2010: 279. Figs. 82, 238, 240, 405-408. ☿ holotype, Peru, Madre de Dios, Cusco Amazónico, 15 km. NE Puerto Maldonado, 29.vi.1991, S.P. Cover [leg.], MCZC: MCZ-ENT00036275, link [image examined].

Combinations. In *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species. Bezděčková et al., 2015: 123.



Fig. 10. *Neoponera coveri*. ☿ (DZUP: DZUP549599). Venezuela: Amazonas. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Worker diagnosis. Posterior head corner round (Fig. 10b); petiolar node somewhat triangular in lateral view, anterior margin straight and strongly inclined, meeting region between anterior and dorsoanterior margins barely discernible, this is, not angulate (Fig. 3f, 10a); top of node placed posterad to nodal vertical midline; posterior nodal margin feebly convex; posterior nodal face mostly flat and bearing piligerous punctae; prora subtriangular in ventral view, broadened basally, acute apically.

Worker (*n* = 2): HW: 1.45-1.6; HL: 1.7-1.9; EL: 0.41-0.5; SL: 1.6-1.75; WL: 2.1-2.65; PrW: 1.0-1.2; MsW: 0.59-0.7; MsL: 0.55-0.7; PW: 0.84-0.95; PH: 1.1-1.2; PL: 0.72-0.85; GL: 1.95-2.8; A3L: 1.03-1.1; A4L: 1.0-1.1; A3W: 1.35-1.6; A4W: 1.28-1.55; TLa: 6.55-7.6; TLr: 6.47-8.2. **Indices.** CI: 84.21-85.29; OI: 28.28-31.25; SI: 109.38-110.34; MsI: 100.0-107.27; LPI: 65.45-70.83; DPI: 111.76-116.67.

Queen and male. Unknown.

Comments. *Neoponera coveri* is a medium-sized taxon in the *N. crenata* group (Fig. 26; ☿: 6.55 – 7.6 mm). This lineage was erected based on a single specimen from Amazonian Cusco in Peru. Its morphology is very similar to that of *N. oberthueri* whose populations are mostly found in the Amazon. Although we have here identified a second specimen from the also Amazonian Alto Orinoco in Venezuela, 23 km west to the political border of Rondônia, Brazil, it is still hard to separate both taxa, which basically differ in only two external features, 1) The petiolar shape: that of *N. coveri* is somewhat triangular in lateral view, while in *N. oberthueri* it is usually somewhat block-shaped, or otherwise subtriangular (queen from Cuyabeno, Ecuador (Fig. 3g, CPDC: ATPFOR2083), as seen in lateral view; and 2) Size: the worker of *N. coveri* is clearly larger than that of *N. oberthueri* (Fig. 23). Mackay and Mackay (2010) point out that the "medial clypeal tooth is large and well-developed" (pg. 279), which is illustrated on their figure no. 406 as an acute, spiniform tooth. The examined holotype, however, does not show this feature as described by M&M, but the typical subtriangular-shaped, carina-like extension of the mid clypeus which is diagnostic for all members in the *N. crenata* group.

M&M also mention that *N. coveri* has "coriaceous and punctate mandible with a dull surface [while the] mandible is shining in *P. oberthueri*" p. 281. We noted that among the *N. oberthueri* specimens here examined (*n* = 39), some show shining mandibles while in others these are dull, but all of them have a mixture of feeble striae, which may seem like a coriaceous

integument, and scattered piligerous punctae. The mandibles of the *Neoponera* material thus far examined can usually vary from dull to shining, but frequently this is deceiving as the specimens are commonly coated with dust or any other microhabitat-derived debris from where they were collected. Moreover, the mandibles of the holotype of *N. coveri* are also relatively shining (link). The relative amount of striae on the mandibular dorsum is apparently a factor to consider while distinguishing between both taxa. The two *N. coveri* specimens have relatively more striae than the average of *N. oberthueri* specimens. However, we advise to the reader to use this trait with caution since it can be plastic, i.e., showing a degree of populational variation, sometimes bearing well-impressed striae or otherwise.

The elevation range of *N. coveri* extends from 200 to near 900 m, and it seems this taxon has a relatively broad distribution, from southern Venezuela to southern Peru.

Since only two specimens are known: the holotype found in 1991, and the other in 2007, we may hypothesize of this as a quite rare lineage, but also due to its similarity to *N. oberthueri* it could have been erroneously determined as such. In addition, since a high-quality image of the holotype was not publicly available, the morphology of this species was hard to picture out even when checking its description. Further specimens of these two forms plus additional lines of evidence, e.g., geometric morphometrics, DNA barcoding, UCE phylogenies, may bring additional light about their specific status.

Natural history notes. Besides being collected from a "dead stick hanging in foliage at forest edge" (note on label of the holotype), nothing is known about this taxon.

Material examined. 2☿. **PERU – Madre de Dios:** • 1☿; 15 km NE Puerto Maldonado; -12.4, -69.1; alt. 200m; 1991-06-29; Cover, S. leg.; hand collected; (MCZC). **VENEZUELA – Amazonas:** • 1☿; Parima B; 2.7765, -64.2321; alt. 895m; 2007-01-07; Escalona, H. leg.; (DZUP).

Geographic range. Venezuela, Peru.

***Neoponera crenata* (Roger, 1861)**

Fig. 25: a (distribution)

Ponera pallipes F. Smith 1858: 98. ♀ Brazil, Pará. Junior primary homonym of *Ponera pallipes* F. Smith, 1858: 87, (BMNH) [type absent from collection].

Ponera crenata Roger, 1861: 3. ♀ [Venezuela], Puerto Caballo [probably Puerto Cabello]. Note: The type should be at MNHU or NHMW but it is absent from both collections.

Neoponera unidentata sulcatula Santschi, 1919: 38. Fig. 2. ☿ [designated as lectotype of *N. moesta* by Mackay & Mackay 2010: 469 (error)], Argentina, [Córdoba], Cruz Grande, v. Steiger [leg.], (NHMB, AntWeb: CASENT0915258) [image examined, link]. Notes: 1) Type published as *N. unidentata sulcatula*, not as *N. carinulata sulcatula* as shown in AntCat.org. **Syn. nov.**

Neoponera crenata confusa Santschi, 1921: 86. ☿ syntype [designated as lectotype of *N. moesta* by Mackay & Mackay 2010: 469 (error)], Brazil, Minas Gerais, Sampaio, NHMB, AntWeb: CASENT0915255 [image examined]. **Syn. nov.**

Neoponera mesorotalis [*recte mesonotalis*] Santschi 1923: 246 (☿, ♂). ☿ syntype [designated as lectotype of *N. moesta* by Mackay & Mackay 2010: 469 (error)], Brazil, Santa Catarina, Blumenau, M. Witte [leg.], NHMB, AntWeb: CASENT0915268 [image examined]; ☿ syntype, Brazil, Santa Catarina, Blumenau, M. Witte [leg.], MZSP [examined]; 2 ☿ syntypes (designated as paralectotypes of *N. moesta* by Mackay & Mackay 2010: 469 [error], same data as for syntype, (MHNG) [not examined]. **Syn. nov.**

Neoponera crenata moesta subcarinata Santschi, 1939: 313. ☿ Brazil, [Santa Catarina], Nova Teutônia, 27°11'B (S), 52°23'L(W), viii.1935, F. Plaumann [leg.], (BMNH(E)1015563, AntWeb: CASENT0902519); ☿ [same data as preceding], (BMNH1937-47, AntWeb: CASENT0915257). Type specimens of unavailable name [images examined]. **Syn. nov.**

Neoponera crenata Roger, 1861. ☿ **neotype** [by present designation], Brazil, Paraná, R. N. [Reserva Natural] Guaricica, beating [method], Nov.2018, Troya, A. [leg.], (MEPN: CASENT0649900). Type notes: specimen subjected to DNA extraction, Ants of the World project, extraction code EX # 2451.

Status as species. Roger, 1863: 18; Mayr, 1863: 448 [list]; Mayr, 1865: 65 [list]; Mayr, 1887: 534 [comments on morphology]; Emery, 1890b: 73 [in key]; Emery, 1911: 73 [synonymic list]; Bruch, 1914: 214 [checklist]; Mann, 1916: 413 [general comments]; Gallardo, 1918: 59 [checklist]; Luederwaldt, 1918: 35 [checklist]; Santschi, 1919: 38 [notes on variant]; Santschi, 1921: 85 [description of variant: male, worker]; Wheeler, 1921: 138 [comments biology]; Mann, 1922: 7 [comments biology]; Borgmeier, 1923: 65 [synonymic list]; Wheeler, 1934: 161 [comments biology and distribution]; Eidmann, 1936: 33 [checklist]; Santschi, 1939: 313 [notes on variant]; Wheeler, 1942: 155 [comments biology]; Brown, 1957: 233 [comments morphology and distribution]; Kusnezov, 1969: 36 [in key]; Kempf, 1970: 326 [comments biology]; Kempf, 1972: 161 [synonymic list]; Kempf & Lenko, 1976: 53 [comments biology and distribution]; Bolton, 1995: 304 [synonymic list]; Wild, 2003: 8 [annotated checklist]; Mariano et al., 2006: 278 [cytogenetic analysis]; Wild, 2007: 39 [checklist]; Mackay et al., 2008: 190 [annotated checklist]; MacKay & MacKay, 2010: 288 **[misidentification]**; Branstetter & Sáenz, 2012 : 263 [checklist, **doubtful record**]; Bezděčková et al., 2015: 123 [checklist based on Kemp, 1972]; Feitosa, 2015: 99 [checklist based on Mackay & Mackay, 2010]; Fernández & Guerrero, 2019: 533 [checklist, **doubtful record**]; Pazmiño-Palomino & Troya, 2022: 9 [annotated checklist, identified as *N. moesta* (**misidentification**)].

Neoponera divaricata: ☿ Brazil, Santa Catarina, Blumenau, Witte [leg.] NHMB, AntWeb: CASENT0915261 [image examined]. Note: syntype (cotype) of unpublished name.

Worker and queen diagnosis. Head usually subquadrate, and less frequently rectangular; distance between mandibular insertion to anterior eye margin longer than **half** eye maximum length (Fig. 4b); antennal scape, when pulled posterad, exceeding posterior head margin by 1 to 1.5 times apical scape width (Fig. 4d); in lateral view, posterior margin of petiolar node slightly convex, while the posterior face is usually straight, anterodorsal margin not inclined (link); posterior face of node bearing piligerous punctae, usually on its entire surface (Fig. 8d); in dorsal view, petiolar node campanulate to subtriangular (Fig. 8d).

Worker. Measurements (n = 37): HW: 1.17-1.62; HL: 1.32-1.8; EL: 0.33-0.44; SL: 1.19-1.59; WL: 2.02-2.7; PrW: 0.72-1.2; MsW: 0.59-0.82; MsL: 0.47-0.71; PW: 0.69-0.94; PH: 0.63-0.98; PL: 0.61-0.82; GL: 1.84-3.27; A3L: 0.76-1.1; A4L: 0.82-1.14; A3W: 1.08-1.43; A4W: 1.06-

1.45; TLa: 5.71-7.43; TLr: 6.08-8.23. **Indices.** CI: 82.05-94.44; OI: 25.54-33.33; SI: 90.91-113.33; MsI: 100.0-133.33; LPI: 75.0-125.0; DPI: 102.38-137.5.

Queen. Measurements (*n* = 19): HW: 1.25-1.85; HL: 1.37-1.85; EL: 0.39-0.5; SL: 1.25-1.67; WL: 2.25-3.35; PrW: 1.02-1.45; MsW: 0.9-1.23; MsL: 1.1-1.65; PW: 0.81-1.1; PH: 0.71-1.0; PL: 0.59-0.98; GL: 2.65-3.5; A3L: 0.99-1.5; A4L: 0.9-1.5; A3W: 1.29-1.6; A4W: 1.31-1.7; TLa: 6.34-9.05; TLr: 7.16-9.55. **Indices.** CI: 79.49-111.43; OI: 27.03-36.36; SI: 86.49-113.89; MsI: 70.97-91.67; LPI: 71.74-138.89; DPI: 84.0-148.48.

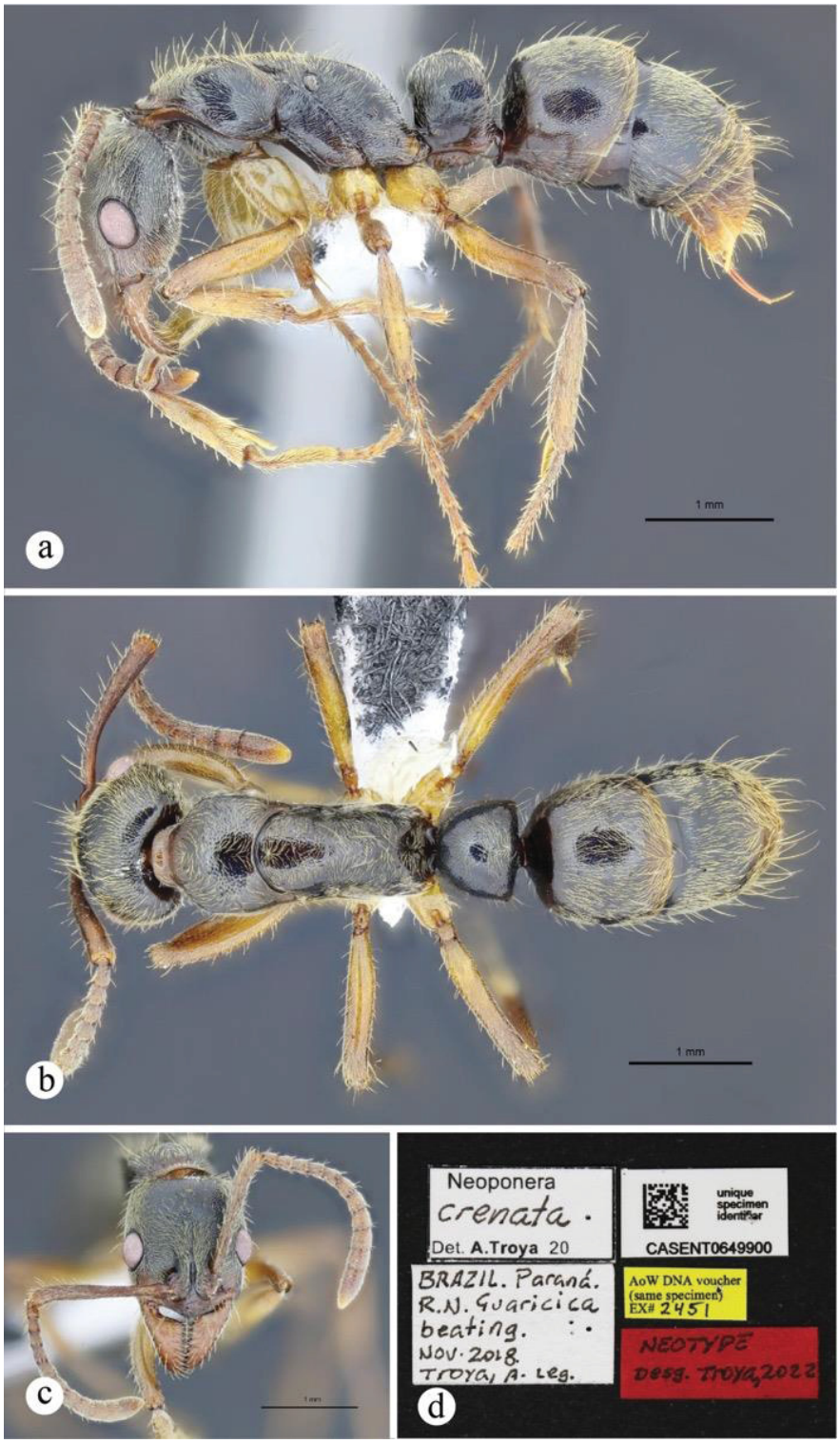


Fig. 11. *Neoponera crenata*. ☿ neotype (MEPN: CASENT0649900), Brazil: Paraná. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Collection labels.

Male. Not examined, but see Santschi (1921) which provides a short glimpse of the morphology for this caste. Mackay and Mackay (2010) redescribed a potential male. It is uncertain, however, if their information actually corresponds to *N. crenata* since their treatment for this species is based on G. Mayr's holotype of *N. moesta*, which is extremely similar to *N. crenata* (see comments below). They state "The specimens from Nicaragua are nearly identical to the types […]" p. 472. We could not find the primary type material for any caste in this species whose distribution range is restricted to South America (see below under distribution). Thus, we cannot confirm the information provided by M&M for this caste. Yet, since *N. crenata* and *N. moesta* are so similar, the features provided by these authors are still useful when eventually confirming the association male-worker or male-queen in *N. crenata*.

Comments. *Neoponera crenata* is a small to medium-sized species (Fig. 26; ☿: TLa = 5.71 – 7.23 mm; ♀: 6.34 – 8.14 mm). Its morphology, including coloration, is quite homogeneous across its distribution range. However, in populations of the Brazilian Atlantic Forest, namely from southern Bahia to western Espírito Santo, the shape of the petiolar node departs, not significantly though, from the observed pattern. In these populations the node is more triangular-shaped, and longitudinally slightly shorter as seen in dorsal view. Workers and queens of *N. crenata* can easily be confused with two highly similar, sympatrically occurring taxa (in South America only): *N. moesta*, and *N. fiebrigi*. The easiest way to differentiate it from *N. moesta* is through the following: *N. crenata* is overall larger (Fig. 26), and has proportionally smaller eyes, so that the distance from their anterior margin to the mandibular insertion is longer than half eye maximum length (smaller or at most equal to such distance in *N. moesta*); the posterior nodal face of *N. crenata* has piligerous punctures (almost absent in *N. moesta*). In regards to *N. fiebrigi*, the user can check the following characters to separate it from *N. crenata*: the fore coxa has a longitudinal carina laterally (Fig. 13c) which can be difficult to discern with lower magnification (absent in *N. crenata*); the anterodorsal nodal margin is inclined (it is not in *N. crenata*), and its posterior face is completely glabrous and polished (bearing piligerous punctae in *N. crenata*); except for two records in southern Paraguay (e.g., Parque Nacional Ybycuí), *N. fiebrigi* is clearly larger than *N. moesta* (Fig. 26).

A third species, *N. cylindrinodis* sp. nov., could also be confused with *N. crenata*, but is certainly easier to distinguish the differences as compared to the previous cases. The user can examine the following: *N. cylindrinodis* has golden pilosity (whitish to pale yellowish in *N.*

crenata); antennal scape, when pulled posterad, exceeding posterior head margin by 2 to 2.5 times apical scape width (antennal scape smaller in *N. crenata*, see diagnosis); *N. cylindrinodis* is overall much larger than *N. crenata* (Fig. 26).

Justification for the neotype designation. This is required since the primary type material is lost, and without a new name-bearing type and its associated diagnostic traits, is impossible to identify this species. The curatorial staff at MNHU in Berlin, and NHMW in Vienna, the probable repositories of J. Roger's type, confirmed to us they could not locate it in those collections. However, we examined the images of two historical, non-type workers at MNHU which were probably identified by G. Mayr, both are from São Paulo, Brazil, one is identified as *N. crenata*, and the other as *N. crenata moesta* Mayr. The first coincides with the diagnostic traits we currently consider as belonging to such species. Likewise, the other specimen coincides with the traits we recognize for *N. moesta*. We chose as neotype the specimen in Fig. 11, which does not belong to the original type locality because: 1) The morphology of this specimen matches that of the specimen aforementioned identified by G. Mayr, who was the first to recognize the close similarity between both *N. crenata* and *N. moesta* (Mayr, 1870: p 396); 2) After careful examination of collection material from Brazilian institutions, no specimens from Pará were found; and 3) The DNA of the proposed neotype is sequenced, thus allowing further testing.

A century-long taxonomic uncertainty. The taxonomy of *N. crenata* is closely linked to that of *N. moesta*, and in less degree to that of *N. fiebrigi*. An untrained eye can easily get confused identifying this triad due to their high similarity, in particular between the first two taxa which, contrary to what could be expected, they are not sister but relatively closely related (Troya et al. unpublished). Their external morphology is almost identical probably due to convergence, thus making its identification challenging or impossible even for experienced taxonomists. Since both *N. crenata* and *N. moesta* occur in sympatry in many South American regions, and are relatively commonly collected, their taxonomic history was the source of an intricate confusion in the genus, perhaps similar to that between *N. verenae* Forel and *N. obscuricornis* Emery (see details on Wild 2005). The complexity in discerning their specific identity explains in part the numerous misidentified records found in all the repository collections visited. Other factors include: 1) Absence of the primary type material of *N. crenata* and *N. pallipes*, which is the reason for the present designation of a neotype for this species; 2) The lack of informative characters in the descriptions of the subspecific names associated to both forms proposed by F. Santschi (1919,

1921, 1923, 1939); and above all, 3) Insufficient amount of examined material not representing the distribution range of this species and its related forms.

The first step, and central to solving the issue, is the examination of all related type material. As Brown (1957) wrote: "I am unable to find any satisfactory characters to separate *stipitum* [= *N. moesta*] from *crenata*, and I incline to the belief that a thorough study, with resort to the scattered types of these and other named variants of the complex, will see them all merged under the name crenata" p. 233. Note that Brown considered *N. crenata* as a species-complex due to its apparent high morphological variation. In this regard, Longino (2010), based on material of the Emery collection at MSNG, Italy, noted that all the material identified as *N. crenata* belonged from Brazil (no specific regions indicated), while the material identified as *N. moesta*, also from Brazil, was composed of smaller individuals which were lighter-colored (as compared to *N. crenata*). According to Longino these latter matched Costa Rican *N. crenata*, as well as Emery's material of *P. stipitum* which match the morphology of Central American specimens, currently identified as *N. crenata*. Longino concludes: "[…] if *crenata s.l.* is revealed to be a species complex, the name could change for Costa Rican material, and would probably be *moesta* or *stipitum*" (no page No.). The material we examined from Central America in deed matches the traits of *N. moesta*. Furthermore, these traits correspond to those of the types (see details under that species).

Mackay and Mackay (2010) revised the type specimens of the five subspecific names erected by Santschi, but they incorrectly synonymized them under *N. moesta*. Among this material, *N. crenata confusa lata* (voucher at NHMB, AntWeb CASENT0915256) in fact represents *N. fiebrigi* (see below under that species). The observations of Brown (1957), based on unspecified number of specimens from Mexico, Guyana and Brazil (Espírito Santo) in regards to the morphology of *N. crenata* and *N. moesta*, match some of the traits we describe for these taxa in the current revision. We tried to examine as much material as possible representing the approximate distribution range of this morphologically very similar triad. This allowed us to get a better resolution of their taxonomic boundaries. Nonetheless, it is beyond our current scope to verify the complete literature sources (see Janicki et al. 2016, Guénard et al. 2017) that report a large number of records of these species, especially for *N. crenata* and *N. moesta*, in the Americas. Since their taxonomic limits are newly proposed here, we recommend a further revision of those sources because they probably contain misidentifications.

Neoponera crenata is restricted to South America with its elevational rage extending from the sea level up to about 1400 m. This species reaches the southernmost distribution range of any species in the genus. The neotype, which was probably collected in the early twentieth century, have its origin from the region of Córdoba, north-central Argentina. Except for two records: one from southern Paraguay in the mid 70's, and another from southwestern Paraná, Brazil in 2017, just at the political border with the province of Misiones, we are unaware of any other report of this species in Argentina. Note that Córdoba is approximately 900 km away from the mentioned sites in Brazil and Paraguay. From northern Rio Grande do Sul, north to the also Brazilian state of Bahia in the Atlantic Forest, we found numerous records composing the majority of our examined material. We found only a single record from the central Cerrado, in the state of Goiás. The remaining scant records, namely four, belong from southern to northwestern Amazonia, with a single record from northern Guyana, in Kartabo (Fig. 28a). Pazmiño-Palomino and Troya (2022) report a doubtful record (MEPN34660) from the Ecuadorian Chocó-Darién. This record probably comes from a mislabeled specimen from Amazonia where we did find specimens for Ecuador.

Natural history notes. This arboreal species seems to prefer well-preserved habitats, being many of the records obtained from a number of natural reserves in some countries. Nests of *N. crenata* have been collected inside live plants like *Eriobotrya japonica* (Rosaceae), *Ipomoea sidifolia* (Convolvulaceae), *Clidemia hirta* (Melastomataceae), *Vriesea friburgensis* (Bromeliaceae), as well as from common *Eucaliptus* sp. (Myrtaceae) in agroforestry systems. Sometimes specimens have been collected few hours before dawn.

Material examined. 157☿, 48♀. **ARGENTINA – Córdoba:** • 1☿; Cruz Grande; -30.9486, -64.4931; alt. 1100m; von Steiger leg.; (NHMB). **BOLIVIA – Beni:** • 1☿; Parque Nacional Noel Kempff, campamento Flor de Oro; -13.3042, -62.4983; alt. 201m; 2002-09-01; Roy, D. leg.; (MEPN). **BRAZIL – Acre:** • 2☿; Fazenda Experimental Catuaba; -10.0667, -67.6167; alt. 226m; 2016-11-07; Lattke, J. leg.; (DZUP). **– Bahia:** • 2☿; Enchuzilhada; -15.5833, -40.9833; alt. 980m; 1975-11-01; Alvarenga, M. leg.; (MZSP). • 1☿; Enchuzilhada; -15.5833, -40.9833; alt. 980m; (MZSP). • 3☿; Ilhéus; -14.7472, -39.2272; alt. 138m; (CPDC). • 1☿; RPPN Serra Bonita, centro de pesquisa; -15.3925, -39.5642; alt. 778m; 2018-07-14; Feitosa, R.; et al. leg.; hand collected; (DZUP). • 1♀; Serra Bonita; -15.3905, -39.5635; alt. 799m; (CPDC). • 1☿;

Universidade Estadual do Sudoeste da Bahia (UESB); -14.8901, -40.8085; alt. 872m; 2001-01-12; Santos, J. R. M. leg.; hand collected; (CPDC). • 1♀; Vitória da Conquista; -14.8619, -40.8445; alt. 882m; (CPDC). – **Espírito Santo:** • 1♂; Estaçao Biológica de Santa Lucia; -19.95, -40.5333; alt. 600m; 2018-11-18; (DZUP). • 3♀; Santa Teresa; -19.9368, -40.5983; alt. 617m; (MZSP). • 1♂; Santa Teresa; -19.9368, -40.5983; alt. 617m; (MZSP). • 1♂; Santa Teresa; -19.1, -40.5833; alt. 697m; Conde, O. leg.; (MZSP). – **Goiás:** • 1♂; Anápolis; -16.3309, -48.9485; alt. 969m; (MZSP). – **Minas Gerais:** • 1♀; Cristina; -22.2, -45.25; alt. 1012m; 1912-07-01; Luederwaldt, H. leg.; (MZSP). • 1♀; Flona Ritapolis - IBAMA; -21.05, -44.25; alt. 905m; 2006-03-24; De Paula, G.A.R . leg.; Malaise; (DZUP). • 1♂; Flona Ritapolis - IBAMA; -21.05, -44.25; alt. 905m; 2006-04-25; De Paula, G.A.R . leg.; Malaise; (DZUP). • 1♂; Guanhães; -18.7771, -42.9375; alt. 777m; (CPDC). • 1♂; Marimbá, Sitio das irmãs; -19.9199, -44.2753; alt. 822m; 1980-05-02; Diniz leg.; (DZUP). • 5♂; Marimbá, Sitio das irmãs; -19.9655, -44.2062; alt. 100m; 1980-11-28; Diniz leg.; (DZUP). • Mata do Paraiso, Universidade Federal do Viçosa; -20.799, -42.8623; alt. 759m; 2017-04-10; Jesus, R. leg.; Malaise aerial; (UFVLABECOL). • 2♂; Mata do Paraiso, Universidade Federal do Viçosa; -20.75, -42.85; alt. 681m; 2019-01-01; Chaul, J. leg.; (DZUP). • 1♂; Mina Tamanduá; -20.0833, -43.9333; alt. 1400m; 2012-12-12; Queiroz; et al. leg.; (DZUP). • 1♀; Parna Caparaó; -20.4192, -41.8514; alt. 1300m; 2011-12-05; Camacho, G. leg.; pitfall; (UFVLABECOL). • 1♂; Parna Caparaó; -20.4192, -41.8514; alt. 1300m; 2011-12-05; Camacho, G. leg.; pitfall; (UFVLABECOL). • 1♂; Região de Itabira, Serra do Fundão; -19.7501, -43.2323; alt. 705m; 2015-06-05; Da Paz, A. leg.; hand collected; (UFVLABECOL). • 1♂; Rodovia MG 355; -21.4833, -44.95; alt. 971m; 2011-09-01; Lasmar et al. leg.; pitfall; (DZUP). • 1♂; Sampaio; -18.0, -44.0; alt. 1200m; Sampaio leg.; (NHMB). • 1♀; Serra do Caraça; -20.1333, -43.4833; alt. 1380m; 1961-11-01; Lenko, K., Martins, Silva leg.; (MZSP). • 4♂; Serra do Caraça; -20.1333, -43.4833; alt. 1380m; (MZSP). • 1♂; Serra do Caraça; -20.1333, -43.4833; alt. 1380m; 1961-11-01; Lenko, K., Martins, Silva leg.; (MZSP). • 1♂; Universidade Federal de Viçosa; -20.765, -42.8639; alt. 710m; 2012-05-01; Chaul, J.; Maccida, A. leg.; (MEPN). • 1♂; Universidade Federal de Viçosa, Mato do Coluni; -20.765, -42.8639; alt. 683m; 2012-06-01; Chaul, J.; Muccida, A. leg.; (UFVLABECOL). • 1♂; Varginha; -21.55, -45.4167; alt. 864m; 1961-09-01; Alvarenga, M. leg.; (DZUP). • 1♂; Varginha;

-21.55, -42.4167; alt. 864m; 1961-09-01; Alvarenga, M. leg.; (DZUP). • 1♀; [no locality given]; -18.5, -44.55; alt. 661m; (MZSP). – **Paraná:** • 1♂; 4km NW of Distrito de Itaiacoca ; -25.1167, -49.9333; alt. 930m; 2017-03-08; Almeida, M.; Tozetto, l. leg.; Malaise; (DZUP). • 1♂; 4km NW of Distrito de Itaiacoca ; -25.1167, -49.9333; alt. 930m; 2017-02-10; Almeida, M.; Tozetto, l. leg.; Malaise; (DZUP). • 1♂; 4km NW of Distrito de Itaiacoca ; -25.1167, -49.9333; alt. 930m; 2017-04-12; Almeida, M.; Tozetto, l. leg.; Malaise; (DZUP). • 1♀; 6.6 km Piraquara, Recreio da Serra; -25.4538, -49.0077; alt. 845m; 2017-03-23; Lopez, R.; Lattke, J. leg.; (DZUP). • 1♂; Apucurana; -23.5537, -51.4588; alt. 864m; (MZSP). • 2♂; Bairro Canguiri; -25.3667, -49.1167; alt. 915m; 2014-12-05; Savaris, M. leg.; (DZUP). • 1♂; Bairro Vila Industrial ; -24.7, -53.75; alt. 541m; 2013-05-31; Musolon, L. M. leg.; (DZUP). • 1♂; Curitiba; -25.43, -49.26; alt. 900m; 1966-02-16; (DZUP). • 1♂; Estrada dos Castelhanos; -25.7995, -48.9108; alt. 294m; 2003-10-18; Melo, G. leg.; Malaise; (DZUP). • 1♀; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1984-10-03; Malaise; (DZUP). • 1♀; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1984-10-17; Malaise; (DZUP). • 1♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1984-10-29; Malaise; (DZUP). • 1♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1984-08-27; Malaise; (DZUP). • 1♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-02-04; Malaise; (DZUP). • 1♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1984-10-29; C.I.I.F leg.; Malaise; (DZUP). • 2♂; Jardim Social; -25.4192, -49.2355; alt. 900m; 2021-02-17; Lattke, J. leg.; hand collected; (DZUP). • 1♂; Mananciais da Serra; -25.4923, -48.9943; alt. 925m; 2010-11-15; Melo, G. leg.; (DZUP). • 1♂; Mananciais da Serra; -25.4923, -48.9943; alt. 975m; 2019-02-21; Araujo, B. leg.; (DZUP). • 1♀; Morretes; -23.708, -51.6392; alt. 644m; 1967-05-14; La Roca, O. M. leg.; (DZUP). • 1♂; Parque Estadual de Campinhos; -25.0333, -49.0833; alt. 860m; 2007-08-25; Melo, G.; Weiss, G. leg.; (DZUP). • 1♂; Parque Estadual de Marumbi; -25.4833, -48.9833; alt. 970m; 2014-12-15; Calixto, J.; et al. leg.; (DZUP). • 1♀; Parque Estadual de Vila Velha; -25.2333, -50.0167; alt. 801m; 2003-09-09; Melo, G.; Gonçalves, R. leg.; (DZUP). • 2♂; Parque Estadual de Vila Velha; -25.2333, -50.0167; alt. 798m; 2016-12-19; Feitosa, R.; et al. leg.; (DZUP). • 1♂; Parque Estadual de Vila Velha; -25.2167, -50.0333; alt. 934m; 2014-11-24; Franco et al. leg.; pitfall; (DZUP). • 5♂; Parque Nacional Iguaçu, 19 Km SE Foz do Iguaçu; -25.65, -

54.4333; alt. 225m; 2017-10-01; Troya, A. leg.; hand collected; (MEPN). • 1♀; Piraquara, BR-277-km 54; -25.5167, -49.0833; alt. 907m; 1985-02-11; Malaise; (DZUP). • 1♂; Piraquara, BR-277-km 54; -25.5167, -49.0833; alt. 907m; 1984-07-30; Malaise; (DZUP). • 1♂; Piraquara, BR-277-km 54; -25.5167, -49.0833; alt. 907m; 1984-10-08; Malaise; (DZUP). • 1♂; Piraquara, BR-277-km 54; -25.5167, -49.0833; alt. 907m; 1984-12-10; C.I.I.F leg.; Malaise; (DZUP). • 4♀; Pão de Ló, 27 Km E Curitiba; -25.4, -49.0; alt. 1242m; 2019-03-01; Troya, A. leg.; (MEPN). • 1♀; RPPN Fazenda Assu; -24.15, -53.95; alt. 321m; 2013-03-23; Gonçalves, R.; Soares, P. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3, -48.65; alt. 300m; 2010-12-15; De Souza, J.M.T leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2010-01-16; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3667, -48.7667; alt. 9m; 2009-12-09; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3667, -48.7667; alt. 9m; 2012-12-12; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3667, -48.7667; alt. 9m; 2010-01-14; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2009-12-09; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2010-11-02; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3, -48.6667; alt. 110m; (DZUP). • 2♂; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2009-12-12; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2010-01-14; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.315, -48.696; alt. 50m; 2015-11-05; Curso de Entomologia UFPR leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3058, -48.6739; alt. 102m; 2015-11-05; Ferreira, A. leg.; hand collected; (DZUP). • 2♂; Reserva Natural Guaricica, Guaricica trail; -25.3667, -48.7667; alt. 9m; 2017-02-11; hand collected; (DZUP). • 1♂; Reserva Natural Guaricica, dos Fornos trail; -25.3, -48.65; alt. 36m; 2018-11-06; Troya, A. leg.; beating; (MEPN). • 1♀; São Camilo; -24.2667, -53.8333; alt. 325m; 2017-05-17; Escárraga, M. leg.; (DZUP). • São José dos Pinhais; -25.605, -49.1936; alt. 898m; 2017-02-18; Domahovski, A. leg.; Malaise suspensa; (DZUP). • 2♂; São José dos Pinhais; -25.6, -49.1833; alt. 880m; 2015-11-18; Domahovski, A. C. leg.; (DZUP). • 1♂; São José dos Pinhais; -25.6, -49.1833; alt. 880m; 2014-12-04; Domahovski, A. C. leg.; Malaise;

(DZUP). • 1♂; São José dos Pinhais; -25.6049, -49.1936; alt. 897m; 2018-01-06; Domahovski, A. leg.; (DZUP). • 2♀; Taquara; -25.283, -49.7001; alt. 740m; 1930-12-01; Wihe, M. leg.; (MZSP). • 1♂; Universidade Federal do Paraná, Centro Politécnico; -25.4333, -49.2333; alt. 916m; 2015-01-20; Martins, A. L. leg.; sweeping; (DZUP). • 2♂; Universidade Federal do Paraná, Centro Politécnico; -25.4333, -49.2333; alt. 916m; 2018-03-16; Feitosa, R. leg.; (DZUP). – **Rio Grande do Sul:** • 1♂; Nova Petrópolis; -29.3667, -51.1; alt. 585m; (MZSP). • 1♂; Três Arroios; -27.4996, -52.1454; alt. 541m; (MZSP). – **Rio de Janeiro:** • 3♀; Corcovado; -22.957, -43.2112; alt. 150m; (MZSP). • 1♀; Corcovado; -22.957, -43.2112; alt. 150m; 1960-04-01; Albertoni, F.; Seabra leg.; (MZSP). • 1♂; Petrópolis; -22.5089, -43.1776; alt. 831m; (MZSP). • Petrópolis, Fazenda das Arcas; -22.3762, -43.0879; alt. 854m; Diniz leg.; (DZUP). – **Santa Catarina:** • 1♀; 4 Km SE of Nova Teutônia; -27.1833, -52.3833; alt. 300m; 1958-12-01; Plaumann, F. leg.; (MZSP). • 2♀; 4 Km SE of Nova Teutônia; -27.1833, -52.3833; alt. 300m; 1974-12-01; Plaumann, F. leg.; (MZSP). • 1♂; Blumenau; -26.9155, -49.0936; alt. 20m; Witte, M. leg.; (NHMB). • 1♂; Blumenau; -26.9166, -49.0717; alt. 18m; (MZSP). • 1♂; Blumenau; -26.9155, -49.0936; alt. 20m; M. Witte leg.; (NHMB). • 1♀; Blummenau; -26.9155, -49.0936; alt. 20m; Witte, M. leg.; (MZSP). • 1♂; Blummenau; -26.9155, -49.0936; alt. 20m; Witte, M. leg.; (MZSP). • 1♂; Gaspar; -26.9341, -48.9539; alt. 25m; (MZSP). • 1♀; Ilha dos Moleques do Sul; -27.845, -48.43; alt. 40m; 2006-01-29; Ulyssea, M. A. leg.; (DZUP). • 1♀; Lagoa Pequena; -27.65, -48.4667; alt. 5m; 2009-03-17; Albertoni, F. leg.; (DZUP). • 1♂; Lagoa Pequena; -27.65, -48.4667; alt. 200m; 2009-03-17; Albertoni, F. leg.; (DZUP). • 1♂; Lagoa Pequena; -27.65, -48.4667; alt. 2m; 2009-03-17; Albertoni, F. leg.; (DZUP). • 1♀; Monte Belo; -27.1, -52.6167; alt. 615m; 2013-02-01; Savaris, M.; Lampert, S. leg.; Malaise; (DZUP). • 1♀; Monte Belo; -27.1, -52.6167; alt. 615m; 2013-03-01; Savaris, M.; Lampert, S. leg.; Malaise; (DZUP). • 1♀; Monte Belo; -27.1, -52.6167; alt. 615m; 2013-02-01; Savaris, M.; Lampert, S. leg.; Malaise; (DZUP). • 2♂; Monte Belo; -27.1, -52.6167; alt. 615m; 2013-03-01; Savaris, M.; Lampert, S. leg.; Malaise; (DZUP). • 1♂; Monte Belo; -27.1, -52.6167; alt. 615m; 2013-01-01; Savaris, M.; Lampert, S. leg.; Malaise; (DZUP). • 2♂; Monte Belo; -27.0833, -52.6; alt. 671m; 2013-01-01; Savaris, M.; Lampert, S. leg.; Malaise; (DZUP). • 1♂; Nova Teutonia; -27.1833, -52.3833; alt. 300m; 1935-08-01; Fritz Plaumann leg.; (NHMUK). • 1♂; Nova

Teutonia; -27.1833, -52.3833; alt. 300m; 1935-08-01; Fritz Plaumann leg.; (NHMB). • 1♀; Nova Teutônia; -27.2333, -52.3833; alt. 400m; Plaumann, F. leg.; (MZSP). • 4♂; Nova Teutônia; -27.2333, -52.3833; alt. 400m; (MZSP). • 1♂; Nova Teutônia; -27.1833, -52.3833; alt. 300m; 1936-04-01; Plaumann, F. leg.; (MZSP). • 1♂; Praia da Lagoinha da Ponta das Canas; -27.3892, -48.4249; alt. 1m; 2013-01-01; Chaul, J. leg.; (UFVLABECOL). – **São Paulo:** • 1♂; 28 km a SE de Barra do Turvo; -24.9333, -48.2833; alt. 700m; 2006-01-07; Melo, A., Faria, J. leg.; (DZUP). • 2♀; Avaré; -23.1027, -48.9175; alt. 778m; 1972-04-22; Lane, F. leg.; (MZSP). • 2♀; Barueri; -23.5097, -46.8731; alt. 734m; 1963-07-02; Lenko, K. leg.; (MZSP). • 4♂; Caraguatatuba; -23.6213, -45.4231; alt. 30m; 1962-05-31; (MZSP). • 1♂; Embu-Guaçu; -23.8276, -46.8148; alt. 749m; (MZSP). • 2♂; Estação Biológica de Boraceia ; -23.6308, -45.8697; alt. 982m; 1960-09-18; Lenko, K. leg.; (MZSP). • 1♀; Ipiranga; -23.5884, -46.6038; alt. 750m; Forel, L. leg.; (MZSP). • 1♀; Ipiranga; -23.5884, -46.6038; alt. 750m; (MZSP). • 3♂; Ipiranga; -23.5884, -46.6038; alt. 750m; (MZSP). • 1♂; Jardim Botánico; -21.2155, -47.7909; alt. 603m; (CPDC). • 1♂; Parque Estadual Carlos Botelho; -24.2008, -47.9675; alt. 600m; 2009-05-11; Esteyes, F.; et al. leg.; hand collected; (MZSP). • 2♂; Pousada Bacury ; -22.7976, -48.1159; alt. 484m; 1969-02-14; Kempf, W.; et al. leg.; (MZSP). • 1♀; Redenção da Serra; -23.2617, -45.5317; alt. 726m; (MZSP). • 1♂; Redenção da Serra; -23.2617, -45.5317; alt. 726m; (MZSP). • 2♂; Reserva Biológica do Alto da Serra de Paranapiacaba; -23.8067, -47.1233; alt. 919m; 1909-06-01; Luederwaldt, H. leg.; (MZSP). • 3♂; Rio Claro; -22.4145, -47.565; alt. 615m; 1962-01-18; Reichardt leg.; (MZSP). • 1♂; Salto; -23.1984, -47.2934; alt. 528m; 1976-03-14; Diniz, J. leg.; (DZUP). • 2♂; Serra da Cantareira; -23.4135, -46.5996; alt. 1063m; 1959-03-01; Kempf, W.; Santos leg.; (MZSP). • 1♂; Trilha do Ouriço; -23.5333, -46.1667; alt. 781m; 1998-12-01; Cassarotti, A. F. M. leg.; hand collected; (MZSP). • 1♂; [no locality given]; -22.4715, -48.9791; alt. 591m; 1953-09-13; Kempf, W. leg.; (DZUP). **ECUADOR – Orellana:** • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-08; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-19; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658,

-76.452; alt. 216m; 1995-02-20; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-09; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-10; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-11; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-12; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-13; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-14; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-15; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-16; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-17; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-18; Erwin, T.; et al. leg.; fogging; (MEPN). **PARAGUAY – Caaguazu:** • 1♀; 18 Km NE Caaguazu; -25.3477, -55.8834; alt. 316m; Duelli, P. leg.; (MZSP). – **Itapúa:** • 3♀; Capitán Meza; -26.8431, -55.3358; alt. 254m; Duelli, P. leg.; (MZSP). • 1♀; Capitán Meza; -26.8431, -55.3358; alt. 254m; 1974-10-31; Duelli, P. leg.; (MZSP).

Geographic range. Guyana*, Ecuador, Bolivia, Brazil (Acre, Bahia, Goiás, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), Paraguay, Argentina (Córdoba, Misiones). *: record from literature.

***Neoponera donosoi* (MacKay & MacKay, 2010)**

Figs. 28: b (distribution)

Pachycondyla donosoi MacKay & MacKay, 2010: 303 (☿, ♂). Figs. 73, 81, 236, 308, 428-432. ☿ holotype, Ecuador, Pichincha, La Unión del Rio Toachi, 15.vii.2005, #21156, and #21179, W. & E. Mackay [leg.], (MCZC) [absent from collection]. Paratypes: 6 ☿, 1 ♂ [same data as for holotype], (IAVH, MZSP, PUCE, USNM, CASC, WEMC) [not examined]. Note: paratypes are absent from IAVH, MZSP, PUCE, and USNM.

Combinations. In *Neoponera*: Schmidt & Shattuck 2014: 151.

Worker diagnosis. Head subquadrate, occipital corner round; antennal scape long, when pulled back exceeding posterior head margin by about three times apical scape width (link); distance between mandibular insertion to anterior margin of eye about as long as maximum eye length (link); in dorsal view, notopropodeal suture forming shallow groove (link); petiolar node somewhat block-shaped in lateral view, with posterior margin broadly convex, anterior margin longitudinally straight, and anterodorsal margin truncate. (Fig. 6f); dome of subpetiolar process medially straight to slightly convex, concavity between keel and dome absent to vestigial (Fig. 6f).

Worker Measurements (n = 4): HW: 1.18-1.31; HL: 1.53-1.65; EL: 0.39-0.43; SL: 1.57-1.69; WL: 2.31-2.43; PrW: 0.94-1.02; MsW: 0.55-0.63; MsL: 0.53-0.57; PW: 0.78-0.82; PH: 0.76-0.84; PL: 0.67-0.74; GL: 2.39-2.86; A3L: 0.86-0.98; A4L: 0.78-0.88; A3W: 1.25-1.33; A4W: 1.22-1.29; TLa: 6.16-6.55; TLr: 6.9-7.61. **Indices.** CI: 76.92-80.25; OI: 32.84-34.38; SI: 124.62-133.33; MsI: 102.19-114.29; LPI: 85.71-90.0; DPI: 105.26-117.65.

Queen. Unknown.

Male. See Mackay and Mackay (2010)

Comments. *Neoponera donosoi* is a small to medium-sized species in the *N. crenata* group (Fig. 26; ☿: TLa = 6.16 – 6.55 mm). We could not locate the holotype which should be at the MCZC in Harvard, nor the six paratype workers and one paratype male. Yet, except for the petiolar node, the characters described for the worker match those shown in the original description. The reader can use the following three characters present in *N. donosoi* to differentiate it from *N. antecurvata*, *N. dejeani* sp. nov., *N rugosula*, and *N. unidentata*, with which it probably

could be confused: 1) The antennal scape is long (see diagnosis), while in the other species it surpasses posterior head margin by approximately two times apical scape width; 2) The notopropodeal suture is present and forms a shallow groove. In the other three species this suture is completely absent or vestigial; 3) The posterior head corners are round, while in the other species these are mostly square.

Mackay and Mackay (2010) point out that "The worker of *P. donosoi* is nearly identical to that of *P. goeldii*" pg. 305. We consider that *N. goeldii* is somewhat similar to *N. donosoi* but these two species cannot be confused with each other since their petiolar nodes are quite different, especially in lateral view. Also, *N. goeldii* is clearly larger than *N. donosoi* (Fig. 26) and its body is furnished with abundant erect hairs which are also longer than those of *N. donosoi*.

We cannot make any robust inference with regards to its morphological variation since we found only four mostly identical specimens in collections. One of these was collected at the type locality in the province of Pichincha, in a protected forest within the Chocó-Darién biome which is virtually surrounded by heavily-impacted areas used mostly for cattle ranching and monoculture farming. The others belong from the nearby province, Santo Domingo de los Tsáchilas, also a quite disturbed region, and from Manglares Churrute, a semi-deciduous forest reserve in the province of Guayas, at the Pacific coastal region of Ecuador.

Natural history notes. See Mackay and Mackay (2010). Although *N. donosoi* probably has arboreal habits, A. Troya collected two workers in northwestern Ecuador from a Melastomataceae shrub without domatia which was growing near the ground surface.

Material examined. 5☿. **ECUADOR – Guayas:** • 1☿; Reserva Manglares Churrute, Sendero Los Monos; -2.53, -79.688; alt. 169m; 2013-07-22; Troya, A. leg.; beating; (MEPN). – **Pichincha:** • 1☿; ENDESA Forest Reserve; 0.13, -79.05; alt. 600m; 2003-12-06; Wild, A. leg.; (UTIC). • 1☿; Reserva Otongachi; -0.3, -78.9333; alt. 850m; 2008-08-04; Donoso, D. leg.; (MEPN). – **Santo Domingo de Los Tsáchilas:** • 2☿; 19 Km SSE Alluriquin; -0.3344, -78.9916; alt. 970m; 2003-09-01; Troya, A. leg.; hand collected; (MEPN).

Geographic range. Western Ecuador.

***Neoponera fiebrigi* Forel,1912**

Figs. 11: a, b; 28: a (distribution)

Neoponera crenata race *fiebrigi* Forel, 1912: 37. Figs. 447 – 450. [Raised to species by MacKay & MacKay, 2010: 324]. Primary type material composed of three specimens on single pin: ☿ lectotype [middle], 2 ☿ paralectotypes [top and bottom] [by designation of MacKay & MacKay, 2010: 324], Paraguay, San Bernardino, Fiebrig [leg.], (MHNG, AntWeb CASENT0907244) [images examined, link].

Neoponera crenata confusa lata Santschi, 1921: 86. ☿ [type specimen of unavailable name], Argentina, Chaco Austral, Formosa, Joergensen [leg.], (NHMB, AntWeb: CASENT0915256) [image examined, link]. **Syn. nov.** Note: Specimen determined as *N. moesta* by W. Mackay [error].

Neoponera latinoda MacKay & MacKay, 2010: 419. ☿ holotype, Brazil, Espírito Santo, Santa Tereza, 700m, 23 Feb 1967, mt. For. WL Brown, (MCZ-ENT00036276) [image examined, link]. **Syn. nov.**

Combinations. In *Pachycondyla*: Mackay and Mackay, 2010:324; In *Neoponera*: Schmidt and Shattuck 2014: 151.

Senior synonym of: *Neoponera crenata*: Brown 1957: 234; Bolton 1995: 305.

Subspecies of: *Neoponera crenata*: Kempf, 1972: 162.

Status as species. Mackay and Mackay, 2010: 324 [redescription].

Worker and queen diagnosis. Distance from anterior eye margin to mandibular insertion longer than maximum eye length (Fig. 4b); in lateral view, fore coxa with feeble to strongly impressed carina which may usually be arched running somewhat parallel to the coxal apical margin before vanishing on the surface, or (not often) may extend distally through the coxal surface, somewhat perpendicular to the apical coxal margin, down to approximately its median region (Fig. 11b); in lateral view, anterodorsal margin of petiolar node inclined, highest nodal point posterior to longitudinal midline (Fig. 3d); posterior face of node glabrous, smooth, and polished (Fig. 8g); in lateral view, node slightly higher than broad (Fig. 3d).

Worker Measurements (n = 26): HW: 1.49-2.0; HL: 1.65-2.25; EL: 0.45-0.59; SL: 1.55-2.1; WL: 2.4-3.35; PrW: 1.1-1.61; MsW: 0.71-1.15; MsL: 0.57-1.1; PW: 0.86-1.32; PH: 0.94-1.4;

PL: 0.75-1.1; GL: 2.74-4.7; A3L: 0.98-1.53; A4L: 1.05-1.51; A3W: 1.37-1.9; A4W: 1.35-1.93; TLa: 6.98-9.69; TLr: 7.84-11.08. **Indices.** CI: 84.62-97.3; OI: 25.0-32.89; SI: 90.0-108.45; MsI: 103.45-137.93; LPI: 75.0-95.45; DPI: 100.0-123.89.

Queen Measurements (*n* = 7): HW: 1.4-2.15; HL: 1.73-2.4; EL: 0.48-0.6; SL: 1.42-2.1; WL: 2.6-3.8; PrW: 1.33-1.65; MsW: 1.05-1.4; MsL: 1.3-1.75; PW: 1.0-1.3; PH: 1.05-1.4; PL: 0.77-1.15; GL: 3.15-5.51; A3L: 1.15-1.7; A4L: 1.15-1.7; A3W: 1.5-2.0; A4W: 1.5-2.0; TLa: 7.41-10.75; TLr: 8.26-12.86. **Indices.** CI: 80.92-95.56; OI: 27.85-34.84; SI: 95.48-105.0; MsI: 80.0-87.86; LPI: 66.96-84.62; DPI: 113.04-142.86.

Male diagnosis. Distance between posterior ocelli slightly longer than that between anterior and posterior ocelli (Fig. 12c); notauli well-impressed, cross ribbed, almost meeting posteriorly (Fig 12b); anapleural sulcus deeply impressed, reaching ventral surface of mesopleuron (Fig. 12a); lateral carina absent on petiolar node; posterior face of petiolar node glabrous and smooth (as in worker and queen).

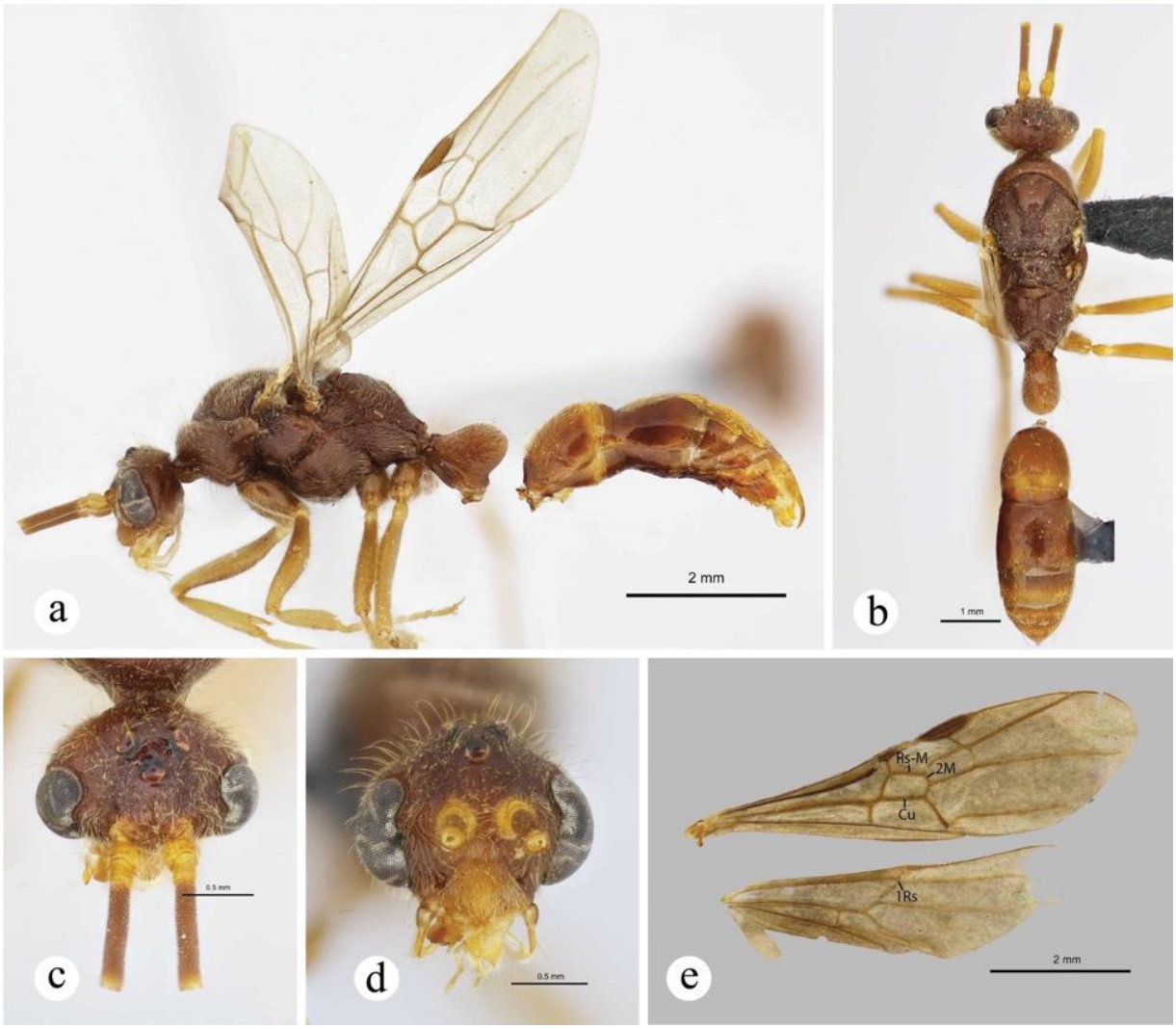


Fig. 12. *Neoponera fiebrigi*. ♂ (MZSP). Brazil: São Paulo. **a.** Lateral view; **b.** Dorsal view; **c.** Head in anterodorsal view; **d.** Head in frontal view; **e.** Fore and hind wings.

Male Measurements (*n* = 3): HW: 1.1-1.2; HL: 1.06-1.29; EL: 0.67-0.78; SL: 0.24-0.25; WL: 2.74-3.14; PrW: 1.1-1.37; MsW: 1.18-1.49; MsL: 1.53-1.88; PW: 0.59-0.63; PH: 0.78-0.86; PL: 0.74-0.9; GL: 2.86-4.51; A3L: 0.94-1.3; A4L: 1.02-1.2; A3W: 1.14-1.29; A4W: 1.33-1.57; TLa: 6.51-7.77; TLr: 7.41-9.8. **Indices.** CI: 91.67-111.11; OI: 56.67-65.45; SI: 19.61-22.73; MsI: 76.92-79.17; LPI: 86.36-113.92; DPI: 68.89-78.95.

Comments. *Neoponera fiebrigi* is a medium-sized to relatively large species (Fig. 26), in particular the queen (☿: TLa = 6.98 – 8.98 mm;♀: 7.08 – 10.97 mm). Except for the absence of pilosity on the nodal posterior face, the fore coxal carina in workers and queens, and its overall size, *N. fiebrigi* is virtually identical to *N. crenata*. This latter has piligerous punctae on the entire nodal surface, lacks fore coxal sculpture, and is clearly smaller than *N. fiebrigi* (Fig. 26). In this case, their morphological similarity could be explained through their phylogenetic relatedness (Troya et al, unpublished).

This species is also very similar to *N. moesta*. Besides the lateral fore coxal carina which is absent in *N. moesta*, the anterodorsal nodal margin of *N. fiebrigi* is inclined, while in *N. moesta* it is only slightly inclined or without slope; the eye of *N. moesta* is proportionally large as compared to its head length, so that the anterior eye margin is very close to the mandibular insertion, while in *N. fiebrigi* the eye is proportionally smaller, very similar to that of *N. crenata*, so that its anterior margin is more distanced from the mandibular insertion.

Mackay and Mackay (2010) erected *N. latinoda* (here considered synonym of *N. fiebrigi*) based on five specimens from southern Brazil. The characters they provide in their description match with those of the examined image of the lectotype of *N. fiebrigi* at MHNG. In this revision, based on more material representing a broader distribution range, including central Mato Grosso do Sul in Brazil, southern Paraguay, and northern Argentina (Fig. 28a), we found new key diagnostic characters, namely the fore coxal carinae and the glabrous posterior nodal face, which are invariably present in all examined specimens. Since the fore coxal carina is hardly discernible from the image of the type, we asked Amanda Dias, our fellow myrmecologist who visited the MHNG. She confirmed this feature is present on the three type specimens, and it is evident on the holotype of *N. latinoda* (MCZ-ENT00036276, link). These two apomorphies mostly characterize *N. fiebrigi* and are very useful for differentiating it from *N. moesta* and *N. crenata*. An additional character, the anterodorsal slope on the petiolar node, is also apomorphic among all examined specimens. This trait, however, can sometimes be confused with that present in *N. moesta*, where it is less pronounced.

Populations of *N. fiebrigi* are morphologically homogeneous across its range, but its body size can vary significantly as compared to most other species in the genus. Only *N. rugosula* shows a similar pattern (Fig. 26). For example, in workers the lowest size range (TLa ~ 7 mm) in the

distribution is represented by specimens from Guairá, southern Paraguay (Fig. 13a), while the upper size range (TLa ~ 10 mm) is represented by a specimen from Parque Nacional Iguazú, northeastern Argentina (Fig. 13b). As for the queens, although we just measured seven individuals, a similar pattern was evident with the largest specimen (TLa ~ 11 mm) on the upper range of the size distribution, and the smallest (TLa ~ 7.5 mm) on the opposite extreme. These variations occur randomly in the geographic distribution of this species, this is, we did not find a particular trend associated to any particular biome or region.



Fig. 13. Size difference among examined *Neoponera fiebrigi* populations: **a.** Smallest worker from Paraguay: Guairá, ca. 7 mm TLa (UTIC: UTIC254630), in contrast to **b.** Largest worker from Argentina: Misiones, ca. 10 mm TLa (CPDC: AT689). Both images at same scale. **c.** Lateral fore coxal carina of the specimen from Argentina.

Mackay and Mackay (2010) report a 14 mm queen (no site provided), which certainly fits into the size distribution we have here shown. We do not consider in our measurements the abdominal segments V to VII in workers and queens, and V to IX in males, since these are frequently contracted or expanded.

Neoponera fiebrigi is a commonly collected species, its populations are restricted to eastern South America, with most records pertaining to the Brazilian Atlantic Forest. Apparently, few populations inhabit the Pampa in the state of Rio Grande do Sul, and in the humid Chaco, southern Paraguay and northern Argentina. We are aware of scant records from the southern range of *N. fiebrigi* but we think this is artifactual since this species has possibly been confused in the past with *N. crenata* and *N. moesta*. Additional factors may be associated with chronic

anthropogenic disturbance leading to this species' populations displacement from their native habitats, as well as the rarity of ant monitoring and/or collection events in this region.

Natural history notes. See Mackay and Mackay (2010). Virtually nothing is known from this taxon but probably it is an arboreal dweller. Most specimens from which we could extract information of their labels were obtained through arboreal Malaise. Some specimens, however, have been collected from twigs and rotten logs on the ground. A worker from Igaratá, São Paulo was collected by T. Fernandes inside a twig with nests of *Pheidole sigillata* Wilson and *Pheidole sospes* Forel.

Material examined. 87☿, 17♀. **ARGENTINA – Chaco:** • 1☿; Chaco Austral; -26.0, -60.5; Joergensen leg.; (NHMB). – **Misiones:** • 17 km E Oberá; -27.4447, -54.9403; alt. 280m; 2013-03-21; Tubaro, P. leg.; (MACN). • 1☿; Iguazú; -25.8454, -54.3436; alt. 257m; 1998-09-21; Leponce leg.; (CPDC). • 1☿; Parque Nacional Iguazú; -25.675, -54.456; alt. 171m; 1998-03-03; Hanisch, P. leg.; (MACN). • 1☿; Reserva Natural Osonunu; -27.2807, -55.5754; alt. 173m; 2015-01-12; Hanisch, P. leg.; (MACN). • 1☿; Reserva Natural Osonunu; -27.2824, -55.5754; alt. 225m; 2015-01-18; Hanisch, P. leg.; (MACN). • 1☿; Reserva Natural Osonunu; -27.2791, -55.5785; alt. 169m; 2015-01-12; Hanisch, P. leg.; (MACN). **BRAZIL – Bahia:** • 1♀; Boa Nova; -14.3656, -40.2076; alt. 729m; (CPDC). • 3☿; Enchuzilhada; -15.5833, -40.9833; alt. 980m; 1975-11-01; Alvarenga, M. leg.; (MZSP). • 1♀; Itororó; -15.1167, -40.05; alt. 255m; (CPDC). • 1☿; Itororó; -15.1167, -40.05; alt. 255m; (CPDC). • 3☿; Parque Nacional de Boa Nova; -14.4169, -40.1161; alt. 842m; 2003-03-05; Santos, J. R. M. leg.; (CPDC). • 3☿; Poções; -14.5203, -40.3637; alt. 815m; 2004-02-05; Maia, J. R. leg.; (CPDC). • 1☿; Vitória da Conquista; -14.8619, -40.8445; alt. 882m; (CPDC). – **Espírito Santo:** • 1☿; Mantena; -18.7547, -40.8908; alt. 201m; (CPDC). • Santa Teresa; -19.9363, -40.5964; alt. 700m; 1967-02-23; Brown, W. leg.; (UTEP). • 3☿; Santa Teresa; -19.9363, -40.5964; alt. 700m; 1967-02-23; Brown, W. leg.; (MCZC). • 1☿; Santa Teresa; -19.9363, -40.5964; alt. 700m; 1967-02-23; Brown, W. leg.; (UTEP). • 1☿; Santa Teresa; -19.9368, -40.5983; alt. 617m; (MZSP). – **Minas Gerais:** • 1☿; 4 km SW Viçosa; -20.777, -42.842; alt. 702m; Chaul, J. leg.; (UFVLABECOL). • 1☿; Itambacuri; -18.0333, -41.6667; alt. 308m; 1958-01-16; Lenko, K. leg.; (MZSP). • 1☿; Lavras; -21.2485, -45.0014; alt. 923m; 2002-02-06; Santos, M. S.; Dias, N. S.

leg.; (CPDC). • 1♀; Mata Cristais, Universidade Federal do Viçosa; -20.777, -42.842; alt. 710m; 2013-05-01; Chaul, J.; Jesus, R. leg.; (UFVLABECOL). • Mata do Paraiso, Universidade Federal do Viçosa; -2080601.0, -42.8514; alt. 781m; 2017-03-01; Jesus, R. leg.; Malaise aerial; (UFVLABECOL). • Mata do Paraiso, Universidade Federal do Viçosa; -20.7968, -42.8613; alt. 782m; 2017-03-31; Jesus, R. leg.; Malaise aerial; (UFVLABECOL). • 3♂; Mata do Paraiso, Universidade Federal do Viçosa; -20.75, -42.85; alt. 681m; 2000-11-23; Nascimento, I.C. leg.; (DZUP). • 1♂; Mata do Paraiso, Universidade Federal do Viçosa; -20.75, -42.85; alt. 704m; 2000-11-23; Nascimento, I. C. leg.; (DZUP). • 1♂; Mata do Paraiso, Universidade Federal do Viçosa; -20.8023, -42.8586; alt. 752m; 2000-11-23; Mariano, C. S. F. leg.; (CPDC). • 1♂; Mata do Paraiso, Universidade Federal do Viçosa; -20.75, -42.85; alt. 681m; 2019-01-01; Chaul, J. leg.; (UFVLABECOL). • 1♂; Parna Caparaó; -20.4192, -41.8514; alt. 1300m; 2011-12-05; Campos, R. leg.; pitfall; (UFVLABECOL). • 5♂; Serra do Caraça; -20.1333, -43.4833; alt. 1380m; 1981-11-01; Lenko, K.; Martins, Silva leg.; (MZSP). • 3♂; Serra do Caraça; -20.1333, -43.4833; alt. 1380m; 1961-11-01; Lenko, K., Martins, Silva leg.; (MZSP). • 1♀; Viçosa; -20.7474, -42.8833; alt. 648m; (CPDC). • 1♂; Viçosa; -20.7474, -42.8833; alt. 648m; (CPDC). • 1♂; Viçosa; -20.8167, -42.8833; alt. 760m; 2010-01-01; Audino, L. leg.; (DZUP). • 1♂; Viçosa; -20.8167, -42.8833; alt. 760m; 1998-02-11; Soares, M. leg.; (UFVLABECOL). – **Paraná:** • 1♀; Bocaiúva do Sul; -25.1833, -49.1333; alt. 1003m; (MZSP). • 1♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-05-27; Malaise; (DZUP). • 1♂; Parque Estadual do Cerrado; -24.1667, -49.6667; alt. 783m; 2015-01-15; Feitosa,; etal. leg.; (DZUP). • 1♀; RPPN Fazenda Assu; -24.15, -53.95; alt. 321m; 2013-03-23; Gonçalves, R.; Soares, P. leg.; (DZUP). • 1♂; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2009-11-14; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♂; Reserva Natural Guaricica, dos Fornos trail; -25.3, -48.65; alt. 36m; 2018-11-01; Troya, A. leg.; hand collected; (MEPN). • 1♂; Rio Negro; -26.0864, -49.7793; alt. 804m; 1925-11-01; Witte, M. leg.; (MZSP). • 1♂; Rolândia; -23.3091, -51.3757; alt. 733m; (MZSP). • 1♂; Serra da Baitaca; -25.3768, -49.0261; alt. 940m; 2021-01-15; Tozetto, L. leg.; (DZUP). • 1♂; São José dos Pinhais; -25.6, -49.1833; alt. 880m; 2014-10-19; Domahovski, A. C. leg.; Malaise; (DZUP). • 1♂; São José dos Pinhais; -25.6, -49.1833; alt. 880m; 2016-07-09; Domahovski, A. C. leg.; (DZUP). • 1♂; São José dos Pinhais; -

25.6049, -49.1936; alt. 897m; 2018-10-13; Domahovski, A. leg.; (DZUP). – **Rio Grande do Sul:** • 1♂; Harmonia; -29.5492, -51.4242; alt. 27m; (MZSP). • 3♂; Mata, Morro de São Pedro; -30.1667, -51.1; alt. 289m; 2008-01-18; Ulyssea, M. A. leg.; (DZUP). • 2♂; Nova Petrópolis; -29.3718, -51.1076; alt. 581m; 1959-09-01; Plaumann, F. leg.; (MZSP). • 1♂; Panambi; -28.2833, -53.4833; alt. 483m; 2018-12-12; Assmann, I. C leg.; (DZUP). • 1♂; Porto Alegre; -30.0346, -51.2177; alt. 10m; (MZSP). • 1♂; Santa Cruz do Sul; -29.7167, -52.4333; alt. 61m; 2009-11-12; Lemes, J. A. R leg.; pitfall; (DZUP). • 1♂; São José do Maratá; -29.61, -51.4744; alt. 17m; (MZSP). – **Rio de Janeiro:** • 1♀; Corcovado; -22.957, -43.2112; alt. 150m; (MZSP). • 2♀; Corcovado; -22.957, -43.2112; alt. 150m; 1958-05-02; Alvarenga, M. leg.; (MZSP). • 1♂; Floresta da Tijuca; -22.9543, -43.2819; alt. 518m; (MZSP). • 1♀; Floresta dos Macacos; -22.9667, -43.2333; alt. 235m; 1961-05-30; Alvarenga, M. leg.; (DZUP). • 1♂; Petrópolis; -22.5089, -43.1776; alt. 831m; 1944-12-12; Kempf, W. leg.; (MZSP). – **Santa Catarina:** • 1♀; 4 Km SE of Nova Teutônia; -27.1833, -52.3833; alt. 300m; 1974-12-01; Plaumann, F. leg.; (MZSP). • 1♂; Chapecó; -27.1002, -52.6153; alt. 674m; 2013-03-01; Belo, M.; Savaris, M. leg.; Malaise; (DZUP). • 1♂; Ibirama; -27.0552, -49.5188; alt. 255m; Luederwaldt, H. leg.; (MZSP). • 1♂; Monte Belo; -27.1, -52.6167; alt. 615m; 2013-03-01; Savaris, M.; Lampert, S. leg.; Malaise; (DZUP). • 1♀; Nova Teutônia; -27.2333, -52.3833; alt. 400m; (MZSP). • 1♂; Nova Teutônia; -27.2333, -52.3833; alt. 400m; (MZSP). • 1♂; Nova Teutônia; -27.1833, -52.3833; alt. 300m; 1960-05-01; Plaumann, F. leg.; (DZUP). • 1♂; Rodeio; -26.9244, -49.3688; alt. 88m; (MZSP). – **São Paulo:** • 1♂; 1km W of Igaratá, Cachoeira Pedra Bonita; -23.2, -46.1667; alt. 717m; 2015-04-14; Fernandes, T. leg.; (MZSP). • 1♀; Caraguatatuba; -23.6213, -45.4231; alt. 30m; (MZSP). • 1♂; Embu-Guaçu; -23.8276, -46.8148; alt. 749m; 1972-01-23; Lane, F leg.; (MZSP). • 4♀; Estação Piaçaguera; -23.8526, -46.3747; alt. 8m; 1911-01-06; Wederwaldt, H. leg.; (MZSP). • 1♂; Ilha dos pescadores (Ilha da Vitória); -23.75, -45.01; alt. 33m; (MZSP). • 1♂; Mogi das cruzes; -23.5333, -46.1667; alt. 781m; (MZSP). • REBIO do Alto da Serra de Paranapiacaba; -23.8067, -47.1233; alt. 919m; 1909-06-01; Wederwaldt, H. leg.; (MZSP). • REBIO do Alto da Serra de Paranapiacaba; -23.8067, -47.1233; alt. 919m; (MZSP). • 1♂; REBIO do Alto da Serra de Paranapiacaba; -23.8067, -47.1233; alt. 919m; 1910-10-01; Iheriug, M. V. leg.; (MZSP). • 2♂; REBIO do Alto da Serra de Paranapiacaba; -23.8067, -

47.1233; alt. 919m; 1909-06-01; Wederwaldt, H. leg.; (MZSP). • Serra da Cantareira; -23.4135, -46.5996; alt. 1063m; 1959-03-01; Kempf; Santos leg.; (MZSP). • Serra da Cantareira; -23.4144, -46.5999; alt. 1103m; 1959-01-03; Kempf; Santos leg.; (MZSP). • 2☿; São Roque; -23.5291, -47.1374; alt. 784m; 1971-12-25; Lane, F. leg.; (MZSP). • 1☿; Vila Formosa; -23.5671, -46.5432; alt. 802m; 1959-04-29; Lane, F. leg.; (MZSP). **PARAGUAY – Caaguazu:** • 1☿; 18 Km NE Caaguazu; -25.3835, -55.8334; alt. 315m; 1974-09-27; Duelli, P. leg.; (MZSP). **– Canindey√∫:** • 1☿; Reserva Natural del Bosque Mbaracay√∫, Jejuim√≠; -24.1, -55.4667; 1996-07-19; A.C.F. Costa leg.; Malaise 5; (ALWC). **– Cordillera:** • 1☿; San Bernardino; -25.2667, -57.3167; Fiebrig leg.; (MHNG). **– Guairá:** • 1☿; Roque Gonzalez; -25.88, -57.287; alt. 133m; 1995-01-14; Garcete, B. leg.; (UTIC). **– Ybycuí:** • 1☿; Parque Nacional Ybycuí; -26.0167, -57.05; alt. 135m; 1994-10-01; Garcete, B. leg.; (UTIC).

Geographic range. Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, Rio Grande do Sul, Paraná, Santa Catarina), Paraguay, Argentina (Formosa, Misiones).

***Neoponera globularia* (MacKay & MacKay, 2010)**

Figs. 14: a – e; 28: a (distribution)

Pachycondyla globularia MacKay & MacKay, 2010: 358 (☿, ♂). Figs. 483 – 487. ☿ holotype, Bolivia, Huachi Beni, viii. W.M. Mann [leg.], USNM [examined]. Paratypes: 6 ☿, 1 ♀ [same data as for holotype], (CASC, AntWeb: CASENT0923100, link) [image examined], (IAVH, MCZC, MZSP, USNM, WEMC). Note: paratype is absent from IAVH.

Combinations. In *Neoponera*: Schmidt & Shattuck, 2014: 151

Status as species. Bezděčková et al. 2015 et al., 2015: 123

Worker and queen diagnosis. Head subquadrate (link); antennal scape, when pulled posterad exceeding posterior head margin by two times apical scape width; in lateral view, distance from anterior eye margin to mandibular insertion about one eye maximum length (link), in queens this distance is slightly shorter; in lateral view, petiolar node block-shaped, subquadrate, anterodorsal margin usually slightly inclined (link); in dorsal view, nodal margin subcircular or ovoid ((Fig. 8a); largest workers and queens of the *N. crenata* group (Fig. 26).

Worker Measurements (*n* = 21): HW: 1.62-2.12; HL: 1.94-2.44; EL: 0.51-0.62; SL: 1.84-2.38; WL: 2.81-3.75; PrW: 1.25-1.62; MsW: 0.81-1.12; MsL: 0.69-0.94; PW: 0.97-1.44; PH: 1.09-1.5; PL: 1.06-1.38; GL: 2.94-5.12; A3L: 1.06-1.41; A4L: 1.28-1.66; A3W: 1.5-2.03; A4W: 1.56-2.0; TLa: 8.22-10.44; TLr: 9.62-12.28. **Indices.** CI: 81.25-97.14; OI: 28.53-32.26; SI: 96.88-118.97; MsI: 103.33-143.48; LPI: 82.61-109.09; DPI: 87.5-105.88.

Queen Measurements (*n* = 8): HW: 1.88-2.38; HL: 2.19-2.69; EL: 0.56-0.74; SL: 2.0-2.38; WL: 3.25-4.25; PrW: 1.38-2.0; MsW: 0.94-1.81; MsL: 1.81-2.25; PW: 1.16-1.62; PH: 1.19-1.66; PL: 1.12-1.44; GL: 4.19-5.31; A3L: 1.19-1.69; A4L: 1.38-1.94; A3W: 1.75-2.38; A4W: 1.81-2.28; TLa: 9.14-12.0; TLr: 11.08-13.41. **Indices.** CI: 83.13-89.19; OI: 30.0-33.33; SI: 92.75-109.09; MsI: 48.39-88.52; LPI: 86.79-102.33; DPI: 95.45-113.04.

Male diagnosis. Notauli well-impressed, not touching posteriorly (Fig. 14b); anapleural sulcus well-impressed, slightly reaching pleural ventral surface (Fig. 14a); in lateral view, petiolar node about as high as broad, lateral carina feebly impressed, anterior margin inclined, posterior margin mostly straight to feebly convex (Fig. 14a); in dorsal view, node relatively circular (Fig. 14b); hindwing bearing 9 hamuli.

Male (first description). Measurements (*n* = 3): HW: 1.1-1.62; HL: 1.3-1.84; EL: 0.75-0.94; SL: 0.24-0.38; WL: 3.1-3.56; PrW: 1.15-1.75; MsW: 1.35-2.06; MsL: 1.1-2.5; PW: 0.75-1.06; PH: 0.8-1.16; PL: 0.9-1.0; GL: 3.85-5.0; A3L: 0.85-1.44; A4L: 0.95-1.69; A3W: 1.25-1.81; A4W: 1.41-2.12; TLa: 7.1-9.41; TLr: 9.15-11.28. **Indices.** CI: 81.86-88.46; OI: 57.69-68.18; SI: 21.59-23.08; MsI: 81.36-122.73; LPI: 86.49-112.5; DPI: 83.33-106.25.

Head. Frontal view: subrhomboid. Mandible spatulate, longer than wide, blunt apically. About two mandalus (maximum length) fit on mandibular dorsum, mandibular apex, when mandible is closed, touches lateral margin of labrum. Prementum lacking transverse dome. Palp formula: 6,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, somewhat globular-shaped in lateral view, covering anteclypeus. Area between posterior margin of clypeus and supraclypeal area weakly concave. Posterior supraclypeal area round. Supraclypeal area slightly protruding from cuticule. Distance between internal margins of antennal sockets approximately one socket diameter. Torular lobe small but well-developed, covering less than 5 % of antennal bulbus. Eye suboval, slightly notched in the dorsal third, maximum length slightly more than half head length, convex, globose, placed at

cephalic mid-length. Ocellar area weakly protruding from cuticle. Ocellar area placed posterad to vertex. Anterior ocellus maximum length subequal to that of posterior ocelli. Ocelli not equidistant to each other, distance between anterior ocellus to posterior ocelli shorter than interposterior ocellar distance, slightly more than one anterior ocellus maximum length. Occipital carina present, well-developed. Scape cylindrical, one third longer than pedicel. Length of first flagellomere longer than second flagellomere. **Mesosoma**. Lateral view: Dorsal margin convex. Pronotum lacking humeral carina, completely rounded. Anterior subalar area approximately as broad as tegular maximum width. Anapleural sulcus well-developed, running laterally on mesopleuron and reaching part of ventral mesopleural region. Metanotal trough deeply impressed. Metapleuropropodeal suture deeply impressed. Posterolateral margin of propodeal declivity carinate, running along the posterodorsal propodeal margin. Anterolateral propodeal corner rounded. Propodeal spiracle slit-shaped. Posteroventral cuticular flap at metapleural gland opening reduced, weakly projecting dorsad, gland orifice completely discernible laterally. Dorsal view: mesoscutum broader than long, about two times length of mesoscutellum. Mesoscutum anterior triangular impression present, weakly impressed. Parapsidal lines strongly impressed, running straight. Notaulus present, strongly impressed, cross ribbed, not meeting posteriorly, not extending to transscutal line. Transscutal sulcus well-developed. Scutoscutellar sulcus present, straight, strongly impressed, cross ribbed, not completely separating mesoscutum from mesoscutellum. Mesoscutellum subtrapezoid, domed. Metascutellum well-developed, clearly discernible dorsally, surface even, convex. Anterodorsal median propodeal sulcus present, strongly impressed. Posterior face of propodeal declivity slightly concave. Propodeal lateral margins parallel at base, convergent dorsad. Ventral view: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process vestigial. Metasternal process well-developed, inclined posterad, ca. 10° in lateral view, fang-shaped, flattened anteroposteriorly, apex about as long as mid height of metacoxal internal margin, space between lobes narrower than width of each, internal margins running parallel. Metasternal process external margins slightly convergent. **Wings**. Hyaline. Slightly iridescent. Forewing venation Ogata type Ia: submarginal cells 1, 2 and discoidal present, vein 2M present, 2r-rs offset from Rs+ m, Rs+M two times longer than 2M, fine setose layer evenly covering surface, except for subbasal and basal cells which bear less pilosity. Hindwing venation Cantone and Von Zuben Type I: basal and subbasal cells and vein 2M present, 1R well-developed, 1Rs poorly developed. Jugal lobe present. **Legs**. Mesofemur

slightly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora flattened roughly on distad half, surface even without groove. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur half-length of posterior spur. Pretarsal claw arched, with two tiny, feebly raised teeth, one near base and another at middle. Arolium present, roughly 0.5 times length of pretarsal claw. **Petiole**. Lateral view: Petiolar node anterior margin straight, inclined ca. 30° posterad; posterior margin vertically straight to weakly convex, anterior and posterior margins reaching approximately same level dorsally, middorsal margin convex, highest point posterior to nodal longitudinal midline, posterior face slightly convex. Subpetiolar process subtriangular, with blunt, keel-shaped, grooved anterior cusp, followed posteriorly by relatively flat region bordered by longitudinal carinae, mostly smooth, with one weakly raised longitudinal carina medially. Lateral projection of anteroventral nodal carina well-developed, with blunt tip projecting dorsad. Lateral nodal carina weakly impressed. Anteroventral nodal carina incomplete, strongly concave medially. **Gaster**. Lateral view: Prora well-developed, with blunt tip projecting anteroventrad; posterior region slightly flattened and broadened. Anterior margin of tergum of A3 convex. Cinctus moderate. Dorsal view: Tergum of A3 longer than A4. Abdominal sternum 7 with even surface, not cancave, bearing scattered erect and suberect hairs. Spine at posterior margin of tergum of A8 well-developed, extending posterad, beyond posterior margin of sternum of A9, acute, flattened laterally. Sternum of A9 longer than broad, posterior margin convex. Pygostyles present, about three times longer than broad. **Color**. Mandibles and legs yellowish brownish or dark brown, antennae ferruginous brown. **Pilosity**. Body with sparse, flexuous, brownish, erect and suberect hairs. Appressed pubescence present, mostly fine small hairs distributed across integument which is easily discernible. Meso- and metatarsi bearing scant spine-like setate and abundant finer setae. **Sculpture**. Integument polished, with abundant, shallowly impressed piligerous punctures. Striae on head absent, mesosoma lacking striae, except for axilar areas and on posterior propodeal face. Petiolar node lacking striae.

Comments. The workers and queens of *Neoponera globularia* are the largest in the *N. crenata* group (Fig. 26; ☿: TLa = 8.22 – 10.44 mm; ♀: TLa = 9.14 – 12 mm). We did not detect morpho-clines in this species across their distribution range. Except for slight differences in the shape of the petiolar node, for example, in some specimens being more ovoid-like than in others, which occur randomly irrespective of geographic location and are attributable to normally

expected populational variations in a broadly distributed species, the remaining external body structure is virtually identical in our examined material. The dark brown coloration of the body also appears to be homogeneous in our material, except for the Costa Rican worker from Heredia which is light brown. Males, on the other hand, are light-colored as compared to workers, mostly brownish and pale yellowish.

Neoponera globularia could be confused with *N. crenata*, especially because their petiolar nodes are very similar in lateral view. In *Neoponera* groups, the nodal shape and plain of view are usually key factors in species discrimination. This is particularly important in the *N. crenata* group. These two species are immediately distinguished when examining the nodal shape in dorsal view, this is, subtriangular in *N. crenata*, and subcircular or ovoid in *N. globularia*. Their size is also a good clue to tell them apart (Fig. 26).

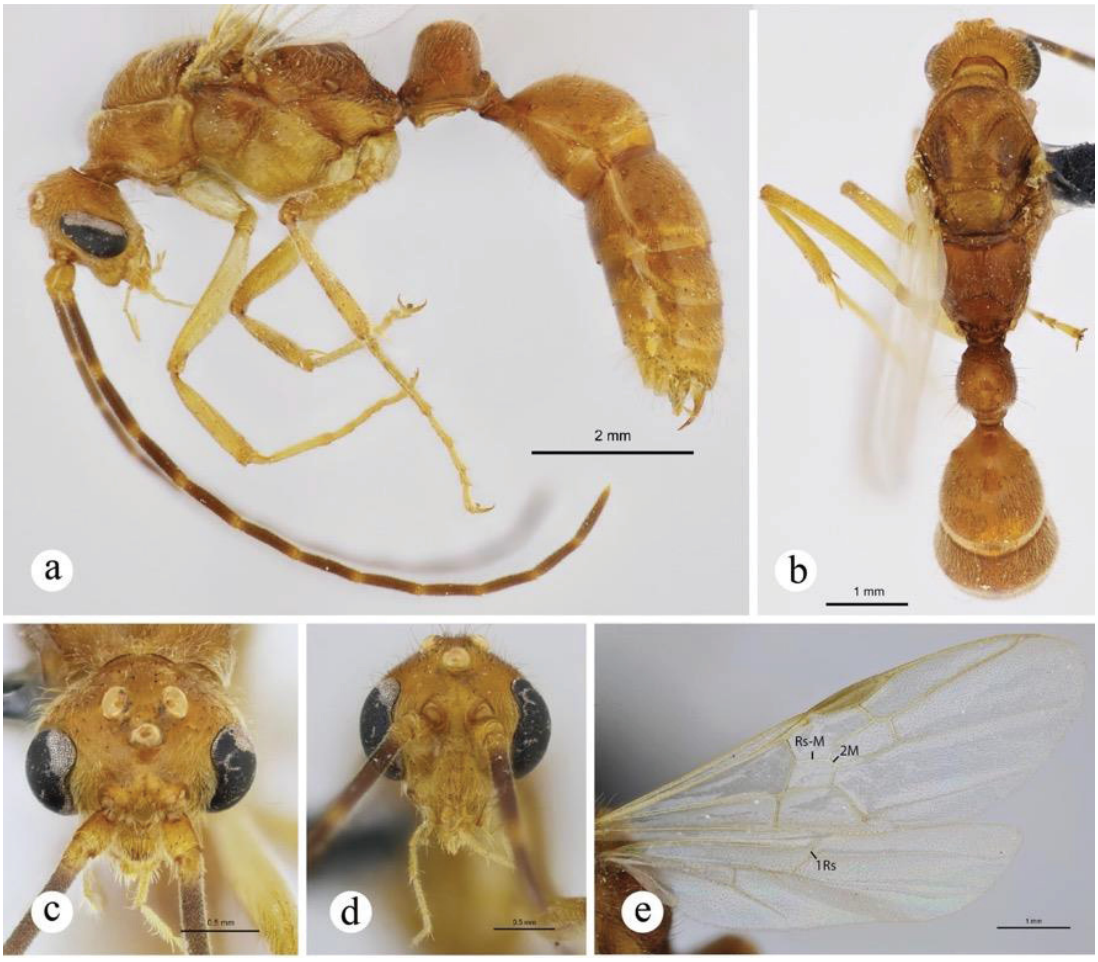


Fig. 14. *Neoponera globularia*. ♂ (MEPN: ATPFOR1967). French Guiana: Saint-Laurent-du-Maroni. **a.** Lateral view; **b.** Dorsal view; **c.** Head in anterodorsal view; **d.** Head in frontal view; **e.** Fore and hind wings.

Another similar species is *N. fiebrigi* which is the second largest taxon in the *N. crenata* group. This species bears a carina on the fore coxa which is absent in *N. globularia*, and also has a glabrous posterior nodal face, which has always piligerous punctae in *N. globularia*, although sometimes are not easily visible. Besides these two species, practically no other has an approximate appearance. However, the user may find doubts when comparing it to *N. moesta* and *N. cylindrinodis* sp. nov. The easiest way to solve any potential issue here is by comparing their size, both are much smaller than globularia (Fig. 26). Second, the eye of *N. moesta* is comparatively large, its anterior margin is very close to the mandibular insertion, and in regards to *N. cylindrinodis* sp. nov., the petiolar node is somewhat elongated in lateral view and barrel-shaped in dorsal view.

Neoponera globularia has not been collected as much as other species in the genus, but it is not a rare taxon either. The only record from Costa Rica, obtained during the ALAS project led by J. Longino, confirms its incursion in Central America and is suggestive of its potential presence in other nearby regions including Nicaragua, Panama and northern Colombia. We hypothesize that it was collected in the past being misidentified as *N. crenata* or any other *N. crenata*-like form. Further revision of already collected Central American material, as well as new expeditions will inform how rare or abundant this species is in that region. In South America its range extends from the lowland rain forests of Trinidad and Tobago, to northern Venezuela in the Cordillera de La Costa, west to the southern Chocó-Darién in Colombia and Ecuador, and part of their Andean region, for example at Parque Nacional Podorcarpus in the latter, and Parque Nacional Serranía de los Churumbelos in Colombia, with this site representing the highest altitudinal range (1400 m). Relatively few records originate from Amazonia but these are quite spread, from the lowland rains forests in northern Guyana to southeastern Perú (Madre de Dios) and northern Bolivia, east to the Brazilian states of Rondônia, Mato Grosso, and Manaus in Amazonas. On northeastern Brazil we found scant records from the Caatinga biome in Ceará and Bahia, and from the Atlantic Forest in Bahia and Espírito Santo. The southernmost range in this continent is represented by few records from the Humid Chaco in southern Paraguay (Mackay and Mackay 2010).

Natural history notes. See Mackay and Mackay (2010). *N. globularia* is a typical arboreal species in the *N. crenata* group, it has been collected through fogging, arboreal Malaise, arboreal pitfall, sweeping, among other methods. A. Mathews found an arboreal nest containing

Microtermes sp. (Termitidae) prey 15 Km N Xavantina in Mato Grosso, Brazil. P. Kazan, while collecting specimens of *Eciton rapax* Smith in Amazonian Ecuador found a worker of *N. globularia*, and on the label is written "prey of *Eciton rapax*". John Lattke collected two workers feeding on honeydew produced by unidentified scale insects in an urban park in Curitiba, Brazil. Benjamin Palm bred a captive colony from French Guiana. He observed that pupae do not require any special substrate, they are just placed by the workers; foraging workers accept both dead and live prey which usually consisted mostly in common house flies; the ants seemed to show preference for similar-sized or even larger prey items; workers were fed with both sugary water and honey; when in danger the workers produce a relatively loud stridulation easily discernible by humans if approaching closer to them.

Material examined. 52☿, 11♀, 6♂. **BOLIVIA** • 1☿; HuachiBeni ; -15.6667, -67.25; Mann, W. leg.; (CASC). **BRAZIL – Acre:** • 1☿; Fazenda Experimental Catuaba; -10.0667, -67.6167; alt. 214m; 2014-01-19; Denicol, M. R.; Santos, A. M. leg.; arboreal pitfall; (DZUP). – **Amapá:** • 1☿; Parque Nacional Montanhas do Tumucumaque; 1.6167, -52.4833; alt. 150m; 2017-07-25; Feitosa, R.; et al. leg.; (DZUP). • 1♀; Serra do Navio; 0.9, -52.0; alt. 152m; 1959-09-01; (MZSP). • 1♀; Serra do Navio; 1.625, -52.4845; alt. 166m; 2017-07-25; Feitosa, R.; et al. leg.; (DZUP). • 1☿; Serra do Navio; 0.9019, -52.0032; alt. 152m; (MZSP). – **Amazonas:** • 1☿; Fazenda Porto Alegre; -2.3667, -59.9333; alt. 133m; (CPDC). • 1♀; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9333, -59.9667; alt. 110m; 1968-05-01; Faustino leg.; (MPEG). • 1☿; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.963, -59.9229; alt. 111m; 2005-10-02; Aguiar, A. leg.; Malaise; (INPA). – **Bahia:** • 1♀; 5.5km W of Gov. Lomanto Junior, Barro Preto IX; -14.8, -39.4166; alt. 133m; 2006-05-05; Santos, et al. leg.; (CPDC). • 1☿; 5.5km W of Gov. Lomanto Junior, Barro Preto IX; -14.8, -39.4166; alt. 133m; 2006-05-05; Santos, et al. leg.; (CPDC). • 1♀; Bahia; -12.5621, -42.686; alt. 910m; 2000-06-16; Santos, J. R. M. leg.; (CPDC). • 1♀; Praia do Norte; -14.6167, -39.0667; alt. 8m; 2004-11-16; Nascimento, I. leg.; (INPA). – **Ceará:** • 1☿; 2km S of Pacoti; -4.25, -38.9167; alt. 700m; 2001-01-01; Hites, N. leg.; (CPDC). – **Espírito Santo:** • 1☿; Linhares; -19.4, -40.0667; alt. 35m; 1972-09-01; Alvarenga, M. leg.; (MZSP). – **Mato Grosso:** • 2☿; 150 Km N Xavantina; -12.85, -53.8333; alt. 350m; 1967-12-08; Mathews, A. G. A. leg.; (MZSP). • 2♂; 65

Km S Sinop; -12.5167, -55.6167; alt. 430m; 1974-10-01; Alvarenga, M.; Roppa leg.; (MZSP). • 1♀; Barra do Tapirapé; -10.6457, -50.6131; alt. 189m; (MZSP). – **Pará:** • 1☿; 15 km SW of Tailândia, Faz. Sta Martha; -2.8799, -48.7994; alt. 48m; 2003-07-30; Elizabeth, A. M. leg.; (CPDC). • 2☿; Jarí-Amazônia; -0.8833, -52.6; alt. 18m; 1905-07-03; Silva, E. A. leg.; (DZUP). • 1♂; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-08-26; Rosa, N. leg.; (MZSP). • 2♂; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-10-24; Rosa, N. leg.; (MZSP). • 1♀; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-07-16; Rosa, N. leg.; (MZSP). • 1☿; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-07-16; Rosa, N. leg.; (MZSP). • 2☿; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-08-26; Rosa, N. leg.; (MZSP). • 1☿; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-10-24; Rosa, N. leg.; (MZSP). • 3☿; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-11-05; Rosa, N. leg.; (MPEG). – **Rondônia:** • 1☿; Ji-Paraná; -10.8787, -61.9334; alt. 138m; (MZSP). • 1☿; Vilhena; -12.7398, -60.1307; alt. 609m; (MZSP). – **Roraima:** • 1☿; Estação Ecológica de Maracá; 3.4167, -61.65; alt. 127m; 2007-02-20; Souza, J. leg.; pitfall; (INPA). **COLOMBIA – Cauca:** • 1☿; Parque Nacional Natural Serranía de los Churumbelos Auka-Wasi; 1.2156, -76.4103; alt. 1400m; 1998-07-02; Bustos, J. leg.; hand collected; (MUSENUV). – **Vaupes:** • 1☿; Estación Biológica Caparú; 1.0756, -69.5136; alt. 96m; 2003-04-25; Benavides, L. leg.; (ICN). **COSTA RICA – Heredia:** • 1☿; 11km SE La Virgen; 10.3333, -84.0667; alt. 500m; 2003-02-18; Brenes, D. leg.; Sweeping; (JTLC). **ECUADOR – Guayas:** • 1☿; Bosque Protector Cerro Blanco; -2.1835, -80.0162; alt. 25m; 2016-11-01; Troya, A. leg.; pitfall; (MEPN). – **Orellana:** • 1☿; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.65, -76.45; alt. 216m; 1995-02-10; Erwin, T.; et al. leg.; fogging; (MEPN). • 1☿; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-11; Erwin, T.; et al. leg.; fogging; (MEPN). • 1☿; Parque Nacional Yasuní, Afluente Río Rumiyacu, Bloque 31; -0.7833, -75.9; alt. 227m; 2006-03-29; Troya, A. leg.; fogging; (MEPN). • 1☿; Parque Nacional Yasuní, Tiputini Biodiversity Station, 288 km SE Quito; -0.6319, -76.1442; alt. 230m; 2001-07-19; Erwin, T.; et al. leg.; fogging; (MEPN). – **Pastaza:** • 1☿; Parque Nacional Yasuní, Lorocachi; -1.6, -75.9667; alt. 172m; 2014-01-13; Chasiliquin, N;

Villacrés, E. leg.; (MEPN). – **Sucumbíos:** • 1☿; Limoncocha; -0.3998, -76.6001; alt. 280m; 1972-07-29; Kazan, P. L. leg.; (QCAZ). • 1☿; Reserva Cofan Bermejo; -0.3009, -77.3846; alt. 920m; 2005-12-27; Troya, A. leg.; fogging; (MEPN). – **Zamora Chinchipe:** • 4☿; 27 km SS of Zamora possada Copalinga; -4.0907, -78.9583; alt. 1060m; 2014-10-26; Tuza, M.; et. al. leg.; (DZUP). **FRENCH GUIANA – Cayenne:** • 3☿; 12km East from the village of Sinnamary, Paracou Station; 5.2667, -52.9167; alt. 50m; 1996-11-01; Corbara, B.; et al. leg.; (CPDC). • 2☿; Les Nourages; 4.0882, -52.6801; alt. 125m; 2006-03-01; Dejean, A. leg.; (CPDC). • 1♀; Montagne dês Chevaux; 4.7333, -52.4333; alt. 75m; 2011-01-01; Team, S. E. A. G. leg.; (DZUP). • 1☿; Montagne dês Chevaux; 4.7333, -52.4333; alt. 75m; 2011-01-01; Team, S. E. A. G. leg.; (DZUP). • 2♀; Petit Saut; 5.0667, -53.0333; (CPDC). • 1☿; Petit Saut; 5.0667, -53.0333; (CPDC). – **Saint-Laurent-du-Maroni:** • 1☿; Belvedere de Saul; 3.6167, -53.2; alt. 326m; 2011-05-20; Team, S. E. A. G. leg.; (DZUP). • 1♂; Kourou; 5.1611, -52.6493; alt. 3m; Palm, B. leg.; hand collected; (MEPN). • 1☿; Kourou; 5.1611, -52.6493; alt. 3m; Palm, B. leg.; hand collected; (MEPN). **PERU – Madre de Dios:** • 1☿; Parque Nacional Paquitza-Manu; -11.9445, -71.283; alt. 329m; 1992-02-09; Quintero, D.; Cambra, R. leg.; (CPDC). • 1☿; [no locality given]; -9.0, -75.0; 1960-10-19; Cunningham leg.; (AVCZ). **VENEZUELA – Miranda:** • 1☿; Yaguapa; 10.3992, -66.2896; alt. 119m; 1982-01-01; Tablante, A. leg.; (MZSP). • 1☿; Yaguapita; 10.3117, -66.303; alt. 66m; Marques, M. leg.; (MZSP).

Geographic range. Costa Rica, Venezuela, Trinidad and Tobago, Guyana, Suriname, French Guiana, Colombia, Ecuador, Peru, Bolivia, Brazil (Acre, Amapá, Amazonas, Bahia, Ceará, Espírito Santo, Mato Grosso, Pará, Rondônia, Roraima), Paraguay.

***Neoponera goeldii* Forel, 1912**

Fig. 28b (distribution)

Neoponera goeldii Forel, 1912: 36. ☿ lectotype [by designation of MacKay & MacKay, 2010: 362], Brazil, Amazonas, Victoria, Goeldi [leg.], (MHNG, AntWeb: CASENT0907240) [image examined, link]; ☿ paralectotype [same data as for lectotype], (MHNG) [not examined].

Combinations. In *Pachycondyla*: Brown, 1995: 305. In *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species. Borgmeier, 1923, 66; Kempf, 1972: 162; MacKay & MacKay, 2010: 362 [redescription]

Worker and queen diagnosis. Head subquadrate, slightly broader posteriorly to eye (Fig. 5c); in frontal view, eye feebly more globose than most species of the *N. crenata* group (Fig. 5c); antennal scape long, when pulled back exceeding posterior head margin by approximately three times apical scape with; in lateral view, anterior margin of petiolar node inclined posterad, posterior margin of node convex, top of node relatively acute and placed at about vertical nodal midlength (Fig. 3e); body, including legs, with abundant, long erect hairs, some as long as maximum fore coxal width (link).

Worker Measurements (n = 14): HW: 1.42-1.65; HL: 1.3-1.8; EL: 0.5-0.55; SL: 1.75-1.9; WL: 2.55-2.85; PrW: 1.03-1.2; MsW: 0.62-0.73; MsL: 0.55-0.7; PW: 0.75-0.9; PH: 0.65-1.0; PL: 0.75-0.85; GL: 2.55-3.5; A3L: 0.95-1.16; A4L: 0.9-1.08; A3W: 1.3-1.55; A4W: 1.25-1.45; TLa: 6.8-7.6; TLr: 7.6-8.7. **Indices.** CI: 88.24-123.08; OI: 31.75-35.34; SI: 109.09-123.67; MsI: 100.0-122.73; LPI: 77.5-115.38; DPI: 96.77-116.13.

Queen. Measurements (n = 4): HW: 1.7-1.8; HL: 1.8-1.95; EL: 0.62-0.7; SL: 1.95-2.02; WL: 3.2-3.35; PrW: 1.4-1.5; MsW: 1.28-1.35; MsL: 1.58-1.65; PW: 1.0-1.05; PH: 1.1-1.25; PL: 0.87-1.0; GL: 3.1-3.95; A3L: 1.35-1.52; A4L: 1.3-1.36; A3W: 1.85-2.0; A4W: 1.75-1.88; TLa: 8.57-9.1; TLr: 9.38-10.2. **Indices.** CI: 89.74-94.44; OI: 34.72-41.18; SI: 112.5-114.71; MsI: 78.79-84.38; LPI: 79.09-88.64; DPI: 105.0-114.94.

Male diagnosis. Interposterior ocellar distance usually 1.5 times as long as the distance between anterior and posterior ocelli (Fig. 15c); anterior ocellus as long as maximum antennal

socket length, sometimes slightly longer (Fig. 15d); notauli relatively well-impressed, not touching posteriorly (Fig. 15b); anapleural sulcus slightly impressed, reaching ventral pleural surface (Fig. 15a); in lateral view, anterior margin of petiolar node strongly inclined posterad, posterior margin feebly convex, carinated and bearing tiny crenulae, posterior face slightly convex, nodal dorsum round (Fig. 15a); posterior propodeal carina sometimes connected dorsally with longitudinal median carina (Fig. 15b); body of all examined individuals yellow to brown yellowish; hindwing bearing 8 – 9 hamuli.

Male. See description by Mackay and Mackay (2010). Measurements (n = 4): HW: 0.85-1.75; HL: 1.15-1.95; EL: 0.6-0.75; SL: 0.22-2.1; WL: 2.7-3.3; PrW: 1.05-1.48; MsW: 1.2-1.35; MsL: 1.55-1.75; PW: 0.65-1.1; PH: 0.68-0.78; PL: 0.8-0.95; GL: 2.8-4.05; A3L: 1.0-1.1; A4L: 1.0-1.05; A3W: 1.15-1.2; A4W: 1.25-1.35; TLa: 6.8-8.35; TLr: 7.58-10.25. **Indices.** CI: 73.91-93.62; OI: 36.86-73.17; SI: 20.45-120.0; MsI: 73.85-84.38; LPI: 103.23-135.71; DPI: 72.22-137.5.

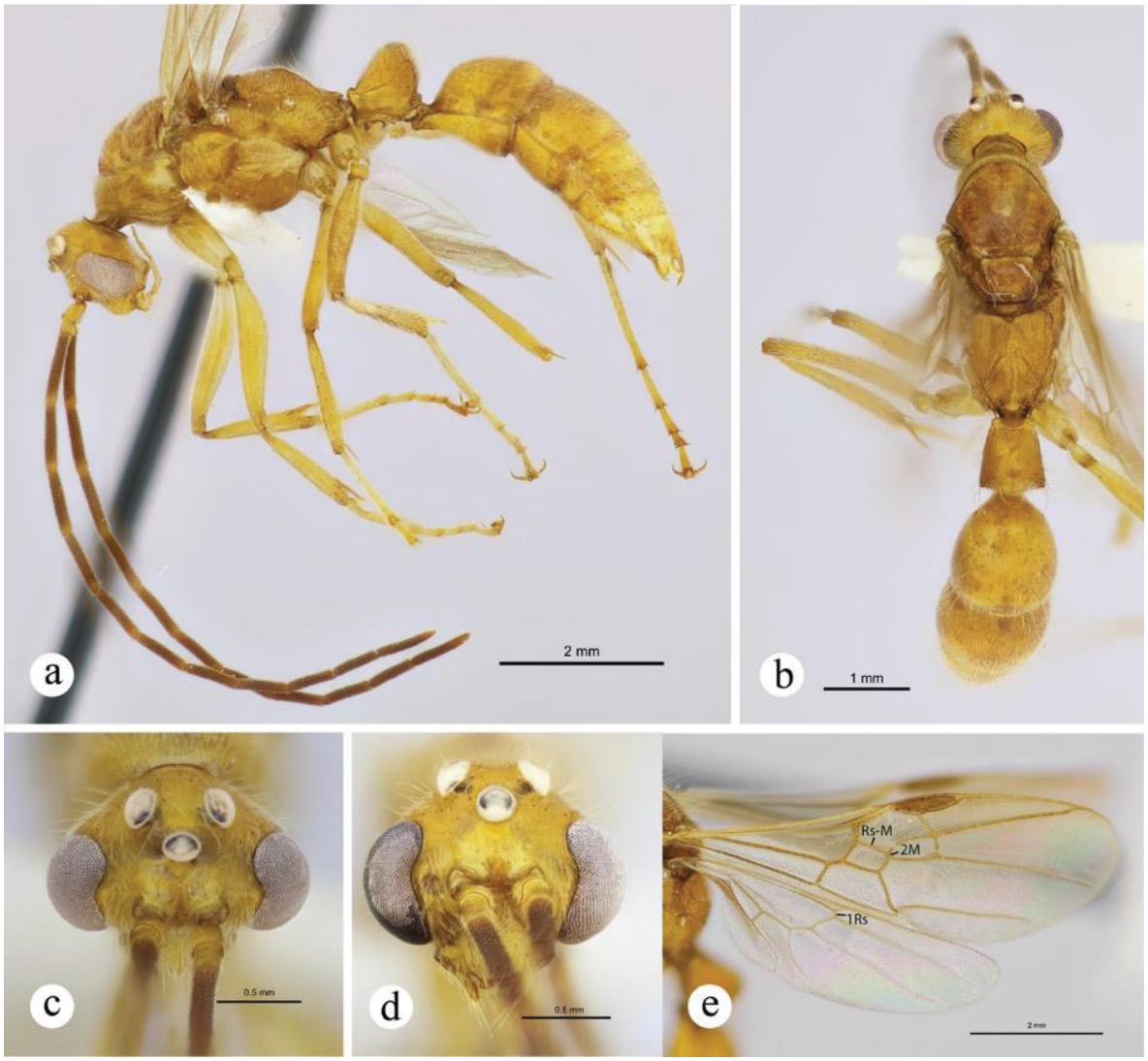


Fig. 15. *Neoponera goeldii*. ♂ (CPDC: AT535). French Guiana: Cayenne. **a.** Lateral view; **b.** Dorsal view; **c.** Head in anterodorsal view; **d.** Head in frontal view; **e.** Fore and hind wings.

Comments. *Neoponera goeldii* is a medium-sized species in the *N. crenata* group (Fig. 26; ☿: TLa = 6.8 – 7.6 mm; ♀: TLa = 8.57 – 9.1 mm). Its morphology, including body color, is remarkably homogeneous across its distribution range. Even the form of the petiole, which is usually intraspecifically variable in most *Neoponera* species, in *N. goeldii* it is quite stable with no detected variations among the examined material. This morphologic stasis is possibly reflecting continuous gene flow between *N. goeldii* populations along their range; this has rarely been seen in broadly ranged *Neoponera*, and perhaps the other known case is exemplified in *N. villosa*.

As with most species in the *N. crenata* group, except for few features like the shape of the petiolar node with an acute dorsum, eye convexity, and antennal scape length, the overall body form of *N. goeldii* is relatively similar to most other conspecifics. Yet, the nodal shape of *N. goeldii* is unique not only in this species-group but among all species in the genus, and this feature should suffice for distinguishing it from other *Neoponera*. In only two species within the *N. crenata* group the top of the node is relatively acute as in *N. goeldii*: *N. carinulata*, and *N. oberthueri*. However, in these species the anterior nodal margin is always vertically straight, and the anterodorsal margin is inclined, usually straight. In *N. goeldii*, the entire anterior margin is inclined posterad. Also, the top of the node in those two species is placed posterad to vertical nodal midline, while in *N. goeldii* it is placed medially, sometimes slightly anterad. Finally, *N. goeldii* is overall brownish castaneous, while *N. carinulata* and *N. oberthueri* show a darker integument, usually black.

This species has the shortest elevational range among our examined material, from near the sea level up to about 220 m. Interestingly, antmaps.org shows four collection records supposedly preserved in ICN; these belong to the Colombian Department of Risaralda, most of which is over 1000 m up to approximately 4000 m at Cerro Tamaná. According to the material we examined, *N. goeldii* reaches as far north in northwestern South America to the northern Ecuadorian Amazonia, but see also Fernandez and Guerrero (2019) who report this species in the southern Colombian Amazonia. If the Risaralda records are confirmed this species could extend its distribution in South America to the Cordillera Occidental which is part of the eastern region of the Colombian Chocó-Darién biome. The remaining records are spread from western to eastern Amazonia, as far east to the coastal forests near the Atlantic region in French Guiana and northern Amapá, in Brazil.

As for Central America, we here report the first record of *N. goeldii* which belongs to the Los Tuxtlas reserve at the eastern coastal region of the Gulf of Mexico, state of Veracruz; this reserve is part of the Sierra de Los Tuxtlas ecoregion (Dinerstein et al 2017), the largest and northernmost intact portion of moist, cloud forests in Mexico (Valero et al. 2019).

Natural history notes. See Mackay and Mackay (2010). As with a number of species in the genus, *N. goeldii* prefers nesting in epiphytes and palms, from well-preserved rain forests, terra firme and seasonal floodplains (varzea), to agriculture systems. We have gathered records from *Aechmea* sp. (Bromeliaceae), *Philodendron solimoesense* (Araceae), *Phytelephas* sp. (Arecaceae).

Leroy et al. (2017) found that epiphyte seeds of *Aechmea mertensii* had higher germination percentages inside carton nests produced by *N. goeldii* in a Brazilian Amazonian site, as compared to carton nests from *Camponotus femoratus* Fabricius. In Parque Nacional Yasuní, Ecuadorian Amazonia, A. Troya found an ant garden build by *N. goeldii*, which was next to a huge *Azteca* sp. carton nest (~ 1 m length) build around an *Anthurium* sp. (Araceae) epiphyte. Workers of *N. goeldii* are fast huntresses, Orivel et al. (2000) observed that preys when subdued by the ants are immediately stung without prior palpation (sensing through antennal tipping), which according to them is a common trait of this species among the Ponerinae which frequently use palpation before seizing their prey (but see Dejean 2011). This hunting strategy is apparently an adaptation of non-dominant, solitary foraging arboreal species to capture agile preys, like flying insects, which otherwise rapidly flee when menaced (Djiéto-Lordon et al. 2001, Dejean 2011).

Material examined. 44☿, 14♀, 8♂. **BRAZIL – Amapá:** • 1♀; Oiapoque; 3.8441, -51.8323; alt. 18m; 1979-05-03; Overal, W. leg.; (MPEG). • 1☿; Oiapoque; 3.8441, -51.8323; alt. 18m; 1979-05-03; Overal, W. leg.; (MPEG). – **Amazonas:** • 1♂; 45 Km SW Manaus, Lago Janauacá; -3.4126, -60.384; alt. 12m; 1988-03-26; Rocha, R. leg.; (INPA). • 2☿; Benjamin Constant; -4.376, -70.0302; alt. 70m; 1962-09-18; Brown, W. leg.; (MPEG). • 1☿; Br. 174, Km 45; -3.0489, -59.9764; alt. 49m; 1987-02-09; Vasconcelos, H. leg.; (CPDC). • 1☿; Br. 174, Km 70; -2.4673, -60.0307; alt. 123m; 1995-04-05; Matsuo, A.; Vasconcelos, H. leg.; (INPA). • 1☿; Manaus; -3.1167, -60.0167; alt. 65m; 1987-12-03; Couturier, G. leg.; (CPDC). • 2☿; Roadside near Boavista, km 60; -2.7269, -59.888; alt. 127m; 1986-12-01; Davidson, D. leg.; hand collected; (INPA). • 1☿; Victoria; -8.0667, -67.2666; Goeldi leg.; (NHMB). – **Bahia:** • 1♂; 5 km of Jeribucaçu. Campo Cheiroso; -14.3667, -39.05; alt. 113m; 2015-03-15; Amorin, A. leg.; (CPDC). • 1☿; 5 km of Jeribucaçu. Campo Cheiroso; -14.3667, -39.05; alt. 113m; 2015-03-15; Amorin, A. leg.; (CPDC). • 1☿; Maraú; -14.103, -39.015; alt. 36m; (CPDC). – **Pará:** • 1☿; Bajurú; 1.516, -48.045; alt. 13m; 1979-10-01; Neto, R. leg.; (MPEG). • 1♀; Marituba; -1.3667, -48.3333; alt. 32m; 2004-10-14; Santos, J. R. M. leg.; (CPDC). • 1☿; Marituba; -1.3667, -48.3333; alt. 32m; 2004-10-14; Santos, J. R. M. leg.; (CPDC). • 1♂; Mojú; -1.8844, -48.7656; alt. 14m; 1967-07-01; E. P. D. Z.; M. G. leg.; (MPEG). • 1♀; PA 408, Km 6; -1.35, -48.25; alt. 31m; 1980-10-21; Torres, M. leg.; (MPEG). • 1♂; Reserva Biológica Trombetas; -1.1375, -56.6924; alt. 73m; 1982-10-06; Harada,

A. leg.; (INPA). • 1♀; São Francisco; -3.8441, -51.8323; alt. 18m; 1978-12-12; Overal, W. leg.; (MPEG). • 1⚧; São Francisco; -3.8441, -51.8323; alt. 18m; 1978-12-12; Overal, W. leg.; (MPEG). • 1⚧; São Francisco; 3.8441, -51.8323; alt. 18m; 1978-12-12; Overal, W. leg.; (MEPN). • 1⚧; São Francisco; -6.2068, -52.7028; alt. 219m; 1978-12-12; Overal, W. leg.; (DZUP). • 1⚧; Xingu river, right shore; -3.8519, -51.8523; alt. 173m; 2001-03-09; Santos, R.; Dias, J. leg.; Malaise; (MPEG). • 3⚧; Área de Pesquisa Ecológica do Guamá; -1.4647, -48.4512; alt. 10m; 1969-11-02; Rosa, N. leg.; (DZUP). • 3⚧; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-11-11; Rosa, N. leg.; (MPEG). **COLOMBIA** • 1⚧; Parque Nacional Natural Amacayacu; -3.4398, -70.144; alt. 103m; 1993-08-01; Barr, J. leg.; (ICN). **ECUADOR – Orellana:** • 1⚧; Francisco de Orellama (Coca); -0.461, -76.993; alt. 250m; Onore, G. leg.; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-07-06; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-07-03; Erwin, T.; et al. leg.; fogging; (MEPN). • 1⚧; Parque Nacional Yasuní, Estación Científica Yasuní; -0.9333, -75.4; alt. 250m; Maza, F. leg.; (QCAZ). • 1⚧; Parque Nacional Yasuní, Guacamayo, saladero; -1.294, -76.06; alt. 215m; 2014-02-02; Troya, A.; Duque, P. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, Tiputini Biodiversity Station, 288 km SE Quito; -0.6319, -76.1442; alt. 230m; 2002-01-31; Erwin, T.; et al. leg.; fogging; (MEPN). – **Sucumbíos:** • 1⚧; Reserva Ecológica Cofán Bermejo; -0.1667, -77.35; alt. 920m; 2009-12-01; Troya, A. leg.; fogging; (MEPN). • 1⚧; Reserva de Producción Faunística Cuyabeno, Trocha Zábalo-Güepi; -0.26, -75.69; alt. 270m; 2000-08-08; Araujo, P. leg.; fogging; (MEPN). **FRENCH GUIANA – Cayenne:** • 2♀; Base Vie; 5.1667, -52.65; alt. 60m; 2000-06-01; Delabie, J. H. C. leg.; (CPDC). • 3♂; Petit Saut; 5.0667, -53.0333; alt. 75m; (CPDC). • 1♂; Petit Saut; 5.0667, -53.0333; alt. 67m; 1998-07-08; Dejean, A. leg.; (CPDC). • 3♀; Petit Saut; 5.0667, -53.0333; alt. 75m; (CPDC). • 1♀; Petit Saut; 5.0667, -53.0333; alt. 67m; 1998-07-08; Dejean, A. leg.; (CPDC). • 3⚧; Petit Saut; 5.0667, -53.0333; alt. 75m; 1998-07-08; Dejean, A. leg.; (DZUP). • 4⚧; Petit Saut; 5.0667, -53.0333; alt. 75m; (CPDC). • 3⚧; Petit Saut; 5.0667, -53.0333; alt. 67m; 1998-07-08; Dejean, A. leg.; (CPDC). • 1⚧; Petit Saut; 5.0667, -53.0333; alt. 67m; 2002-10-01; Orivel, J.; Dejean, A. leg.; (CPDC). • 1♀; Sinnamary; 5.3746, -52.9547; alt. 7m; 1999-08-15; Durou, S. leg.; (CPDC). **MEXICO –**

Veracruz: • 1☿; Reserva de la Biosfera Los Tuxtlas; 18.4476, -95.2044; alt. 345m; 1994-12-01; Fresneau, D. leg.; (CPDC). **PERU – Loreto:** • 3☿; Jenaro Herrera; -4.9082, -73.6668; alt. 108m; 1989-10-11; Couturier, G. leg.; (CPDC).

Geographic range. Mexico (Veracruz), Colombia, Trinidad and Tobago*, Guyana*, Suriname*, French Guiana, Ecuador, Peru, Brazil (Amapá, Amazonas, Pará). *: record from literature (see distribution map).

***Neoponera luteola* (Roger, 1861)**

Figs. 29: a (distribution)

Ponera luteola Roger, 1861: 166. ☿ syntype, Peru, Pampa del Sacramento [-7.992, -75.834], de Castelnau [leg.], (MNHN, AntWeb: CASENT0915467) [image examined, link]

Combinations. In *Pachycondyla*: Roger, 1863: 18; Brown, 1995: 307; In *Neoponera*: Emery, 1901: 47; Schmidt & Shattuck, 2014: 151.

Status as species. Roger, 1863: 18; Mayr, 1863: 449; MacKay & MacKay, 2010: 447 [redescription].

Worker diagnosis. Head subtrapezoidal, slightly broadened posteriorly to eye, posterior head margin concave (link); eye relatively small, distance from anterior margin to mandibular insertion longer than one eye maximum length (link); anterior mid clypeal margin without acute cuticular extension overhanging the mid basal mandibular margin, instead a tiny pointed tip is emerging from cuticle (Fig. 2a); malar carina faintly impressed (link); humerus with feeble, blunt carina, almost indistinguishable; notopropodeal suture present, slightly grooved; petiolar node block-shaped with anterodorsal margin feebly inclined, anterior margin vertically straight, posterior margin convex; posterior nodal face glabrous, devoid of sculpture; subpetiolar process longitudinally carinate; body color of workers light brownish, while queens are dark ferruginous.

Worker Measurements (*n* = 3): HW: 1.65-1.8; HL: 1.86-2.0; EL: 0.4-0.45; SL: 1.7-1.75; WL: 2.75-3.1; PrW: 1.2-1.3; MsW: 0.85-0.88; MsL: 0.7-0.82; PW: 0.95-1.0; PH: 0.9-0.95; PL: 0.85-0.9; GL: 3.7-3.75; A3L: 1.2-1.33; A4L: 1.18-1.25; A3W: 1.65-1.7; A4W: 1.7-1.8; TLa: 7.94-8.57; TLr: 9.26-9.7. **Indices.** CI: 88.47-90.26; OI: 23.32-25.0; SI: 97.22-103.03; MsI: 106.06-121.43; LPI: 94.44-98.36; DPI: 111.11-111.76.

Queen. See Mackay and Mackay (2010).

Comments. *Neoponera luteola* is a medium-sized species (☿: TLa = 6.8 – 7.6 mm), and within the *N. crenata* group is approximate as large as *N. cavinodis*, *N. fiebrigi*, and *N. cylindrinodis* sp. nov. (Fig. 26). The combination of its diagnostic traits makes *N. luteola* a peculiar taxon. This is the only species in the *N. crenata* group with a subtrapezoidal head with relatively small eyes, and reduced both mid clypeal and humeral carinae. These traits are useful for easily distinguishing this species from any other in this group, and even in the genus. The large size of the queen (~ 12 mm sensu Mackay and Mackay 2010) versus respective workers is also remarkable. In all other lineages in the genus the size ratio worker/queen is smaller. The reader can find the only known image of the queen of this species in (AntWiki.org, link)

The head and anterior clypeal shape, and the presence of notopropodeal groove, although shallow, resembles most species in the *N. foetida* group, which in general are similarly sized or larger, and most of them are significantly hairier, in particular with regards to the erect hairs. In addition, the lobes of the metasternal process of the species in the *N. foetida* group are broader than those of the *N. crenata* group, and the space between the lobes is greater than the width of each (shorter in those of the *N. crenata* group).

We only gathered 12 records of *N. luteola*, three of which are from literature search, two examined through images in AntWeb.org, and only seven were physically examined, all of these belonging from the same site in Mato Grosso, Brazil. Thus, a robust inference on morphological variation across its distribution range is not possible here. The worker from Ecuadorian Amazonia is practically identical to that from southern Peru, and to those of Brazil. The only differing feature is the body color, with the latter showing a brighter integument. Although this is mostly an Amazonian lineage, Emery (1911) reports a record from the Atlantic Forest in Rio de Janeiro. Since that date no further records have been reported from such biome.

Natural history notes. See Mackay and Mackay (2010). The records we examined were collected from river banks, possibly in the proximities of *Cecropia* spp. (Urticaceae) trees. The colonies of *N. luteola* can contain several thousand workers (Yu and Pierce 1998), however, despite their abundance this species is rarely encountered in the field, possibly because of its facultative association to *Cecropia* trees. According to Gutiérrez-Valencia et al. (2017) *N. luteola* is beginning to replace *Azteca* ants as mutualistic partners in *C. membranacea* in Peru. Alluding

to this mutualism with *Cecropia* plants, *N. luteola* could well be called the "cecropia ant" in the genus.

Material examined. 9☿. **BRAZIL – Mato Grosso:** • 4☿; Fazenda São Nicolau; -9.85, -58.2333; alt. 222m; 2011-11-01; Vicente, R. E. leg.; (DZUP). • 2☿; Fazenda São Nicolau; -9.85, -58.2333; alt. 222m; 2011-05-01; Vicente, R. E. leg.; (DZUP). **ECUADOR – Orellana:** • 1☿; Avila Viejo; -0.6375, -77.4356; alt. 739m; 1998-06-19; Kohn, E. leg.; (QCAZ). **PERU – Madre de Dios:** • 1☿; Rio Tambopata Reserve, 30 km. (air) SW Puerto Maldonado; -12.8333, -69.3333; alt. 290m; 1982-11-01; Ross, E. S. leg.; (CASC). • 1☿; Pampa del Sacramento; -7.992, -75.834; alt. 1400m; 1847-12-31; De Castelnau leg.; (MNHN).

Geographic range. Ecuador, Peru, Bolivia*, Brazil (Mato Grosso, Mato Grosso do Sul*, Rio de Janeiro*). *: record from literature (see distribution map).

***Neoponera moesta* (Mayr, 1870)**

Fig. 28: a (distribution)

Pachycondyla moesta Mayr, 1870: 395 – 396. ☿ holotype, Colombia, S. Fe Bogota, Lindig [leg.], [identified as *pallidipes* (*recte pallipes*) by G. Mayr], (NHMW, AntWeb: CASENT0915658) [image examined, link].

Neoponera stipitum Forel, 1901: 348 – 349 (☿ ♀). ☿ lectotype [by designation of Mackay & Mackay, 2010: 468], Colombia, Nevada [Sierra Nevada de Santa Marta], St. Antonio, Forel [leg.], tiges [plant stem], (MHNG, AntWeb: CASENT0907246) [image examined]. Note: additional type material [paralectotypes] designated by Mackay & Mackay, 2010: 468, consists of 5 ☿, 2 ♀ at MHNG [not examined], and 2 ☿ at NHMB [not examined].

Combinations. In *Neoponera*: Emery, 1901: 47; Schmidt & Shattuck, 2014: 151.

Subspecies of *Neoponera pallipes*: Emery, 1890a: 42 [checklist]; Dalla Torre, 1893: 34 [checklist]; Emery, 1894: 48 [checklist]; Forel, 1895: 115 [checklist]; Forel, 1899: 13 [checklist]; Forel, 1901a: 349 [comments morphology]; Forel, 1908: 345 [checklist]; Forel, 1909: 252 [checklist].

Subspecies of *Neoponera crenata*: Forel, 1899: 13 [checklist]; Emery, 1911: 73 [checklist]; Forel, 1912: 37 [checklist]; Mann, 1916: 413 [checklist]; Luederwaldt, 1918: 35 [checklist]; Santschi,

1921: 86 [checklist, comments morphology]; Borgmeier, 1923: 66 [checklist]; Wheeler & Bequaert, 1929: 31[comments biology]; Santschi, 1939: 313 [**misidentification, synonym of *N. crenata***]; Brown, 1957: 233 [comments morphology and distribution]; Kempf, 1972: 162 [checklist].

Junior synonym of *Neoponera crenata*: Mayr, 1887: 534; Brown, 1957: 234 [**not formally established**]; Bolton, 1995: 307 [**misidentification**].

Status as species. Kempf & Lenko, 1976: 54 [comments biology and distribution in Brazil]; MacKay & MacKay, 2010: 468 [redescription based on types of both *N. crenata* and *N. moesta*]; Branstetter & Sáenz, 2012: 263 [checklist based on Mackay & Mackay, 2010]; Bezděčková et al., 2015: 124 [checklist based on Kemp, 1972]; Feitosa, 2015: 99 [checklist based on Mackay & Mackay, 2010]; Fernández & Guerrero, 2019: 534 [checklist]; Pazmiño-Palomino & Troya, 2022: 9 [**misidentification, Fig. 17 is of *N. crenata***].

Worker and queen diagnosis. Head rectangular to subquadrate; distance between mandibular insertion to anterior eye margin equal to- or shorter than *half* eye maximum length (Fig. 4a); antennal scape, when pulled posterad, exceeding posterior head margin by about one apical scape width; in lateral view, posterior margin and posterior face of petiolar node convex, anterodorsal margin usually feebly inclined; posterior face of node always mostly completely glabrous and polished, this feature usually extends over part of the nodal posterodorsal face (Fig. 8c); in dorsal view, petiolar node subtriangular (Fig. 8c); in lateral view, nodal length subequal to its width.

Worker Measurements ($n = 27$): HW: 1.01-1.32; HL: 1.13-1.49; EL: 0.35-0.44; SL: 1.04-1.32; WL: 1.7-2.27; PrW: 0.79-1.02; MsW: 0.47-0.71; MsL: 0.39-0.55; PW: 0.57-0.88; PH: 0.61-0.88; PL: 0.6-0.8; GL: 1.73-3.14; A3L: 0.63-0.9; A4L: 0.76-1.0; A3W: 0.82-1.26; A4W: 0.94-1.25; TLa: 5.1-6.35; TLr: 5.38-7.51. **Indices.** CI: 74.42-111.0; OI: 30.03-42.19; SI: 87.09-112.5; MsI: 96.88-139.29; LPI: 84.09-110.0; DPI: 94.74-116.67.

Queen Measurements ($n = 7$): HW: 1.1-1.48; HL: 1.26-1.71; EL: 0.42-0.47; SL: 1.1-1.32; WL: 2.11-2.41; PrW: 0.96-1.16; MsW: 0.86-1.1; MsL: 1.07-1.29; PW: 0.78-1.01; PH: 0.68-0.82; PL: 0.63-0.79; GL: 2.23-3.37; A3L: 0.85-1.02; A4L: 0.94-1.13; A3W: 1.18-1.46; A4W: 1.2-1.48; TLa: 6.01-7.0; TLr: 6.47-8.19. **Indices.** CI: 78.16-111.9; OI: 31.91-40.28; SI: 78.72-103.57; MsI: 77.78-87.14; LPI: 83.33-100.0; DPI: 105.26-128.0.

Male. Not examined but see Mackay and Mackay (2010). The user, however, should direct its attention to the information provided on pages 290-291 on M&M work because it apparently refers to the actual male caste of this species. We cannot confirm this though, since M&M based their treatment of *N. moesta* on mixed type material representing both *N. moesta* and *N. crenata*, and even *N. fiebrigi*. In addition, the worker and queen descriptions depict features of the first two taxa.

Comments. *Neoponera moesta* is the third smallest species in the *N. crenata* group (Fig. 26; ☿: TLa = 5.1 – 6.35 mm; ♀: TLa = 6 – 7 mm), after *N. dejeani* sp. nov. and *N. recava* (Fig. 16), and is among the smallest in the genus. Its morphology and integument coloration are relatively homogeneous across its distribution range. We found scant specimens, one from Oaxaca, Mexico and few from Orellana, Amazonian Ecuador showing a blackish to dark brownish integument, instead of the usual brownish to ferruginous castaneous which characterizes this taxon.

The taxonomy of *N. moesta* is closely linked to that of *N. crenata* since these are morphologically highly similar (see comments under *N. crenata*). Mackay and Mackay (2010) revised the names and type material associated to *N. moesta*, and solved some inconsistencies but also created further challenges due to incorrect synonymization of the subspecific names linked to their morphology, plus that of *N. fiebrigi* which is another very similar form. We re-examined all available images of correspondent type material. Under the taxonomic history of each species, we re-assigned the type names to the respective correct form, i.e., either to *N. moesta*, *N. crenata*, or *N. fiebrigi*. Current taxonomic acts in this revision are also supported by the comprehensive examination of material which represents the known distribution range of this lineage and its similar forms.

The user can safely separate *N. crenata* from *N. moesta* by using the taxonomic key and the diagnoses combined, but the following two characters are crucial: 1) The distance from anterior eye margin to mandibular insertion is shorter than, or at most equal to half eye maximum length in *N. moesta* (always longer in *N. crenata*); 2) The posterior face of the petiolar node is almost entirely glabrous in *N. moesta*, except for the margins (always with piligerous punctae in *N. crenata*).

In regards to *Neoponera fiebrigi*, which is also similar in color to *N. moesta* (mostly brownish castaneous), the user can first note its size (☿ TLa = 6.98 – 8.98 mm; ♀TLa = 7.08 – 10.97 mm) which is significantly bigger than the latter (Fig. 26; ☿ TLa = 5.1 – 6.35 mm; ♀TLa = 6.01 – 7 mm). *Neoponera fiebrigi* also bears a carina laterally on the fore coxa (Fig. 13c), which is absent in *N. moesta*.

A fourth taxon, *N. cylindrinodis* sp. nov., could also be confused with *N. moesta*. However, the following features characterizes the former: 1) Black integument with golden piligerous punctures, 2) Barrel-shaped node which is laterally longer in lateral view than that of *N. moesta*, 3) This is a medium-sized to relatively large species (☿ TLa = 7.35 – 9 mm; ♀TLa = 8 – 10.33 mm; Figs. 20, 21).

The elevational range of *N. moesta* extends from near the sea level to about 2550 m, this latter from the city of Bogotá, Colombia, a worker (ICN080665) collected in 2007 in a kitchen's apartment!. The examined collection records span from across Central and South America. The northernmost record lies in a pre-mountainous subtropical site from the southern region of the Sierra Madre Oriental mountain range, near the forests of the Gulf of Mexico, in Oaxaca. Mackay and Mackay (2010) report two sites further north in that country: the first in the state of Durango, at Villa Montemorelos (not Monte Morelos), a semi-arid site at about 1850 m elevation, and the second from Xilitla, close to the southern limit of the state of San Luis de Potosí, a subtropical site at the central region of Sierra Madre Oriental. Nonetheless, we consider unlikely for current *N. moesta* populations extending far north to the state of Durango, especially because the habitat of that region strongly departs from the usually find for this species, which is mostly tropical humid to wet forests. Since the authors did not provide specific details, nor museum vouchers for their records, it is hard to confirm them. In Central and South America, *N. moesta* is broadly occurring on most biomes, including the Chocó-Darién, Amazonia, Atlantic Forest, and even in the Brazilian Cerrado (a single record from Mato Grosso do Sul). The southernmost range reaches the island of Florianopolis in the Brazilian state of Santa Catarina.

Natural history notes. According to Wheeler and Bequaert (1929) this species usually nests inside live twigs. These authors found some workers inside foliar domatia of *Tococa* sp. (Melastomataceae). Mackay and Mackay (2010), found two nests in dead twigs containing winged reproductive castes and brood. From the presently examined material: nests have been collected

in *Goupia glabra* (Goupiaceae), a native South American tree. From J. Longino observations (AntWeb 2022): records from México in live stems of Urticaceae shrubs with carton partitions inside; in eastern Costa Rica, from Cerro Plátano, Longino found a nest occupying two internodes of a *Cecropia* sp. (Urticaceae), which was also hosting nests of *Azteca xanthochroa* (Roger), and *Camponotus* sp. The striking ICN080665 record from Bogotá, by C. Martínez and F. Fernández, represents a potential extreme case of altitudinal expansion, perhaps denoting climate change shifts for a species which is mostly adapted to tropical, mostly undisturbed habitats. It is worth doing further research around this observation.

Material examined. 142☿, 8♀. **BOLIVIA – Santa Cruz:** • 1☿; Las Gamas, P. N. Noel Kempff Mercado; -14.8, -60.3833; alt. 700m; 1993-12-03; P.S. Ward leg.; (PSWC). **BRAZIL – Acre:** • 1☿; Fazenda Experimental Catuaba- UFAC; -10.0667, -67.6167; alt. 214m; 2014-03-04; Denicol, M. R.; Santos, A. M. leg.; arboreal pitfall; (DZUP). • 3☿; Porto Walter; -8.2667, -72.7333; alt. 199m; 1961-10-01; Herbst, P. L. leg.; (MZSP). • 1☿; Rio Branco-Res; -9.9745, -68.4299; alt. 219m; (CPDC). – **Amapá:** • 1☿; Mazagão; -0.1157, -51.2862; alt. 14m; 1981-11-21; arboreal Malaise; (MPEG). – **Amazonas:** • 1☿; 2 Km SW São Antonio do Içá; -3.1138, -67.9626; 2004-09-18; Venticinque, E. leg.; beating; (INPA). • 5☿; Benjamin Constant; -4.376, -70.0302; alt. 70m; (MZSP). • Fazenda Esteio, 80 km NNE Manaus ; -2.4167, -59.8667; alt. 80m; 1987-09-16; Ward, P. leg.; hand collected; (INPA). • 1☿; Fazenda Esteio, 80 km NNE Manaus ; -2.4167, -59.8667; alt. 80m; 1987-09-16; Ward, P. leg.; hand collected; (INPA). • 1☿; Fazenda Porto Alegre; -2.3333, -60.0; alt. 129m; 2001-05-17; Vilhena, J.; Vasconcelos, H. leg.; (INPA). • 1☿; Igarapé Cururu; -3.1167, -59.9333; alt. 52m; 2006-10-09; Souza, J.; Araujo, J. leg.; beating; (INPA). • 1☿; Ilha Jaraqui, Japurá river; -1.917, -65.4669; alt. 53m; 1988-10-18; Dias, J. leg.; arboreal Malaise; (MPEG). • 8☿; Manaus; -3.1167, -60.0167; alt. 65m; 1962-09-08; Lenko, K. leg.; (MZSP). • 1☿; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9333, -59.9667; alt. 61m; 1991-08-21; Adis, J. leg.; (CPDC). • 1☿; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9167, -59.9833; alt. 65m; 1992-02-23; Adis, J.; et al. leg.; fogging; (INPA). • 2☿; Sto. Antônio; -3.1167, -60.0333; alt. 61m; 1971-06-11; (MZSP). – **Bahia:** • 6☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75,

-39.2167; alt. 61m; (CPDC). • 1♂; Camaçã; -15.4201, -39.4964; alt. 158m; (CPDC). • 1♂; Camaçã; -15.4201, -39.4964; alt. 158m; 1980-03-22; Benton, F. leg.; (INPA). • 1♀; Porto Seguro; -16.4444, -39.0654; alt. 4m; (CPDC). – **Espírito Santo:** • 3♂; Linhares; -19.3947, -40.0653; alt. 31m; (CPDC). – **Maranhão:** • 1♂; Ribeirão; -21.166, -47.8499; alt. 605m; 1989-08-01; Ramos, F. leg.; Malaise; (MPEG). – **Mato Grosso:** • 2♂; 65 Km S Sinop; -12.5167, -55.6167; alt. 430m; 1974-10-01; Alvarenga, M.; Roppa leg.; (MZSP). – **Mato Grosso do Sul:** • 1♂; Batimento; -20.4, -54.5; alt. 600m; (CPDC). – **Pará:** • 1♂; 12 Km N, Tucurui; -3.6566, -49.6762; alt. 31m; 1979-08-20; Overal, W. leg.; (MPEG). • 1♂; Alenquer; -1.9466, -54.7388; alt. 28m; 1979-07-02; Ramos, F. leg.; (MPEG). • 1♀; Fazenda Florentino; -7.1167, -55.3833; alt. 967m; 2011-02-09; Krinsk, D. leg.; pitfall; (DZUP). • 1♂; Floresta Nacional Caxiuanã; -1.7333, -51.45; alt. 21m; 2011-12-01; Cunha, D. et al. leg.; pitfall; (MPEG). • Floresta Nacional Caxiuanã, Estação Científica Ferreira Pennna; -1.7333, -51.45; alt. 27m; 1999-04-26; Silveira, O.; Dias, J. leg.; Malaise; (MPEG). • 1♂; Floresta Nacional Caxiuanã, Estação Científica Ferreira Pennna; -1.7167, -51.4167; alt. 34m; 2003-10-26; Souza, J.; Moura, C. leg.; Winkler; (INPA). • 1♂; Rebio do Rio Trombetas - ICMBio; -1.4667, -56.3667; alt. 26m; Feitosa, R. leg.; hand collected; (DZUP). • 1♀; Río Telles Pires; -8.85, -57.4167; alt. 133m; 2009-06-21; Albertoni, F. leg.; (DZUP). • São Francisco; -3.8441, -51.8323; alt. 18m; 1979-06-02; Neto, R. leg.; (MPEG). • 1♂; Tailândia; -2.9382, -48.9511; alt. 52m; (CPDC). • 1♂; Xingu river, left shore; -2.8817, -52.0095; alt. 4m; 2001-02-16; Maciel, C.; Dias, J. leg.; Malaise; (MPEG). • 1♂; Xingu river, right shore; -3.8519, -51.8523; alt. 173m; 2001-02-25; Santos, R.; Dias, J. leg.; Malaise; (MPEG). • 1♀; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-10-09; Rosa, N. leg.; (MZSP). • 1♀; same data as precedent except for: 1969-10-13; (MZSP). • 3♂; same data as precedent except for: 1969-07-16; (MZSP). • 2♂; same data as precedent except for: 1969-10-09; (MZSP). • 2♂; same data as precedent except for: 1969-07-25; (MZSP). • 2♂; same data as precedent except for: 1969-10-13; (MZSP). • 3♂; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1969-11-17; Rosa, N. leg.; (MPEG). – **Rondônia:** • 1♂; Linha 212; -10.7, -62.2333; alt. 433m; 1985-04-01; Ramos, F. leg.; Malaise; (MPEG). • 1♀; Parque Estadual do Guajara-Mirim; -10.3167, -64.55; alt. 152m; 1998-02-25; Santos, J. R. M. leg.; Malaise; (CPDC). • 1♂; Vilhena; -12.7398, -60.1307; alt. 609m;

1973-11-01; Alvarenga, M. leg.; (MZSP). – **Roraima:** • 1♀; Estação Ecológica de Maracá; 3.4167, -61.65; alt. 127m; (CPDC). • 1♀; Estação Ecológica de Maracá; 3.4167, -61.65; alt. 127m; 1987-10-29; Benton, F. P. leg.; (CPDC). • 1♀; Estação Ecológica de Maracá; 3.4167, -61.65; alt. 127m; 2007-02-20; Souza, J. leg.; pitfall; (INPA). – **Santa Catarina:** • 1♀; Praia Lagoinha; -27.389, -48.425; alt. 2m; 2013-01-01; Chaul, J. leg.; (UFVLABECOL). – **São Paulo:** • 1♀; Sete Barras; -24.3833, -47.9167; alt. 38m; 2005-03-24; Melo, G. leg.; Malaise; (DZUP). **COLOMBIA** • 1♀; Parque Nacional Natural Cahuinarí; 1.4248, -71.1186; alt. 120m; 1989-09-01; Ospina, A. leg.; (MUSENUV). – **Cauca:** • 1♀; Popayán-Calibío; 2.5319, -76.5631; alt. 1700m; Negrett, A. J. leg.; (MZSP). – **Cundinamarca:** • 1♀; Guayabetal; 4.2, -73.8; alt. 960m; Mackay, W.; Mackay, E. leg.; (MZSP). – **La Guajira:** • 1♀; Sierra Nevada de Santa Marta, San Antonio; 7.2073, -75.61; Forel leg.; (MHNG). • 1♀; St. Antonio Nevada; 11.3, -72.5; alt. 70m; (MZSP). – **Meta:** • 1♀; Acacias, Finca el Araguaney; 3.888, -73.713; alt. 470m; 2004-04-23; Florez, E. leg.; (ICN). – **Risaralda:** • 1♀; Parque Regional Natural Ucumarí; 4.7102, -75.4877; alt. 2509m; 1992-01-28; (MUSENUV). – **Valle del Cauca:** • 1♀; 4 km W Yotoco; 3.8579, -76.4215; alt. 1525m; 2006-08-13; Mera-Velasco, Y. leg.; hand collected; (MUSENUV). • 1♀; Bocas del Río Bravo; 3.916, -76.648; alt. 900m; 1989-10-15; Castaño, F. leg.; (IAvH). • 1♀; Buga; 3.8, -76.3; (CPDC). – **Vaupes:** • 1♀; Estación Biológica Caparú; 1.0756, -69.5136; alt. 96m; 2003-04-25; Benavides, L. leg.; (ICN). • 1♀; Bogotá, Entreríos; 4.6822, -74.0748; alt. 2540m; 2007-04-08; Martínez, C.; Fernández, F. leg.; hand collected; (ICN). • 1♀; Santa Fé, Bogotá; 4.25, -74.1833; Lindig leg.; (NHMW). • 1♀; Sierra Nevada de Santa Marta, San Antonio; 7.2073, -75.61; Forel leg.; (MZSP). • 1♀; St. Antonio, Nevada; 7.2073, -75.61; Forel leg.; (MHNG). • 1♀; [no locality given]; 4.0, -72.0; G. Mayr leg.; (NHMW). **COSTA RICA – Limon:** • 2♀; Hamburg Farm; 10.244, -83.454; alt. 13m; Nevermann, F. leg.; (MZSP). – **Limón:** • Cerro Platano, 26km WSW Limón; 9.8722, -83.2394; alt. 990m; 2015-06-17; Longino, J. leg.; hand collected; (MUCR). • 1♀; Cerro Platano, 26km WSW Limón; 9.8722, -83.2394; alt. 990m; 2015-06-17; Longino, J. leg.; hand collected; (MUCR). – **Osa Peninsula:** • 1♀; 2.5 mi SW Rincón; 8.698, -83.484; alt. 40m; 1967-03-06; Thomas, E. leg.; (QCAZ). – **Puntarenas:** • 5♀; 6 Km S San Vito; 8.7, -83.0; alt. 500m; 1967-03-13; OTS course leg.; (QCAZ). **ECUADOR – Esmeraldas:** • Reserva Ecológica Cotacachi Cayapas, Charco

Vicente 2, 5 Km S San Miguel; 0.696, -78.91; alt. 230m; 2001-04-01; Araujo, P.; et al. leg.; fogging; (MEPN). • 2♀; Reserva Ecológica Cotacachi Cayapas, La Tabla, 7 km EES Playa de Oro; 0.845, -78.744; alt. 120m; 2001-04-01; Araujo, P.; et al. leg.; fogging; (MEPN). – **Guayas:** • 1♀; Cerro Cimalón; -2.53, -79.71; alt. 80m; 2013-07-01; Troya, A. leg.; beating; (MEPN). – **Napo:** • 1♀; 1km N Tena; -0.9833, -77.8167; alt. 500m; 2003-12-11; Wild, A.; Donoso, D. leg.; (UTIC). – **Orellana:** • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-08; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1994-01-26; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, Estación Científica Yasuní; -0.9333, -75.4; alt. 250m; 1995-09-23; Baquero, E.; Maza, F. leg.; (QCAZ). • 1♀; Parque Nacional Yasuní, Guiyero, a 4 km del centro de la comunidad Waorani. Laguna Waorani.; -0.625, -76.496; alt. 129m; 2007-10-23; Troya, A. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, Guiyero, a 4 km del centro de la comunidad Waorani. Laguna Waorani.; -0.625, -76.496; alt. 129m; 2008-05-21; Troya, A. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, Tiputini Biodiversity Station, 288 km SE Quito; -0.6319, -76.1442; alt. 230m; 2000-10-01; Erwin, T.; et al. leg.; fogging; (MEPN). – **Pastaza:** • 1♀; Puyo; -1.49, -77.99; alt. 900m; Weyrauch, W. leg.; (MZSP). – **Santa Elena:** • 1♀; La Rinconada; -1.5333, -80.7833; alt. 11m; Vargas, A. leg.; fogging; (QCAZ). – **Sucumbíos:** • 1♀; Reserva de Producción Faunística Cuyabeno, Trocha Zábalo-Güepi; -0.26, -75.69; alt. 270m; 2000-08-08; Araujo, P. leg.; fogging; (MEPN). **FRENCH GUIANA – Cayenne:** • 1♀; 12km East from the village of Sinnamary, Paracou Station; 5.2667, -52.9167; alt. 50m; 1996-11-01; Corbara, B.; et al. leg.; (CPDC). • 1♀; 200m E Nouragues Station, Grand Plateau, Nouragues Natural Reserve; 4.088, -52.6798; alt. 145m; 2018-08-21; (DZUP). • 1♀; Montagne dês Chevaux; 4.7333, -52.4333; alt. 75m; 2013-11-16; Team, S. E. A. G. leg.; (DZUP). • 1♀; Petit Saut; 5.0667, -53.0333; alt. 75m; 1998-07-08; Dejean, A. leg.; (DZUP). • 1♀; Petit Saut; 5.0667, -53.0333; (CPDC). • 5♀; Petit Saut; 5.0667, -53.0333; alt. 70m; 1998-07-08; Dejean, A. leg.; (CPDC). • 1♀; Saint Elie-K; 4.8228, -53.2764; alt. 126m; 2002-04-01; Orivel, J.; Le Breton, J. leg.; (CPDC). – **Saint-Laurent-du-Maroni:** • 1♀; Itoupe, P1; 3.2639, -53.7616; alt. 800m; 2014-09-11; Orivel, J.; Fichaux, M. leg.; Pitfall72h;

(EcoFoG). • 1♂; Mitaraka, P10; 2.2164, -54.457; alt. 392m; 2015-02-28; Orivel, J.; Petitclerc, F. leg.; Winkler48h; (EcoFoG). **GUYANA – Essequibo:** • 1♀; Bartica; 6.4046, -58.6257; alt. 26m; 1920-07-01; Wheeler, W. M leg.; (MZSP). • 2♂; Bartica; 6.4046, -58.6257; alt. 26m; 1920-07-01; Wheeler, W. M leg.; (MZSP). • 3♂; Kartabo; 6.4046, -58.6257; alt. 26m; (MZSP). • 1♂; Kartabo; 6.4046, -58.6257; alt. 26m; 1920-07-01; Wheeler, W. leg.; (MPEG). **MEXICO – Oaxaca:** • 1♂; Temascal; 18.2375, -96.404; alt. 37m; 1967-03-11; Janzen, O. M. leg.; (MZSP). • Uluapan, 4km NE San Bartolomé Ayautla; 18.0594, -96.6462; alt. 430m; 2016-06-08; Longino, J. leg.; hand collected; (JTLC). • Uluapan, 4km NE San Bartolomé Ayautla; 18.0594, -96.6462; alt. 430m; 2016-06-08; Longino, J. leg.; hand collected; (JTLC). • 1♂; Uluapan, 4km NE San Bartolomé Ayautla; 18.0594, -96.6462; alt. 430m; 2016-06-08; Longino, J. leg.; hand collected; (JTLC). • 1♂; Uluapan, 4km NE San Bartolomé Ayautla; 18.0594, -96.6462; alt. 430m; 2016-06-08; J. Longino leg.; search; (JTLC). • 1♂; Uluapan, 4km NE San Bartolomé Ayautla; 18.0594, -96.6462; alt. 430m; 2016-06-08; J. Longino leg.; search; (Lattke). – **Veracruz:** • 1♂; Los Tuxtlas, 10km NNW Sontecomapan; 18.5833, -95.0833; alt. 500m; 1985-03-21; P.S. Ward leg.; (PSWC). **NICARAGUA – Matagalpa:** • 1♀; Hotel Selva Negra; 12.998, -85.909; alt. 1270m; 2003-07-07; Mackay, W.; Mackay, E. leg.; (ICN). • 1♂; Hotel Selva Negra; 12.998, -85.909; alt. 1270m; 2003-07-07; Mackay, W.; Mackay, E. leg.; (ICN). **PANAMA – Canal Zone:** • 1♂; Frijoles; 9.176, -79.7989; alt. 41m; Wheeler, W. M. leg.; (MZSP). – **Colón:** • 2♂; Bosque Protector San Lorenzo; 9.3167, -80.0; alt. 20m; (CPDC). **PERU – Junin:** • 1♂; Chanchamayo; -11.1, -75.3; alt. 900m; Weyrauch, W. leg.; (MZSP). – **Madre de Dios:** • 2♂; 15 Km NE Puerto Maldonado; -12.4733, -69.1025; alt. 254m; 1989-06-01; Cover, S.; Tobin, J. leg.; hand collected; (UNMSM). • 1♂; Reserva Nacional Tambopata, Sachavacayoc; -12.8558, -69.3619; alt. 210m; 2012-07-19; Chaul, J. leg.; (MEPN). **VENEZUELA – Miranda:** • 1♂; Instituto Nacional De Investigaciones Agrícolas; 10.2293, -66.3126; alt. 48m; 1982-01-01; Brandão, C.; et al. leg.; (MZSP).

Geographic range. Mexico (Oaxaca, Veracruz, Chiapas), Guatemala*, Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Ecuador, Guyana, French Guiana, Peru, Bolivia, Brazil (Acre, Amapá, Amazonas, Bahia, Espírito Santo, Mato Grosso, Mato Grosso do Sul, Pará, Rondônia, Roraima, São Paulo, Santa Catarina). *: record from literature.

***Neoponera oberthueri* (Emery, 1890)**

Fig. 27: b (distribution)

Pachycondyla oberthueri Emery, 1890: 74. ☿ holotype, Brazil, Pará, Bragance, R. Oberthür [leg.], (MSNG, AntWeb: CASENT0903886) [image examined, link].

Combinations. In *Pachycondyla*: Brown, 1995: 307; In *Neoponera*: Emery, 1901: 47; Schmidt & Shattuck, 2014: 151

Status as species. Dalla Torre, 1893: 34; MacKay & MacKay, 2010: 474 [redescription].

Worker and queen diagnosis. Head subquadrate, posterior head corner round (Fig. 5b); eye slightly more globose than many species in the *N. crenata* group; in lateral view, anterior margin of petiolar node vertically straight, making obtuse-, occasionally nearly straight angle with dorsoanterior margin which is straight (Fig. 3h), posterior margin vertically straight, top of node placed posterad to nodal vertical midline (Fig. 3h); in lateral view, posterior face of node usually convex, bearing weak tumulus (usually), always glabrous (except marginally), and devoid of sculpture.

Worker Measurements (*n* = 14): HW: 1.01-1.29; HL: 1.16-1.61; EL: 0.35-0.47; SL: 1.24-1.64; WL: 1.89-2.27; PrW: 0.76-1.01; MsW: 0.5-0.66; MsL: 0.36-0.62; PW: 0.63-0.86; PH: 0.72-0.94; PL: 0.58-0.72; GL: 1.67-2.99; A3L: 0.72-1.04; A4L: 0.69-0.94; A3W: 1.04-1.35; A4W: 1.01-1.29; TLa: 5.16-6.47; TLr: 5.38-7.51. **Indices.** CI: 77.78-90.24; OI: 33.33-38.65; SI: 121.21-136.84; MsI: 97.3-147.83; LPI: 68.97-86.09; DPI: 103.54-126.98.

Queen Measurements (*n* = 4): HW: 1.1-1.26; HL: 1.29-1.51; EL: 0.44-0.5; SL: 1.2-1.45; WL: 2.2-2.82; PrW: 0.94-1.16; MsW: 0.9-1.06; MsL: 1.09-1.23; PW: 0.72-0.91; PH: 0.8-1.01; PL: 0.6-0.71; GL: 2.1-2.55; A3L: 0.87-1.07; A4L: 0.82-0.98; A3W: 1.18-1.37; A4W: 1.13-1.42; TLa: 5.9-6.9; TLr: 6.3-7.47. **Indices.** CI: 78.57-85.37; OI: 40.0-40.91; SI: 109.09-121.67; MsI: 81.82-88.52; LPI: 63.16-87.8; DPI: 115.0-133.33.

Comments. *Neoponera oberthueri* is amongst the smallest species in the *N. crenata* group (Fig. 26; ☿: TLa = 5.16 – 6.47 mm; ♀: TLa = 5.9 – 6.9 mm), and among the smallest in the genus. We detected some variations in the shape of the petiolar node: with a flat posterior face in three of the four specimens from Amazonian Ecuador (Fig. 3h), while in the remaining examined

material this nodal region has a truncate tumulus. (Fig. 6e). In addition, the dorsoanterior nodal margin of a dealate queen (Fig. 3g) from Parque Nacional Cuyabeno in Ecuador, does not form the characteristic obtuse angle with its anterior margin (e.g., MEPN2944, Fig. 3h). Also, the node of said queen is narrower than the average seen in other queens. Excepting these differences, including those illustrated in Figures 3g and 3h with respect to the dorsoanterior nodal margin, all the body features are virtually identical in the present material of this species, including the holotype. Current evidence does not support a potential split of these forms in two or more species. Due to the small size of the population sample from Ecuador we cannot make deeper inferences related to a potential morpho-cline in *N. oberthueri*. However, among the potential factors explaining these variations, perhaps the occurrence of random mutations on populations inhabiting relatively isolated regions could find support in further research. The specimen from Cuyabeno was obtained from a seasonally to permanently flooded várzea (sediment-rich white water) forest which distinguishes this site from other local lowland Amazonian forests. Flooded habitats differ from those of terra firme in various aspects, for example, nutrient availability which is higher on seasonally inundated forests making them exceptionally productive as compared to terra firme forests which in general are nutrient poor (Haugaasen and Peres 2005). Fluctuating conditions in these inundated habitats may lead to continuous adaptation by some organisms and can be the driving force initiating diversification (Ferreira et al. 2010). This could the case for these forms which maybe are in process of morphological differentiation. *Neoponera oberthueri*, on the other hand, is overall rarely collected, its arboreal habits together with hypothetical small populated nests may be the cause for not finding more material. In the northern Ecuadorian Amazon the arboreal strata has been intensely sampled in several sites including the well-known Parque Yasuní (see for example Erwin and Geraci 2009). The output of this sampling efforts produced enormous amount of material from where scant specimens of this taxon have been detected (A. Troya, pers. obs.).

Besides its high similarity to *N. coveri* (see comments under that species), *N. oberthueri* can also be confused with *N. carinulata* and *N. cavinodis*. The posterior head corners of *N. carinulata* are squared, in contrast to those in *N. oberthueri* which are round, this is the easiest form to separate them. *Neoponera cavinodis*, in the other hand, is very similar to *N. oberthueri*, the reader can examine the petiolar node in lateral view to distinguish them: that of the former

species has a pointed dorsum which is directed posterad, and also its posterior margin is sinuous, convex basally and concave distally. The node of *N. oberthueri* is either flat or convex posteriorly.

The elevational range of *N. oberthueri* extends between the sea level to approximately 700 m. Mackay and Mackay report a record from the region of Kamakusa in Guayana, a mountain with ca. 1400 m of altitude. We could not verify this record but it seems plausible. *N. oberthueri* is clearly an Amazonian species, and despite been scantly collected, its range is relatively broad from western to eastern Amazonia, reaching its southernmost limit in Madre de Dios, Peru.

Natural history notes. *Neoponera oberthueri* records belong mostly from well-preserved second-growth to mature forests. Besides fogging, other collecting methods include Winkler, pitfall, and directly by hand. M. Naumann and P. Kazan collected few specimens from a lowland rain forest reserve in Sucumbíos, Ecuador, their specimen labels read "prey of *Eciton hamatum* and *E. rapax*" (QCAZ: QCAZ50479, QCAZ50486, QCAZ50505).

Material examined. 34☿, 5♀. **BRAZIL – Acre:** • 2☿; 6 km E of Porto Walter; -8.25, -72.8; alt. 239m; 1997-02-05; Caldwell, J. P. leg.; (CPDC). • 1☿; Parque Nacional da Serra do Divisor; -7.4525, -73.6662; alt. 254m; 2016-11-15; Feitosa, R.; et al. leg.; (DZUP). • 1☿; Parque Nacional da Serra do Divisor, Barreiro; -7.4524, -73.6662; alt. 255m; 2016-11-15; Feitosa, R.; et al. leg.; winkler; (DZUP). – **Amazonas:** • 1☿; 80 Km NNE Manaus, ZF3-Km 24, Fazenda Esteio; -2.4167, -59.7667; alt. 115m; 1983-03-21; Harada, A. leg.; (INPA). • 1♀; Br. 319, Km 300; -4.9833, -61.5667; alt. 62m; 2009-10-15; Baccaro, F. leg.; Winkler; (INPA). • 1☿; Br. 319, Km 300; -4.9833, -61.5667; alt. 62m; 2009-10-15; Baccaro, F. leg.; Winkler; (INPA). • 1☿; Parque Nacional do Jaú - PNJ, Carabinai river; -2.2504, -62.651; alt. 64m; 1995-04-27; Santos, A. leg.; pitfall; (INPA). • 1☿; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9333, -59.9667; alt. 106m; 1999-07-29; Melo, G. leg.; (DZUP). – **Pará:** • 1☿; Belém; -1.457, -48.4875; alt. 17m; 1962-08-12; Lenko, K leg.; (MZSP). • 1☿; Bragança; -1.0539, -46.7727; alt. 14m; de Mathan leg.; (MSNG). • 1♀; Floresta Nacional Caxiuanã; -1.7001, -51.45; alt. 48m; 2003-10-01; Harada, A.; et al. leg.; Winkler; (INPA). • 1☿; Mocambo Reserve; -1.4333, -48.4; alt. 29m; 1980-01-17; Torres, M. leg.; (MPEG). • 1☿; PA 408, Km 6; -1.4608, -48.2329; alt. 14m; 1980-06-21; Torres, M. leg.; (MPEG). • 1☿; Porto Trombetas; -1.46, -56.37; alt. 35m; 1992-

01-08; Majer, J.D. leg.; (CPDC). • 2♂; Río Gurupí; -2.7131, -46.6742; alt. 61m; 1906-02-27; Malkin, B. leg.; (MZSP). • 1♂; Utinga; -1.4242, -48.4454; alt. 18m; 1962-08-05; Darlington, P. leg.; (MPEG). • 1♀; Utinga State Park; -1.4258, -48.4442; alt. 15m; 1980-01-29; Torres, M. leg.; (MPEG). – **Rondônia:** • 1♂; Parque Estadual do Guajara-Mirim, 18 km SW of Nova Dimensão; -10.3167, -64.55; alt. 152m; 1998-02-20; Santos, J. R. M. leg.; hand collected; (CPDC). • 1♂; Área Abunã; -9.6333, -65.4333; alt. 96m; 2013-04-28; Mazão, G. R.; Mendoça R. T. leg.; (DZUP). • 1♂; Área Abunã; -9.6, -65.3667; alt. 111m; 2010-09-08; Silva, R.; Feitosa, R. leg.; Winkler; (MPEG). – **Roraima:** • 1♂; Parque Nacional do Viruá; 1.5099, -60.7163; alt. 100m; 2017-12-06; Lattke, J.; et al. leg.; winkler; (DZUP). **COLOMBIA – Nariño:** • 1♂; Orito, Territorio Kofán; 0.4999, -77.2167; alt. 620m; 1998-09-19; Gonzales, E. leg.; hand collected; (IAvH). **ECUADOR – Napo:** • 1♂; 1km NNE Archidona; -0.8833, -77.8; alt. 600m; 2003-12-09; Wild, A. leg.; (UTIC). – **Orellana:** • 2♂; Parque Nacional Yasuní, Tiputini Biodiversity Station, 288 km SE Quito; -0.6319, -76.1442; alt. 230m; 2002-02-03; Erwin, T.; et al. leg.; fogging; (MEPN). – **Sucumbíos:** • 2♂; Limoncocha; -0.3998, -76.6001; alt. 280m; 1972-08-03; Chadab, R. leg.; (QCAZ). • 1♂; Limoncocha; -0.3998, -76.6001; alt. 280m; 1970-06-30; Naumann, M. G. leg.; (QCAZ). • 1♂; Limoncocha; -0.3998, -76.6001; alt. 280m; 1973-07-01; Chadab, R. leg.; (QCAZ). • 1♂; Limoncocha; -0.3998, -76.6001; alt. 280m; 1970-07-28; Kazan, P. L. leg.; (QCAZ). • 1♂; Reserva de Producción Faunística Cuyabeno; -0.2707, -75.7532; alt. 224m; 1994-10-12; Caldwell, J. P. leg.; (CPDC). **FRENCH GUIANA – Cayenne:** • 1♂; 9km W of Kaw Camp Patawa, Kaw Mountains; 4.5342, -52.1516; alt. 284m; 2008-09-01; Groc, S.; Dejean, J. leg.; Winkler; (CPDC). • 1♂; Base Vie; 5.0667, -53.0333; alt. 67m; 2000-12-06; Durou, S.; et al. leg.; (CPDC). • 1♀; Petit Saut; 5.0667, -53.0333; alt. 67m; 2000-06-28; Delabie, J. leg.; (CPDC). – **Saint-Laurent-du-Maroni:** • 1♂; Maipouri, mai-02; 5.143, -53.9974; alt. 131m; 2019-11-20; Jackie, O.; Petitclerc, F.; Troispoux, V.; Lepage, P. leg.; Winkler48h; (EcoFoG). • 1♀; Saul-Limonade, P7; 3.5629, -53.1903; alt. 278m; 2013-10-16; Orivel, J.; Donald, J. leg.; Pitfall72h; (EcoFoG). **PERU – Madre de Dios:** • 1♂; Sachavacayoc Centre, 24.39 km SW Puerto Maldonado; -12.8499, -69.3664; alt. 186m; 2012-07-20; Mackay, W. leg.; (UTIC).

Geographic range. Colombia, Guayana*, French Guiana, Ecuador, Peru, Brazil (Acre, Amapá*, Amazonas, Pará). *: record from literature.

***Neoponera recava* (MacKay & MacKay, 2010)**

Figs. 28: b (distribution)

Pachycondyla recava MacKay & MacKay, 2010: 493. Figs. 76, 225, 615-617. ☿ holotype Colombia, Valle del Cauca, Calima Cuenca media Río Calima campo, 3°56’48’’N, 76°40’30’’W, 550 m., vegeta., v.1993, R. Aldana [leg.], (IAVH) [absent from collection].

Combinations. In *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species. Fernández & Guerrero, 2019: 534.

Worker and queen diagnosis. Head subquadrate; eye relatively small, distance from mandibular insertion to anterior eye margin approximately as long as maximum eye length (Fig. 16a); posterolateral propodeal margin with salient carina (Fig. 6g); in lateral view, anterior margin of petiolar node vertically straight, anterodorsal margin horizontally straight, and posterodorsal margin broadly convex (Fig. 16a); posterior face of node concave, glabrous, polished and devoid of sculpture (Fig. 6g, 16a, c); prora longitudinally carinate (keel-shaped). AntWeb image of non-type worker UTIC00212810, link.

Worker Measurements (n = 4): HW: 1.18-1.35; HL: 1.33-1.5; EL: 0.36-0.4; SL: 1.18-1.4; WL: 2.0-2.05; PrW: 0.85-0.95; MsW: 0.55-0.56; MsL: 0.47-0.55; PW: 0.78-0.9; PH: 0.65-0.75; PL: 0.55-0.63; GL: 1.25-2.51; A3L: 0.67-0.9; A4L: 0.71-0.85; A3W: 1.18-1.35; A4W: 1.15-1.3; TLa: 5.33-5.85; TLr: 5.35-6.47. **Indices.** CI: 88.24-96.3; OI: 29.63-32.67; SI: 96.3-107.69; MsI: 100.0-116.67; LPI: 78.95-85.56; DPI: 128.12-163.64.

Queen description. Measurements (n = 1): HW: 1.22; HL: 1.41; EL: 0.39; SL: 1.33; WL: 2.35; PrW: 1.06; MsW: 0.95; MsL: 1.22; PW: 0.9; PH: 0.78; PL: 0.63; GL: 2.98; A3L: 1.0; A4L: 0.9; A3W: 1.33; A4W: 1.29; TLa: 6.29; TLr: 7.37. **Indices.** CI: 86.11; OI: 32.26; SI: 109.68; MsI: 78.39; LPI: 80.0; DPI: 143.75.

Head. Frontal view: subrectangular. Mandible triangular, longer than wide, distal region moderately bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with five to six teeth alternating with four to six smaller teeth, proximal region with one or two denticles.

Prementum with reduced transverse dome. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, with dorso-ventrally relatively flat, subtriangular-shaped, acute, extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina not reaching ocular mid-length. Torular lobe subtriangular, covering approximately 50% of acetabulum of antennal socket, posterolateral margin straight. Malar carina well-developed, not reaching anterointernal eye margin. Eye suboval, maximum length ca. one-fourth head length, convex, exceeding lateral margin of head, placed at cephalic mid-length. Anterior ocellus maximum length subequal to that of posterior ocelli. Ocelli not equidistant to each other, distance between anterior ocellus to posterior ocelli longer than interposterior ocellar distance. Distance from posterior ocellar margin to posterior margin of head roughly 1.5 times apical scape width. Distance between anterior and posterior ocelli approximately 3 times anterior ocellus maximum length. Posterior margin of head straight. Occipital carina vestigial. Scape , when pulled posterad, exceeding posterior margin of head by approximately two times apical scape width. **Mesosoma**. Lateral view: Dorsal margin convex. Pronotum carinate, with carina not projecting from cuticle. Anterior subalar area shorter than tegular maximum width. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum. Metanotal trough weakly impressed. Posterolateral margin of propodeal declivity with blunt, salient carina. Anterolateral propodeal corner rounded. Propodeal spiracle slit-shaped. Ventrolateral propodeal declivity with shallow groove just dorsad to metapleural gland opening. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Dorsal view: mesoscutum about as long as broad, close to three times length of mesoscutellum. Parapsidal lines evident, slightly divergent. Transscutal sulcus well-developed. Scutoscutellar sulcus present, slightly arched posterad, shallowly impressed, with scrobiculate sculpture, not separating mesoscutum from mesoscutellum. Mesoscutellum subtrapezoid, flat dorsally. Metascutellum well-developed, clearly discernible dorsally, surface flat. Anterodorsal median propodeal sulcus absent. Posterior face of propodeal declivity slightly concave. Propodeal lateral margins subparallel, not converging dorsomedially. Ventral view: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process poorly developed, tooth-shaped, internal margins of lobes convergent,

relatively flattened anteroposteriorly, space between lobes approximately equal to width of each. Metasternal process well-developed, inclined posterad, 20°-30° in lateral view, fang-shaped, flattened anteroposteriorly, apex about as long as mid height of metacoxal internal margin, space between lobes narrower than width of each, internal margins running parallel, process external margins slightly convergent. **Legs**. Mesofemur roughly equally thick as metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora slighlty flattened roughly on distad two thirds. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about three times shorter than posterior spur. Pretarsal claw arched, unarmed (without accesory teeth on surface). Arolium present, roughly three times shorter than pretarsal claw. **Petiole**. Lateral view: Petiolar node with straight anterior margin and convex posterior margin, posterior margin higher than anterior margin, middorsal margin horizontally relatively straight, highest point anterior to nodal longitudinal midline, posterior face convex. Subpetiolar process subtriangular, with blunt, keel-shaped, grooved anterior cusp, followed posteriorly by slightly convex dome, dome with transverse, well-impressed striae. Lateral projection of anteroventral nodal carina well-developed, with blunt tip feebly projecting dorsad. Lateral nodal carina weakly impressed, straight line. Anteroventral nodal carina incomplete, feebly concave medially. Node of petiole similar in size and shape as that of worker. **Gaster**. Lateral view: Prora well-developed, with truncate tip projecting anteroventrad. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 slightly below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin slightly convex. Anterodorsal margin of tergum of A3 usually broadly convex. Cinctus weak. Dorsal view: Tergum of A3 approximately equal in length to A4. Posterior dorsum of epipygium completely smooth. **Color**. Mandibles and legs light brown, antennae ferruginous brown. **Pilosity**. Body with moderately abundant, flexuous, golden to dark golden, erect and suberect hairs. Appressed pubescence moderately abundant, except on posterior face of node which is almost glabrous, integument always discernible. Most erect hairs on body dorsum slightly shorter than maximum eye length. Scape pilosity mostly composed of erect and suberect hairs and pruinose pubescence, erect hairs mostly shorter than apical scape width. Meso- and metatarsi bearing stiff setae (ventrally only) interspersed with suberect and appressed fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, longer than eye maximum length, and a row of tiny, stiff setae about one fifth length of those hairs. Posterior

dorsum of epipygium surrounded by 20–30 long flexuous hairs, longer than eye maximum length. **Sculpture**. Integument polished, with abundant, shallowly impressed piligerous punctures, except for head dorsum where punctures are more densely and strongly impressed. Striae on head absent except on mid clypeal dorsum bearing feebly impressed longitudinal striae, mandibles finely striate dorsally, mesosoma lacking striae except for axilar areas and laterally on propodeum and part of mesopleurum. Striae on petiolar node absent.

Male. unknown.

Comments. *Neoponera recava* is the second smallest taxon in the *N. crenata* group (Fig. 26; ☿: TLa = 5.33 – 5.85 mm; ♀: TLa = 6.29 mm). Since our material is composed of only five specimens, we cannot make general inferences about morphological variation in this species. We noted though, the petiolar node of workers from Ecuador is slightly shorter laterally as compared to that of workers and the only examined queen from Colombia. The Colombian specimens are overall darker than those from Ecuador which also show brown yellowish legs.

Although the nodal outline of this species may be similar to that of some others like *N. antecurvata*, *N. rugosula*, *N. unidentata*, its posterior face is unique due to the concavity which reaches the nodal dorsum. No other species in *Neoponera* has a similar node, thus making it unlikely to get confused with other taxa. The three species above are all bigger than *N. recava*.

The elevational range of this species spans from ca. 500 m up to ca. 1400 m. The material belongs from the Chocó-Darién biome, with the specimens obtained from well-preserved, pre-mountainous forests at the western hills of the Andes which collide with the lowland, more disturbed habitats off the Pacific coast in western South America.

Natural history notes. In contrast to most species in the *N. crenata* group, none of the specimens of *N. recava* were collected with canopy-aimed techniques. However, all of them show well-developed aroliae which is suggestive of arboreal life.



Fig. 16. *Neoponera recava*. ♀ (MUSENUV: MUSENUV-HOR1212), Colombia: Nariño. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Material examined. 4☿. **COLOMBIA – Nariño:** • 1☿; Reserva Natural de las Aves El Pangán; 1.3303, -78.082; alt. 1469m; 2006-08-04; Miranda, A.; Reyes, O. leg.; Winkler; (IAvH). • 1☿; Reserva Natural de las Aves El Pangán; 1.3303, -78.082; alt. 1451m; 2006-08-06; Miranda, A.; et al. leg.; hand collected; (IAvH). • Reserva Rio Ñambi; 1.2667, -78.1; alt. 1300m; 1993-07-

01; Bustos, J. leg.; hand collected; (MUSENUV). **ECUADOR – Pichincha:** • 2☿; ENDESA Forest Reserve; 0.1311, -79.043; alt. 600m; 2003-12-05; Wild, A. leg.; hand collected; (UTIC).

Geographic range. Western Colombia, and northwestern Ecuador.

***Neoponera rugosula* Emery, 1902**

Figs. 17: a – c (♀); 29: b (distribution)

Neoponera unidentata var. *rugosula* Emery, 1902: 30. [Raised to species by MacKay & MacKay, 2010: 324]. ☿ syntype, Peru, Marcapata, (MSNG, AntWeb: CASENT0903885) [image examined, link]; ☿ syntype, Brazil, Mato Grosso, (MSNG) [not examined]. Note: Marcapata probably refers to an Amazonian river in Peru, not to the town at ca. 3100 m elevation. The river is at the Department of Cusco where Marcapata town belongs to.

Combinations. In *Pachycondyla*: Mackay & Mackay, 2010: 499; in *Neoponera* Schmidt & Shattuck, 2014: 151.

Senior synonym of *Neoponera laevinodis* André, 1902: 14.

Status as subspecies. *Neoponera unidentata* Emery, 1911: 72.

Status as species. MacKay &MacKay, 2010: 499 [redescription].

Worker and queen diagnosis. Head subquadrate, posterior margin straight to slightly concave (Fig. 29b); antennal scape, when pulled posterad exceeding posterior head margin by about 2.5 times apical scape width; dorsum of pronotum and mesonotum either densely covered with well-impressed piligerous punctae which touch each other, or with horizontal striae (only seen in specimens from some Amazonian habitats, see comments below); propodeum laterally with strong longitudinal striae (faintly impressed in Central American populations) which usually reach dorsum; in lateral view, anterior margin of petiolar node vertically straight, usually making acute angle with dorsal margin which is inclined posterad and slightly round posteroventrally (Fig. 17c); petiolar node usually longitudinally striated laterally (Fig. 17c).

Worker Measurements (n = 29): HW: 1.14-1.8; HL: 1.34-1.9; EL: 0.35-0.51; SL: 1.27-1.8; WL: 1.95-2.82; PrW: 0.91-1.37; MsW: 0.56-0.95; MsL: 0.43-0.71; PW: 0.78-1.16; PH: 0.6-1.02; PL: 0.55-1.02; GL: 2.16-4.31; A3L: 0.84-1.33; A4L: 0.71-1.3; A3W: 1.1-1.65; A4W: 1.1-

1.65; TLa: 5.39-8.27; TLr: 6.0-9.88. **Indices.** CI: 82.93-100.0; OI: 25.0-31.43; SI: 93.75-112.07; MsI: 116.43-158.62; LPI: 80.95-133.33; DPI: 111.54-144.44.

Queen Measurements (*n* = 3): HW: 1.57-1.92; HL: 1.73-1.92; EL: 0.47-0.55; SL: 1.55-1.78; WL: 2.94-3.14; PrW: 1.33-1.57; MsW: 1.18-1.35; MsL: 1.45-1.57; PW: 0.0-1.18; PH: 0.86-1.14; PL: 0.82-0.9; GL: 2.71-4.08; A3L: 1.43-1.53; A4L: 1.22-1.37; A3W: 1.57-1.65; A4W: 1.61-1.69; TLa: 8.14-8.86; TLr: 8.43-10.04. **Indices.** CI: 88.89-100.0; OI: 28.57-30.23; SI: 91.86-102.5; MsI: 81.08-90.67; LPI: 79.31-95.45; DPI: 0.0-138.1.

Male. See Mackay and Mackay (2010)

Comments. *Neoponera rugosula* is a medium-sized species in the *N. crenata* group (Fig. 26; ☿: TLa = 5.39 – 8.27 mm; ♀: TLa = 8.14 – 8.86 mm). Morphologically, this is the most variable taxon not just in this species group but among species in the genus. Although the mesosomal striae and the shape of the petiolar node are potential intraspecific apomorphies, these are only valid, in general, for South American populations. In the two examined specimens from Costa Rica, which is the only region from where this species is thus far known from Central America, the striae are only present on the propodeum and these are less strongly impressed than their conspecifics from the south. Also, the outline of the node is less pronounced posterad than in the material from South America. We also noted feebly impressed horizontal striae medially on their clypeus. These specimens are similar to *N. unidentata*, which is possibly closely related to *N. rugosula* and to *N. antecurvata* (Troya et al. unpublished). In South American populations the body size, number of striae, and nodal shape vary significantly. For example, a specimen from Cauca (MUSENUV-HOR1213), southern Colombian Chocó-Darién, the pronotum, mesonotum and petiole lack striae, and instead it shows tiny, shallow punctae which are typical of *N. unidentata*. This specimen is also very small (TLa = 5.39 mm) as compared to the biggest known in *N. rugosula* (MUSENUV-HOR1249, TLa = 8.27 mm) found in the same biome, approximately 240 Km north of Cauca. This latter has a less pronounced node posterad and lacks nodal striae laterally but shows dense piligerous punctae on the pronotum and mesonotum, a common trait seen in the material from Cordillera de La Costa in Venezuela (e.g., LACM-ENT142422), and from Parque Nacional Tayrona (e.g., IAvH-E-79043) in the Colombian Caribe. In specimens from Amazonian Ecuador (e.g, MEPN33716), Peru, and Brazil (e.g., ATPFOR1825), the dorsal pronotal punctae is transformed into horizontal striae or a mix of those (e.g., ATPFOR1820), and this trait is

apparently shared by some populations of the Atlantic Forest. For example, a specimen from Sooretama (UFV-LABECOL000518), in Espírito Santo, has a densely punctate pronotum dorsally.

Whether these variations represent two or more species which are under ongoing differentiation, for example, amidst hybridization with hypothetically structured populations in Central America and Amazonia, or be this an unusually morphologically variable form, our observations are insufficient to properly tackle the problem. Additional lines of evidence using, for example, DNA and geometric morphometrics may clear the path towards getting a better resolution.

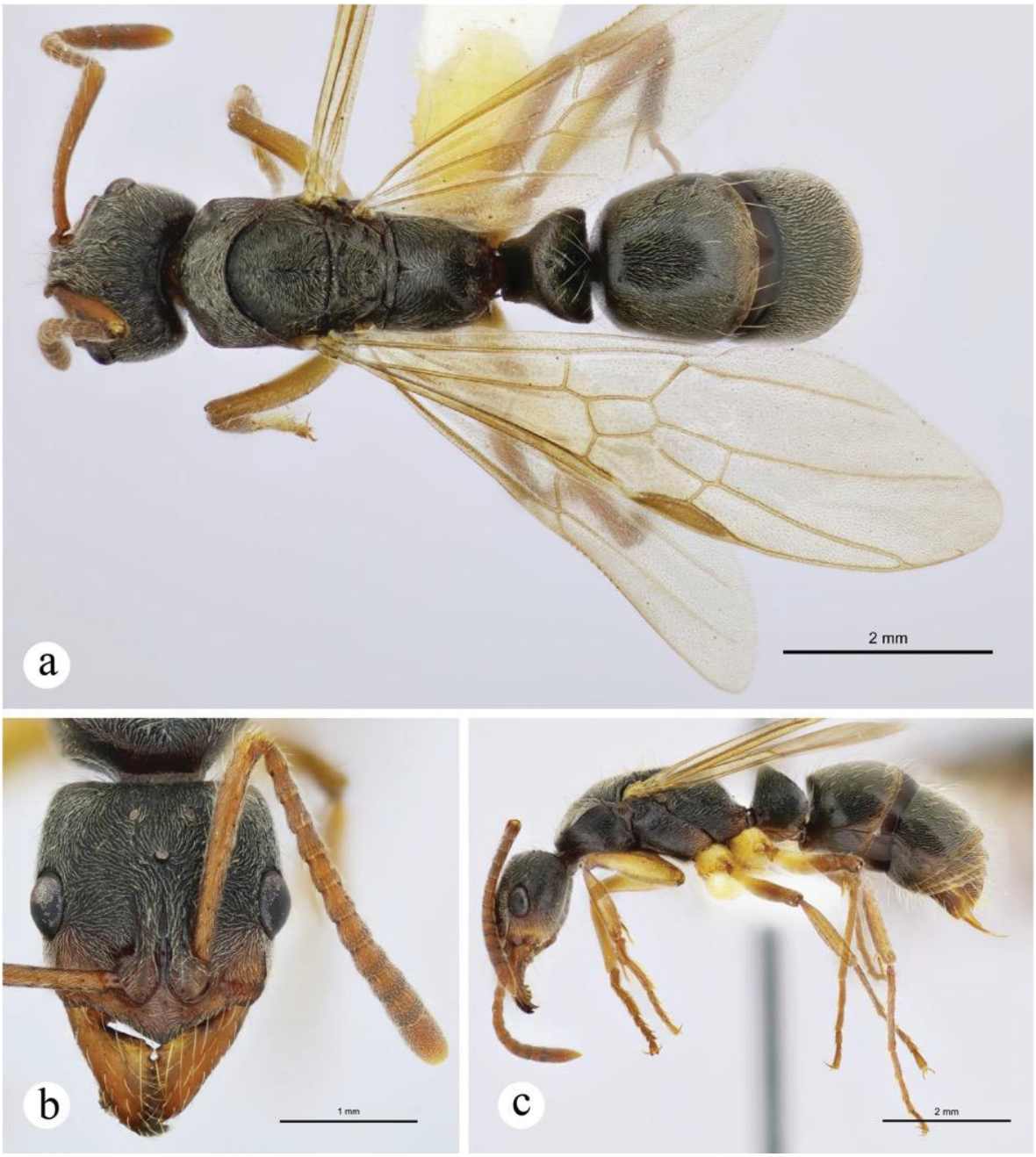


Fig. 17. *Neoponera rugosula*. ♀ (JTLC: LACMENT142422), Venezuela: Trujillo. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Neoponera rugosula is very similar to *N. unidentata*, and in lesser extent to *N. antecurvata*. The easiest way to separate them is by examining the shape of the petiolar node, the dorsoposterior margin of which is not as inclined posterad in these two species, as is in *N. rugosula*. Also, the posterior nodal face of *N. rugosula* lacks striae, while in *N. antecurvata* are always present. The node of *N. unidentata* usually is slightly higher than broad, but in *N. rugosula* is broader than high, except for the Costa Rican specimens whose petiole is highly similar to that of *N. unidentata*. A third species, *N. recava*, could also be confused with *N. rugosula*, but the concavity on the posterior nodal face of the former is sufficient to separate it from *N. rugosula*.

The elevational range of *N. rugosula* extends from near the sea level up to approximately 1400 m. Its has a broad latitudinal range from the eastern hills of the Cordillera de Guanacaste in Costa Rica, thus far the only Central American country where this species has been recorded, south to the Caribbean regions of Colombia and Venezuela, to the western and eastern sides of the tropical Andes in Colombia, Ecuador and Peru. In regards to this latter, the Calango specimens collected by Staudinger (at MZSP) from an arid region nearby the city of Lima, are probably mislabeled. To the east of the continent *N. rugosula* extends its distribution to Amazonia in Bolivia and Brazil, as far as the Xingu river, central-eastern Pará. The southernmost limit reaches the Atlantic Forests on the states of Minas Gerais, and Espírito Santo.

Natural history notes. See Mackay and Mackay (2010). In addition, J. Longino collected specimens from *Cecropia insignis* and from a *C. palmatisecta* (Uritcaceae) sapling in a second growth forest in Costa Rica. P. Araujo, collected specimens through fogging in a well-preserve seasonally flooded forest in Cuyabeno, Ecuador.

Material examined. 66☿, 4♀. **BOLIVIA – Santa Cruz:** • 1☿; Santa Anita, 7km WSW Concepci√≥n; -16.1667, -62.0833; alt. 490m; 1993-11-25; Ward, P. S. leg.; (PSWC). **BRAZIL – Bahia:** • 1☿; Fazenda esperança, Guarupa Mirim; -15.695, -3962412.0; alt. 265m; 2009-02-05; Marquezs, T. leg.; arboreal pitfall; (UFVLABECOL). **– Espírito Santo:** • 1☿; Reserva Natural Vale; -19.15, -40.0499; alt. 55m; 2009-03-08; Schmidt, F. leg.; (UFVLABECOL). **– Mato Grosso:** • 1☿; 85km W of Alta Floresta, rio dos Apiacás; -9.9, -56.9; alt. 209m; 2017-09-01; Lopes, F. J. A.; Araujo, C. B. leg.; (DZUP). **– Minas Gerais:** • 1☿; Paraopeba; -19.2784, -44.4062; alt. 730m; 2005-02-20; Santos, I.; Lino-Neto, J. leg.; (UFVLABECOL). • 1☿; Paraopeba; -19.2784, -

44.4062; alt. 730m; 2005-02-20; Santos, I. A. leg.; (DZUP). • 1♂; Paraopeba; -19.2784, -44.4062; alt. 730m; 2005-02-18; Santos, I. A. leg.; (UFVLABECOL). – **Pará:** • 1♀; Cachimbo; -8.9498, -54.9025; alt. 511m; 1954-09-01; Alvarenga, M. leg.; (MZSP). • 2♂; Floresta Nacional de Carajás, Mina de Arenito; -6.0856, -50.2313; alt. 653m; 2017-10-14; Albuquerque, E.; Monteiro, M. leg.; hand collected; (MPEG). • 1♂; Mina do Palito; -6.3, -55.7833; alt. 261m; 2018-02-03; Silva, R.; Prado, L. leg.; hand collected; (MPEG). • 1♀; São Felix de Xingu; -7.0079, -52.3643; alt. 222m; 1991-11-15; Mascarenhas, B. leg.; (MPEG). • 1♂; Xingu river, right shore; -3.8519, -51.8523; alt. 173m; 2001-03-05; Santos, R.; Dias, J. leg.; Malaise; (MPEG). – **Rondônia:** • 1♂; Ouro Preto do Oeste; -10.7096, -62.2379; alt. 337m; 1985-03-24; Dias, J. leg.; (MPEG). • 1♂; Área Mutum; -9.5833, -65.0333; alt. 101m; 2013-07-17; Mazão, G. R.; Probst, R. S. leg.; (DZUP). **COLOMBIA – Cesar:** • 1♂; [no locality given]; 9.99, 73.0; (ICN). – **Chocó:** • 5♂; Nuqui; 5.7167, -77.2667; alt. 30m; 1997-04-01; Alvarez, G. leg.; pitfall; (MUSENUV). – **Magdalena:** • 1♂; Parque Nacional Tayrona; 11.3, -74.06; alt. 350m; 1977-08-30; Kugler, C. leg.; (IAvH). – **Meta:** • 1♂; Jardín Botánico; 3.8, -74.2; alt. 3700m; 2002-01-04; Vargas, H. leg.; (IAvH). • 1♂; Jardín Botánico; 3.8, -74.2; alt. 3700(?)m; 2002-01-04; Vargas, H. leg.; Malaise; (IAvH). • 1♂; Reserva Natural El Caduceo San Martin, 400 m of Rio Camoa; 3.6653, -73.6578; alt. 380m; 2006-05-10; Cortés, J leg.; (ICN). – **Risaralda:** • 1♂; Miralindo II; 4.9328, -75.8523; alt. 964m; 1997-10-03; García, R. leg.; hand collected; (MUSENUV). – **Valle del Cauca:** • 1♂; Puerto Bello; 3.9, -76.6833; alt. 549m; 1997-02-23; Bustos, J. leg.; Winkler; (MUSENUV). **COSTA RICA – Heredia:** • 1♂; 11km SE La Virgen; 10.3333, -84.0667; alt. 500m; 2003-02-16; ALAS leg.; fogging; (INBC). • 1♂; Casa Plastico, 17km S Pto. Viejo; 10.3, -84.0333; alt. 550m; 1989-01-24; Longino, J. leg.; (JTLC). **ECUADOR – Esmeraldas:** • 1♂; 13 Km S Quininde; 0.2074, -79.4946; alt. 140m; 2010-09-01; Tituana, M. leg.; hand collected; (MEPN). – **Napo:** • 1♂; Río Hollin; -0.7, -77.6667; alt. 1100m; 1999-12-05; Pontero, C. leg.; (QCAZ). – **Orellana:** • 2♂; Parque Nacional Yasuní, Estación Científica Yasuní; -0.671, -76.4; alt. 300m; 2004-12-02; hand collected; (ICN). – **Sucumbíos:** • 1♂; Limoncocha; -0.4, -76.6; alt. 280m; 1972-07-25; Chadab, R. leg.; (QCAZ). • 1♂; Limoncocha; -0.4, -76.6; alt. 280m; 1973-08-13; Morales, L. leg.; (QCAZ). • 1♂; Limoncocha; -0.4, -76.6; alt. 280m; 1973-12-13; Morales, L. leg.; (QCAZ). • 1♂; Limoncocha; -0.4, -76.6; alt. 280m; 1972-08-

06; Chadab, R. leg.; (QCAZ). • 1☿; Limoncocha; -0.4, -76.6; alt. 280m; 1973-07-01; Chadab, R. leg.; (QCAZ). • 1☿; Limoncocha; -0.4, -76.6; alt. 280m; 1973-08-01; Chadab, R. leg.; (QCAZ). • 2☿; Limoncocha; -0.4, -76.6; alt. 280m; 1972-07-25; Morales, L. leg.; (QCAZ). • 2☿; Limoncocha; -0.3998, -76.6001; alt. 280m; 1973-08-13; Morales, L. leg.; (MZSP). • 4☿; Reserva de Producción Faunística Cuyabeno, Trocha Zábalo-Güepi; -0.26, -75.69; alt. 270m; 2000-08-08; Araujo, P. leg.; fogging; (MEPN). **PERU – Cusco:** • 1☿; Marcapata; -13.5914, -70.9785; alt. 3163(?)m; Staudinger leg.; (MSNG). – **Junin:** • 1☿; Chanchamayo; -11.1, -75.3; alt. 900m; (MZSP). • 1☿; Chanchamayo; -11.0632, -75.3412; alt. 1052m; 1939-01-01; Weyrauch leg.; (MZSP). – **Lima:** • 1♀; Calango; -12.526, -76.545; alt. 300m; Satudinger leg.; (MZSP). • 1☿; Calango; -12.526, -76.545; alt. 300m; (MZSP). – **Madre de Dios:** • 1☿; Reserva Nacional Tambopata, Sachavacayoc, Condenado trail; -12.85, -69.3663; alt. 186m; 2012-07-20; Fernandes, I. leg.; Winkler; (INPA). **VENEZUELA – Aragua:** • 1☿; Parque Nacional Henri Pittier, Estación Biológica Rancho Grande; 10.3499, -67.6841; alt. 1184m; 1982-03-10; Brandão, R.; et al. leg.; (MZSP). • 1☿; Parque Nacional Henri Pittier, Estación Biológica Rancho Grande; 10.3494, -67.6844; alt. 1100m; 2008-08-09; Ant course leg.; (UTIC). – **Falcon:** • 1☿; Finca Rita, 36.7 km W Chichiriviche; 10.8833, -68.6; alt. 336m; 2008-06-27; Lattke, J. leg.; (DZUP). – **Miranda:** • 1☿; Estación Experimental de Caucagua; 10.2833, -66.3667; alt. 74m; 1982-03-16; Brandão, C. R. F.; et al. leg.; (MZSP). • 1☿; Estación Padrón, Instituto Nacional de Investigaciones Agrícolas, 11 Km SSE Caucagua; 10.2206, -66.2993; alt. 37m; 1982-01-01; Brandão, C.; Jaffé, K.; Campos, L.; Valenzuela, J.; Jaisson, P. leg.; (MZSP). – **Trujillo:** • 1♀; Guaramacal, 15 ESE Boconó; 9.1833, -70.15; alt. 1160m; 1987-08-24; Longino, J. leg.; (JTLC). • 1☿; Guaramacal, 15 ESE Boconó; 9.1833, -70.15; alt. 1160m; 1987-08-24; Longino, J. leg.; (CUIC). • 1☿; Guaramacal, 15 ESE Boconó; 9.1833, -70.15; alt. 1160m; 1987-08-24; Longino, J. leg.; (JTLC). • 1☿; Guaramacal, 15 ESE Boconó; 9.1833, -70.15; alt. 1160m; 1987-08-04; Longino, J. leg.; (MZSP). • 6☿; Guaramacal, 15 ESE Boconó; 9.1833, -70.15; alt. 1160m; 1987-08-04; Longino, J. leg.; (CASC). – **Vargas:** • 2☿; La Peñita; 10.45, -67.2333; alt. 1150m; 2012-07-28; Lattke, J. leg.; (DZUP).

Geographic range. Costa Rica, Colombia, Guyana, Ecuador, Peru, Bolivia, Brazil (Espírito Santo, Mato Grosso, Minas Gerais, Pará, Rondônia), northern Venezuela.

***Neoponera striatinodis* (Emery, 1890)**

Figs. 29: a (distribution)

Pachycondyla striatinodis Emery, 1890: 75. ☿ syntype, Costa Rica, Alajuela and Jiménez, A. Alfaro [leg.], (MSNG, AntWeb: CASENT0903884) [image examined, link].

Combinations. In *Neoponera*: Emery, 1901: 47; Schmidt & Shattuck, 2014: 152; in *Pachycondyla*: Brown, 1995: 310.

Status as species. Emery, 1890: 13; MacKay & MacKay, 2010: 533 [redescription].

Senior synonym of: *Neoponera bakeri* (MCZC) [syntype examined]: Kempf, 1960: 391; Bolton, 1995: 310; MacKay & MacKay, 2010: 533; *Neoponera rugosinodis*: MacKay & MacKay, 2010: 533

Worker and queen diagnosis. Head subquadrate with mid lateral margin weakly convex, posterior head margin concave (link); posteroventral head corner slightly protruding and laterally bearing concentric striae (fig. 7a); humeral carina salient, shelf-like (strongly salient); posterolateral propodeal margin carinate and bearing piligerous crenulae (link); petiolar node completely covered with horizontal, coarsely impressed striae, posterolateral nodal margin bearing piligerous crenulae (Fig. 6b); prora keel-shaped, usually with sharp acute tip directed anterad (Fig. 6b).

Worker Measurements (n = 19): HW: 1.41-1.69; HL: 1.57-1.84; EL: 0.39-0.47; SL: 1.53-1.78; WL: 2.43-2.86; PrW: 1.06-1.37; MsW: 0.69-0.86; MsL: 0.55-0.67; PW: 0.82-1.06; PH: 0.84-1.1; PL: 0.78-0.98; GL: 2.47-3.72; A3L: 1.0-1.37; A4L: 0.98-1.22; A3W: 1.35-1.57; A4W: 1.29-1.57; TLa: 6.76-8.16; TLr: 7.25-9.02. **Indices.** CI: 84.09-95.56; OI: 25.43-30.0; SI: 103.53-115.79; MsI: 124.52-141.94; LPI: 80.77-100.0; DPI: 100.0-120.0.

Queen Measurements (n = 3): HW: 1.69-1.96; HL: 1.9-2.12; EL: 0.48-0.55; SL: 1.76-1.96; WL: 3.14-3.49; PrW: 1.45-1.71; MsW: 1.25-1.49; MsL: 1.45-1.61; PW: 1.06-1.33; PH: 1.06-1.24; PL: 0.92-1.06; GL: 3.49-4.27; A3L: 1.49-1.69; A4L: 1.37-1.49; A3W: 1.71-1.88; A4W: 1.69-1.9; TLa: 8.9-9.84; TLr: 9.57-10.94. **Indices.** CI: 88.66-92.59; OI: 27.95-29.53; SI: 100.0-106.82; MsI: 83.12-92.68; LPI: 81.03-92.59; DPI: 108.0-125.93.

Male. unknown.

Comments. *Neoponera striatinodis* is a medium-sized species in the *N. crenata* group (Fig. 26; ☿: TLa = 6.76 – 8.16 mm; ♀: TLa = 8.9 – 9.84 mm), its size-range varies little with no extremes departing from its general morpho-plan. In addition, the traits characterizing this species are quite homogeneous among the material examined. Even the striae, which are usually quite variable among the *Neoponera*, as well as in many other ant genera, are remarkably stable in workers and queens of *N. striatinodis*. The only characters showing certain degree of variation are the posterolateral propodeal carinae as well as the crenulae present on them and on the nodal posterior margin. The specimens from Costa Rica and Panama show a less raised propodeal carinae with reduced crenulae as compared to the populations from South America. The prora also varies in certain degree, from sharply pointed to a blunt keel-shaped form. However, this apparently occurs randomly and we did no detect clines among its known distribution range.

The acute posterolateral head corners and the gross nodal striae of this species is sufficient evidence to differentiate it from all known forms in the *N. crenata* group. The diagnostic traits of *N. striatinodis* are also peculiar among species in the genus, which facilitates its identification at a glance. Perhaps, only *N. yasuni* sp. nov. is its most similar taxon as it also has striae dorsally on the mesosoma and on the nodal surface, but lacks the crenulae on the propodeum and node, and does not have acute posterolateral head corners.

This species inhabits on relatively low-elevation regions, from the sea level to approximately 900 m, from the Pacific of southern Guatemala south to most biomes in South America including the Chocó-Darién, the tropical Andes, Amazonia, and the Atlantic Forest. The southernmost distribution reaches the state of Rio de Janeiro in Brazil.

Natural history notes. See Mackay and Mackay (2010). Much of the examined material has been obtained either with fogging, beating, or arboreal Malaise, on mostly well-preserved rain forests, in either second-growth or mature habitats. We found one record from a Colombian dry forest in Pereira, and two from the Restingas, in Maranhão, which are mostly composed of coastal shrubby vegetation typical of semi-arid zones, usually associated with sand-dunes in the Brazilian Atlantic region (Santos-Filho et al. 2015).

Material examined. 40☿, 3♀. **BRAZIL – Amapá:** • 1☿; Oiapoque; 3.8441, -51.8323; alt. 18m; 1979-05-02; Overal, W. leg.; (MPEG). – **Amazonas:** • 1☿; Estação Experimental de Silvicultura Tropical, ZF2, Km 19; -2.5892, -60.115; alt. 100m; 1979-08-18; Adis, J.; et al. leg.;

fogging; (INPA). • 1♀; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9167, -59.9833; alt. 65m; 1994-07-26; Adis, J.; et al. leg.; fogging; (INPA). • 1♀; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9167, -59.9833; alt. 65m; 1991-08-21; Adis, J.; et al. leg.; fogging; (INPA). – **Bahia:** • 1♀; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 2004-08-24; Carmo, J. C. S. leg.; (DZUP). • 1♀; Japu, Fazenda Duas Barras; -14.8832, -39.1933; alt. 130m; 1988-11-27; (DZUP). – **Goiás:** • 1♀; Niquelândia; -14.0796, -48.394; alt. 494m; 1995-09-24; Dietz, S.; Brandão leg.; (MZSP). – **Maranhão:** • 2♀; Reserva da Merck; -2.552, -44.0686; alt. 13m; 2010-08-14; Ferreira, B. leg.; arboreal Malaise; (DZUP). • 1♀; Reserva da Merck; -2.552, -44.0686; alt. 13m; 2009-09-01; Ferreira, B.; et al. leg.; arboreal Malaise; (DZUP). – **Mato Grosso:** • 1♀; 85km W of Alta Floresta, rio dos Apiacás; -9.9, -56.9; alt. 209m; 2017-09-01; Lopes, F. J. A.; Araujo, C. B. leg.; (DZUP). • 1♀; Vila vera; -12.2804, -55.2946; alt. 440m; 1973-10-01; Alvarenga, M. leg.; (MZSP). – **Minas Gerais:** • 1♀; Parque Estadual do Río Doce; -19.75, -42.6167; alt. 307m; 2015-10-14; Leponce, M, et al. leg.; (DZUP). – **Pará:** • 1♀; 10 km N Tucurui; -3.6762, -49.6816; alt. 31m; 1979-08-17; Overal, W. leg.; (MPEG). • 1♀; Cuiú-Cuiú; -5.9167, -56.5667; alt. 161m; 2018-06-18; Siqueira, E. leg.; arboreal pitfall; (MPEG). • 1♀; Fazenda Florentino; -7.1167, -55.3833; alt. 967m; 2011-02-09; Krinsk, D. leg.; pitfall; (DZUP). • 1♀; Floresta Nacional de Carajás, Mina de Arenito; -6.0856, -50.2313; alt. 653m; 2018-04-07; Albuquerque, E.; Siqueira, E. leg.; hand collected; (MPEG). • 1♀; Jarí-Amazônia; -0.8833, -52.6; alt. 18m; 1905-07-03; Silva, E. A. leg.; (DZUP). • 1♀; Quatipuru, Fazenda Feitoria; -0.8962, -47.0054; alt. 15m; 1992-11-28; Dias, J. leg.; arboreal Malaise; (MPEG). – **Rondônia:** • 1♀; Rio Madeira; -8.7372, -63.8744; alt. 90m; Mann; Baker leg.; (MCZC). • 1♀; Vilhena; -12.7412, -60.1305; alt. 594m; 1983-07-31; Harada, A. leg.; (INPA). **COLOMBIA** • 1♀; Caquetá; 0.8, -73.8; alt. 200m; 1994-10-01; Gangi, G. leg.; (IAvH). – **Caqueta:** • 1♀; Parque Nacional Natural La Serrania de Chiribiquete, Río Sarraramano; 0.1797, -72.6234; alt. 153m; 2000-04-06; Gonzales, E. leg.; hand collected; (IAvH). – **Chocó:** • 1♀; Aruzi; 7.0406, -77.3378; alt. 149m; 1998-11-25; Jimenez, E. leg.; hand collected; (MUSENUV). • 1♀; Chocó; 7.4406, -77.1189; alt. 7m; 1994-10-20; Fernandez, F. leg.; (IAvH). • 1♀; Estación Silvicultura al Bajo Atrato; 7.0406, -77.3378; alt.

149m; 1994-03-01; Mendoza, L. leg.; hand collected; (ICN). • 3☿; Estación Silvicultura al Bajo Atrato; 7.0406, -77.3378; alt. 149m; 1994-03-01; Ferro, L. leg.; hand collected; (ICN). – **Putumayo:** • 1☿; Parque Nacional Natural La Playa, Finca Charapa; 0.1333, -7494996.0; alt. 187m; 2002-04-12; Cobete, R. leg.; Malaise; (IAvH). – **Risaralda:** • 1☿; Alejandria; 7.0406, -77.3378; alt. 149m; 1997-04-12; Aldana, R. leg.; hand collected; (MUSENUV). **COSTA RICA – Limón:** • 1☿; Reserva Biológica Hitoy-Cerere; 9.6656, -83.0226; alt. 220m; 2015-06-12; Heacox, S. leg.; beating; (MUCR). • 1☿; Reserva Biológica Hitoy-Cerere; 9.6716, -83.0243; alt. 160m; 2015-06-12; Krissy Dominguez leg.; beating; (INBC). • 1☿; Jimenez; 10.2093, -83.7413; (MSNG). **ECUADOR – Orellana:** • 1☿; Estación Chiruisla; -0.6139, -75.8761; alt. 200m; 2005-09-15; Donoso, D. leg.; pitfall; (QCAZ). • 2☿; Parque Nacional Yasuní, Afluente Río Rumiyacu, Bloque 31; -0.7936, -75.902; alt. 227m; 2002-03-29; Troya, A. leg.; fogging; (MEPN). – **Pastaza:** • 1☿; Parque Nacional Yasuní, Lorocachi, Batallón de Selva 48 Sangay; -1.609, -75.968; alt. 172m; 2014-01-13; Chasiliquín, N.; Villacrés, E. leg.; fogging; (MEPN). – **Pichincha:** • 1☿; ENDESA Forest Reserve; 0.13, -79.05; alt. 600m; 2003-12-05; Wild, A. leg.; (UTIC). **FRENCH GUIANA – Saint-Laurent-du-Maroni:** • 1♀; Belvedere de Saul; 3.6167, -53.2; alt. 326m; 2011-08-25; Team, S. E. A. G. leg.; (DZUP). • 1☿; Belvedere de Saul; 3.6167, -53.2; alt. 326m; 2011-03-22; Team, S. E. A. G. leg.; (DZUP). • 1☿; Belvedere de Saul; 3.6167, -53.2; alt. 326m; 2011-09-15; Team, S. E. A. G. leg.; (DZUP). **PANAMA – Canal Zone:** • 1☿; Barro Colorado Island; 9.1509, -79.8453; alt. 124m; 1924-06-23; Wheeler, W. M leg.; (MZSP).

Geographic range. Guatemala*, Costa Rica, Panama, Guyana*, French Guiana, Colombia, Peru, Bolivia*, Brazil (Acre*, Amapá, Amazonas, Bahia, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro, Tocantins). *: record from the literature.

***Neoponera unidentata* (Mayr, 1862)**

Figs. 18: a – b (☿); 19: a – e (♂); 29: b (distribution)

Pachycondyla unidentata Mayr, 1862: 720 (☿, ♀). ☿ lectotype [by designation of MacKay & MacKay, 2010: 551], Brazil [Amazonas] “Aus dem Gebiete des Amazonenstroms”, (NHMW,

AntWeb: CASENT0915676) [image examined, link]; 5 ☿ and 1 ♀ paralectotypes [by designation of MacKay & MacKay, 2010: 551], same data as for lectotype, (NHMW) [not examined].

Combinations. In *Pachycondyla* Brown, 1995: 311; in *Neoponera* Emery, 1901: 47; Schmidt & Shattuck, 2014: 152.

Status as species. Roger, 1836: 18; Mayr, 1863: 439; MacKay & MacKay, 2010: 551 [redescription].

Senior synonyms. *Neoponera unidentata eburneipes*: Brown, 1957: 232; Kempf, 1972: 163; Bolton, 1995: 311; MacKay & MacKay, 2010: 551; *Neoponera unidentata maya*: Brown, 1957: 232; *Neoponera unidentata trinidadensis*: Brown, 1957: 232; Kempf, 1972: 163.

Worker and queen diagnosis. Head subquadrate, usually slightly narrowing posteriorly to eyes, posterior head margin feebly concave (Fig. 5c); distance from anterior eye margin to mandibular insertion about as long as maximum eye length; pronotum, mesonotum and petiolar node with micro piligerous punctae **not** touching each other; in lateral view, anterior nodal margin vertically straight, dorsal margin inclined (~ ° 70), broadly curved posterad (Fig. 6c); meeting point of vertical and dorsal margins blunt (not acute, Fig. 6a, b, nor truncate, Fig. 6e, f); posterior face of node feebly convex, not forming tumulus (Fig. 6c, d); prora blunt, keel-shaped, pointing anteroventrad, never spiny-shaped.

Worker Measurements (n = 46): HW: 1.25-1.65; HL: 1.35-1.84; EL: 0.35-0.47; SL: 1.35-1.73; WL: 2.08-2.63; PrW: 0.94-1.25; MsW: 0.61-0.86; MsL: 0.45-0.63; PW: 0.78-1.06; PH: 0.7-0.94; PL: 0.67-0.82; GL: 1.92-4.04; A3L: 0.94-1.22; A4L: 0.78-1.1; A3W: 1.22-1.53; A4W: 1.15-1.53; TLa: 5.92-7.57; TLr: 6.35-8.35. **Indices.** CI: 86.49-100.0; OI: 25.93-32.35; SI: 94.22-115.15; MsI: 113.33-155.56; LPI: 79.07-100.0; DPI: 109.52-141.18.

Queen Measurements (n = 10): HW: 1.41-1.61; HL: 1.59-1.76; EL: 0.45-0.51; SL: 1.39-1.7; WL: 2.51-2.8; PrW: 1.18-1.41; MsW: 0.9-1.22; MsL: 0.85-1.45; PW: 1.02-1.14; PH: 0.78-1.02; PL: 0.71-0.86; GL: 2.69-3.72; A3L: 1.25-1.45; A4L: 1.07-1.15; A3W: 1.55-1.72; A4W: 1.53-1.65; TLa: 7.16-7.96; TLr: 7.59-9.14. **Indices.** CI: 88.24-96.43; OI: 29.63-33.33; SI: 98.61-113.33; MsI: 80.0-105.88; LPI: 75.0-100.0; DPI: 127.27-145.0.

Male diagnosis. Interposterior ocellar distance about 1.5 times longer than the distance between anterior and posterior ocelli (Fig. 19c); notaulus well-impressed, cross ribbed, not meeting

posteriorly (Fig. 19b); anapleural sulcus deeply impressed, reaching ventral surface of mesopleuron (Fig. 19a); in lateral view, anterior margin of petiolar node straight but inclined posterad, posterior margin convex, anterior and dorsal margins meet in acute angle, lateral nodal carina well-impressed (Fig. 19a); prora keel-shaped, longitudinally sharp; posterior wing bearing 8 hamuli.

Male Measurements (*n* = 3): HW: 0.89-0.92; HL: 1.05-1.1; EL: 0.6-0.6; SL: 0.21-0.22; WL: 2.2-2.4; PrW: 1.2-1.23; MsW: 1.1-1.1; MsL: 1.4-1.55; PW: 0.55-0.6; PH: 0.6-0.7; PL: 0.6-0.7; GL: 2.3-2.5; A3L: 0.85-0.95; A4L: 0.95-1.05; A3W: 1.0-1.05; A4W: 1.1-1.2; TLa: 5.7-6.15; TLr: 6.28-6.55. **Indices.** CI: 81.82-85.19; OI: 65.22-67.42; SI: 23.6-24.44; MsI: 70.97-78.57; LPI: 92.31-100.0; DPI: 85.71-100.0.

Comments. *Neoponera unidentata* is a medium-sized species in the *N. crenata* group (Fig. 26; ☿: TLa = 5.92 – 7.57 mm; ♀: TLa = 7.16 – 7.96 mm). This is the most commonly collected form in this species-group, and is amongst the commonest in the genus after *N. verenae*, *N. apicalis*, and *N. villosa*. Its morphological diagnostic traits, including the nodal shape, are relatively stable across its distribution range. Slight differences occurring randomly among the whole examined material, with no detected geographic patterns were observed mainly in the shape of the head margin and of the petiolar node. This latter sometimes showing a slightly more convex posterior face, similar to that of *N. antecurvata*. As for the head, we noted that scant specimens from Mexico and Costa Rica have the margin posterior to eyes more straight, approximating that of such species. However, we consider these variations lie within the normal spectrum of morphological plasticity for a typical broadly distributed taxon.

Only two specimens from Pereira, Colombia (MSENUV: HOR1222, HOR1228, Fig. 18) showed a petiolar node that could perfectly be diagnostic for a different, potentially new species. This specimen, however, also shows all the characteristic traits of *N. unidentata*. Both the margin and posterior nodal face of this specimen are vertically straight, instead of convex as in *N. unidentata*. This variation could be the result of hybridization between *N. unidentata* and its potentially closest species *N. antecurvata* and *N. rugosula* (Troya et al., unpublished), or maybe these are just specimens with aberrant node shapes which depart from the known *N. unidentata* pattern. Further sampling in the area, preferably using canopy-aimed techniques, will undoubtedly yield additional clues.



Fig. 18. *Neoponera unidentata* (variant). ☿ (MUSENUV: HOR1222), Colombia: Risaralda. **a.** Lateral view; **b.** Petiolar node in lateral view.

Neoponera unidentata can only be confused with two species in the *N. crenata* group: *N. antecurvata*, and *N. rugosula*. Both are so similar that we found a considerable amount of misidentified material from the examined collections, as well as in the images from AntWeb.org illustrating *N. unidentata*. The following five specimens actually represent this species: CASENT0249164, CASENT0106307, CASENT0246022, CASENT0178709, USNMENT00412162. *N. antecurvata* differs from *N. unidentata* in the shape of the posterior head margins, posterior to eyes, which are straight, while in in *N. unidentata* are slightly narrowed. In addition, the posterior face of the node in *N. antecurvata* has a tumulus, while in *N. unidentata* it is just convex, not salient. On the other hand, in *N. rugosula* the petiolar node is slightly protruded posteroventrally, so that it is almost always higher than long, while the node of *N. unidentata* is somewhat symmetrical. The propodeum of *N. rugosula* is frequently coarsely striated laterally and dorsally (except, apparently, for Central American populations), while that of *N. unidentata* is mostly punctate.

Neoponera unidentata has a broad elevational range which spans from the sea level up to approximately 2500 m at Parque Regional Natural Ucumarí in Colombia (record MUSENUV19249 collected in 1989), a tropical mountainous region at the western limits of the Andes and the Chocó-Darién. Latitudinally, this species reaches as far north as San Luis Potosí in central-eastern Mexico, and to the south it has been found in virtually all Central American

countries but El Salvador. In South America it has been reported from Trinidad and Tobago, to the Cordillera de La Costa in Venezuela, south to the tropical Andes, Amazonia, and the Atlanctic Forest. The southernmost record is from eastern São Paulo in Brazil.

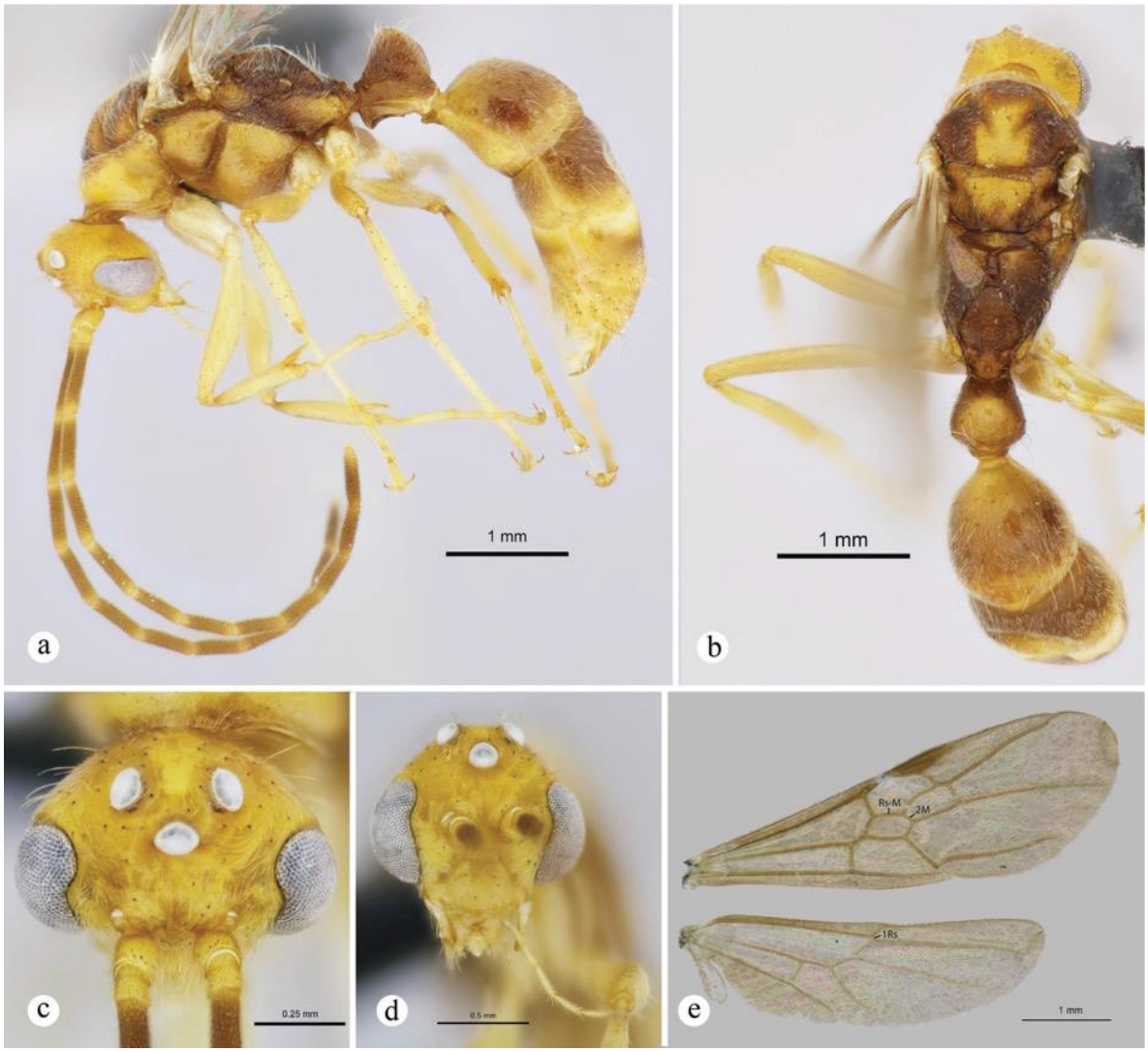


Fig. 19. *Neoponera unidentata*. ♂ (MEPN: ATPFOR2018). Mexico: Oaxaca. **a.** Lateral view; **b.** Dorsal view; **c.** Head in anterodorsal view; **d.** Head in frontal view; **e.** Fore and hind wings.

Natural history notes. See Mackay and Mackay (2010) who provide a rich compilation of information on this topic. Most records from which we could get information regarding habitat type are linked to well-preserved forests. This species has been captured with a variety of methods including ground and arboreal pitfall and Malaise, beating, sweeping, fogging, with Winkler extractors, pan and light traps, and by hand (active search). Interestingly, despite the number of specimens revised (*n* = 164) we found scant information recorded on specimen labels in regards to microhabitat. In one label it was written "*Cordia* sp." (Boraginaceae), from Manaus, and in another "on Palmeira Inajá", probably *Attalea maripa* (Arecaceae), a common native palm from Amazonia (Govaerts et al. 2022). Macedo-Reis et al. (2019) found some specimens in *Erythrochiton brasiliensis* (Rutaceae), a common ground treelet from the Brazilian Atlantic Forest which captures considerable amounts of litter from nearby trees which serves as nesting habitat to a number of ant species.

Material examined. 143☿, 12♀, 3♂, 1 larva. **BOLIVIA – La Paz:** • 1☿; Zongo; -16.1, -68.05; alt. 1980m; Staudinger, J. leg.; (MZSP). **BRAZIL – Acre:** • 1☿; Fazenda Experimental Catuaba; -10.0667, -67.6167; alt. 214m; 2014-02-23; Denicol, M. R.; Santos, A. M. leg.; arboreal pitfall; (DZUP). • 1☿; Fazenda Experimental Catuaba; -10.0667, -67.6167; alt. 214m; 2014-02-24; Denicol, M. R.; Santos, A. M. leg.; arboreal pitfall; (DZUP). • 1☿; Parque Nacional da Serra do Divisor; -7.4525, -73.6662; alt. 254m; 2016-11-15; Feitosa, R.; et al. leg.; winkler; (DZUP). • 1☿; Parque Nacional da Serra do Divisor, Barreiro; -7.4858, -73.6661; alt. 270m; 2016-11-15; Feitosa, R.; et al. leg.; pitfall; (DZUP). • 1☿; Parque Nacional da Serra do Divisor, Barreiro; -7.4525, -73.6662; alt. 254m; 2016-11-15; Feitosa, R.; et al. leg.; (DZUP). • 1☿; Parque Nacional da Serra do Divisor, Formosa; -7.438, -73.6576; alt. 252m; 2016-11-15; Feitosa, R.; et al. leg.; pitfall; (DZUP). – **Amapá:** • 1☿; Macapá; 0.0358, -51.6702; alt. 23m; 1982-12-14; Torres, M. leg.; (MPEG). • 1☿; Oiapoque; 3.8441, -51.8323; alt. 18m; 1979-05-01; Overal, W. leg.; (MPEG). • 1☿; Pacoval; -0.0571, -51.0523; alt. 17m; 1978-10-20; Torres, M. leg.; (MPEG). • 2☿; Parque Nacional Montanhas do Tumucumaque; 1.625, -52.4845; alt. 166m; 2017-07-25; Feitosa, R.; et al. leg.; winkler; (DZUP). • 1☿; Río Amaparí; 1.0822, -52.2044; alt. 125m; 1959-06-21; Lane, Bicellian leg.; (MZSP). • 1☿; Serra do Navio; 0.9019, -52.0032; alt. 152m; 1957-09-27; Lenko, K. leg.; (MPEG). – **Amazonas:** • 1☿; 80 Km N Manaus, BDFF project, Cabo Frio; -2.9333, -59.95; alt.

97m; 2006-07-25; Winkler; (INPA). • 1♀; Br. 174, Km 46; -3.0489, -59.9764; alt. 49m; 1992-02-11; Harada, A. leg.; (INPA). • 1♀; Colosso Camp; -2.4037, -59.8657; alt. 106m; 2016-08-12; Boudinot, B.; et al. leg.; (UFVLABECOL). • 1♀; Dimona Reserve, 80 Km N Manaus; -2.9012, -60.005; alt. 81m; 1986-11-01; Davidson, D. leg.; hand collected; (INPA). • 1♀; Instituto Nacional de Pesquisas da Amazôna (INPA), BR 174, KM 70; -3.0948, -59.9887; alt. 91m; 1976-11-01; Daniels, V. P. leg.; (MZSP). • 1♀; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9667, -59.9; alt. 109m; 2006-03-30; Baccaro, F. leg.; Winkler; (INPA). – **Bahia:** • 1♀; 1.5 km E Itororó; -15.1167, -40.05; alt. 255m; 2000-08-08; Santos, J. R. M. leg.; (DZUP). • 1♀; 12 Km NW Porto Seguro; -16.3833, -39.1667; alt. 90m; 2000-06-16; Santos, J. R. M.; Soares, J. C. leg.; Winkler; (MZSP). • 1♀; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; Maia, J. R. leg.; (CPDC). – **Goiás:** • 1♀; 17 km NE of Jataí, Fazenda Rio Paraíso; -17.7333, -51.6333; alt. 869m; 2011-01-28; Diniz, J. leg.; pan trap; (DZUP). • 1♀; 7 km SE of Jataí. Faz. Gertrudes; -17.8333, -51.7167; alt. 876m; 2009-02-02; Diniz, J. leg.; (DZUP). • 1♀; Mata do Açude; -17.8587, -51.727; alt. 788m; 2001-02-14; Diniz, J.; et al. leg.; (DZUP). • 2♀; Mata do Açude; -17.8587, -51.727; alt. 788m; 2005-08-20; Paniago, G. leg.; (DZUP). • 1♀; Mata do Açude; -17.8587, -51.727; alt. 788m; 2000-08-24; Diniz, J.; et al. leg.; (DZUP). • 6♀; Parque Natural Municipal Mata Do Açude; -17.8605, -51.728; alt. 791m; 2001-05-12; Élio, A.,L.; Rone, S. G. F. leg.; (MZSP). • 3♀; Parque Natural Municipal Mata Do Açude; -17.8605, -51.728; alt. 791m; 2001-05-12; Silva, J. G.; Filho, L. F. leg.; (MZSP). • 1♀; Pequena Central Hidrelétrica (PCH) Retiro Velho; -18.8222, -52.174; alt. 565m; 2011-04-14; Gilmar; James leg.; (DZUP). • 1♀; Universidade Federal de Goiás; -16.6061, -49.2614; alt. 780m; 2003-03-05; Diniz leg.; (DZUP). – **Maranhão:** • 1♀; Buriticupu; -4.3128, -46.4588; alt. 177m; 1978-09-30; Torres, M. leg.; (MPEG). – **Mato Grosso:** • 1♀; 65 Km S Sinop; -12.5167, -55.6167; alt. 430m; 1974-10-01; Alvarenga, M. leg.; (MPEG). • 1♀; Alta floresta; -9.95, -55.8667; alt. 249m; 2017-09-01; Lopez, F.; Araujo, C. leg.; beating; (MPEG). • 1♀; Chapada dos Guimarães; -15.5, -55.75; alt. 690m; 1983-11-18; (DZUP). – **Pará:** • 1♀; 10 Km N Benevides, Faz. Morelândia; -1.4608, -48.2329; alt. 14m; 1991-01-23; França, W. leg.; arboreal Malaise; (MPEG). • 1♀; 10 Km N Benevides, Faz. Morelândia; -1.4608, -48.2329; alt. 14m; 1991-09-17; Andrade, H. leg.;

arboreal Malaise; (MPEG). • 1♂; 2 Km South Jacundá; -4.463, -49.1154; alt. 104m; 1984-05-12; Overal, W., et al. leg.; hand collected; (MPEG). • 3♂; Belém; -1.457, -48.4875; alt. 17m; 1962-08-12; Lenko, K leg.; (MZSP). • 1♀; Campus pesquisa MPEG; -1.45, -48.4667; alt. 23m; 2018-01-09; Almeida, R.; Alves, D. leg.; beating; (MPEG). • 1♂; Campus pesquisa MPEG; -1.45, -48.4667; alt. 23m; 2018-01-01; Prado, L. leg.; hand collected; (MPEG). • 1♂; Campus pesquisa MPEG; -1.45, -48.4667; alt. 23m; 2018-01-09; Almeida, R.; Alves, D. leg.; beating; (MPEG). • 1♂; Campus pesquisa MPEG; -1.45, -48.4667; alt. 23m; 1989-04-26; De Sá, D. leg.; (MPEG). • 1♂; Caripi; -1.4868, -48.6978; alt. 8m; 2001-11-13; Gorayeb, I.; et al. leg.; Malaise; (MPEG). • 1♂; Floresta Nacional Caxiuanã; -1.7333, -51.45; alt. 21m; 2018-03-15; Almeida, R.; et al. leg.; pitfall; (MPEG). • 1♀; Floresta Nacional Caxiuanã, Estação Científica Ferreira Pennna; -1.7333, -51.45; alt. 21m; 2002-12-23; Martins, M. leg.; sweeping; (MPEG). • 1♀; Floresta Nacional Caxiuanã, Estação Científica Ferreira Pennna; -1.7167, -51.4167; alt. 34m; 2003-10-26; Souza, J.; Moura, C. leg.; Winkler; (INPA). • 1♂; Floresta Nacional Caxiuanã, Estação Científica Ferreira Pennna; -1.7333, -51.45; alt. 27m; 1999-04-26; Silveira, O.; Dias, J. leg.; Malaise; (MPEG). • 1♂; Mocambo Reserve; -1.4333, -48.4; alt. 29m; 1983-07-15; Sardinha, A. leg.; (MPEG). • 1♂; Mocambo Reserve; -1.4333, -48.4; alt. 29m; 1980-01-17; Torres, M. leg.; (MPEG). • 1♂; Mocambo Reserve; -1.4333, -48.4; alt. 29m; 1979-08-23; Torres, M. leg.; (MPEG). • 1♂; Mocambo Reserve; -1.4333, -48.4; alt. 29m; 1978-03-27; Torres, M leg.; (DZUP). • 1♀; Parque Ambiental, Macaco trail; -1.4246, -48.4299; alt. 35m; 2004-04-19; Nunes, A.; et al. leg.; Malaise; (MPEG). • 1♂; Pto. IGA, Reserva Gavião; -5.162, -48.9318; alt. 142m; 1981-08-11; hand collected; (INPA). • 1♂; Tucuruí; -3.7655, -49.6702; alt. 35m; 1979-03-10; Overal, W. leg.; (MPEG). • 1♂; Utinga State Park; -1.4258, -48.4442; alt. 15m; 1978-03-03; Torres, M. leg.; (MPEG). • 1♂; Área de Pesquisa Ecológica do Guamá; -1.4647, -48.4512; alt. 10m; 1969-08-26; Rosa, N. leg.; (DZUP). • 1♂; Área de Pesquisa Ecológica do Guamá-APEG; -1.4667, -48.45; alt. 13m; 1989-06-28; Torres, M. leg.; (MPEG). – **Pernambuco:** • 3♂; Caruaru; -8.2737, -35.9803; alt. 900m; 1972-05-01; Lima, T. leg.; (MZSP). – **Rio de Janeiro:** • 3♂; Silva Jardim; -22.647, -42.3954; alt. 13m; 1974-03-01; Oliviera, M. F. leg.; (MZSP). – **Rondônia:** • 1♂; Área Caiçara; -9.4331, -64.8333; alt. 85m; 2010-09-08; Silva, R.; Feitosa, R. leg.; Winkler; (MPEG). • 1♂; Área de Mata, quadrante 3; -11.4833, -61.4333;

alt. 226m; 2013-07-01; Silva, L. S. leg.; hand collected; (DZUP). • 1♂; Área de Mata, quadrante 5; -11.4833, -61.4333; alt. 226m; 2013-07-01; Silva, L. S. leg.; hand collected; (DZUP). – **Roraima:** • 1♂; Estação Ecológica do Maracá; 3.4167, -61.65; alt. 127m; 2007-02-21; Souza, J. leg.; pitfall; (INPA). • 1♀; Parque Nacional do Viruá; 1.51, -60.7163; alt. 100m; 2017-12-06; Lattke, J.; et al. leg.; (DZUP). • 5♂; Parque Nacional do Viruá; 1.4412, -61.0436; alt. 56m; 2017-12-06; Lattke, J. leg.; (DZUP). • 1♂; Parque Nacional do Viruá; 1.51, -60.7163; alt. 100m; 2017-12-06; Lattke, J.; et al. leg.; winkler; (DZUP). • 1♂; Parque Nacional do Viruá; 1.51, -60.7163; alt. 100m; 2017-12-06; Lattke, J.; et al. leg.; (DZUP). – **Sergipe:** • 1♂; São Cristovão; -10.9, -37.1833; alt. 21m; 2014-11-01; Almeida, R. P. S. leg.; (DZUP). – **São Paulo:** • 1♂; Parque Natural da Grota de Mirassol; -20.8243, -49.509; alt. 551m; 1976-06-16; Diniz, J. leg.; (DZUP). – **Tocantins:** • 1♂; Araguacema; -8.8082, -49.557; alt. 172m; 1983-01-28; Harada, A. leg.; (INPA). • 1♂; [no locality given]; -10.0, -55.0; (NHMW). **COLOMBIA** • 1♂; Reserva Forestal del Río Calderón, Estación Biológica El Zafire; -4.0, -69.9833; alt. 146m; 2007-12-06; Franco, L. E.; et al. leg.; (ICN). – **Caldas:** • 1♂; Finca Santagueda; 5.06, -75.66; alt. 1055m; 1975-05-01; Negrett, A. J. leg.; (MZSP). – **Putumayo:** • 1♂; Puerto Asis; 0.498, -76.497; alt. 2250m; 1972-08-20; (MUSENUV). – **Risaralda:** • 1♂; Alejandria; 4.8092, -75.2973; alt. 1408m; 1997-09-13; Osorio, L. leg.; Winkler; (MUSENUV). • 1♂; Parque Regional Natural Ucumarí; 4.7102, -75.4877; alt. 2509m; 1989-09-01; (MUSENUV). – **Valle del Cauca:** • 1♂; Puerto Bello; 3.9, -76.6833; alt. 549m; 1997-02-11; Bustos, J. leg.; pitfall; (MUSENUV). **COSTA RICA – Cartago:** • 1♂; Centro Agronómico Tropical de Investigación y Enseñanza; 9.8904, -83.6557; alt. 614m; Novermann, F. leg.; (MZSP). – **Heredia:** • 1♂; Casa Plastico, 17km S Pto. Viejo; 10.3, -84.0333; alt. 550m; 1989-01-24; Longino, J. leg.; (JTLC). • 1♀; La Selva Biological Station; 10.4333, -84.0167; alt. 50m; 1992-07-14; Longino, J. leg.; (INBC). • 1♂; La Selva Biological Station; 10.4333, -84.0167; alt. 50m; 1992-07-14; Longino, J. leg.; (INBC). – **Puntarenas:** • 1♂; 15 km SSW Pto. Jimenez; 8.4082, -83.3277; alt. 170m; 2010-03-07; J. Longino leg.; miniWinkler; (JTLC). • 1♂; Osa Península, 2.5 Mi SW Rincón; 8.6987, -83.4845; alt. 40m; 1967-02-21; (QCAZ). – **San José:** • 2♀; San José; 9.9294, -84.0903; alt. 1171m; 1940-01-01; Schmidt, H. leg.; (MZSP). • 1♂; San José; 9.9294, -84.0903; alt. 1171m; Schmidt, H. leg.; (MZSP). • 2♀; [no locality given]; 9.82, -83.7508; alt.

929m; Nevermann, F. leg.; (MZSP). **ECUADOR – Napo:** • 1♀; Reserva Jatun Sacha, 7 km ESE Puerto Misahualli; -1.05, -77.6; alt. 450m; 2008-12-05; Troya, A.; Vizuete, J. leg.; fogging; (MEPN). • 1♀; Río Hollin; -0.7, -77.6667; alt. 1100m; 1994-11-05; Barragán, J. leg.; (QCAZ). – **Orellana:** • 1♀; Parque Nacional Yasuní, Estación Científica Yasuní, Parcela Dinámica Bosque; -0.6833, -76.4; alt. 230m; 2004-04-03; Millow, C.; Brenes, T. leg.; (MEPN). – **Pastaza:** • 1♀; Parque Nacional Yasuní, Bameno, sendero Curaray 2; -1.3, -76.1333; alt. 240m; 2014-01-31; Troya, A.; Duque, P. leg.; fogging; (MEPN). • 1♀; Parque Nacional Yasuní, Lorocachi, Batallón de Selva 48 Sangay; -1.609, -75.968; alt. 172m; 2014-01-13; Chasiliquín, N.; Villacrés, E. leg.; fogging; (MEPN). • 1♀; Villano; -1.485, -77.538; alt. 400m; 1996-07-07; Naranjo, J. leg.; (QCAZ). – **Sucumbíos:** • 2♀; Limoncocha; -0.3998, -76.6001; alt. 280m; 1973-08-08; Morales, L. leg.; (MZSP). **FRENCH GUIANA – Cayenne:** • 1♀; 200m E Nouragues Station, Grand Plateau, Nouragues Natural Reserve; 4.088, -52.6798; alt. 145m; 2018-08-21; (DZUP). • 3♀; Petit Saut; 5.0667, -53.0333; alt. 75m; 2000-07-06; Corbara, B.; et al. leg.; (DZUP). – **Saint-Laurent-du-Maroni:** • 1♀; Galbao, P500-1; 3.6042, -53.2674; alt. 525m; 2018-10-16; Fichaux, M.; Jackie, O.; Touchard, A. leg.; Pitfall48h; (EcoFoG). • 1♀; Galbao, P500-3; 3.6008, -53.2668; alt. 465m; 2018-10-13; Fichaux, M.; Jackie, O.; Touchard, A. leg.; Winkler48h; (EcoFoG). • 1♀; Laussat, P4; 5.4819, -53.5754; alt. 50m; 2015-08-24; Orivel, J.; Fichaux, M.; Jackie; Milhomme, N. leg.; Pitfall72h; (EcoFoG). • 2♀; Laussat, P6; 5.4683, -53.5809; alt. 50m; 2015-08-25; Orivel, J.; Fichaux, M.; Jackie; Milhomme, N. leg.; Winkler48h; (EcoFoG). • 1♀; Laussat, P9; 5.4759, -53.5735; alt. 50m; 2015-08-24; Orivel, J.; Fichaux, M.; Jackie; Milhomme, N. leg.; Winkler48h; (EcoFoG). • 1♀; Mitaraka, P7; 2.2332, -54.4438; alt. 445m; 2015-02-27; Orivel, J.; Petitclerc, F. leg.; Pitfall72h; (EcoFoG). • 1♀; Trinite, G48; 4.62, -53.41; alt. 400m; 2017-04-17; Orivel, J.; Petitclerc, F. leg.; Pitfall72h; (EcoFoG). **GUATEMALA** • 1♀; [no locality given]; 15.0, -90.0; Forel, A. leg.; (MZSP). **MEXICO – Chiapas:** • 1♀; Laguna Ocotal ; 16.7959, -91.4303; alt. 950m; Dressler, R. L. leg.; (MZSP). • 1♀; Laguna Ocotal ; 16.7959, -91.4303; alt. 950m; Dressler, R. L. leg.; (MZSP). – **Oaxaca:** • 3♂; 6km S Valle Nacional; 17.7209, -96.3151; alt. 800m; 2014-08-14; Prebus, M. leg.; hand collected; (MEPN). • 2♀; 6km S Valle Nacional; 17.7209, -96.3151; alt. 800m; 2014-08-14; Prebus, M. leg.; hand collected; (MEPN). • 1 larva; Cafetal Carlota, 3km NW

Ayautla; 18.0479, -96.6896; alt. 1050m; 2016-06-13; Longino, J. leg.; hand collected; (JTLC). • 1♀; Cafetal Carlota, 3km NW Ayautla; 18.0479, -96.6896; alt. 1050m; 2016-06-13; Longino, J. leg.; hand collected; (JTLC). – **Veracruz:** • 4♀; 0.5 Km Los Tuxtlas Biological Station; 18.5827, -95.0776; alt. 280m; 2014-08-16; Prebus, M. leg.; hand collected; (MEPN). • 1♀; 1km SW Los Tuxtlas BS; 18.5786, -95.0811; alt. 450m; 2014-08-16; Prebus, M. leg.; hand collected; (MEPN). • 1♀; 1km SW Los Tuxtlas BS; 18.5786, -95.0811; alt. 450m; 2014-08-16; Prebus, M. leg.; hand collected; (MEPN). • 4♀; Reserva Los Tuxtlas; 18.5829, -95.0768; alt. 256m; 2016-05-06; Ahuatzin, D. leg.; winkler; (DZUP). • 1♀; Reserva Los Tuxtlas; 18.5829, -95.0768; alt. 256m; 2016-05-06; Corro, E.; et al. leg.; beating; (DZUP). • 3♀; Tezonapa; 18.6065, -96.6844; alt. 232m; 1953-08-11; Wilson, E. O. leg.; (MZSP). **NICARAGUA – Granada:** • 1♀; Mombacho Volcano; 11.8333, -85.9667; alt. 1150m; 2003-07-18; Mackay, W.; Mackay, E. leg.; (MZSP). **PANAMA – Colón:** • 1♀; Bosque Protector San Lorenzo; 9.2522, -79.9894; alt. 96m; (CPDC). **PERU – Cusco:** • 1♀; Estación Biológica Villa Carmen, 1.5 Km N Pillcopata; -12.8833, -71.4; alt. 521m; 2013-08-08; Lattke, J. leg.; (DZUP). – **Madre de Dios:** • 1♀; 15 Km NE Puerto Maldonado; -12.4733, -69.1025; alt. 254m; 1989-06-01; Cover, S.; Tobin, J. leg.; hand collected; (UNMSM). • 1♀; Vivero Universidad Nacional Amazonica de Madre de Dios; -12.5833, -69.2; alt. 207m; 2011-04-14; Salcedo, J. M. C. leg.; (DZUP). **VENEZUELA – Sucre:** • 1♀; El Rincón, 30 Km S Carupano; 10.6167, -63.2; alt. 606m; 1986-11-01; (MZSP). • 1♀; Rio Cuyuni, SE Venezuela; 6.086, -61.496; alt. 140m; 2008-01-01; Alonso, L. E. leg.; (ICN).

Geographic range. Mexico, Belize*, Guatemala*, Honduras*, Nicaragua, Costa Rica, Panama, Venezuela, Guyana*, Suriname*, French Guiana, Colombia, Ecuador, Peru, Bolivia, Brazil (Acre, Alagoas, Amapá*, Bahia, Espírito Santo, Goiás, Mato Grosso, Maranhão, Mato Grosso do Sul, Minas Gerais, Pernambuco, Rio de Janeiro, Rondônia, São Paulo, Sergipe, Tocantins). *: record from literature.

***Neoponera cylindrinodis* sp. nov.**

[zoobank link]

Figures. 20: a – e (☿); 21: a – c (♀); 28: a (distribution)

Type material. ***Holotype*.** 1 ☿; **BRAZIL**: **Paraná**: São José dos Pinhais, 25°36'18"S, 49°11'37"W, 880 m, Malaise, 1-7.iii.2015, A. C. Domahovski leg. (DZUP: DZUP549367). ***Paratypes***. 9 ☿, 1 ♀. **BRAZIL**: **Paraná**: same data as for holotype except, 18-28.ii.2017, Malaise suspensa, (DZUP: 1 ♀DZUP549401); same data as for holotype except, 19.x.2014, (USNM: 1 ☿ DZUP549434); same data as for holotype, except, 11.vii.2018, (UFV-LABECOL: 1 ☿ DZUP549732); same data as for holotype, except, 18.xi.2015 (INPA: 1 ☿ DZUP549382); same data as for holotype, except, 19.x.2014 (MCZC: 1 ☿ DZUP549477); same data as for holotype, except, 28.vii.2018, sweep, (MPEG: 1 ☿ DZUP549690); Piraquara Mananciais da Serra, 25°29'46"S, 49°58'54"W, 17-31.x.2007, arm. interceptação de vôo [flight interception trap]; P.C. Grossi & D.R. Parizotto, (ICN: 1 ☿ DZUP549614); P. N. Guaricana, APUFPR, 40 km SSE Curitiba, 880 m, search, jan 2019, J Lattke 3920, 18.xi.2015 (CPDC: 1 ☿ DZUP549350); same data as preceding, (MEPN: 1 ☿ ATPFOR0876).

Etymology. From the Latin *cylindrus* meaning "roller, cylinder", and *nodus* meaning "knot", referring to the somewhat barrel-shaped petiolar node as seen in dorsal view.

Worker and queen diagnosis. Head subquadrate, posterior margin straight (Fig. 20b); antennal scape, when pulled posterad exceeding posterior head margin by two times apical scape width (Fig. 20b), sometimes slightly more; distance from anterior eye margin to mandibular insertion about as long as maximum eye length (Fig. 20a); notopropodeal suture either present but faintly impressed, not forming groove, or vestigial (Fig. 20d); in lateral view, petiolar node block-shaped, about as high as broad (Fig. 20c), while in dorsal view, somewhat cylindric or barrel-shaped (Fig. 20d); integument black with golden piligerous punctae.

Worker description. Measurements (n = 10; holotype in parenthesis): HW: 1.41-1.9 (1.69); HL: 1.65-2.06 (1.9); EL: 0.39-0.47 (0.42); SL: 1.8-2.0 (1.9); WL: 2.55-3.1 (2.9); PrW: 1.1-1.35 (1.3); MsW: 0.78-0.9 (0.9); MsL: 0.47-0.95 (0.78); PW: 0.82-0.94 (0.9); PH: 0.9-1.08 (1.05); PL: 0.88-1.0 (0.91); GL: 3.0-4.25 (3.7); A3L: 1.1-1.3 (1.2); A4L: 1.06-1.3 (1.2); A3W: 1.37-1.65

(1.49); A4W: 1.37-1.7 (1.51); TLa: 7.35-8.61 (8.11); TLr: 8.33-10.3 (9.41). **Indices.** CI: 80.9-100.0 (88.95); OI: 24.39-29.03 (24.85); SI: 105.26-127.78 (112.43); MsI: 94.74-166.67 (115.38); LPI: 86.67-105.56 (86.67); DPI: 89.47-102.22 (98.9).

Head. Frontal view: subquadrate. Mandible triangular, longer than wide, distal region slightly bent ventrad, dorsolateral margin mostly straight, even surface, without groove or rim. Masticatory margin of mandible with five to six teeth alternating with four to six smaller teeth, proximal region usually with one or two denticles. Prementum with reduced transverse dome. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, with dorso-ventrally relatively flat, subtriangular-shaped, usually acute, extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina reaching, but not exceeding ocular mid-length. Torular lobe subtriangular, covering approximately 70% of acetabulum of antennal socket, posterolateral margin slightly convex. Malar carina well-developed, usually reaching anterointernal eye margin. Eye suboval, maximum length ca. one-fourth head length, convex, slightly globose, exceeding lateral margin of head, placed at cephalic mid-length. Posterior margin of head straight. Occipital carina reduced. Scape , when pulled posterad, exceeding posterior margin of head by two times apical scape width, somtimes slightly more. **Mesosoma**. Lateral view: Dorsal margin slightly convex. Pronotum carinate, with carina slightly projecting from cuticle. Anapleural sulcus weakly impressed. Posterolateral margin of propodeal declivity with feeble, blunt carina, without crenulae. Propodeal spiracle slit-shaped. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Notopropodeal suture vestigial, although faint line visible, hard to distinguish posterior margin of mesonotum and anterior margin of propodeum. Posterior face of propodeal declivity flat. Propodeal lateral margins parallel at base, convergent dorsad. Ventral view: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process strongly reduced to vestigial, when present, stump-shaped, space between lobes broader than width of each. Metasternal process well-developed, inclined posterad, ca. 45° in lateral view, fang-shaped, flattened anteroposteriorly, apex higher than half height of metacoxal internal margin, space between lobes narrower than width of each, internal margins running parallel. Metasternal process external margins convergent. **Legs**.

Mesofemur thickened medially, feebly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora flattened roughly on distad half, surface even without groove. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur about 2.5 times shorter than posterior spur. Pretarsal claw arched, unarmed (without accesory teeth on surface). Arolium present, roughly 0.5 times length of pretarsal claw. **Petiole**. Lateral view: Petiolar node anterior and posterior margins straight from base to top, anterior and posterior margins reaching approximately same level dorsally, middorsal margin convex, highest point at nodal longitudinal midline, anterodorsal margin convex, posterior face flat. Subpetiolar process subtriangular, with blunt, keel-shaped, anterior cusp without groove, followed posteriorly by slightly convex dome, dome with transverse, usually three to five, strong striae, followed posteriorly by few tenuously impressed striae; region between anterior keel and striae always smooth. Lateral projection of anteroventral nodal carina well-developed, with acute to slightly blunt tip moderately bent dorsad. Lateral nodal carina strongly impressed, slighlty arched ventrad. Dorsal view: Anterior margin of petiolar node approximately one third shorter than posterior margin. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. Lateral view: Prora well-developed, with blunt to acute tip projecting ventroposterad. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 slightly below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin relatively angled. Anterodorsal margin of tergum of A3 slightly convex. Cinctus moderate. Dorsal view: Tergum of A3 slightly shorter than A4. Posterior dorsum of epipygium completely smooth. **Color**. Appendages black to ferruginous black, to brownish. **Pilosity**. Body with moderately abundant, flexuous, golden to dark golden, erect and suberect hairs. Appressed pubescence abundant. Most erect hairs on body dorsum approximately equal to maximum eye length. Scape pilosity mostly composed of moderately abundant erect hairs and abundant appressed pubescence, erect hairs mostly shorter than apical scape width. Meso- and metatarsi bearing stiff setae (ventrally only) interspersed with suberect and appressed fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, longer than eye maximum length, and a row of setae about half length of those hairs. Posterior dorsum of epipygium surrounded by 20–30 long flexuous hairs, longer than eye maximum length.

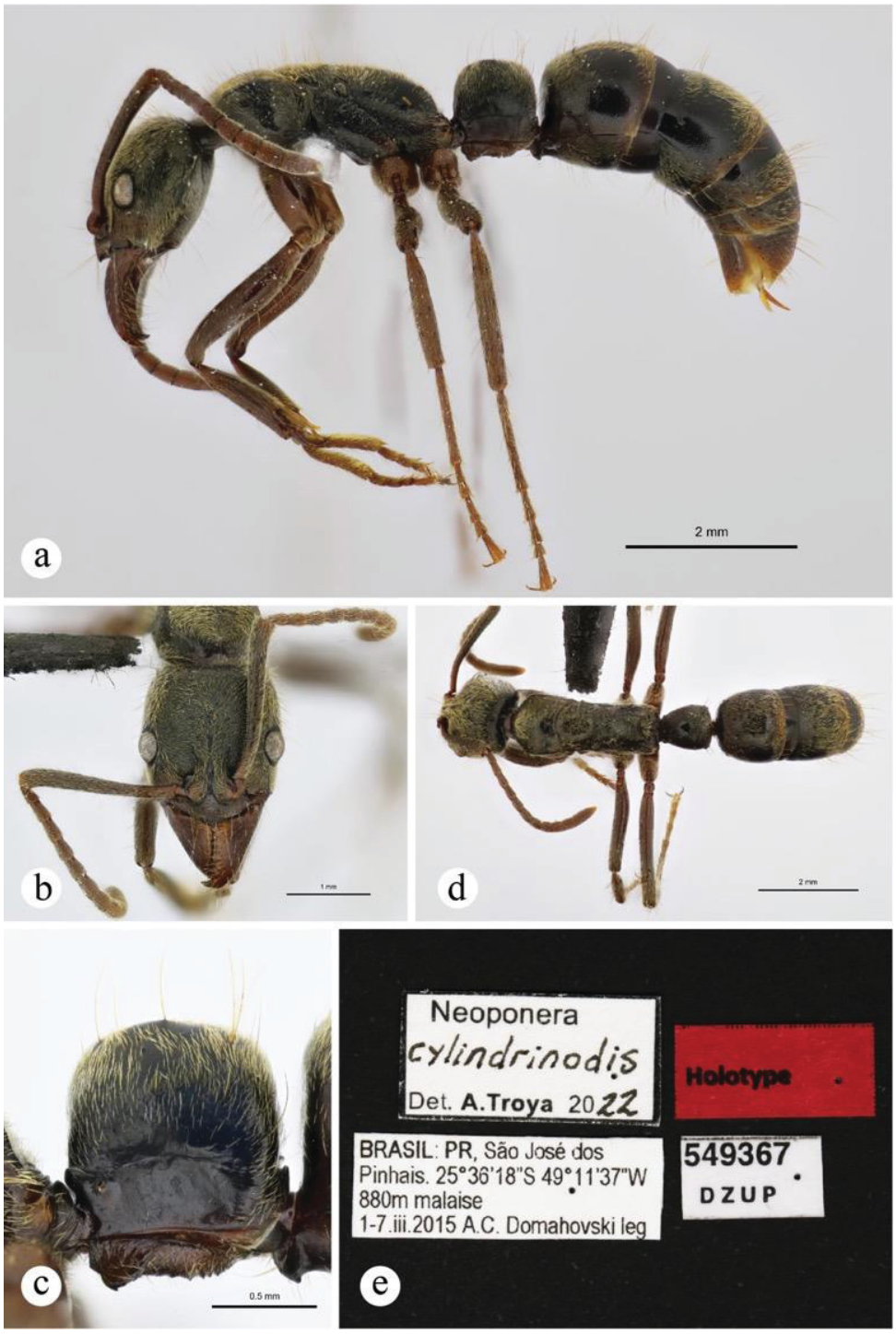


Fig. 20. *Neoponera cylindrinodis*. Holotype ☿ (DZUP: DZUP549367). Brazil: Paraná. **a.** Lateral view; **b.** Head in frontal view; **c.** Petiolar node in lateral view; **d.** Dorsal view; **e.** Collection labels.

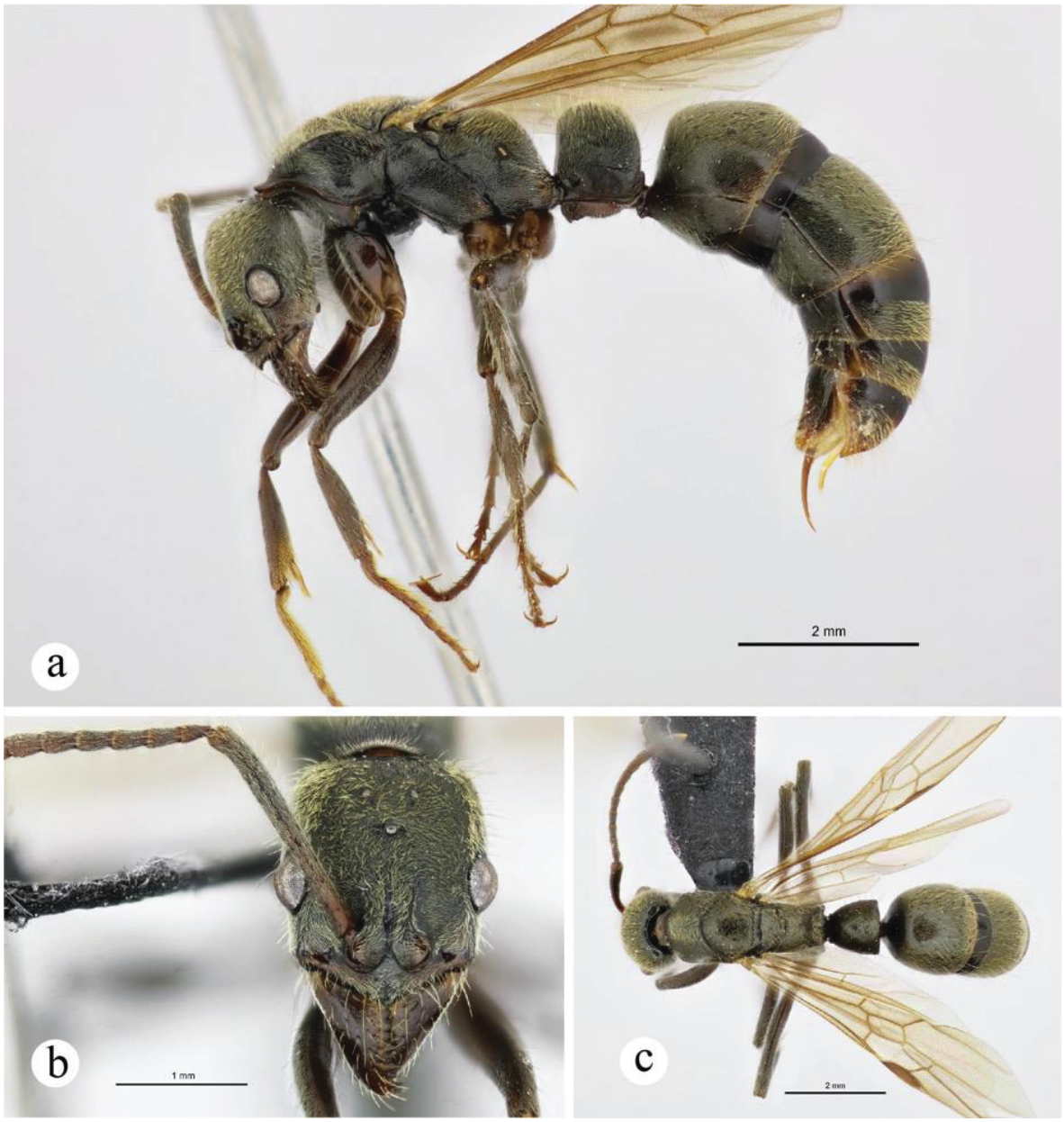


Fig. 21. *Neoponera cylindrinodis*. Paratype ♀ (DZUP: DZUP549401). Brazil: Paraná. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Sculpture. Integument polished, with abundant, shallowly impressed piligerous punctures, except for head dorsum where punctures are more densely and strongly impressed. Striae on head absent except on mid clypeal dorsum which usually shows longitudinal and/or transverse, usually feebly defined striae, mandibles usually finely striate dorsally, mesosoma lacking striae. Striae on petiolar node absent.

Queen description. Measurements (*n* = 7; paratype in parenthesis): HW: 1.49-2.02 (1.61); HL: 1.76-2.2 (1.9); EL: 0.43-0.55 (0.49); SL: 1.63-2.2 (1.85); WL: 2.82-3.75 (3.0); PrW: 1.25-1.65 (1.4); MsW: 1.1-1.5 (1.2); MsL: 1.41-1.8 (1.53); PW: 0.86-1.1 (1.09); PH: 0.98-1.15 (1.1); PL: 0.86-1.08 (0.92); GL: 3.14-5.1 (4.4); A3L: 1.18-1.7 (1.38); A4L: 1.25-1.68 (1.45); A3W: 1.51-1.9 (1.8); A4W: 1.51-1.95 (1.78); TLa: 8.0-10.32 (8.65); TLr: 8.67-12.1 (10.22). **Indices.** CI: 84.44-94.59 (84.74); OI: 25.93-33.33 (30.43); SI: 101.23-114.91 (114.91); MsI: 72.97-85.94 (78.43); LPI: 83.64-97.73 (83.64); DPI: 95.24-118.48 (118.48).

Morphology as in worker, except for: **Head**. Masticatory margin of mandible with five to six teeth alternating with four to five smaller teeth, proximal region usually with one denticle. Anterior ocellus maximum length subequal to that of posterior ocelli. Ocelli not equidistant to each other, distance between anterior ocellus to posterior ocelli slightly shorter than interposterior ocellar distance. Distance from posterior ocellar margin to posterior margin of head close to twice apical scape width. Distance between anterior and posterior ocelli close to 2.5 times anterior ocellus maximum length. **Mesosoma**. Lateral view: Dorsal margin convex. Anterior subalar area approximately as broad as tegular maximum width. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum. Metanotal trough weakly impressed. Dorsal view: mesoscutum about as long as broad, close to twice length of mesoscutellum. Parapsidal lines weakly impressed, slightly divergent. Transscutal sulcus feebly developed. Scutoscutellar sulcus present, slightly arched posterad, shallowly impressed, with scrobiculate sculpture, not separating mesoscutum from mesoscutellum. Mesoscutellum subtrapezoid, flat dorsally. Metascutellum well-developed, clearly discernible dorsally, surface flat. **Wings**. Hyaline. Slightly iridescent. Forewing venation Ogata type Ia: submarginal cells 1, 2 and discoidal present, vein 2M present, highly reduced though, 2r-rs offset from Rs+m, Rs+M ca. ten times longer than 2M, fine setose layer evenly covering surface, except for basal cell which has less pilosity than remaining wing area. Hindwing venation Cantone and Von Zuben Type I: basal and subbasal cells and vein 2M present, 1R well-developed, 1Rs well-developed. Jugal lobe present. Hindwing bearing 9 hamuli. **Legs**. Anterior mid tibial spur about three times shorter than posterior spur. Anterior hind tibial spur about three times shorter than posterior spur. **Petiole**. Node of petiole proportionally shorter and broader than in worker. **Sculpture**. Mesosoma lacking striae, except for axilar areas and few feebly impressed anterolaterally on propodeum.

Male. Unknown.

Comments. *Neoponera cylindrinodis* sp. nov. is a medium-sized species in the *N. crenata* group (Fig. 26; ☿: TLa = 7.35 – 8.61 mm; ♀: TLa = 8 – 10.33 mm). Although not many specimens were examined (*n* = 28) its size distribution is relatively homogeneous as compared to other congenerics in this group which show much greater size variation, for example *N. fiebrigi* (Fig. 13). The diagnostic morphological features of *N. cylindrinodis* are also relatively homogeneous across its range. Variations were detected only in the size and shape of the petiolar node, in some specimens the node is sometimes slightly longer than others. In regards to the nodal shape, some specimens show a feebly carinate posterior margin, while in others this carina is absent.

Neoponera cylindrinodis can only be confused with *N. crenata*, *N. fiebrigi*, and *N. moesta*, with the former being its most similar form thus far known, which is also its putative sister species (Troya et al, unpublished). The following four traits present in *N. cylindrinodis* are useful to separate it from *N. crenata*: 1) The antennal scape passes the posterior head margin by two times apical scape width (1 – 1.5 times in *N. crenata*); 2) The petiolar node is somewhat barrel-shaped, and slightly longer than broad in dorsal view (subtriangular in *N. crenata*); 3) Integument with golden piligerous punctae (pale yellowish to white yellowish in *N. Crenata*); It is clearly larger than *N. crenata*.

In regards to *N. fiebrigi*, the fore coxal carina, the inclined nodal dorsoanterior margin, and the glabrous nodal posterior face are sufficient to separate it from *N. cylindrinodis*. *N. moesta*, on the other hand, is overall smaller than *N. cylindrinodis* and has proportionally large eyes (as compared to its head) which are very close to the mandibular insertion, while the eyes of *N. cylindrinodis* are proportionally smaller and clearly more distanced from the mandibular insertion.

The elevational range of *N. cylindrinodis* spans from ca. 100 m up to ca. 1000 m. Its latitudinal range is restricted mostly to the Brazilian southern Atlantic Forest, with only one record from the Cerrado of Minas Gerais. The southernmost limit reaches the northeastern region of Rio Grande do Sul.

Natural history notes. As its closest congenerics, *Neoponera cylindrinodis* is probably arboreal, most of the examined specimens with labels containing information about the collecting technique, were obtained using arboreal Malaise and Malaise. One alate queen was collected in *Rhipsalis elliptica* (Cactaceae). Besides this nothing else is known about this taxon.

Other material examined. 12☿, 6♀. **BRAZIL – Minas Gerais:** • 1♀; [no locality given]; -18.5, -44.55; alt. 661m; 1929-04-01; (MZSP). – **Paraná:** • 1☿; Lago de Malaquara; -24.8833, -50.7167; alt. 911m; (DZUP). • 1☿; Parque Nacional Guaricana, Chacara da APUFPR, 40 Km SSE Curitiba; -25.837, -49.0489; alt. 880m; 2019-01-06; Lattke, J. leg.; hand collected; (JTLC). • 1☿; São José dos Pinhais; -25.6, -49.1833; alt. 877m; 2013-03-10; Domahovski, A. C. leg.; Malaise; (DZUP). • 1☿; São José dos Pinhais; -25.6, -49.1833; alt. 880m; 2014-12-04; Domahovski, A. C. leg.; Malaise; (DZUP). – **Rio Grande do Sul:** • 2♀; Nova Petrópolis; -29.3667, -51.1; alt. 585m; Buck, P. leg.; (MZSP). • 1☿; Nova Petrópolis; -29.3667, -51.1; alt. 585m; Buck, P. leg.; (MZSP). – **Rio de Janeiro:** • 1♀; Corcovado; -22.957, -43.2112; alt. 150m; 1958-05-02; Alvarenga, M.; Seabra leg.; (MZSP). – **Santa Catarina:** • 1♀; Nova Teutônia; -27.2333, -52.3833; alt. 400m; Plaumann, F. leg.; (MZSP). – **São Paulo:** • 3☿; Estação Biológica de Boraceia ; -23.6291, -45.8685; alt. 991m; 1964-08-18; Rabello, E. X. leg.; (MZSP). • 3☿; Guapiara; -24.1833, -48.5167; alt. 740m; Lenko, K. leg.; (MZSP). • 1☿; Parque Estadual Carlos Botelho; -24.1833, -47.9833; alt. 800m; 2009-05-11; Esteves, et al. leg.; (MZSP). • 1♀; Reserva Biológica do Alto da Serra de Paranapiacaba; -23.7667, -46.3; alt. 793m; 2012-01-23; Mendes, Z.R. leg.; (DZUP).

Distribution. Brazil (Minas Gerais, Paraná, Santa Catarina, São Paulo, Rio de Janeiro, Rio Grande do Sul).

***Neoponera dejeani* sp. nov.**

Figs. 22: a – e (☿); 23: a – c (♀); 24: a – e (♂); genitalia XX: x – x (♂); 27: a (distribution)

Type material. ***Holotype*.** 1 ☿, top label: BRAZIL: Pará: Benevides, FAZ MORELANDIA [Moreilândia farm], 2 a 4 – VII – 1988; second label from top: F. F. Ramos [leg.], (MPEG: ATPFOR1761). ***Paratypes***. 6 ☿, 1♀, 1 ♂. **BRAZIL**: **Pará**, Melgaço, Caxiuanã – ECFPn [Estação Científica Ferreira Pennna], 1°44'27.6"S, 51°27'34.2"W, 27 – 28 – XI – 2000, Mata Oeste [habitat], Malaise 2, D.M.T., S.H. Borges col [leg.], (INPA: 1 ☿ ATPFOR1799); **FRENCH GUIANA**: **Petit Saut**, Piste de Relaché. Km 7, Montagne Plomb, 25/06/2000, B. Corbara [leg.], Reg.: 5294, *Cordia nodosa* Borraginaceae [*recte* Boraginaceae] [host plant], (DZUP: 2 ☿, 1♀ ATPFOR1963); Petit Sant Basse Vie, VI.VII.2000, BM 7A, S. Durou, J. Delabie, A. Dejean, A.

Gibernau [leg.], (MCZC: 1 ♀ ATPFOR2104); Les Nouragues, # 5575, x.2009, Boulay, R., Orivel, J. [leg.], (CPDC: 1 ♀, 1 ♂ ATPFOR1978); [same collection data as precedent], (MEPN: 1 ♀ ATPFOR1978).

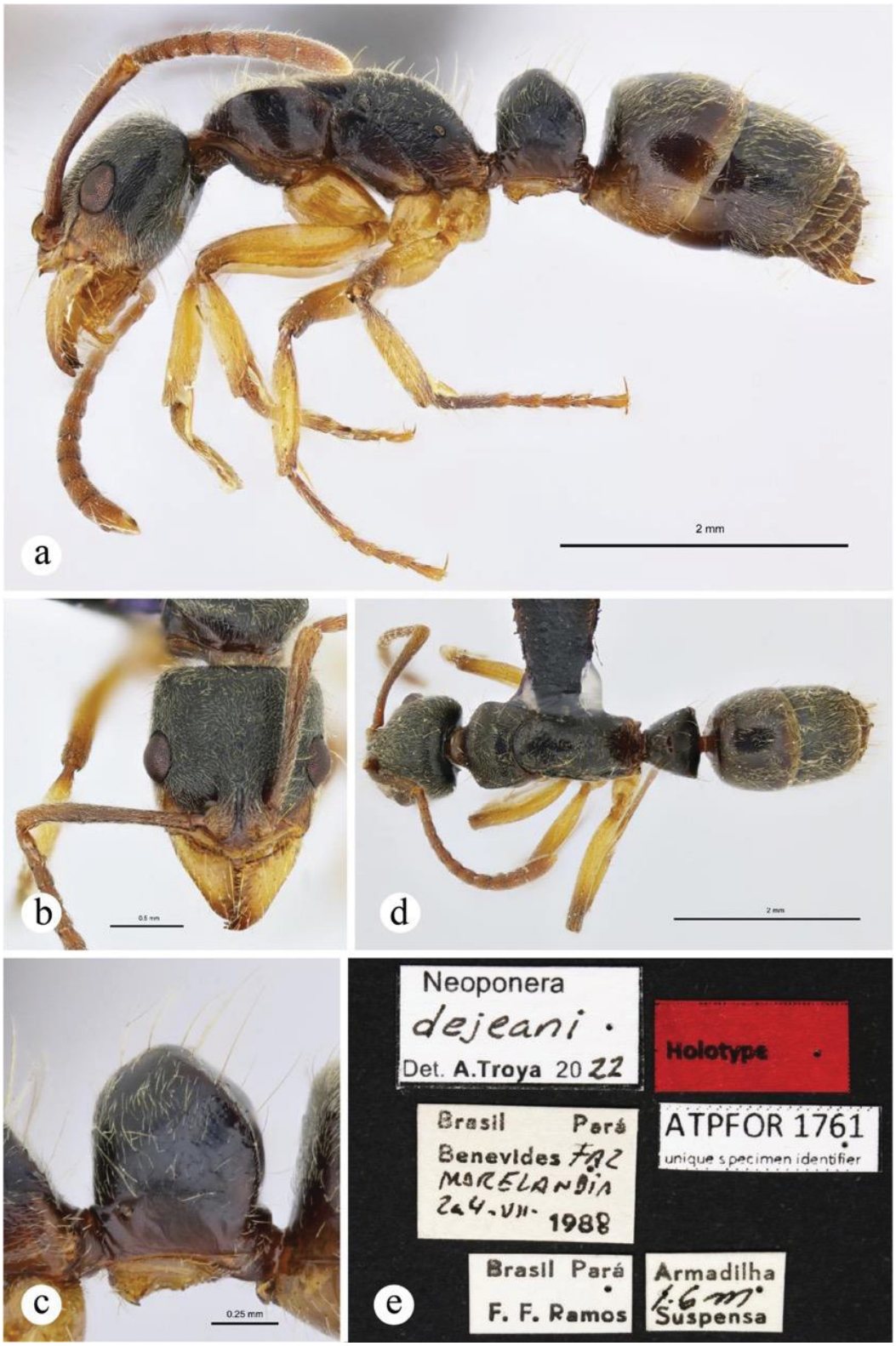


Fig. 22. *Neoponera dejeani*. Holotype ☿ (MPEG: ATPFOR1761). Brazil: Paraná. **a.** Lateral view; **b.** Head in frontal view; **c.** Petiolar node in lateral view; **d.** Dorsal view; **e.** Collection labels.

Etymology. Honoring Professor Alain Dejean, at Université Toulouse III – Paul Sabatier, France, for his many contributions on the ecology of ants and their associated organisms. Prof. Dejean is a pioneer on ant inventorying and monitoring in French Guiana, where most paratypes of this new species were found. Alain led a number of broad-spectrum projects in that country, the results of which deepened our understanding about organismal communities in a changing, human-driven world. The species name is the genitive of his family name.

Worker and queen diagnosis. Head subquadrate, posterior head margin straight, antennal scape exceeding posterior head margin by about 1.5 times apical scape width (Fig. 22b); in lateral view, anterior margin of petiolar node vertically straight, anterodorsal margin feebly convex, not meeting in angle with anterior margin, posterior margin convex (Fig. 22c); dorsum of node relatively acute and placed at about median vertical line (workers only, Fig. 22c), in the queen the nodal top is placed anterior to midline (Fig. 23a); posterior nodal face bearing a truncate, feebly salient tumulus which is glabrous, smooth, and polished (Figs. 6e, 22d); subpetiolar process with faintly impressed striae; prora keel-shaped, mostly round anteriorly (Fig. 6e); body dorsum and pleural plates devoid of striae.

Worker description. Measurements (n = 6; holotype in parenthesis): HW: 1.12-1.31 (1.12); HL: 1.16-1.31 (1.25); EL: 0.34-0.38 (0.34); SL: 0.97-1.25 (1.19); WL: 1.78-1.92 (1.78); PrW: 0.88-0.97 (0.88); MsW: 0.53-0.66 (0.53); MsL: 0.47-0.56 (0.47); PW: 0.72-0.8 (0.72); PH: 0.75-0.78 (0.75); PL: 0.56-0.61 (0.61); GL: 1.72-2.5 (2.34); A3L: 0.67-0.84 (0.81); A4L: 0.69-0.75 (0.72); A3W: 1.06-1.19 (1.09); A4W: 1.03-1.16 (1.06); TLa: 5.06-5.33 (5.17); TLr: 5.55-6.23 (5.98). **Indices.** CI: 88.1-113.51 (90.0); OI: 28.57-32.43 (30.56); SI: 73.81-106.67 (105.56); MsI: 100.0-126.67 (113.33); LPI: 73.47-81.25 (81.25); DPI: 117.95-141.67 (117.95).

Head. Frontal view: subquadrate. Mandible triangular, longer than wide, distal region slightly bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with five to six teeth alternating with four to five smaller teeth, proximal region usually with one denticle. Prementum with well-developed transverse dome. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, with dorso-ventrally relatively flat, triangular-shaped, acute, extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina reaching, but not exceeding ocular mid-length. Torular lobe subtriangular, covering

approximately 70% of acetabulum of antennal socket, posterolateral margin slightly convex. Malar carina well-developed, usually reaching anterointernal eye margin. Eye suboval, maximum length ca. one-fourth head length, convex, slightly globose, exceeding lateral margin of head, placed at cephalic mid-length. Ocelli not equidistant to each other, distance between anterior ocellus to posterior ocelli shorter than interposterior ocellar distance. Posterior margin of head straight. Occipital carina reduced. Scape, when pulled posterad, exceeding posterior margin of head by about one and half apical scape width. **Mesosoma**. Lateral view: Dorsal margin straight to slightly convex. Pronotum carinate, with carina slightly projecting from cuticle. Anapleural sulcus vestigial. Posterolateral margin of propodeal declivity with feeble, blunt carina, without crenulae. Propodeal spiracle slit-shaped. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Notopropodeal suture completely absent. Posterior face of propodeal declivity flat. Propodeal lateral margins parallel at base, convergent dorsad. Ventral view: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process vestigial. Metasternal process well-developed, inclined posterad, ca. 45° in lateral view, fang-shaped, flattened anteroposteriorly, apex slightly higher than half height of metacoxal internal margin, space between lobes narrower than width of each, internal margins running parallel. Metasternal process external margins convergent. **Legs**. Mesofemur thickened medially, feebly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora flattened roughly on distad half, surface even without groove. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about 2.5 times shorter than posterior spur. Pretarsal claw arched, unarmed (without accesory teeth on surface). Arolium present, roughly 0.5 times length of pretarsal claw. **Petiole**. Lateral view: Petiolar node with straight anterior margin and convex posterior margin, posterior margin higher than anterior margin, middorsal margin relatively acute, highest point at nodal longitudinal midline, anterodorsal margin slightly convex to feebly flattened, posterior face convex. Subpetiolar process subtriangular, with acute anterior cusp, sometimes keel-shaped, followed posteriorly by usually straight to slightly convex dome, dome with transverse, usually tenuously impressed striae. Lateral projection of anteroventral nodal carina usually well-developed, with acute to slightly blunt tip moderately bent dorsad. Lateral nodal carina usually

weakly impressed, slighlty arched ventrad. Dorsal view: Anterior margin of petiolar node approximately half width of posterior margin. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. Lateral view: Prora well-developed, with round tip projecting anteroventrad. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin relatively angled. Anterodorsal margin of tergum of A3 slightly convex. Cinctus weak. Dorsal view: Tergum of A3 equal in length to A4. Posterior dorsum of epipygium completely smooth. **Color**. Appendages mandibles and legs brownish, antennae black ferruginous. **Pilosity**. Body with moderately abundant, flexuous, tenuously golden, erect and suberect hairs. Appressed pubescence abundant. Most erect hairs on body dorsum approximately equal to maximum eye length. Scape pilosity mostly composed of scattered erect hairs and appressed pubescence, erect hairs about as long as apical scape width. Meso- and metatarsi bearing stiff setae (ventrally only) interspersed with suberect and appressed fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, longer than eye maximum length, and a row of setae about half length of those hairs. Posterior dorsum of epipygium surrounded by ca. 20 long flexuous hairs, longer than eye maximum length. **Sculpture**. Integument polished, with abundant, shallowly impressed piligerous punctures, except for head dorsum where these are feebly coarser and more densely distributed; posterior face of petiolar node completely smooth and mostly glabrous. Striae on head absent, mandibles finely striate dorsally, mesosoma lacking striae. Striae on petiolar node absent.

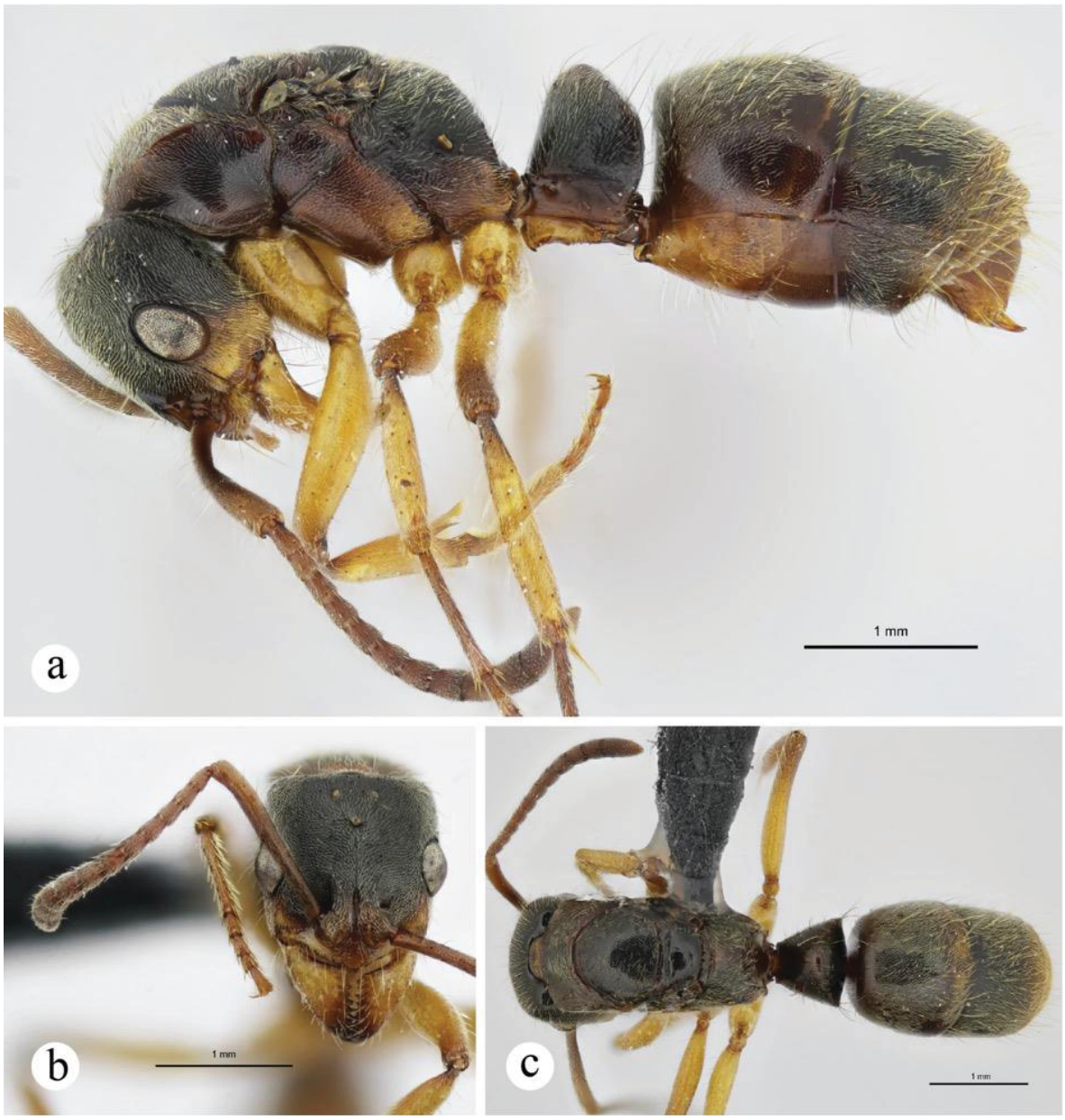


Fig. 23. *Neoponera dejeani*. Paratype♀ (DZUP: ATPFOR1963). French Guiana: Cayenne. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Queen description. Measurements (n = 1): HW: 1.31; HL: 1.38; EL: 0.44; SL: 1.3; WL: 2.28; PrW: 1.12; MsW: 1; MsL: 1.28; PW: 0.91; PH: 0.72; PL: 0.62; GL: 2.19; A3L: 0.97; A4L: 0.94; A3W: 1.41; A4W: 1.34; TLa: 6.19; TLr: 6.47. **Indices.** CI: 95.45; OI: 33.33; SI: 98.81; MsI: 78.05; LPI: 86.96; DPI: 145.

Morphology as in worker except for: **Head**. Ocelli approximately equidistant to each other. Distance from posterior ocellar margin to posterior margin of head roughly one apical scape width. Distance between anterior and posterior ocelli about 2 times anterior ocelus maximum length. **Mesosoma**. Lateral view: Dorsal margin convex. Anterior subalar area approximately as broad as tegular maximum width. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum. Metanotal trough deeply impressed. Dorsal view: mesoscutum broader than long, close to twice length of mesoscutellum. Parapsidal lines weakly impressed, slightly divergent. Transscutal sulcus well-developed. Scutoscutellar sulcus present, slightly arched posterad, strongly impressed, not separating mesoscutum from mesoscutellum. Mesoscutellum subtrapezoid, slightly flat dorsally. Metascutellum well-developed, clearly discernible dorsally, surface even, slightly flat. Anterodorsal median propodeal sulcus present, weakly impressed. **Petiole**. Lateral nodal carina strongly impressed, slighlty arched ventrad. Node of petiole proportionally shorter and broader than in worker.

Male diagnosis. Notaulus deeply impressed on cuticle, lacking internal sculpture; notauli not meeting posteriorly (Fig. 24b); anapleural sulcus feebly impressed on cuticle, and feebly sculptured, just reaching ventral pleural surface (Fig. 24a); in lateral view, anterior margin of petiolar node slightly convex, inclined posterad ca. 45°, posterior margin feebly convex and inclined anterad ca. 30 °, dorsal margin convex (Fig. 24a); lateral nodal carina absent; hindwing bearing 7 hamuli.

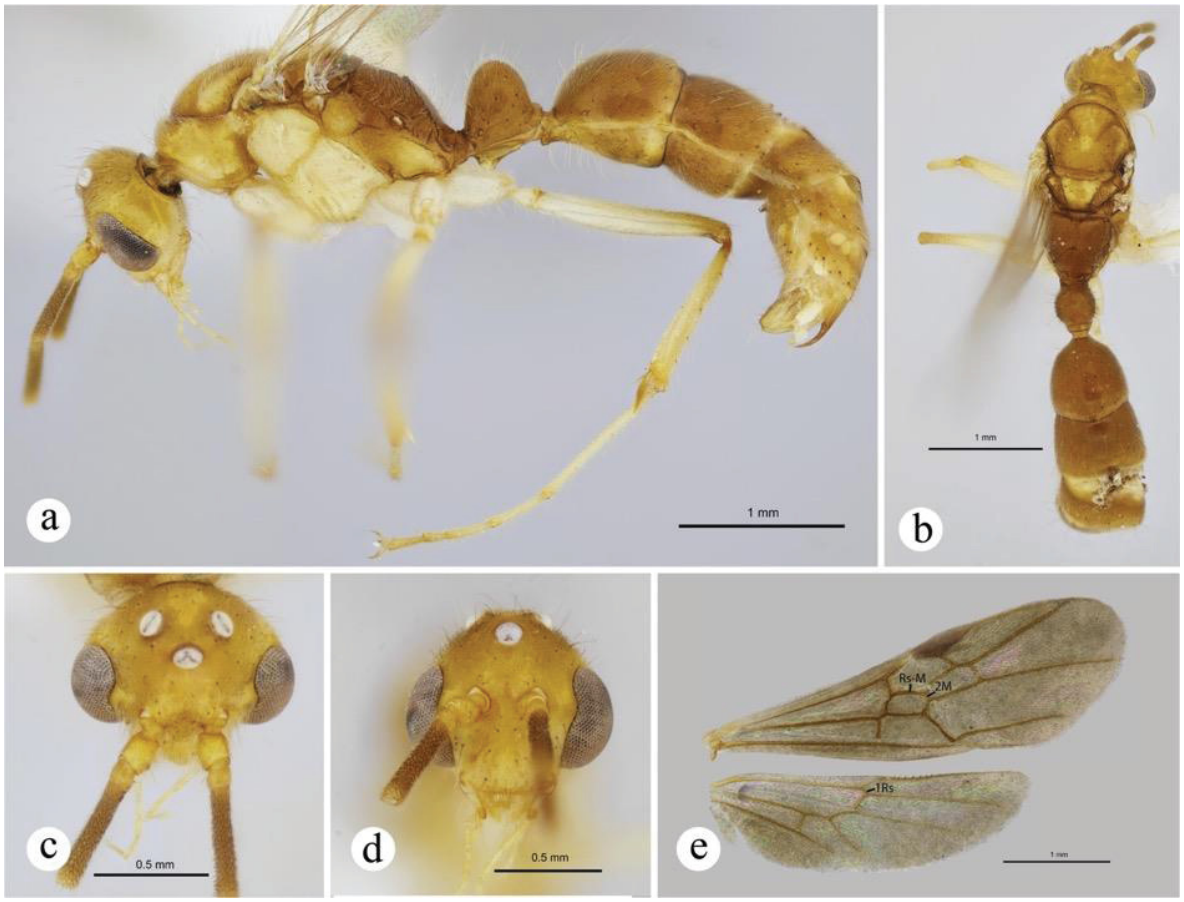


Fig. 24. *Neoponera dejeani*. Paratype ♂ (CPDC: ATPFOR1978). French Guiana: Cayenne. **a.** Lateral view; **b.** Dorsal view; **c.** Head in anterodorsal view; **d.** Head in frontal view; **e.** Fore and hind wings.

Male description. Measurements (n = 1): HW: 0.75; HL: 0.84; EL: 0.09; SL: 0.45; WL: 1.84; PrW: 0.75; MsW: 0.91; MsL: 1.09; PW: 0.41; PH: 0.47; PL: 0.48; GL: 2.38; A3L: 0.64; A4L: 0.62; A3W: 0.75; A4W: 0.88; TLa: 4.44-; TLr: 5.55. **Indices.** CI: 88.89; OI: 12.5; SI: 60.42; MsI: 82.86; LPI: 103.33; DPI: 83.87.

Head. Frontal view: subrhomboid. Mandible spatulate, longer than wide, blunt apically. About 1.5 mandalus (maximum length) fit on mandibular dorsum, mandibular apex, when mandible is closed, barely touches lateral margin of labrum. Palp formula: 6,4. Labrum dorsum smooth. Area between posterior margin of clypeus and supraclypeal area with evident depression. Posterior supraclypeal area acute. Supraclypeal area slightly protruding from cuticule, followed posteriorly by tenuously impressed longitudinal carina. Distance between internal margins of antennal sockets less than one socket diameter. Torular lobe strongly reduced. Eye suboval,

slightly notched in the dorsal third, placed slightly anterior to cephalic mid-length. Ocellar area not protruding from cuticle. Ocellar area placed posterad to vertex. Ocelli not equidistant to each other, distance between anterior ocellus to posterior ocelli shorter than interposterior ocellar distance. Distance between anterior and posterior ocelli approximately 0.5 times anterior ocellus maximum length. Occipital carina reduced. Scape cylindrical, about twice as long as pedicel. Length of first flagellomere longer than second flagellomere. **Mesosoma**. Lateral view: Dorsal margin convex. Pronotum lacking humeral carina, completely rounded. Anterior subalar area shorter than tegular maximum width. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum. Metanotal trough deeply impressed. Metapleuropropodeal suture relatively shallow. Posterolateral margin of propodeal declivity carinate, running along the posterodorsal propodeal margin. Anterolateral propodeal corner marginate. Propodeal spiracle slit-shaped. Ventrolateral propodeal declivity without deep groove. Dorsal view: mesoscutum about as long as broad, close to twice length of mesoscutellum. Mesoscutum anterior triangular impression present, weakly impressed. Parapsidal lines weakly impressed, slightly divergent. Notaulus present, strongly impressed, smooth or at most with feeble rugosities, not meeting posteriorly, not extending to transscutal line. Transscutal sulcus well-developed. Scutoscutellar sulcus present, straight, strongly impressed, without internal sculpture, not separating mesoscutum from mesoscutellum. Mesoscutellum subtrapezoid, convex. Metascutellum well-developed, clearly discernible dorsally, surface slightly uneven, with feeble dome medially. Anterodorsal median propodeal sulcus present, strongly impressed. Posterior face of propodeal declivity flat. Propodeal lateral margins parallel at base, convergent dorsad. Ventral view: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process vestigial. Metasternal process well-developed, inclined posterad, ca. 45° in lateral view, fang-shaped, flattened anteroposteriorly, apex slightly higher than half height of metacoxal internal margin, space between lobes narrower than width of each, internal margins running parallel. Metasternal process external margins convergent. **Wings**. Hyaline. Slightly iridescent. Forewing venation Ogata type Ia: submarginal cells 1, 2 and discoidal present, vein 2M present, 2r-rs offset from Rs+ m, Rs+M ca. three times longer than 2M, setose layer evenly covering surface. Hindwing venation Cantone and Von Zuben Type I: basal and subbasal cells and vein 2M present, 1R well-developed, 1Rs well-developed. Jugal lobe present. Hindwing bearing 6 hamuli. **Legs**. Mesofemur roughly equally thick as metafemur, in dorsal or ventral view. Ventral

surface of meso- and metafemora slighlty flattened roughly on distad two thirds. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about 2.5 times shorter than posterior spur. Pretarsal claw arched, unarmed (without accesory teeth on surface). Arolium present, roughly 0.5 times length of pretarsal claw. **Petiole**. Lateral view: Petiolar node with straight anterior margin and slightly convex posterior margin, anterior and posterior margins reaching approximately same level dorsally, middorsal margin convex, highest point posterior to nodal longitudinal midline, anterodorsal margin convex, posterior face slightly convex. Subpetiolar process subtriangular, with round to blunt anterior cusp, followed posteriorly by straight, concave slope, completely smooth, concave longitudinally. Lateral projection of anteroventral nodal carina well-developed, with acute tip strongly bent dorsad. Lateral nodal carina vestigial. Dorsal view: Anterior margin of petiolar node roughly as broad as posterior margin. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. Lateral view: Prora well-developed, with slightly acute tip projecting anterad. Anterior margin of tergum of A3 slightly convex. Dorsalmost limit of anterior tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin broadly convex. Anterodorsal margin of tergum of A3 broadly convex. Cinctus moderate. Dorsal view: Tergum of A3 slightly shorter than A4. Abdominal sternum 7 with concave surface. Abdominal sternum 7 mostly glabrous. Spine at posterior margin of tergum of A8 well-developed, extending posterad, beyond posterior margin of sternum of A9, acute. Sternum of A9 longer than broad, posterior margin convex. Pygostyles present, about five times longer than broad. **Color**. Appendages mostly light brown to pale yellowish. **Pilosity**. Body with moderately abundant, flexuous, golden, erect and suberect hairs. Appressed pubescence abundant. Most erect hairs on body dorsum smaller than maximum eye length. Scape pilosity mostly with abundant appressed pubescence. Meso- and metatarsi mostly with abundant fine- and few stiff setae. **Sculpture**. Integument polished, with abundant, piligerous micro punctae, except laterally on propodeum where few rugosities are present. Striae on head absent, mesosoma lacking striae. Striae on petiolar node absent.

Comments. *Neoponera dejeani* sp. nov. is the smallest species in the *N. crenata* group (Fig. 26; ☿: TLa = 5.06 – 5.33 mm; ♀: TLa = 6.19 mm), and the second smallest in the genus after the smallest workers of the polymorphic, termite-raiding *N. laevigata* Smith. The few workers (*n*

= 6) we could gather from Brazil and French Guiana vary little in size, and are almost identical morphologically.

In the genus, only three species could probably be confused with *N. dejeani*: *N. antecurvata*, *N. carinulata*, and *N. donosoi*. These taxa show the following differing features: 1) *N. antecurvata*: top of node placed anterior to vertical midline (placed medially in *N. dejeani*), anterodorsal nodal margin truncate (relatively convex in *N. dejeani*), posterior nodal face with piligerous punctae (glabrous in *N. dejeani*), propodeum striated laterally; 2) *N. carinulata*: posterior head corners angulate (less so in *N. dejeani*), nodal dorsum placed posterior to midline, dorsoanterior margin of tergite of A3 broadly convex in lateral view (feebly convex in *N. dejeani*); 3) *N. donosoi*: posterior head corners round (relatively squared in *N. dejeani*), notopropodeal suture present (absent or vestigial in *N. dejeani*), posterior nodal face bearing piligerous punctae.

Neoponera dejeani has a reduced elevational range, from near the sea level up to ca. 300 m. Thus far it has only been recorded from well-preserved Amazonian habitats of northern French Guiana, south to northern Mato Grosso in Brazil.

Natural history notes. Almost certainly this species is arboreal. The few specimens bearing information about collection method were obtained through Malaise. Two workers and one queen were collected in *Cordia nodosa* (Boraginaceae).

Other material examined. 1☿. **FRENCH GUIANA – Saint-Laurent-du-Maroni**: • 1☿; Papaichton; 4.1637, -53.9996; alt. 100m; 2021-03-15; Petitclerc, F. leg.; hand collected; (EcoFoG).

Distribution. French Guiana, Brazil (Mato Grosso, Pará).

***Neoponera yasuni* sp. nov.**

Figs. 25: a – e (☿); 29: a (distribution)

Type material. ***Holotype***. ☿ [absent from body: fore right- and three left legs, 7th to 12th left antenomeres] ECUADOR: Pastaza: P.N. Yasuní, Lorocachi s. [trail] Cononaco, 204 m., 01°36’45”S, 75°58’13”W, T. luz. [light trap], 12–Ene–2014, N. Chasiliquín & E. Villacrés [leg.], voucher barcoding ADN, May – 2017 [written on second label], (MEPN: MEPNINV28815). ***Paratype***. ☿ ECUADOR: Sucumbíos: Reserva Cuyabeno, trocha [trail] Zábalo – Guepi km 10,

fumigación, b. tierra firme [*terra firme* forest], 8–Ago–2000, P. Araujo [leg.], (DZUP: MEPNINV3375).

Etymology. The specific epithet is derived from the (probably) indigenous Waorani word "yasuni", which according to the native peoples living at Parque Nacional Yasuní, the Ecuadorian reserve where the holotype was collected, means "sacred place". We thus acknowledge this Amazonian region which is reputed as being among the world's most biodiverse places of the planet (see Bass et al. 2010), but also threatened by oil-drilling and forest fragmentation.

Worker diagnosis. Head dorsum densely covered with well-impressed piligerous punctae, posterior margin straight (Fig. 25b); antennal scape exceeding posterior head margin by about 2.5 times apical scape width (Fig. 25b); mesosomal dorsum completely covered with somewhat irregularly-shaped, horizontal striae (Fig. 25d); petiolar node completely covered with coarse horizontal striae (Fig. 25c); in lateral view, anterior nodal margin straight, meeting dorsal margin in blunt, convex angle, dorsoposterior margin convex, posterior nodal face feebly convex (Fig. 6d, 25c); subpetiolar process with well-developed, blunt keel anteriorly, dome with few strongly impressed striae (Fig. 6d, 25c); prora keel-shaped, with acute tip directed ventrad (Fig. 6d, 25c).

Worker description. Measurements (n = 3; holotype in parenthesis): HW: 1.62-1.69 (1.69); HL: 1.84-1.91 (1.91); EL: 0.44-0.47 (0.47); SL: 1.75-1.78 (1.75); WL: 2.72-2.84 (2.84); PrW: 1.28-1.31 (1.28); MsW: 0.72-0.77 (0.77); MsL: 0.66-0.69 (0.66); PW: 0.97-1.03 (1.0); PH: 0.94-1.0 (1.0); PL: 0.81-0.84 (0.84); GL: 3.12-3.75 (3.12); A3L: 1.31-1.34 (1.34); A4L: 1.19-1.22 (1.19); A3W: 1.62-1.69 (1.69); A4W: 1.5-1.59 (1.59); TLa: 7.91-8.12 (8.12); TLr: 8.72-9.16 (8.72). **Indices.** CI: 87.5-88.52 (88.52); OI: 26.67-27.78 (27.78); SI: 103.7-108.57 (103.7); MsI: 104.55-116.67 (116.67); LPI: 83.87-86.67 (84.38); DPI: 118.52-126.92 (118.52).

Head. Frontal view: subquadrate. Mandible triangular, longer than wide, distal region slightly bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with six to eight teeth interspersed with two to four slightly smaller teetth; teeth on posterior third significantly smaller than precedent teeth; basal margin edentate. Prementum with well-developed transverse dome. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, with dorso-ventrally flat, subtriangular-shaped, acute extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus

not reaching ocular mid-length. Frontal carina not reaching ocular mid-length. Torular lobe subtriangular, covering approximately 80% of acetabulum of antennal socket, posterolateral margin slightly convex. Malar carina poorly developed, faintly emerging from cuticle, not reaching anterointernal eye margin. Eye suboval, maximum length ca. one-fourth head length, convex, slightly globose, exceeding lateral margin of head, placed slightly posterior to cephalic mid-length. Posterior margin of head straight to slightly concave. Occipital carina reduced. Scape, when pulled posterad, exceeding posterior margin of head by approximately two times apical scape width. **Mesosoma**. Lateral view: Dorsal margin slightly convex. Pronotum carinate, with carina slightly projecting from cuticle. Anapleural sulcus present, merged with surrounding striae. Posterolateral margin of propodeal declivity with feeble, blunt carina, without crenulae. Propodeal spiracle slit-shaped. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Notopropodeal suture vestigial, although faint line visible, hard to distinguish posterior margin of mesonotum and anterior margin of propodeum. Posterior face of propodeal declivity mostly flat. Propodeal lateral margins parallel at base, convergent dorsad. Ventral view: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process well-developed, tooth-shaped, internal margins of lobes running relatively parallel, relatively flattened anteroposteriorly, inclined posterad ca. 20 degrees in lateral view, space between lobes broader than width of each. Metasternal process well-developed, inclined posterad, 20°-30° in lateral view, fang-shaped, flattened anteroposteriorly, apex slightly higher than half height of metacoxal internal margin, space between lobes narrower than width of each, internal margins running parallel. Metasternal process external margins convergent. **Legs**. Mesofemur thickened medially, feebly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora flattened roughly on distad half, surface even without groove. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about three times shorter than posterior spur. Pretarsal claw arched, unarmed (without accessory teeth). Arolium present, roughly 0.5 times length of pretarsal claw. **Petiole**. Lateral view: Petiolar node with straight anterior margin and convex posterior margin, anterior margin feebly higher than posterior margin, middorsal margin convex, highest point anterior to nodal longitudinal midline, anterodorsal margin slightly convex to feebly

flattened, posterior face convex. Subpetiolar process subtriangular, with blunt, keel-shaped, grooved anterior cusp, followed posteriorly by slightly convex dome, dome with transverse, usually three to four, strong striae, followed posteriorly by few feebly impressed striae. Lateral projection of anteroventral nodal carina well-developed, with acute to slightly blunt tip moderately bent dorsad. Lateral nodal carina strongly impressed, slightly arched ventrad. Dorsal view: Anterior margin of petiolar node approximately one third shorter than posterior margin. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. Lateral view: Prora well-developed, convex anteriorly, with acute tip projecting ventrad. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin relatively angled. Anterodorsal margin of tergum of A3 slightly convex. Cinctus weak. Dorsal view: Tergum of A3 equal in length to A4. Posterior dorsum of epipygium completely smooth. **Color**. Appendages mostly black, mandibles feebly lighter than remaining body. **Pilosity**. Body with moderately abundant, flexuous, golden, erect and suberect hairs. Appressed pubescence abundant. Most erect hairs on body dorsum approximately equal to maximum eye length. Scape pilosity mostly composed of scattered erect hairs and appressed pubescence, erect hairs mostly shorter than apical scape width. Meso- and metatarsi bearing stiff setae (ventrally only) interspersed with suberect and appressed fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, shorter than eye maximum length, and a row of setae about one third of eye maximum length. Posterior dorsum of epipygium surrounded by 20–30 long flexuous hairs, longer than eye maximum length. **Sculpture**. Integument mostly polished, with abundant, shallowly impressed piligerous punctures, except for head dorsum where punctures are more densely and strongly impressed. Tiny striae present on head, but only on mid clypeus, on torular lobes, and posterior to these, mandibles finely striate dorsally, mesosoma bearing strong striae on anepisternum, katepisternum, metapleurum, laterally on propodeum, and dorsally on mesonotum and pronotum.

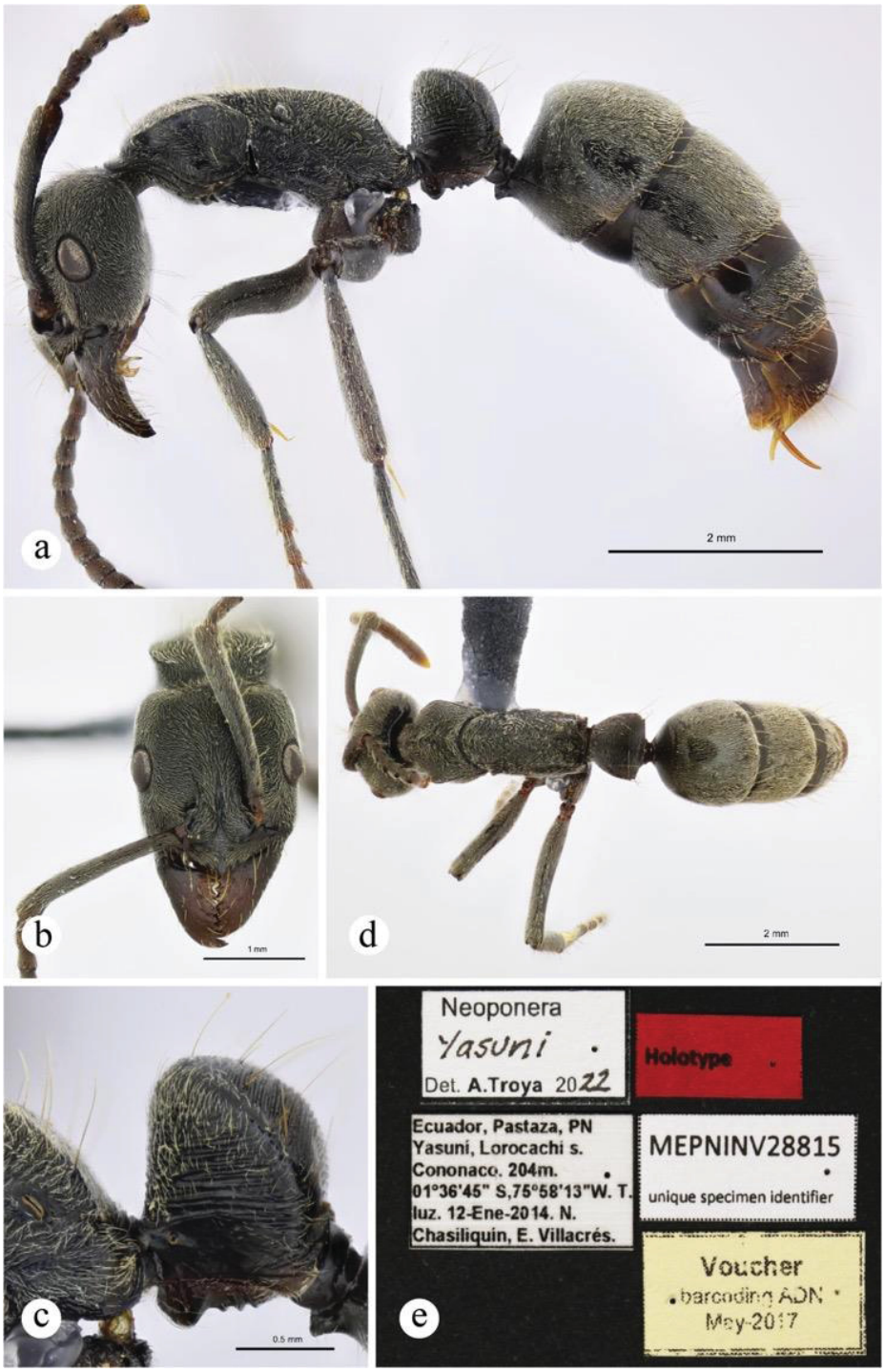


Fig. 25. *Neoponera yasuni*. Holotype ☿ (MEPN: MEPNINV28815). Ecuador: Pastaza. **a.** Lateral view; **b.** Head in frontal view; **c.** Petiolar node in lateral view; **d.** Dorsal view; **e.** Collection labels.

Queen and male. Unknown.

Comments. *Neoponera yasuni* sp. nov. is a medium-sized taxon in the *N. crenata* group (Fig. 26; ☿: TLa = 7.91 – 8.13 mm). Only three specimens are known, all from Amazonian Ecuador. It has a unique combination of diagnostic traits which are useful to differentiate this taxon from all others in the *N. crenata* group. The shape and sculpture of the petiolar node should suffice to distinguish *N. yasuni* from all others in the genus. Yet, *N. antecurvata*, *N. rugosula*, and *N. striatinodis* are relatively similar and could potentially be confused with it. The following characters present in these species facilitate their separation from *N. yasuni*: 1) *N. antecurvata*: dorsum of pronotum, mesonotum, and petiolar node devoid of striae, except for the posterior nodal face where these are feebly impressed, anterodorsal face of node truncate (anterodorsal face of node relatively angulate to feebly convex in *N. yasuni*); 2) *N. rugosula*: petiolar node sometimes bearing feebly impressed striae laterally (entirely striate in *N. yasuni*), nodal shape slightly protruded posteroventrally (just convex in *N. yasuni*); 3) *N. striatinodis*: head corner angulate and slightly protruding posterad (subquadrate, not protruding in *N. yasuni*), posterolateral propodeal margin and posterior nodal margin bearing well-developed crenulae (absent in *N. yasuni*).

Neoponera yasuni is known only from the western Amazon basin (ca. 200 m elevation) in South America.

Natural history notes. As with most species in the *N. crenata* group, this species is probably arboreal. The specimens were captured while at night in well-preserved, mature forests, two of them using insecticidal canopy knockdown, and the other with mercury light trap.

Other material examined. **ECUADOR – Sucumbíos**: • 1 ☿ Reserva de Producción Faunística Cuyabeno, Trocha Zábalo-Güepi; -0.26, -75.69; alt. 270 m; 2000-08-08; Araujo, P. leg.; fogging; (MEPN).

Distribution. Northeastern Ecuador.

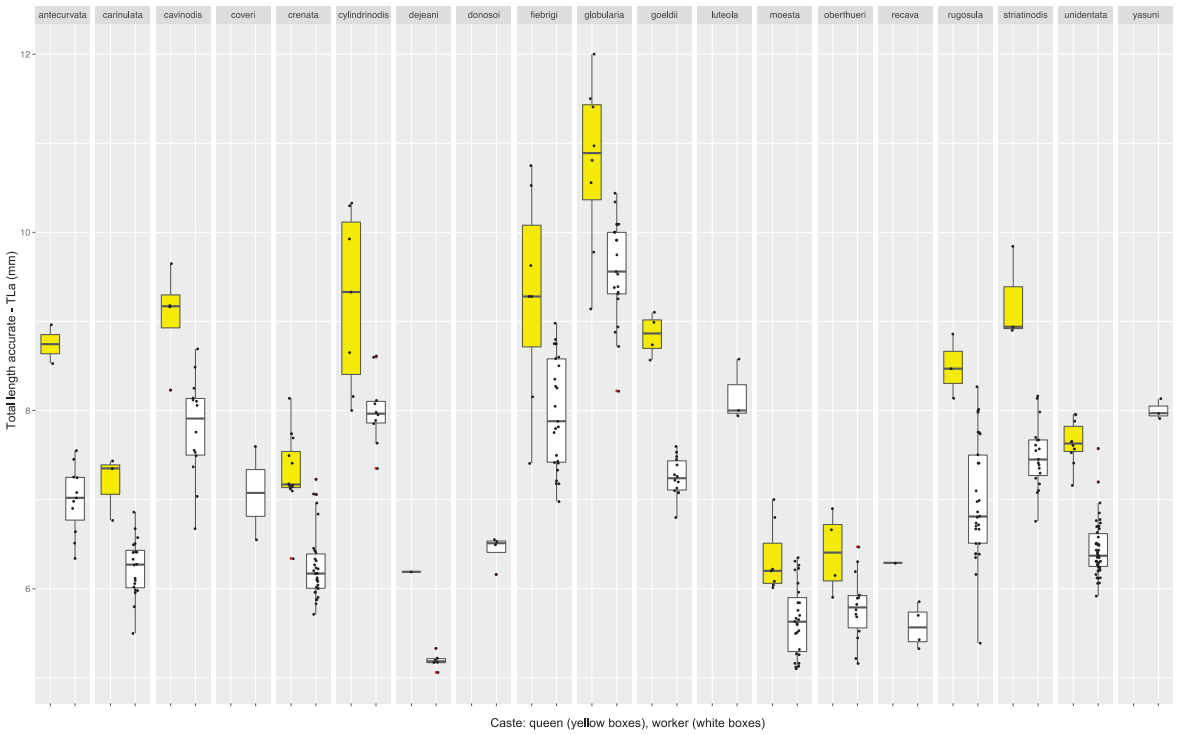


Fig. 26. Worker and queen size variation range, as estimated by the variable TLa (total length accurate), of the currently recognized species in the *N. crenata* group. Measured material *n* = 310 specimens. The red dots are outliers. ♀= yellow boxes; ☿ = white boxes.

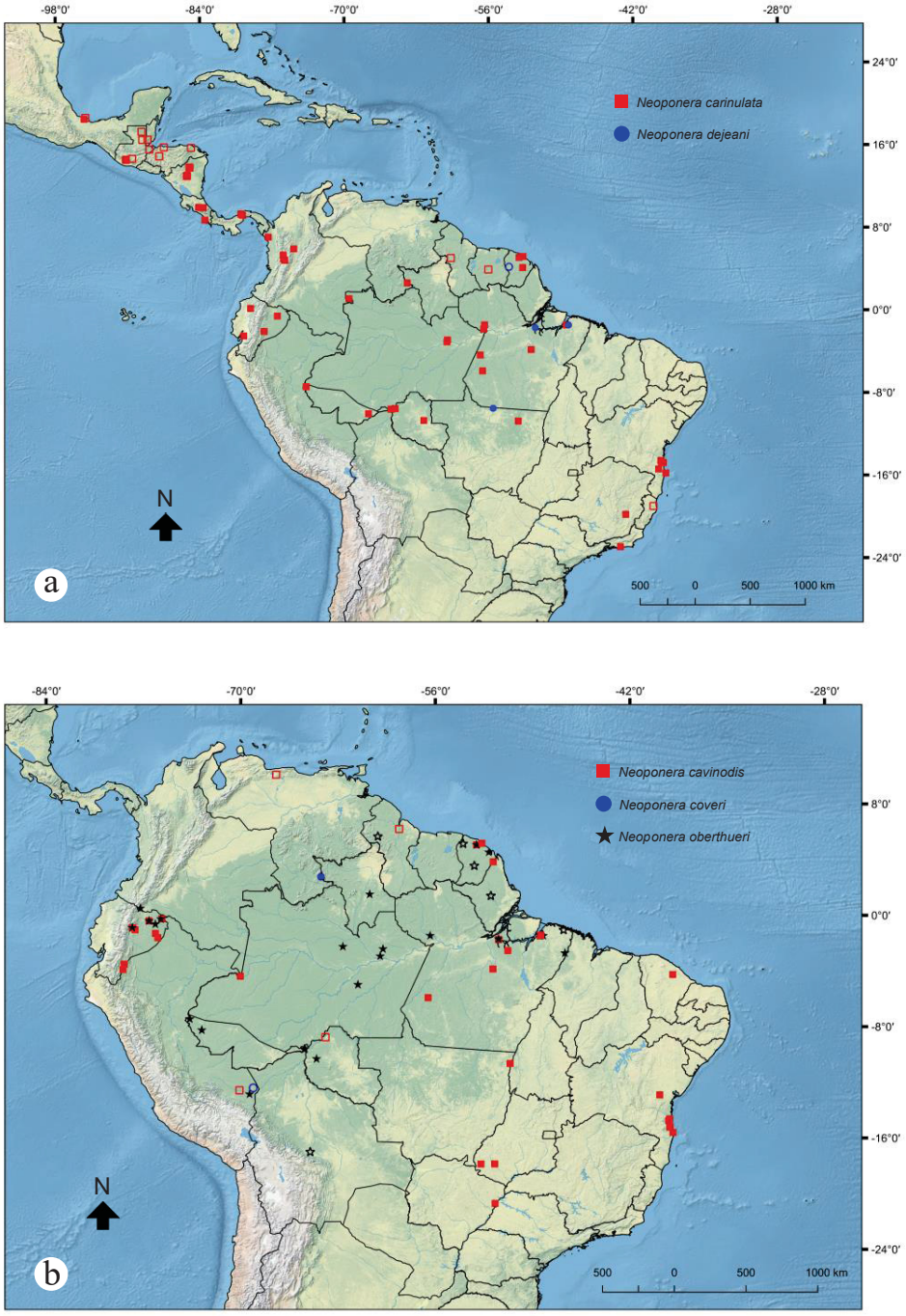


Fig. 27. Distribution of species in the *Neoponera crenata* group. **a.** *Neoponera carinulata*, *N. dejeani* sp. nov.; **b.** *Neoponera cavinodis*, *N. coveri*, *N. oberthueri*. Empty icons belong to the same species as those with filled icons in each figure, but these represent records obtained from the literature (see references below).

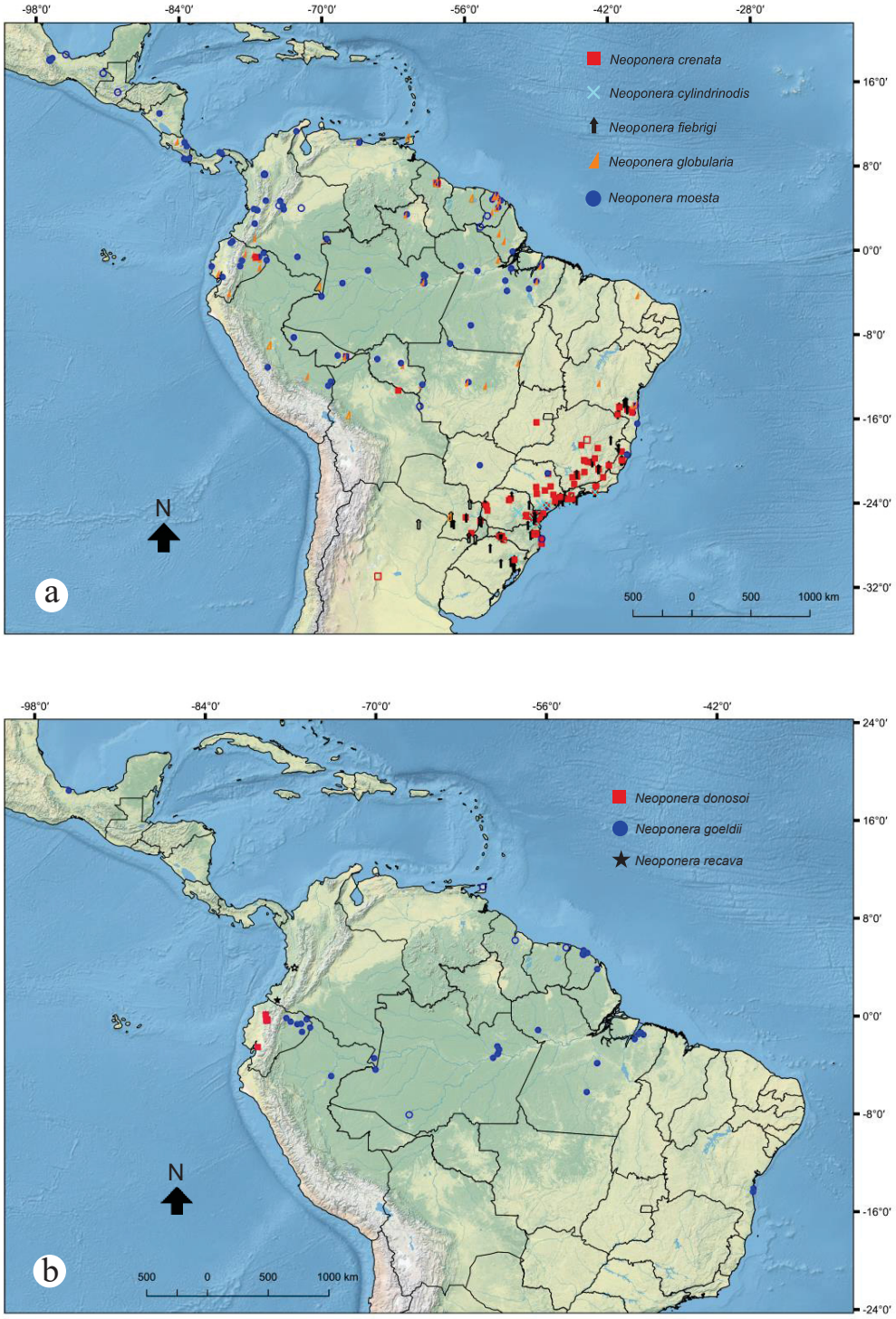


Fig. 28. Distribution of species in the *Neoponera crenata* group. **a.** *Neoponera crenata*, *N. cylindrinodis* sp. nov., *N. fiebrigi*, *N. globularia*, *N. moesta*; **b.** *Neoponera donosoi*, *N. goeldii*, *N. recava*. Empty icons belong to the same species as those with filled icons in each figure, but these represent records obtained from the literature (see references below).

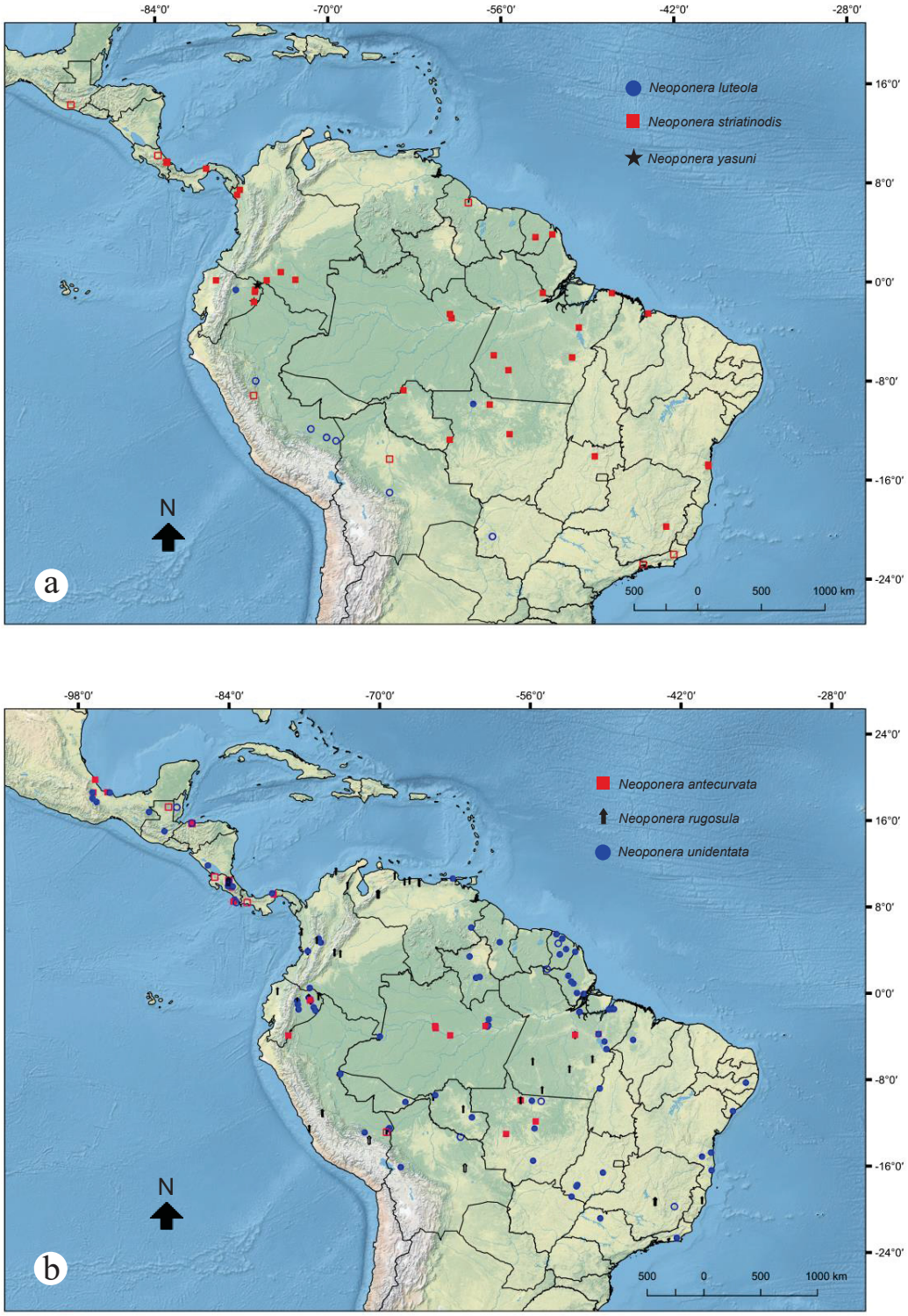


Fig. 29. Distribution of species in the *Neoponera crenata* group. **a.** *Neoponera luteola*, *N. striatinodis*, *N. yasuni*; **b.** *Neoponera antecurvata*, *N. rugosula*, *N. unidentata*. Empty icons belong to the same species as those with filled icons in each figure, but these represent records obtained from the literature (see references below).

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REFERENCES

AntCat. **2022**. AntCat (2022) An online catalogue of the ants of the world by Barry Bolton. Available from https//www. antcat.org. (accessed Mar 2022).

AntWeb. **2022**. AntWeb. Calif. Acad. Sci. online https//www.antweb.org. Accessed 14 July 2022.

AntWiki.org. **2022**. AntWiki. (https://antwiki.org/wiki/Category:Neoponera_species).

Arnold, M. L. 1992. Natural hybridization as an evolutionary process. Annu. Rev. Ecol. Syst. 23: 237–261.

Bass, M. S., M. Finer, C. N. Jenkins, H. Kreft, D. F. Cisneros-Heredia, S. F. McCracken, N. C. a Pitman, P. H. English, K. Swing, G. Villa, A. Di Fiore, C. C. Voigt, and T. H. Kunz. **2010**. Global conservation significance of Ecuador's Yasuní National Park. PLoS One. 5:

e8767.

Bezděčková, K., P. Bezděčka, and I. Machar. **2015**. A checklist of the ants (Hymenoptera: Formicidae) of Peru. Zootaxa. 4020: 101–133.

Bolton, B. 1994. Identification guide to the ant genera of the world, Harvard Univ. Press.

Boudinot, B. E. 2013. The male genitalia of ants: Musculature, homology, and functional morphology (Hymenoptera, Aculeata, Formicidae). J. Hymenopt. Res. 30: 29–49.

Boudinot, B. E. 2015. Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata): a new diagnosis of the family, the first global male-based key to subfamilies, and a treatment of early branching lineages. Eur. J. Taxon. 120: 1–62.

Branstetter, M. G., and J. T. Longino. **2022**. UCE Phylogenomics of New World Cryptopone (Hymenoptera: Formicidae) Elucidates Genus Boundaries, Species Boundaries, and the Vicariant History of a Temperate–Tropical Disjunction. Insect Syst. Divers. 6.

Cantone, S. 2017. Winged ants – The male. Dichotomous key to genera of winged male ants in the world. Behavioral ecology of mating flight. São Paulo: Autopubblicato.

Cantone, S., and C. J. Von Zuben. **2019**. The Hindwings of Ants: A Phylogenetic Analysis. Psyche (London). 2019.

Dallwitz, M. 1980. A general system for coding taxonomic descriptions. Taxon. 29: 41–46.

Dejean, A. 2011. Prey capture behavior in an arboreal african ponerine ant. PLoS One. 6.

Dinerstein, E., D. Olson, A. Joshi, C. Vynne, N. D. Burgess, E. Wikramanayake, ... and M. Saleem. 2017. An ecoregion-based approach to protecting half the terrestrial realm. BioScience, 67(6), 534-545.

Djiéto-Lordon, C., J. Orivel, and A. Dejean. **2001**. Consuming large prey on the spot: The case of the arboreal foraging ponerine ant Platythyrea modesta (Hymenoptera, Formicidae). Insectes Soc. 48: 324–326.

Emery, C. 1911. Hymenoptera. Fam. Formicidae. Subfam. Ponerinae, p. 124. *In* Wytsman, P. (ed.), Genera Insectorum. Bologne.

Erwin, T., and C. Geraci. **2009**. Amazonian rainforests and their richness of Coleoptera, a

dominant life form in the critical zone of the neotropicsitle, pp. 49–67. *In* Insect Biodivers. Sci. Soc. Blackwell Publishing Ltd.

Fernandes, I. O., M. L. De Oliveira, and J. H. C. Delabie. **2014**. Description of two new species in the Neotropical Pachycondyla foetida complex (Hymenoptera: Formicidae: Ponerinae) and taxonomic notes on the genus. Myrmecological News. 19: 133–163.

Ferreira, C. S., A. V. Figueira, R. Gribel, F. Wittmann, and M. T. Piedade. **2010**. Genetic variability, divergence and speciation in trees of periodically flooded forests of the Amazon: a case study of Himatanthus sucuuba (SPRUCE) WOODSON. In Amazonian Floodplain Forests, pp. 301–312. *In* Amaz. Floodpalin For.

Field, D. L., D. J. Ayre, R. J. Whelan, and A. M. Young. **2011**. Patterns of hybridization and asymmetrical gene flow in hybrid zones of the rare Eucalyptus aggregata and common E. rubida. Heredity (Edinb). 106: 841–853.

Fresneau, D. 1985. Individual foraging and path fidelity in a ponerine ant. Insectes Soc. 32: 109–116.

Gómez, P. A., and L. A. Garcés. **2013**. Cultivos celulares de Choibá Dipteryx oleifera Benth. Rev. Colomb. Biotecnol. 15: 124–131.

Google. **2022**. Google Earth. (https://earth.google.com.).

Govaerts, R., J. Dransfield, S. Zona, D. Hodel, and A. Henderson. **2022**. World Checklist of Selected Plant Families. Facil. by R. Bot. Gard. Kew. (http://wcsp.science.kew.org/).

Guénard, B., M. D. Weiser, K. Gómez, N. Narula, and E. P. Economo. **2017**. The Global Ant Biodiversity Informatics (GABI) database: Synthesizing data on the geographic distribution of ant species (Hymenoptera: Formicidae). Myrmecological News. 24: 83–89.

Gutiérrez-Valencia, J., G. Chomicki, and S. S. Renner. **2017**. Recurrent breakdowns of mutualisms with ants in the neotropical ant-plant genus Cecropia (Urticaceae). Mol. Phylogenet. Evol. 111: 196–205.

Harris, R. A. 1979. Glossary of surface sculpturing. Occas. Pap. Entomol. 32.

Haugaasen, T., and C. A. Peres. **2005**. Mammal assemblage structure in Amazonian flooded and unflooded forests. J. Trop. Ecol. 21: 133–145.

Janicki, J., N. Narula, M. Ziegler, B. Guénard, and E. P. Economo. **2016**. Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. Ecol. Inform. 32: 185–193.

Keller, R. A. 2011. A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. Bull. Am. Museum Nat. Hist. 2011: 1–90.

Leroy, C., F. Petitclerc, J. Orivel, B. Corbara, J. F. Carrias, A. Dejean, and R. Céréghino. **2017**. The influence of light, substrate and seed origin on the germination and establishment of an ant-garden bromeliad. Plant Biol. 19: 70–78.

Longino, J. 2010. Ants of Costa Rica. (https://ants.biology.utah.edu/AntsofCostaRica.html).

Longino, J. T., and M. G. Branstetter. **2020**. Phylogenomic Species Delimitation, Taxonomy, and 'Bird Guide' Identification for the Neotropical Ant Genus Rasopone (Hymenoptera: Formicidae), Insect Syst. Divers.

Luebert, F. 2021. The two South American dry diagonals. Front. Biogeogr. 13: 0–14.

Macedo-Reis, L. E., A. C. Leite, T. J. Guerra, R. Antoniazzi, and F. D. S. Neves. **2019**. Suspended leaf litter in an understorey treelet as habitat extension for ground-dwelling ants in the Atlantic Forest, south-eastern Brazil. J. Trop. Ecol. 35: 247–250.

MacKay, W., and E. Mackay. **2010**. The systematics and biology of the New World ants of the genus Pachycondyla (Hymenoptera: Formicidae). Edwin Mellen Press.

Mayr, E. 1942. Systematics and the Origin of Species, 14th Editi. ed. Columbia University Press, New York.

Mill, A. E. 1982. Faunal studies on termites (Isoptera) and observations on their ant predators (Hymenoptera: Formicidae) in the Amazon Basin. Rev. Bras. Entomol. 26: 253–260.

Mill, A. E. 1984. Predation by the ponerine ant Pachycondyla commutata on termites of the genus Syntermes in Amazonian rain forest. J. Nat. Hist. 18: 405–410.

Neves, D. M., K. G. Dexter, R. T. Pennington, M. L. Bueno, and A. T. Oliveira Filho. **2015**. Environmental and historical controls of floristic composition across the South American Dry Diagonal. J. Biogeogr. 42: 1566–1576.

Ogata, K. 1991. A generic synopsis of the poneroid complex of the family Formicidae

(Hymenoptera). Part II. Subfamily Myrmicinae. Bull. Inst. trop. Agric. Kyushu Univ. 14: 61–149.

Orivel, J., A. Souchal, P. Cerdan, and A. Dejean. **2000**. Prey capture behavior of the arboreal ponerine ant Pachycondyla goeldii.pdf. Sociobiology. 35: 131–140.

Pazmiño-Palomino, A., and A. Troya. **2022**. Ants of Ecuador : new species records for a megadiverse country in South America. Rev. Bras. Entomol. 66: 1–15.

Rakotonirina, J. C., and B. L. Fisher. **2013**. Revision of the Pachycondyla sikorae species-group (Hymenoptera: Formicidae) in Madagascar. Zootaxa. 3683: 447–485.

Ratnasingham, S., and P. D. N. Hebert. **2007**. BOLD: The Barcode of Life Data System: (www.barcodinglife.org). Mol. Ecol. Notes. 7: 355–364.

Santos-Filho, F. S., E. B. de Almeida, P. B. Lima, and C. J. dos R. S. Soares. **2015**. Checklist of the flora of the restingas of Piauí state, Northeast Brazil. Check List. 11.

Santschi, F. 1919. Nouveaux formicides de la République Argentine. An. la Soc. Cient. Argentina. 87: 37–57.

Santschi, F. 1921. Ponerinae, Dorylinae et quelques autres formicides néotropiques. Bull. Soc. Vaudoise Sci. Nat.

Santschi, F. 1923. Solenopsis et autres fourmis néotropicales. Rev. Suisse Zool. 30: 245–273.

Santschi, F. 1939. Études et descriptions de fourmis néotropiques. Rev. Entomol. 10: 312–330.

Valero, A., Schipper, J., and T. Allnut. 2019. Sierra de los Tuxtlas. In One Earth: Terrestrial Ecorregions of the World (https://www.worldwildlife.org/ecoregions/nt0161).

Schmidt, C. 2013. Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). 3647: 201–250.

Schmidt, C. A., and S. O. Shattuck. **2014**. The Higher Classification of the Ant Subfamily Ponerinae (Hymenoptera: Formicidae), with a Review of Ponerine Ecology and Behavior.

Serna, F., and W. MacKay. **2010**. A descriptive morphology of the ant genus Procryptocerus (Hymenoptera: Formicidae). J. Insect Sci. 10.

Tozetto, L., and J. E. Lattke. **2020**. Revealing male genital morphology in the giant ant genus

Dinoponera with geometric morphometrics. Arthropod Struct. Dev. 57: 100943.

Troya, A., and J. Lattke. **2022**. Neoponera Emery, 1901 (Hymenoptera: Formicidae) revisited: 1. The N. laevigata species-group. Insect Syst. Evol. 1901: 1–76.

Wheeler, W. 1936. Ecological relations of ponerine and other ants to termites. Proc. Am. Acad. Arts Sci. 71: 158–243.

Wheeler, W. M., and J. C. Bequaert. **1929**. Amazonian myrmecophytes and their ants. Zool. Anz. 82: 10–39.

Wild, A. L. 2005. Taxonomic revision of the Pachycondyla apicalis species complex (Hymenoptera: Formicidae). 25: 1–25.

Wilson, E. O. 1955. A Monographic Revision of the Ant Genus Lasius. Bull. Mus. Comp. Zool.

Yoder, M. J., I. Mikó, K. C. Seltmann, M. A. Bertone, and A. R. Deans. **2010**. A gross anatomy ontology for hymenoptera. PLoS One. 5: e15991.

Yu, D. W., and N. E. Pierce. **1998**. A castration parasite of an ant ± plant mutualism.

SUBCHAPTER III

Neoponera Emery, 1901 (Hymenoptera, Formicidae) revisited: 3. The *N. foetida* and *N. emiliae* species-groups

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***Neoponera* Emery, 1901 (Hymenoptera, Formicidae) revisited: 3. The *N. foetida* and *N. emiliae* species-groups**

ABSTRACT

Neotropical ants of the genus *Neoponera* are best known for their diverse behavior and external morphology. Seven species-groups are currently recognized: aenescens, *apicalis*, *crenata*, *emiliae*, *foetida*, *laevigata*, and *rostrata*. The *apicalis* group was taxonomically treated by Wild in 2005, the *foetida* group was partially revised by Fernandes et al in 2014, the *laevigata* group was revised by Troya and Lattke in 2022, and as part of the genus *Pachycondyla*, W. and E. Mackay reviewed *Neoponera* in 2010. An ongoing, deeper revision of all known species in the genus is revealing new taxa and taxonomic issues, undescribed castes, and previously unknown locality records some of which represent new populational variants which probably are new species. Together, these still unpublished novelties demonstrate the necessity of reviving the work with this fantastic ponerine genus. In the present contribution I taxonomically revise all known species in the *foetida* and *emiliae* groups, provide new diagnoses and update their distribution. Among the results, the following taxa are described as new: *N. prasiosomis* **sp. nov.** (Panama and Ecuador) belonging to the *foetida* group, and *N. caxiuana* **sp. nov.** (Colombia and Brazil), *N. dorsilinea* **sp. nov.** (eastern Brazil), *N. dropsy* **sp. nov.** (eastern Brazil), and *N. glabra* **sp. nov.** (eastern Brazil), belonging to the *emiliae* group. *Neoponera bactronica* Fernandes et al. **syn. nov.** and *N. billemma* Fernandes et al. **syn. nov.** are synonymized under *N. curvinodis* Forel; I propose a neotype for this latter which coupled with comprehensive comments about comparative anatomy, facilitate the distinction of this morphologically highly variable taxon from closely related taxa. In addition, I construct new user friendly, fully illustrated taxonomic keys, and describe the first male of the *emiliae* group. This is the third contribution towards gleaming the taxonomy, systematics and distribution of *Neoponera*.

Keywords: ants, arboreal, epigeic, Neotropical Region, male caste.

INTRODUCTION

Within the Ponerinae, the Neotropical *Neoponera* Emery is a moderately rich genus, currently represented by 58 valid taxa (AntCat 2023, www.antcat.org), and in terms of behavior and morphology its species probably show the broadest variation among all ponerines (MacKay and Mackay 2010, Schmidt and Shattuck 2014, pers. obs.). Some species are specialist termite huntresses and can conduct mass raiding parties as those of the *N. laevigata* group which was recently revised by (Troya and Lattke 2022), others are generalist predators, and hunt mostly in solitary as those of the *N. apicalis* group, whereas a number of other species, which form the bulk in the genus, are adapted to tree-living as those in the *N. crenata* and *N. foetida* groups.

Neoponera was erected by Carlo Emery in 1901 (Emery 1901), it remained valid in ant nomenclature until 1973 when Brian Brown synonymized it under *Pachycondyla* (Brown 1973) without justification though. In 2014 Chris Schmidt and Steve Shattuck (Schmidt and Shattuck 2014) resurrected Emery's name as part of a major revision of the subfamily. By then, the genus was reasonably well-categorized taxonomically, with the combination of the following two traits allowing its distinction from other closely related genera: a cuticular flap at the orifice of the metapleural gland, and in at least three fourths of the species, a malar carina running from the anterior mandibular insertion to the anterior eye margin. Although these traits, plus others that are homoplastic at the subfamily level like the eyes placed at about head midlength, proved useful to identifying the *Neoponera* from other ponerines, a recent study showed that the flap at the metapleural gland orifice can be highly variable as in the *N. laevigata* clade (Troya and Lattke 2022), while in species of the *N. aenescens* clade it is displayed as a vertically-oriented carina (pers. obs.).

Besides these findings which added a level of complexity to the taxonomic comprehension of the genus, new lineages have been discovered which require formal description, but also numerous issues have been detected in regards to the taxonomy of the presently known species in all the seven recognized *Neoponera* groups. Troya and Lattke (2022) revised the *N. laevigata* group, and another revisionary work is planned to be published soon for the *N. crenata* group by the same authors. Here, I provide a treatment of the *N. foetida* and *N. emiliae* groups. The first, which was partially revised by Fernandes et al. (2014), is composed of species with arboreal habits, and are among the most difficult to identify due to the lack of reliable diagnostic

characters. Some taxonomic problems were solved in the cited study, but others arose as additional material became available; among these, a number of species are usually misidentified, while in other cases it is impossible to assign a specific epithet without incurring in errors. Some good examples of these are *N. curvinodis* Forel, *N. inversa* Smith, *N. bugabensis* Forel, *N. bactronica* Fernandes et al., and *N. billemma* Fernandes et al. The first three taxa are commonly collected, broadly distributed, and usually extremely difficult to identify because their populations show quite variable external morphology. As for *N. bactronica* and *N. billemma*, their status is doubtful because their diagnostic features coincide with the definition of *N. curvinodis*.

In regards to the *N. emiliae* group (*sensu* Mackay and Mackay 2010), recent evidence suggests that it should be split in one group containing *N. emiliae* Forel, *N. magnifica* Borgmeier, and *N. metanotalis* Luederwaldt, whereas the remaining taxa, this is, *N. concava* Mackay and Mackay, *N. schultzi* Mackay and Mackay, and *N. venusta* Forel should be placed in a new genus (Troya and Lattke 2022). Furthermore, prior observations of recent new material of *N. magnifica* showed that this lineage is in fact composed of more than one species.

In this study I address all of these issues, revise the taxonomic status of all known species in both groups, provide notes on their biology and distribution, and in some cases, comments on their evolution, and elaborate new taxonomic keys.

MATERIALS AND METHODS

Repositories of examined material

Examined specimens, either physically and/or through images, are deposited in the below institutions. Part of this material is represented through images of the types available on the database of the MCZC, and AntWeb.org. Most museum abbreviations are based on Arnett et al (2019).

ALWC	Alexander L. Wild collection, TX, USA.
AMNH	American Museum of Natural History, NY, USA.
BMNH	The British Museum of Natural History, London, United Kingdom.

CASC	California Academy of Sciences, San Francisco, CA, USA.
CPDC	Coleção do Laboratório de Mirmecologia, Centro de Pesquisas do Cacau, Ilhéus, BA, Brazil.
DZUP	Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, PR, Brazil
ECOFOG	EcoFoG–Joint Research Unit Ecology of Guianan Forests, Kourou, French Guiana.
IAVH	Instituto Alexander von Humboldt, Villa de Leyva, Colombia.
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia.
INBC	Instituto Nacional de Biodiversidad, Heredia, Costa Rica.
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil.
JTLC	John T. Longino Collection, University of Utah, Salt Lake City, UT, USA.
MCZC	Museum of Comparative Zoology, Harvard University, MA, USA
MEPN	Museo de Historia Natural “Gustavo Orcés V.”, Escuela Politécnica Nacional, Quito, Ecuador.
MHNG	Muséum d'histoire naturelle Genève, Switzerland.
MIZA	Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
MPEG	Museu Paraense Emílio Goeldi, Belém, PA, Brazil.
MSNG	Museo Civico di Storia Naturale di Genova "Giacomo Doria", Genova, Italy
MUCR	Colección de Insectos, Universidad de Costa Rica, San Pedro, Costa Rica.

MUSENUV	Museo de Entomología de la Universidad del Valle, Cali, Colombia.
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
NHMW	Naturhistorisches Museum Wien, Vienna, Austria.
PSWC	Philip S. Ward Collection, University of California, CA, USA.
QCAZ	Museo de Zoología de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
SNSB	Zoologische Staatssammlung München, Munich, Germany.
UCDC	Bohart Museum of Entomology, University of California, CA, Davis.
UFVLABECOL	Laboratório de Ecologia de Comunidades, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.
UTEP	University of Texas at El Paso Entomology Collection, TX, USA.
UNMSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.
UTIC	The University of Texas at Austin, TX, USA.

Imaging

Images were taken using a Canon® EOS DSLR 70D with a Laowa® 25mm F2.8, 2.5X – 5.0X macro lens, coupled to a Cognisys StackShot® macro rail system which enabled depth–focus shooting through Helicon Remote v. 3.9.9, and posterior stacking in Helicon Focus v. 7.5.6 (Helicon Soft Ltd.). A dome–shaped, cold–light (LED) source was used for illumination. Images of type material and some non–type specimens, as well as collection data of all examined specimens are available online on AntWeb.org.

Images and illustrations by the author, except those in Figures: 18a – e (Bernard Landry), 23a – d (Museum of Comparative Zoology, Harvard University, ©President and Fellows of Harvard College).

In this work I only provide images for the newly described taxa, as well as for the castes of certain species, morphospecies and/or variants for which no high-resolution digital images are available thus far on the internet. As for the rest of known, described species I provide an internet link to access the image of the respective type at its original source, in this case, AntWeb.org.

Morphometric variables

All observations and measurements of the following morphological variables were taken using a pin–holding stage, allowing rotations around the X, Y, and Z axes at magnifications from 8X to 50X with an ocular micrometer incorporated to a Zeiss® Stemi SV6 stereo microscope. Measurements are presented in mm with an accuracy of two decimal places, minimum and maximum values are indicated when more than one specimen was measured. All measurements are in line with those of Troya and Lattke (2022).

HL Head length. In frontal view, maximum distance from the posterior margin of head to the anterior margin of clypeus.

HW Head width. In frontal view, maximum width of head, excluding the eyes.

EL Eye length. In lateral view, measured along its maximum length.

SL Scape length. In frontal view, maximum length of scape excluding its basal condyle and neck.

PrW Pronotum width. In dorsal view, maximum width of pronotum.

WL Weber's length. In lateral view, distance between the anterior margin of pronotum, excluding collar, to the posteroventral margin of metapleuron.

MsW Mesonotum width. In dorsal view, maximum width of mesonotum.

MsL Mesonotum length. In a dorsal view, the maximum distance from the anterior margin of the mesonotum to its posterior margin.

PW Petiolar width. In dorsal view, maximum width of the petiolar node.

PH Petiolar height. In lateral view, the perpendicular distance from the posteroventral lobe of the petiolar tergite to its maximum dorsal margin.

PL Petiolar length. In a lateral view, the distance between the anteriormost margin of petiole to its posterior margin, excluding the posteroventral ridge.

GL Gaster length. In lateral view, the oblique distance between the anterior margin of abdominal segment III to the posterior margin of the pygidium, excluding the sting. This is a relative measure since it can vary in relation to the extension or contraction of abdominal segments IV to VII.

A3L Abdominal segment III length. In dorsal view, the distance between the anterior and posterior margin of abdominal tergite III.

A3W Abdominal segment III width. In dorsal view, maximum width of tergite of abdominal segment III.

A4L Abdominal segment IV length. In dorsal view, the distance between the anterior and posterior margins of abdominal tergite IV.

A4W Abdominal segment IV width. In dorsal view, maximum width of tergite of abdominal segment IV.

TLa Total accurate length of body: HL + WL + PL + A3L + A4L

TLr Total relative length of body: HL + WL + PL + GL

Indices

The following ratios were multiplied by 100:

CI	Cephalic index: HW/HL
OI	Ocular index: EL/HW
SI	Scape index: SL/HW
MsI	Mesonotum index: MsW/MsL
LPI	Lateral petiolar index: PL/PH
DPI	Dorsal petiolar index: PW/PL

Distribution maps

I used the open–source package Quantum GIS 2.18 to generate maps of distribution, based on coordinates written on specimen labels. All localities were transformed to decimal degrees. I used Google Earth (Google 2022) as information source to check and confirm locality names. In regards to unusual records without specific localities, this is, below the administrative circumscription of state, province, or similar, the center of the next most specific site was georeferenced. In addition, I included in the maps selected literature records, mostly belonging to prior taxonomic treatments, for example from Mackay and Mackay (2010).

Morphological terms

General morphological terminology follows mainly Bolton (1994), Keller (2011), Boudinot (2015), and the Hymenoptera Anatomy Ontology – HAO Yoder et al. (2010). Surface sculpture is based mainly on Harris (1979). Male and female forewing venation on Ogata (1991), and Cantone (2017); hind wing venation on Cantone and Von Zuben (2019). Degree of pilosity inclination follows Wilson (1955), Serna and MacKay (2010): 0°– 5°for appressed hairs running parallel or nearly parallel to body surface; 10°– 20° for decumbent hairs slightly standing from surface; 20°– 40° for subdecumbent hairs; 40°– 70° for suberect hairs; and more than 70° for erect hairs when these stand vertical or nearly vertical. For male genitalia we followed Boudinot (2013)

and Tozetto and Lattke (2020). Palp formula is denoted by "PF" followed by the number of maxillary and labial segments, for example, PF: 4, 4, which means that both appendices have four segments. Tibial spur formula is denoted by "s" – simple, and "p" – pectinate, for example, 2(1s, 1p) which means that two spurs are present, one simple, and 1 pectinate.

Descriptions and material examined

I used the computer package DELTA Dallwitz (1980) for encoding the character states of each newly described caste and/or taxon. This package allows subsequent translation of such encoding into natural language (rich text format – RTF) taxonomic descriptions, which requires further editing from the user. I used TAXOMATA (Ambrosio and Troya, unpublished) a python script which makes a fast conversion of spreadsheet data (e.g., XML, CSV formats) into RTF. In this case, the spreadsheet dataset contained the measured morphometric variables, and the collection information shown in the "Material examined" section.

In the first paragraph of the taxonomic history per species, i.e. the type material, I included inside [ ] my notes, and inside ( ) the repository Collections of such material. Under "status as species" only the first appearance of the species name in the taxonomic literature is cited, as well as relevant redescriptions which are usually part of revisionary studies. The user can access the full history of literature mentions for each species on the Online Catalogue of the Ants of the World – AntCat (AntCat by B. Bolton 2022).

The format of the type material follows: # specimens examined and caste, country, first administrative region, second administrative region or, if known, specific locality, coordinates in decimal degrees, elevation in meters, collection date in format yyyy–mm–dd, collector followed by the word "leg.", method of collection (if known), habitat (if known), and institution where the material is located, usually represented by a unique specimen identifier composed of capitalized letters and numbers. The format for "Other material examined" is essentially equal except that unique specimen identifiers are not shown, but museum acronyms are.

The "Material examined" section contains the complete set of recorded localities and specimens revised in this work.

Relationships among taxa

I provide brief comments about the relationships between species in the present *Neoponera* groups. My statements are grounded on prior studies by Schmidt (2013) and Branstetter and Longino (2022), as well as on molecular-based preliminary results (A. Troya, J. Longino, M. Branstetter et al. unpublished) which are part of a larger ongoing collaborative study about the phylogeny of the genus *Neoponera* which will be published separately. This additional information is not to be treated as conclusive, nevertheless I think it adds support to my morphology–based arguments around the species hypotheses shown here.

Species delimitation

I follow the biological species concept *sensu* Mayr (1942) by considering species as population assemblages which are under presumed continuous gene flow. Since I did not directly assess this process, my criterion for species delimitation was to detect a continuum of expected character gradations lacking discontinuities among distinctive populations. In sympatry, interspecific gene flow can obscure populational distinctness (Arnold 1992, Field et al. 2011). In such case species can be detected by consistently grouping morphologically similar individuals assumed to belong to structured populations, which is a proxy for gene flow (Wild 2005).

Both new and currently known species hypotheses shown in this study should be further evaluated using additional lines of evidence. These will add objectivity and will aid in the discrimination of species boundaries among cryptic populations which may potentially be under differing selective pressures that are suspected, yet here untested.

RESULTS

The *N. foetida* species group

Worker- and queen-based key to species of the *N. foetida* species-group

1 Antennal scape short, when pulled posterad, fails to reach posterior head margin; eye placed slightly anteriorly on head (Fig. 1a); known only from Panama …… ***N. fisheri***

– Antennal scape longer that previous lead, when pulled posterad, always exceeding posterior head margin; eye placed at head midlength (Fig. 1b) ……..… 2

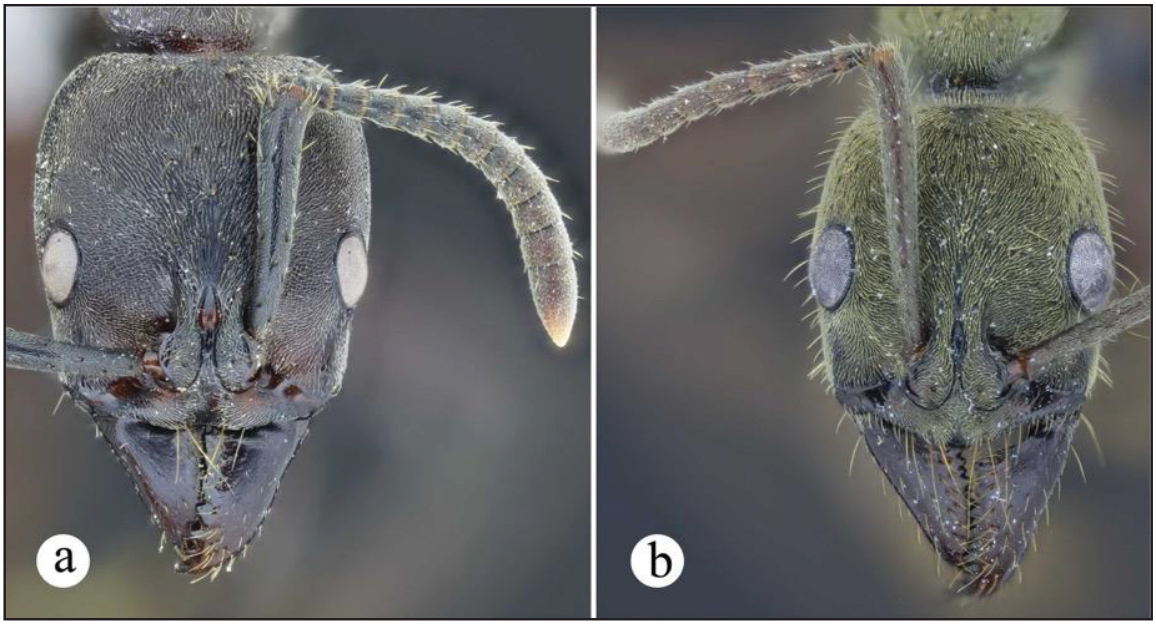


Fig. 1. Antennal scape. **a.** Short, not reaching posterior head margin (☿ *N. fisheri*, MZSP); **b.** Longer, always exceeding posterior head margin (☿ *N. bugabensis*, JTLC: JTL7357).

2 (1) Petiolar node subtriangular in lateral view, posterolateral margin carina-less (Fig. 2a); malar carina highly reduced, hard to distinguish from surrounding rugose sculpture (Fig. 20e); known only from Costa Rica ……..……..……. ***N. dismarginata***

– Petiolar node block-shaped (Figs. 2b, 2c) in lateral view, posterolateral margin either carina-less or carinate; malar carina present or reduced but never as described above …… 3

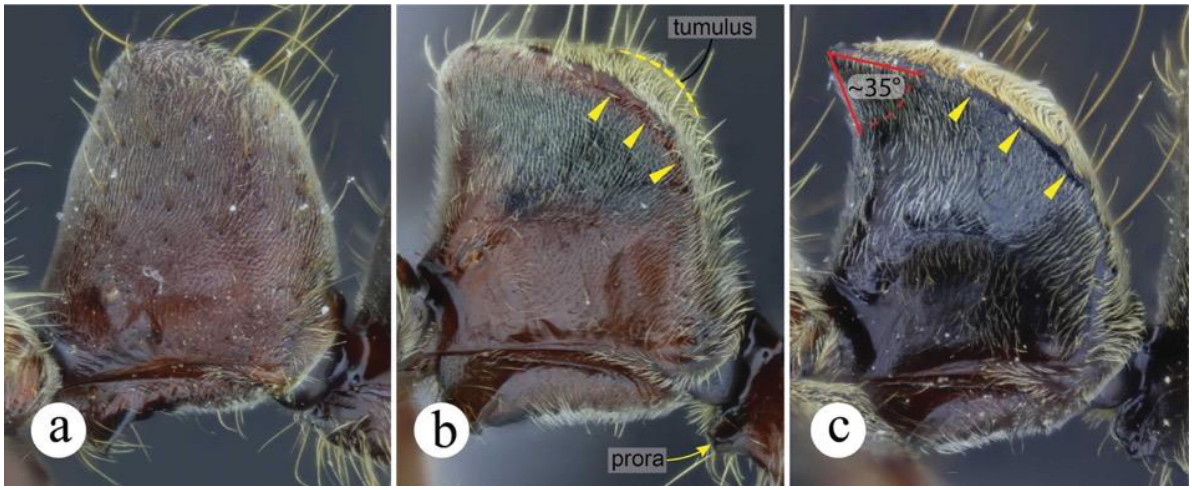


Fig. 2. Node shape in lateral view. **a.** Subtriangular (☿ *N. dismarginata*, JTLC: JTL9295); **b.** Block-shaped (☿ *N. villosa*, JTLC: JTL7597-1); **c.** Scale-shaped (☿ *N. inversa*, CPDC: AT1094). Yellow arrowheads show the posterolateral carina.

3 (2) Petiolar node almost completely covered with well-impressed, horizontal striae, except for the midventral lateral face which is usually devoid of sculpture (Fig. 3a); posterior head margin concave; southern Central America, northern and central South America……..... ***N. foetida***

– Petiolar node not as above, if striae are present, then either on anterior face (Fig. 3b), laterally (Fig. 3c), or tenuously impressed on posterior face (only seen in *N. prasiosomis*, Figs. 5c, 28g); posterior head margin either straight or concave……..……. 4

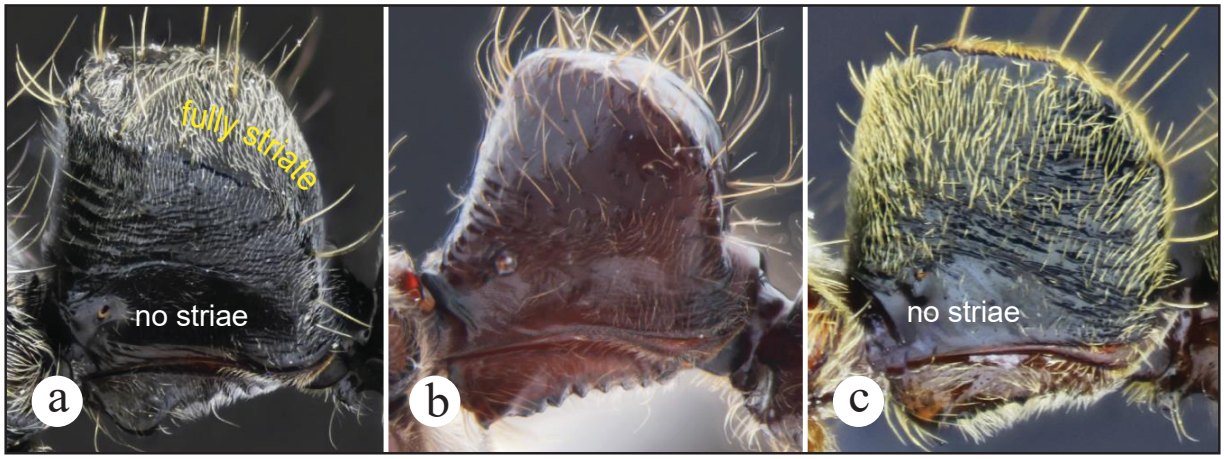


Fig. 3. Node sculpture. **a.** Almost completely striate (☿ *N. foetida*, JTL: JTL944564); **b.** Striate anteriorly (☿ *N. solisi*, INBC: INBIO003662417); **c.** Striate laterally (☿ *N. theresiae*, JTLC: GO-E-08-1-03).

4 (3) Head dorsum costate, costae particularly noticeable on vertex (Fig. 4a); posterior face of petiolar node with patch of feebly impressed, irregular costae; southeastern Mexico to Central America, Colombia (?)……..…..… ***N. lineaticeps***

– Head dorsum without costae, though it may have well-impressed striae (Fig. 4b), or punctae (Fig. 1b); posterior face of petiolar node without patch of well-impressed, vertical striae…… 5

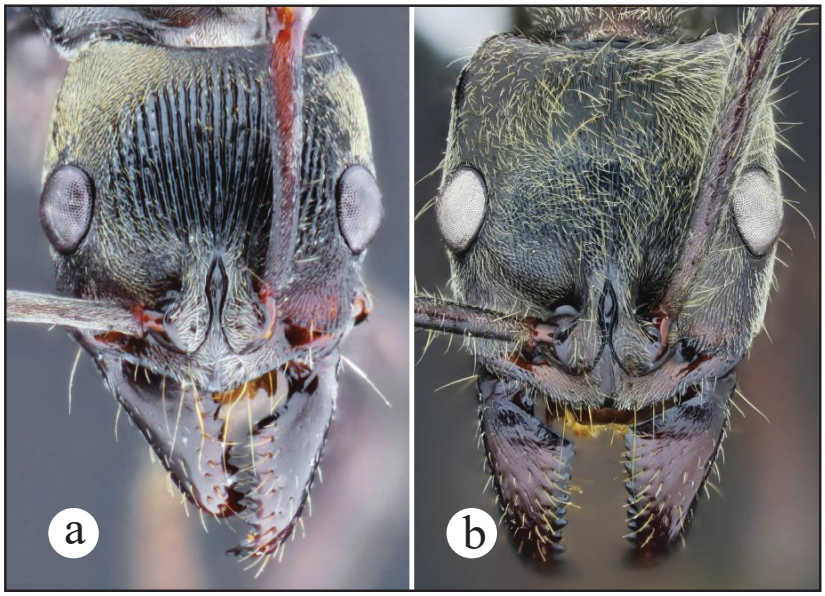


Fig. 4. Dorsal head sculpture. **a.** Costate (☿ *N. lineaticeps*, JTL: CASENT0610994); **b.** Striate (☿ *N. solisi*, JTL: INBIO3662424).

5 (4) Posterior face of petiolar node mostly glabrous (Fig. 5a); posterior head margin concave, with posterior corner convex but feebly protruding posterad (Fig. 4b); known only from Costa Rica…….……..…… ***N. solisi***

– Posterior face of petiolar node not glabrous, either punctate or tenuously striate; posterior head margin either concave or straight ……..…..… 6

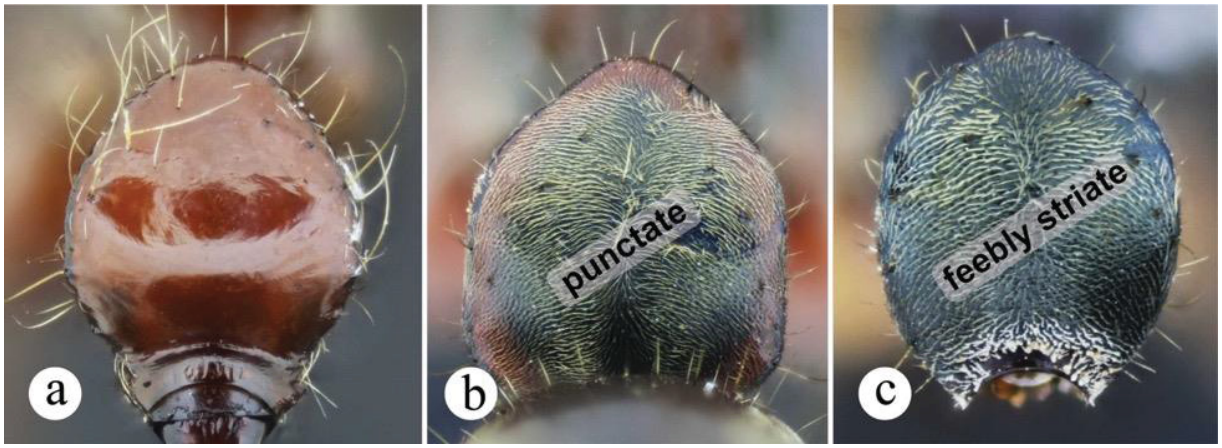


Fig. 5. Posterior nodal face. **a.** Mostly glabrous ((☿ *N. solisi*, JTL: INBIO3662424); **b.** Punctate (☿ *N. bugabensis*, JTLC: CASENT0632922); **c.** Feebly striate (☿ *N. prasiosomis*, DZUP: ATPFOR2001).

6 (5) Dorsum of proximal mandibular region with well-impressed, divergent striae (Fig. 6a); lateral face of petiolar node striate (Fig. 3c); southern Central America, northwestern South America, Ecuador (?), Peru (?), Brazil (?) …… ***N. theresiae***

– Dorsum of mandible without divergent, well-impressed striae, if striae are present, then feebly to moderately impressed (Figs. 4a – b, 9a – c); lateral face of petiolar node without striae ……..…… 7

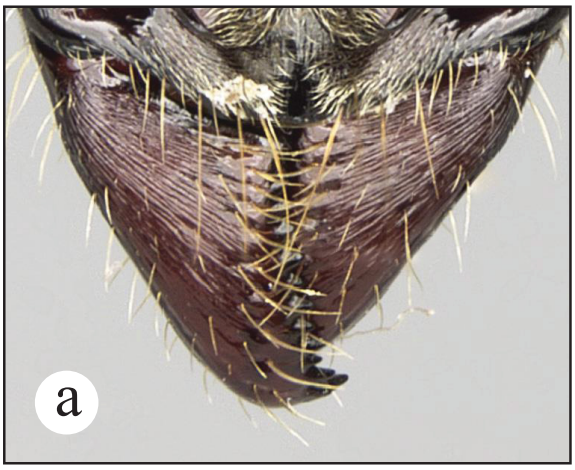


Fig. 6. Mandible sculpture. **a.** Well-marked, divergent (☿ *N. theresiae*, BMNH: CASENT0281902).

7 (6) Anterior margin of mesopleuron with lamellate (Fig. 7a), or lobate (Fig. 7b) cuticular extension; and posterior face of petiolar node with tumulus (Fig. 2b); humeral carina not salient (Fig. 7d); South America (western and central Amazonia) ……..…. ***N. zuparkoi***

– Anterior margin of mesopleuron without anterior lobe or lamella; posterior face of petiolar node either with or without tumulus; humeral carina either slightly to strongly salient (Fig. 7c)…… 8

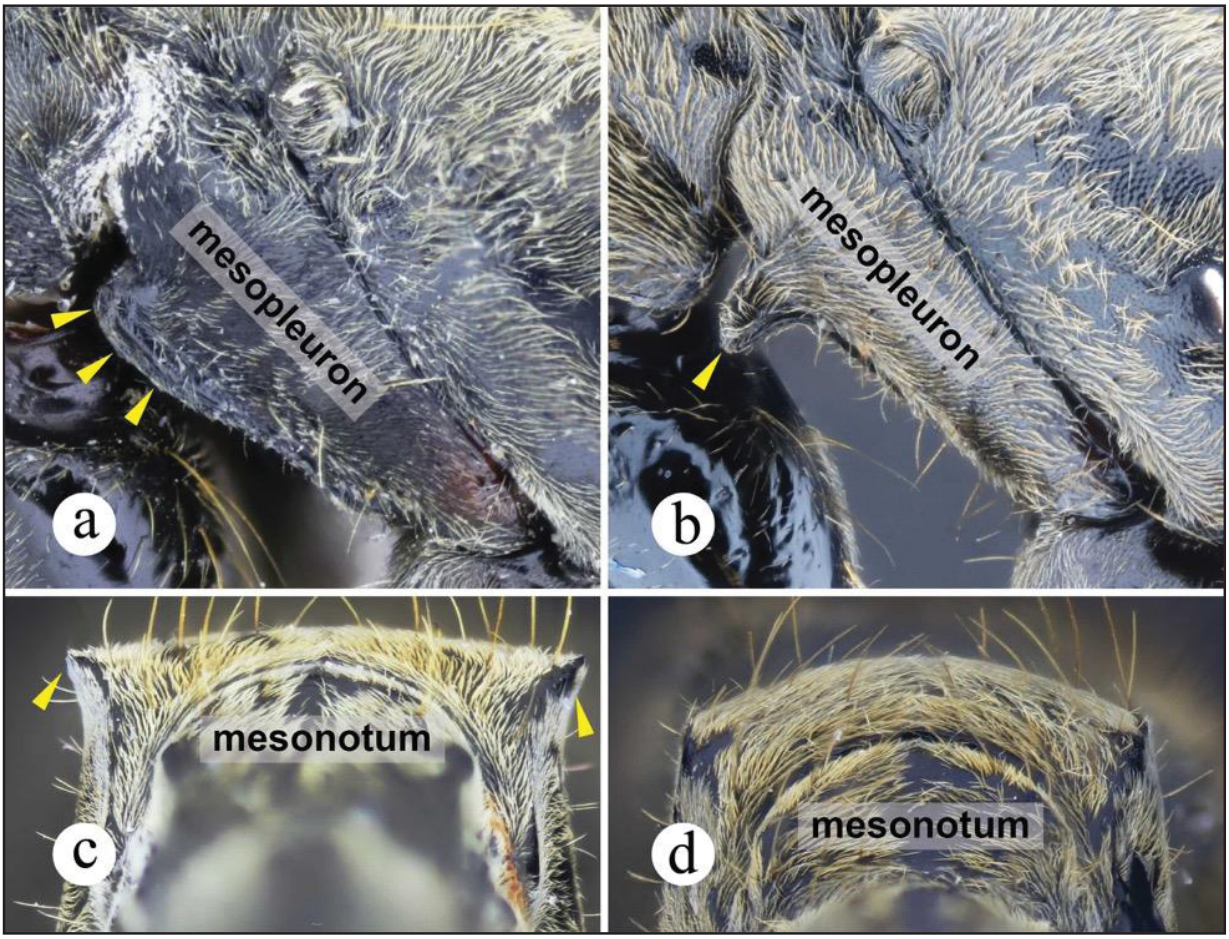


Fig. 7. Mesopleural anterior margin (a – b). **a.** Lamellate (☿ *N. zuparkoi* (variant), MEPN: MEPNINV2923); **b.** Lobate (☿ *N. zuparkoi*, DZUP: DZUP549348); Humeral carina (c – d). **c.** Salient (☿ *N. curvinodis*, MEPN: ATPFOR2105); **d.** Present but not salient (☿ *N. zuparkoi*, DZUP: DZUP549348). Yellow arrowheads show the protruding carinae.

8 (6) Posterior face of petiolar node with tumulus (Fig. 2b); prora well-developed, with truncate tip (Fig. 2b); Nearctic Region (central eastern Texas to northern Mexico, except the Plateau), and Neotropical Region (southern Mexico to northern Argentina) …… ……..…. ***N. villosa***

– Posterior face of petiolar node without tumulus; prora highly variable, either tiny and pointed (Fig. 10b), to well-developed and anteriorly round ……..…… 9

9 (8) In lateral view, anterior and posterolateral margins of petiolar node forming angle between ≂ 60° to ≂ 90° (Fig. 8a) ……..……...…..…… 10

– In lateral view, anterior and posterolateral margins of petiolar node forming angle between ≂ 40° to ≂ 50° (Fig. 8b) ……...…..……...… 12



Fig. 8. Node in lateral view: anterior margin vs. dorsolateral margin. **a.** Forming ca. 90° (☿ *N. bugabensis*, MUSENUV: MUSENUVHOR0985); **b.** forming ca. 45° (☿ *N. curvinodis*, INPA); c. forming ca. 45° (☿ *N. curvinodis*, INPA). Specimens from **b** & **c** belong to the same colony.

10 (9) Antennal scape exceeding posterior head margin by 0.5 X to 1 X apical scape width (Fig. 9a); in lateral view, petiolar node length (PL) ☿ ≂ 0.7 mm to ≂ 0.8 mm (queen unknown); body integument tenuously greenish; central Panama and northwestern Ecuador ..... ***N. prasiosomis***

– Antennal scape exceeding posterior head margin by more than 1 X apical scape width (see next couplet); in lateral view, petiolar node length (PL) longer than previous lead: ☿, ♀≃ 1 mm to ≃ 1.5 mm; body integument castaneous, brownish, black ……..… 11

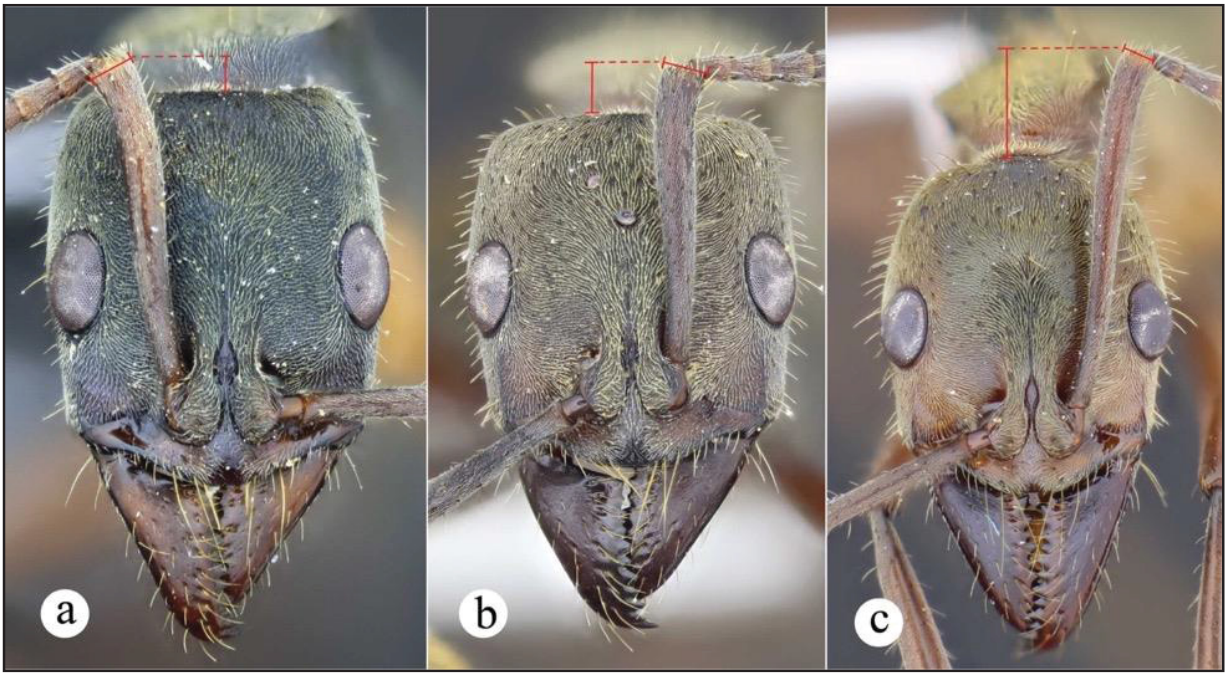


Fig. 9. Antennal scape exceeding posterior head margin by X times apical width: **a.** Between 0.5 to 1 X (☿ *N. prasiosomis*, DZUP: ATPFOR2001); **b.** About 1 X (♀*N. insignis*, LACM: LACMENT142417); **c.** Between 2 X to 3 X (☿ *N. bugabensis*, MUSENUV: MUSENUV22595).

11 (10) Antennal scape exceeding posterior head margin by about 1.5 X apical scape width (Fig. 9b); in lateral view, posterolateral nodal margin moderately sharp (Fig. 10a); southern Central America to northwestern Colombia.....……..... ***N. insignis***

– Antennal scape exceeding posterior head margin by about 2 X to 3 X apical scape width (Fig. 9c); in lateral view, posterolateral nodal margin blunt (populations from Central America, Fig. 10b) or moderately sharp, approximating that of *N. insignis* (populations from South America); mid-eastern Mexico, Central America, northwestern and central South America ……..... ***N. bugabensis***

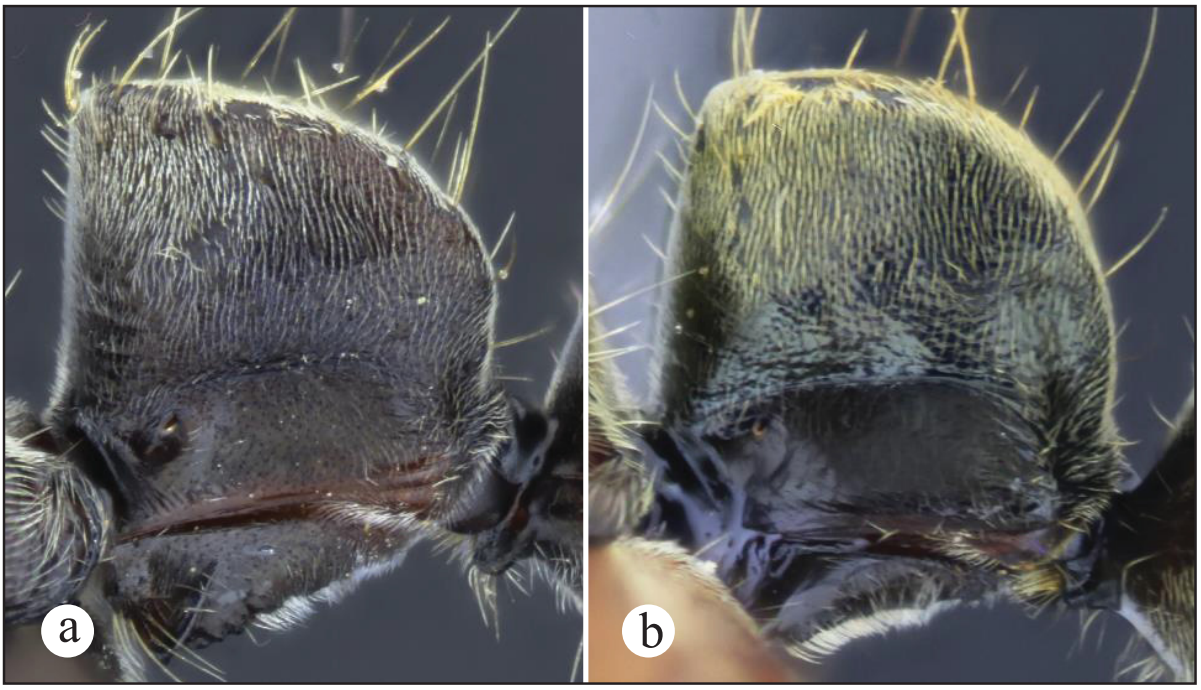


Fig. 10. Petiolar node in lateral view. **a.** Posterolateral margin sharp (☿ *N. insignis*, JTLC: JTL9077-1); **b.** Posterolateral margin blunt (☿ *N. bugabensis*, CASENT0647684).

12 (9) Posterolateral propodeal margin with raised carina, usually crenulate (Fig. 11a); anterolateral distal petiolar node face feebly to moderately deflate, nodal top projected anterodorsad (Fig. 8b); largest species in the *N. foetida* group (TLa: ☿≂11 mm to 14 mm; ♀≂13 mm to 15.5 mm, see also Fig. 12); southern Mexico to southeastern Brazil ..... ***N. curvinodis***

– Posterolateral propodeal margin without (or feebly) raised, carina, without crenulae (Fig. 11b); anterolateral distal petiolar node face strongly deflate (frequently, Fig. 2c), or feebly deflate (less frequently, Fig. 8c), nodal top usually projected anterad (Fig. 2c); smaller body length than previous lead (TLa: ☿≂10 mm to 12 mm; ♀≂11 mm to 14 mm, see also Fig. 12); northern Honduras to southeastern Brazil ……...… ***N. inversa***

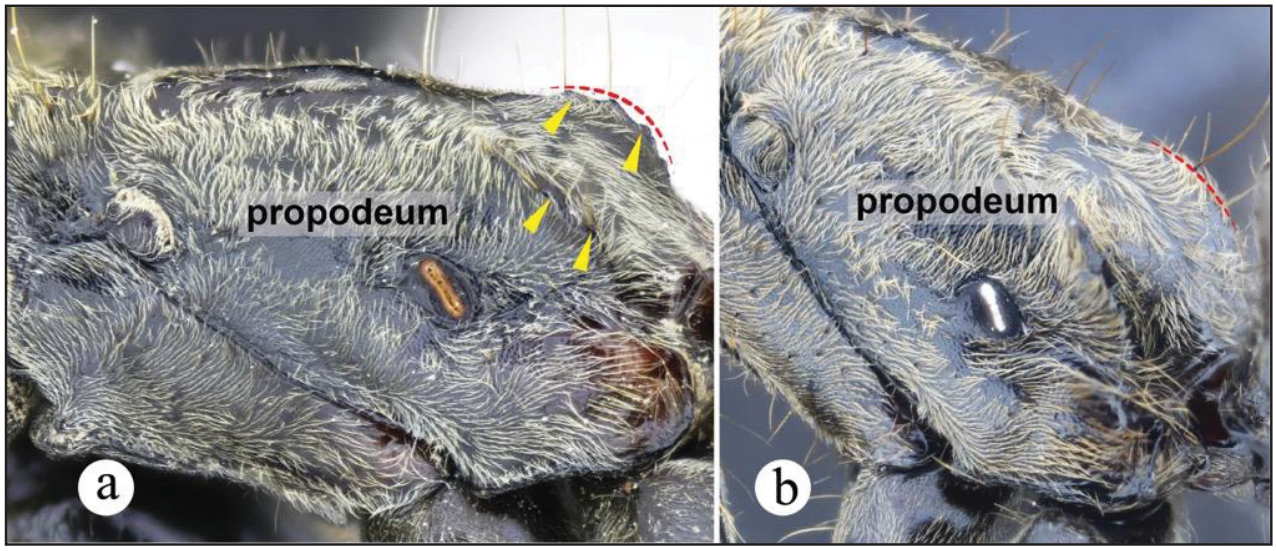


Fig. 11. Propodeum posterolaterally **a.** Bearing raised carina, usually crenulate (☿ *N. curvinodis*, MEPN: ATPFOR2105); **b.** Carina-less, or at most feebly raised, without crenulae (☿ *N. zuparkoi*, DZUP: DZUP549348). Yellow arrowheads point to the raised crenulae of the propodeal carinae. The red-stripped line shows the convexity of the propodeal carina.

TAXONOMY

Synoptic list

In parentheses the known castes per species: ☿ – worker; ♀ – queen; ♂ – male.

Neoponera bugabensis (Forel, 1899) (☿)

Neoponera curvinodis (Forel, 1899) (☿, ♀, ♂)

= *N. bactronica* Fernandes et al., 2014: 136 (☿, ♂) **syn. nov.**

= *N. billemma* Fernandes et al., 2014: 140 (☿) **syn. nov.**

= *N. subversa* Lucas et al., 2002: 256 (☿) **syn. nov.** (*nomen nudum*, unavailable)

Neoponera dismarginata (Mackay & Mackay, 2010) (☿)

Neoponera fisheri (Mackay & Mackay, 2010) (☿, ♀, ♂)

Neoponera foetida (Linnaeus, 1758) (☿, ♀)

= *Neoponera lobata* De Geer, 1773 (♀) synonymy by Retzius, 1783: 75

= *N. pedunculata* (Smith, 1858) (☿) **syn. nov.**

Neoponera insignis (Mackay & Mackay, 2010) (☿, ♀, ♂)

Neoponera inversa (Smith, 1858) (☿, ♀, ♂)

Neoponera lineaticeps (Mayr, 1866) (☿, ♀, ♂)

Neoponera prasiosomis Troya, **sp. nov.** (☿)

Neoponera solisi (Mackay & Mackay, 2010) (☿, ♀)

Neoponera theresiae (Forel, 1899) (☿)

Neoponera villosa (Fabricius, 1804) (☿, ♀, ♂)

= *Neoponera bicolor* (Guérin-Méneville, 1844) (♀) synonymy by Roger, 1861: 1

Neoponera zuparkoi (Mackay & Mackay, 2010) (☿)

Neoponera foetida species-group differential diagnosis

Worker and queen. This group includes the shiniest ants among the *Neoponera*, especially when placed against light. The dorsal cuticle of most species is covered by abundant, golden appressed pilosity which reflects light very well. Because of this the name "golden *Neoponera*" could perfectly be applied to them. In most species, the workers and queens are relatively large as compared to the body size of other species in the genus. The largest lineage, *N. curvinodis*, can easily exceed 12 mm (☿ = ~ 11 – 14 mm; ♀ = ~ 13 – 16 mm), whereas the smallest, *N. lineaticeps*, barely exceeds 8 mm (☿ = 7.2 – 8.3 mm; ♀= 11 mm, this latter sensu Mackay and Mackay, 2010). These two castes are overall very similar to each other, but the queen shows the following differing features with respect to the worker: 1) The head vertex carries three comparatively small ocelli, which are smaller than the antennal acetabulum diameter; 2) The mesonotum is formed by the typical ponerine sclerites for flight function: scutum, scutellum and associated structures; 3) The metanotum is plenty discernible, as in all *Neoponera* queens, and lacks a median carina or tumulus; 4) The mesopleuron is usually divided in anepisternum and katepisternum by a well-marked mesopleural, frequently grooved suture. This suture normally runs uninterrupted through the entire plate, though sometimes it may fade before reaching the anterior mesopleural margin. The only exception to this plate division is found in *N. fisheri* where the suture is vestigial to completely absent (Fig. 21a), as judged by the only two known queens. A concavity is present, however, in the region where the suture is supposed to be placed; 5) The propodeum is almost always more robust, and sometimes the sculpture (when present) is more

abundant; 6) The general body size is larger, including the eye which is ca. 5% larger than that of the worker.

No differences between workers and queens were noted in regards to the malar carina which, according to Fernandes et al. (2014) is sharper in queens. In contrast to some species of other species-groups like the *N. aenescens*, *N. crenata*, *N. laevigata* groups, the petiolar node of the queens of the *N. foetida* group is not slightly narrowed laterally as compared to that of the workers.

Features distinguishing species in this group from others in the genus

Worker and queen. The following characters can be used in combination: 1) The mid clypeal region of most species is either feebly convex (e.g., Figs. 4a, 6a, 9b) or horizontally straight – truncate (e.g., Figs. 1b, 9c). Three species, namely *N. fisheri*, *N. solisi*, and *N. villosa* have a concave mid clypeus, with the former showing the deepest concavity (e.g., Fig. 4b) from all taxa in this group. In contrast, *N. dismarginata* (Fig. 20c, e) has a relatively acute mid clypeus which is reminiscent, though not necessarily similar, to most species of the *N. crenata* group where this clypeal section protrudes anterad in the form of a subtriangular cuticular extension. 2) The globose eye breaks the lateral head margin, and is placed approximately on the mid longitudinal region of the head, as is the case for all species in the *N. crenata* group. The only exception to the rule is *N. fisheri* whose eye is much less globose than the norm in this group, somewhat flat, but also breaks the head margin, and is placed slightly anteriorly on head (Fig. 1a). Also, in some *N. insignis*, the eye barely reaches the head margin. In all other *Neoponera* the eye is slightly displaced from the horizontal median plane of the head, either slightly posterad, e.g., species in the *N. apicalis* group, or slightly anterad, e.g., most species of the *N. aenescens* group. 3) The malar carina is well-marked on the cuticle, slightly raised and in few species like *N. villosa* and *N. curvinodis* it usually touches the anterointernal eye margin (link). In three species, *N. dismarginata*, *N. fisheri*, and *N. solisi*, this carina is reduced (Figs. 4b, 20e), this is, it is not raised, and it merges with the surrounding cuticle before reaching the anterior eye margin. In this case this reduced carina is more like a swelling rather than a true sharp margin. Among Neotropical Ponerinae, the malar carina is a hallmark of most *Neoponera* taxa. It is not present, however, in species of the *N. aenescens* and *N. laevigata* groups (expect for *N. commutata* Roger), where it is transformed into a swelling or is completely absent (link). In *N. concava*, *N. schultzi*, and *N. venusta*, which will now it is known do not belong

to *Neoponera* (Troya and Lattke 2022), but comprise its putative sister group (pers obs.), the carina runs over the anterointernal eye margin, instead of in front of it as in all other species in the genus. 4) The humerus is carinate, except for *N. fisheri* which shows a tenuous, blunt margin (Fig. 21a). The humeral carina varies highly interspecifically, it can either be strongly salient (shelf-like) and sharp as in *N. foetida* (e.g., Fig. 7c), anteriorly acute with posterior irregular margins as in *N. solisi*, or just marginate, not laterally salient as in *N. theresiae* and *N. zuparkoi* (Fig. 7d). In all cases, however, this marginate border fades away before the cuticle reaches the anterodorsal anepisternal margin (upper plate of the mesopleuron). The humeral carina is also depicted in most species of the *N. aenescens*, *N. crenata*, and *N. emiliae* groups, in all of them, however, this structure is never strongly salient, except for *N. striatinodis* where it is shelf-like. In some species of these groups the humeral carina is replaced by a tiny blunt border as in *N. chyzeri* (Forel) (link). In *N. curvinodis* and *N. inversa* the humeral carina varies extraordinarily. Especially in the former, it can be anteriorly acute, laterally sharp, and shelf-like (Fig. 7c) or just barely emerging from the cuticle as a relatively blunt line which can be difficult to discern due to the surrounding pilosity (Fig. 7d). Yet, the first form (shelf-like) is more commonly found. This high degree of plasticity has only been evidenced in these two species across the genus, and this is just part of the picture in regards to their overall morphological variation since it has been noticed in other structures as well (see more details under those species). 5) The notopropodeal suture is always present and forms a groove which is usually easily discernible both dorsally and laterally despite the abundant surrounding pilosity of some species. Although this groove is sometimes considered “deep” (see Fernandes et al. 2014), a more proper term would be well-marked as usually used by MacKay and Mackay (2010). In Ponerinae, a good example of a deep groove is exemplified in *Mayaponera constricta* (link). In *Neoponera*, the notopropodeal groove vary from vestigial or completely absent, to well-marked on the cuticle. This character is present in the *N. apicalis*, *N. laevigata*, and *N. aenescens* groups, but also in *N. rostrata* (Emery). In species of the former the cuticle is opaque and usually devoid of erect hairs except for *N. cooki* (Mackay and Mackay), while in the *N. laevigata* group the cuticle is completely polished, very much like a mirror, and scantly hairy. In species of the *N. aenescens* group the groove is evident despite the usually abundant appressed pilosity on the mesosoma, but all of them lack the characteristic abundant erect hairs of the species in the *N. foetida* group. As for *N. rostrata*, the groove is well-marked and perfectly discernible since it lacks abundant appressed pilosity in such body region. 6) The anterior margin of the

petiolar node is straight, or nearly so, and inclined posterad. Three species, however, show variations of this trait: *N. villosa*, *N. curvinodis, N. inversa*, and also some queens of *N. bugabensis* (Figs. 14, 17). In the former, the margin is virtually perpendicular to the horizontal body plane, although this may vary geographically with some populations showing a slight inclination. As for the latter two taxa, usually the distal region of the whole anterolateral nodal face may be either relatively straight to strongly deflate, frequently observed in *N. inversa*, so that the top of the node is directed anterad somewhat resembling a hood (Fig. 2c). The nodal margin of *N. fisheri* appears to be nearly vertical as in a specimen from Panama (CASENT0217559, link) but with closer examination a slope is noted. 7) Well-developed, fang-shaped metasternal process. This is the only character considered apomorphic for the *N. foetida* group and varies little interspecifically. The configuration of both spine-shaped appendices (or spiny lobes) is relatively similar to that present in species of the *N. crenata* and *N. laevigata* groups. However, in species of the *N. foetida* group the lobes are broad: their mid vertical region is about three times broader than the space separating them. In the *N. crenata* and *N. laevigata* groups the lobes are comparatively narrower than in the *N. foetida* group.

Male. This caste is known from seven species, *N. bugabensis*, *N. curvinodis*, *N. fisheri*, *N. inversa*, *N. lineaticeps*, *N. villosa*, and *N. insignis*. The latter is newly described in this treatment. Males of the *N. foetida* group are in general rarely collected for most species. Perhaps, the only exceptions are *N. villosa* and *N. curvinodis* for which the worker and queen castes abound in museum collections and are frequently encountered in the field.

In this work, male specimens of only four species were examined, *N. curvinodis*, *N. insignis*, *N. villosa*, and *N. fisheri* (this latter through images of UTEPENTO3519-01 in AntWeb.org) for which the association male/queen – worker was confident since the specimens belong from the same nest series. Out of these, only for *N. villosa* and *N. curvinodis* a relatively good amount of material (19 and 11 specimens, respectively) representing some regions of Brazil and Mexico, was examined (see the material examined for those species). Therefore, the following few characters (see further below) are added and/or commented to those reported in prior treatments, namely MacKay and Mackay (2010) and Fernandes et al. (2014).

Troya and Lattke (unpublished) detected that a number of external morphological characters in the males of the *N. crenata* group were variable even intraspecifically, which

complicates species distinction. Characters like ocellar size, length and depth of notauli and mesopleural groove, among others, were not homogeneous, i.e., showing a distinctive morphology pattern, among examined specimens. Populational variations in such traits are, apparently, too plastic for diagnostic consideration. Although in this study a less abundant (# specimens) and diverse (# species) material was examined as compared to said work, I detected here a similar issue in the males of *N. villosa*, with some specimens showing, for example, more deeply impressed notauli than others.

The notauli sometimes meet posteriorly and sometimes do not. Except for *N. villosa* and *N. curvinodis*, the male caste in the *N. foetida* group is still rarely found in either museum samples and in the field. Maybe many specimens preserved in ethanol in museum collections, for example, from Malaise traps, still await discovery. Nevertheless, since most males in this species-group remain unassociated with their respective workers/queens, little progress is expected from morphological examination alone. Future male descriptions and especially diagnoses will require more detail and accuracy coupled with high-definition images made available through free-access platforms.

1) The inter-antennal socket carina, also called "short median longitudinal swelling of the frontal carina" (Dias and Lattke 2021, p. 8), and cited in Fernandes et al. (2014) as a "fine carina present between insertion of antennae", p. 136, is present in the males from all species groups in the genus. This carina is usually feebly impressed, e.g., in *N. aenescens*, *N. globularia*, *N. marginata*, some specimens of *N. villosa*, and sometimes slightly raised but clearly discernible, e.g., in *N. rostrata*, and *N. commutata*. Males from other closely related genera also show this structure, e.g., *Dinoponera grandis*, *Pachycondyla crassinoda*. It is unknown if this feature is present in other ponerine males outside the *Pachycondyla* genus-group, where *Neoponera* is placed, but it appears to be plesiomorphic, therefore not useful for diagnosing species-groups in the genus. However, further specimens from a number of additional species are required to test this assumption. 2) The eye is relatively small, smaller or approximately equal to half head length. This is similar to known males of the *N. laevigata* group where the eye is even smaller, except for *N. commutata* where it is approximately equal such distance. In the males of the remaining *Neoponera* groups the eye is longer than half head length. 3) The mesopleural sulcus (sometimes also called "anapleural sulcus", see for example Delsinne et al. 2019) does not extend into the ventral pleural surface. This condition is certainly similar to the observed in the *N. crenata* group.

In known males of the *N. aenescens* and *N. apicalis* groups, and in *N. rostrata*, the sulcus clearly extends into the ventral mesopleural surface. In contrast, in the *N. laevigata* group, this sulcus is poorly developed, extending approximately to just the median region of the lateral mesopleural plate. 4) The notauli [= mayrian sutures, in Mackay and Mackay (2010), and Fernandes et al. (2014)], are well-marked on the cuticle, slightly cross ribbed, these may meet or "touch" each other posteriorly and form a weakly impressed longitudinal groove (e.g, *N. insignis* from Costa Rica, INBIOCRI002278907, Fig. 25b), or not (remaining examined males). In contrast to such Costa Rican male, the notauli in another from Panama (JTL9077-2) do not meet posteriorly. This is another case of plasticity in *Neoponera* males.

Finally, the following characters cited as diagnostics in Fernandes et al. (2014) are considered apomorphic for all known males in *Neoponera*, thus not informative for diagnosing the *N. foetida* group: "body black or brown; palps covered by sparse pubescence, with palpal formula 6:4; eye well-developed and expanded dorsolaterally; malar carina absent; clypeus convex medially; lateral pronotal carina absent; well-marked mesometanotal and metanotal-propodeal grooves; stridulatory file of abdominal pretergite IV well-developed; parameres well-developed with apex round and sparse hairs on surface", p. 136.

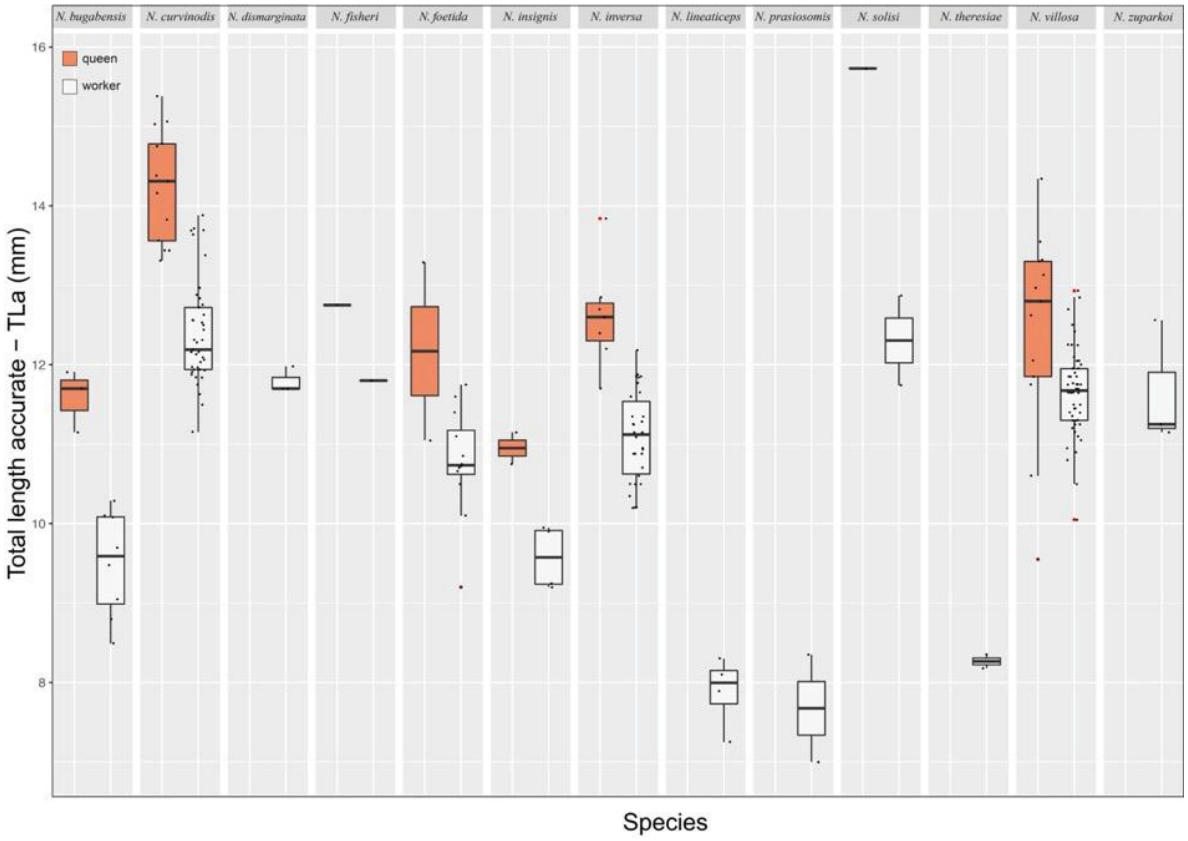


Fig. 12. Approximate body size range of species in the *N. foetida* group as estimated by the variable Total Length accurate – TLa. *n*: ☿ = 191, ♀= 47. Red dots are outliers.

Species accounts

Neoponera bugabensis (Forel, 1899)

Figures. 1b (head ☿); 13, 15, 16: a – c (☿); 14, 17: a – c (♀); 30a (distribution)

Pachycondyla theresiae var. *bugabensis* Forel, 1899: 14. ☿ lectotype [by designation of Mackay & Mackay, 2010: 224], Panama, Bugaba, Champion [leg.], (MHNG, AntWeb: CASENT0907242) [image examined, link].

Combinations. In *Pachycondyla*: Brown, 1995: 303; in *Neoponera*: Emery, 1901: 47; Schmidt and Shattuck, 2014: 151.

Subspecies of *Neoponera theresiae*: Emery, 1911: 72; Kempf 1972: 162; Bolton 1995: 303; Mackay, 2008: 198.

Status as species: MacKay and Mackay, 2010: 224 (redescription).

Worker and queen diagnosis. Head subquadrate (Figs. 14b, 17b), sometimes slightly longer than broad (Fig. 15b), with longitudinal, weakly to well-impressed, irregular striae (Figs. 16b, 17b); antennal scape, when pulled posterad, exceeding posterior head margin by approximately 1.5 times (Figs. 14b, 16b) to 3 times (Fig. 15b) apical scape width; malar carina well-marked, it usually fades away before reaching anterior eye margin; humeral carina present, slightly salient; posterolateral margin of propodeum weakly carinate (Figs. 15a, 16a) or without carina; anterior margin of petiolar node either slightly inclined posterad (Figs. 8a, 10b) or steeper (Fig. 17a); posterolateral margin of node weakly carinate, carina usually blunt (Figs. 10b, 14a) mostly in Central American populations; anterior margin of node straight (Figs. 10b, 14a, 15a, 16a) or slightly concave, this latter only seen in queens from South America (Fig. 17a); dorsal appressed pilosity varying from pale yellowish-brownish (Fig. 16), to intense, brilliant golden (Figs. 14, 15), erect and suberect hairs on head and mesosomal dorsum either shorter or about as long as maximum eye length.

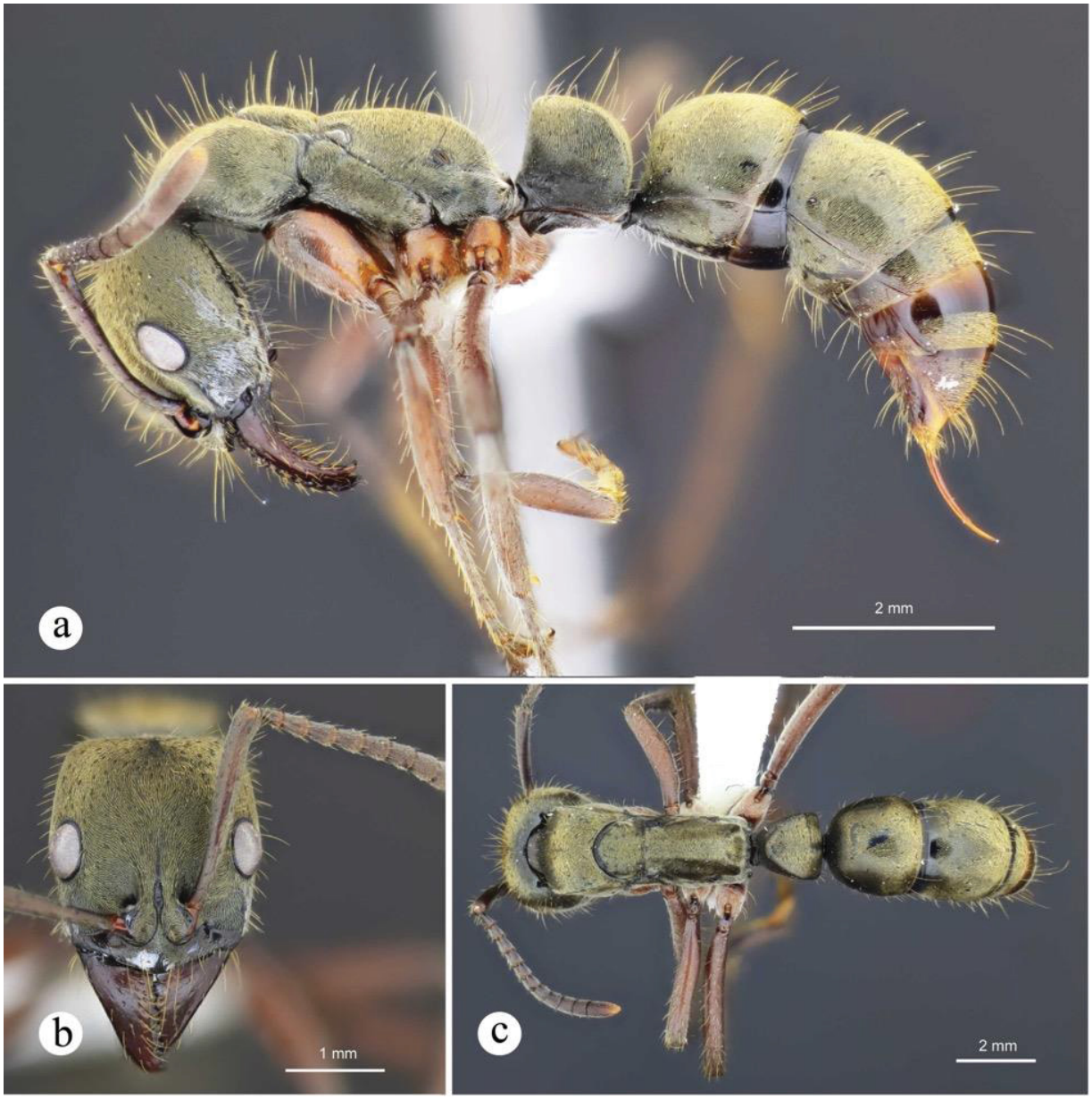


Fig. 13. *Neoponera bugabensis*. ☿ (MUCR: CASENT0637852), Costa Rica: Limón. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

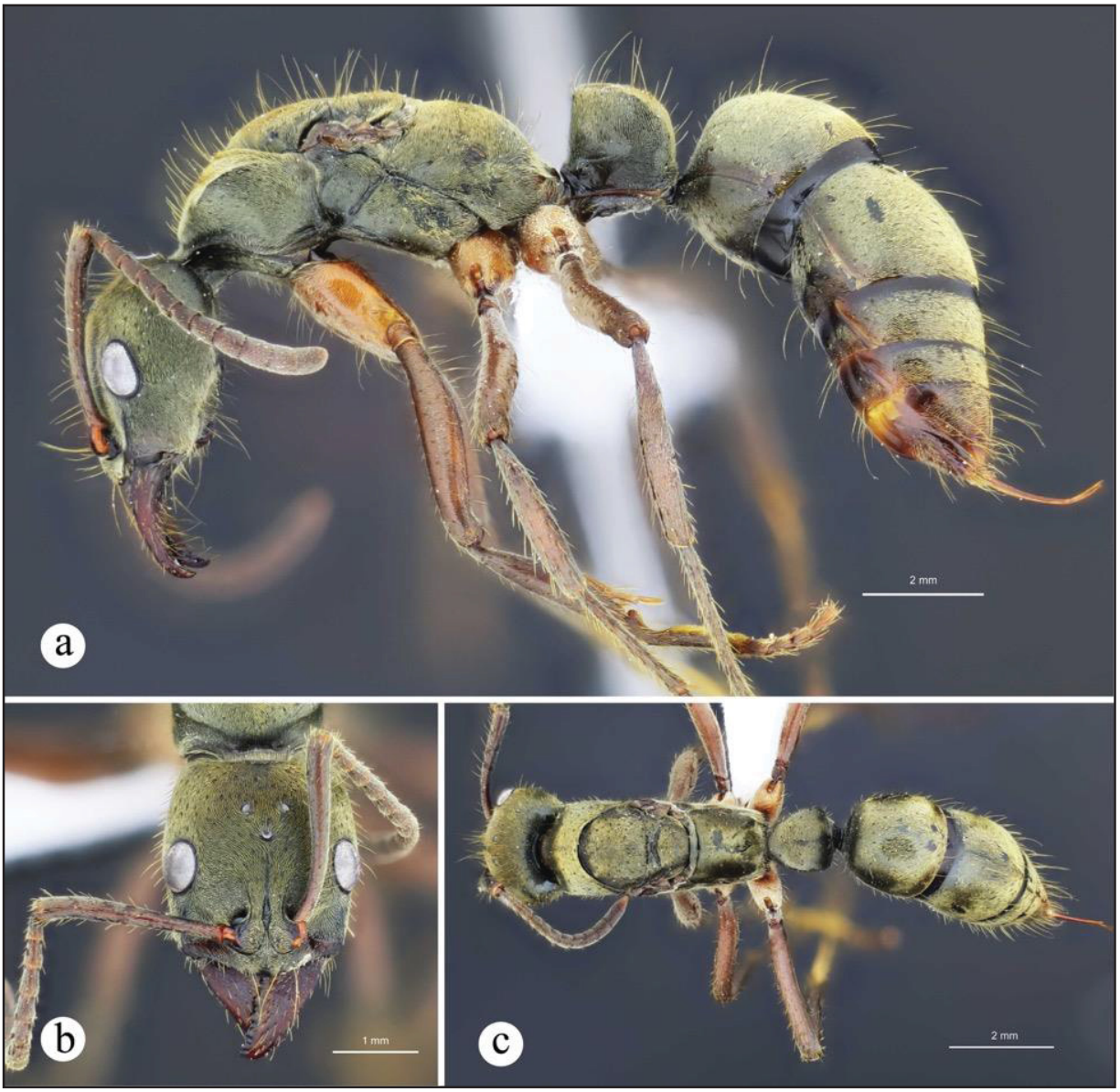


Fig. 14. *Neoponera bugabensis*. ♀ (JTLC: CASENT0617486), Honduras: Comayagua. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

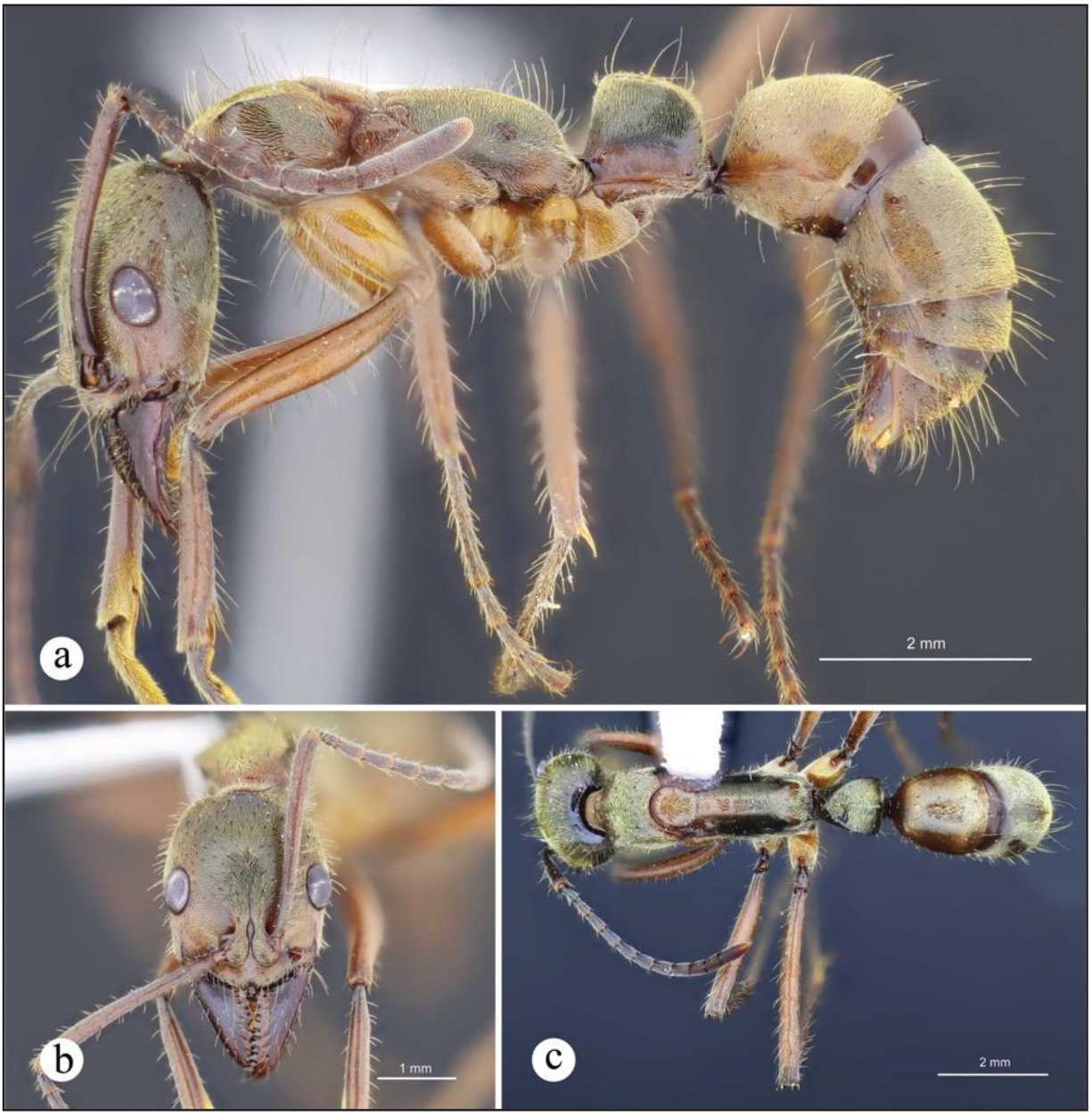


Fig. 15. *Neoponera bugabensis*_var1. ☿ (MUSENUV: MUSENUV22595), Colombia: Valle del Cauca. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.



Fig. 16. *Neoponera bugabensis*_var2. ☿ (MUSENUV: HOR0985), Colombia: Valle del Cauca. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

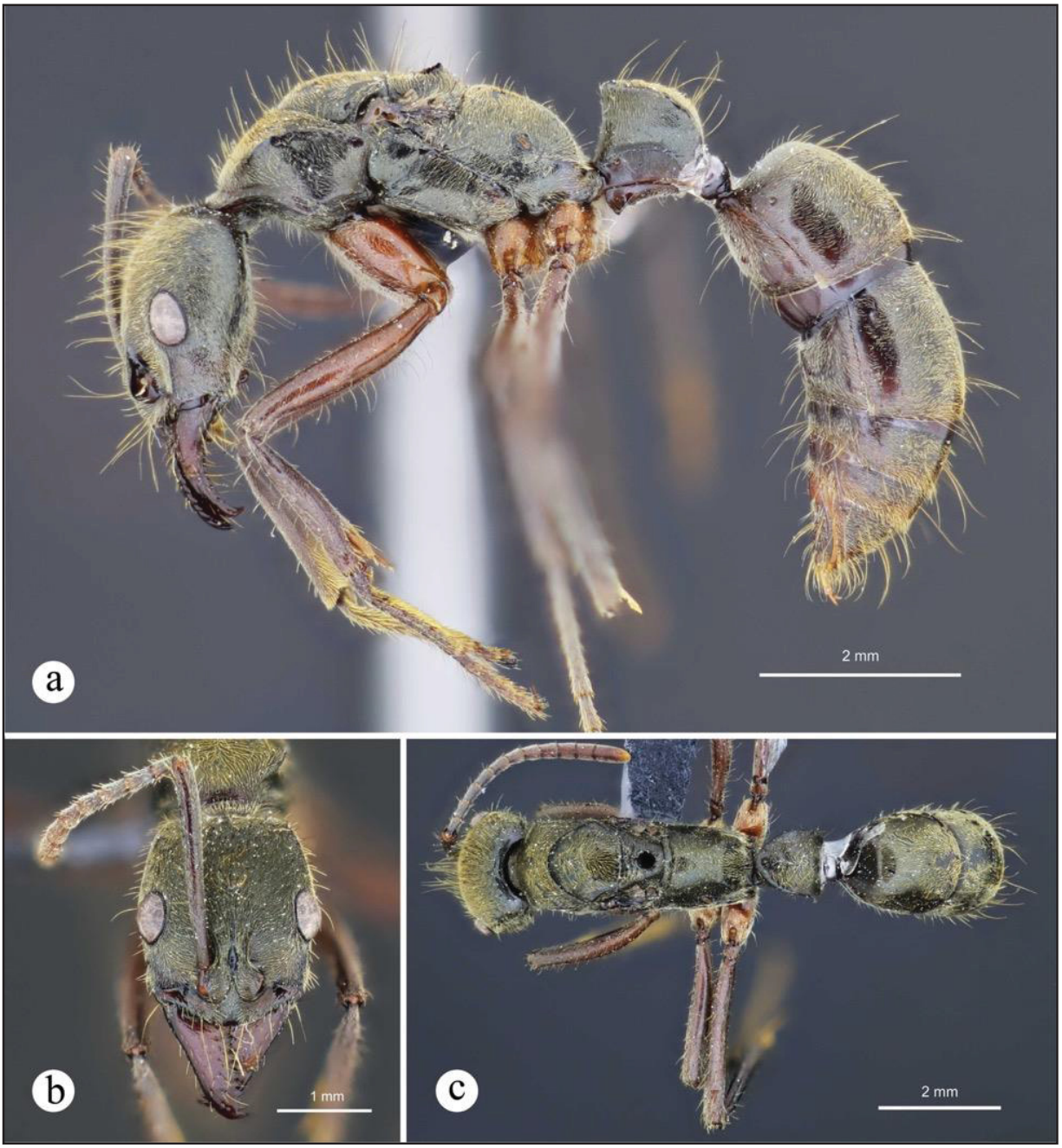


Fig. 17. *Neoponera bugabensis*_var2. ♀ (MUSENUV: HOR0983), Colombia: Valle del Cauca. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Worker. Measurements (*n* = 14): HW: 1.73-2.1; HL: 2.02-2.45; EL: 0.5-0.65; SL: 1.72-2.7; WL: 3.15-3.8; PrW: 1.25-1.55; MsW: 0.76-0.95; MsL: 0.63-0.88; PW: 0.9-1.15; PH: 0.6-1.2; PL: 0.9-1.25; GL: 3.29-4.7; A3L: 1.18-1.5; A4L: 1.23-1.7; A3W: 1.4-1.7; A4W: 1.45-1.75; TLa: 8.49-10.7; TLr: 9.61-11.68. **Indices.** CI: 79.35-88.64; OI: 28.21-34.29; SI: 97.56-131.71; MsI: 105.71-123.33; LPI: 91.67-150.0; DPI: 80.0-111.11.

Queen. Measurements (*n* = 6): HW: 1.84-2.31; HL: 2.23-2.69; EL: 0.59-0.72; SL: 1.98-2.45; WL: 3.65-4.44; PrW: 1.45-1.81; MsW: 1.33-1.69; MsL: 1.3-2.25; PW: 1.04-1.2; PH: 1.02-1.25; PL: 1.1-1.28; GL: 4.2-5.5; A3L: 1.45-1.8; A4L: 1.6-1.95; A3W: 1.61-2.0; A4W: 1.69-2.12; TLa: 10.14-11.91; TLr: 11.21-13.91. **Indices.** CI: 82.0-90.2; OI: 29.27-33.68; SI: 95.65-121.28; MsI: 73.91-111.54; LPI: 97.78-109.52; DPI: 92.68-104.35.

Male. Described by MacKay and Mackay (2010).

Comments. *Neoponera bugabensis* is a medium-sized taxon in the *N. foetida* group (Fig. 12; ☿: TLa = 8.5 – 10.7 mm; ♀TLa: 10.1 – 11.9 mm). Populations of Central America have a cuticle with more intense golden pilosity than those from South America, and are amongst the most brilliant in the genus when light is directed against their body. In a similar fashion to *N. curvinodis*, the examined material of *N. bugabensis* shows relatively large size variation as judged by the variable TLa in workers (Fig. 12). In addition, some body traits also show variations somewhat correlated with geographic distribution making this species one of the most hard-to-diagnose in the genus together with *N. curvinodis*.

Based on the below variations, this species can be categorized under three forms: the first matches the traits of the lectotype from Panama, thus this is the "true" *N. bugabensis* (Figs. 13, 14), and is the most widely distributed form. The other two, which here are called "variant – 1" (Fig. 15), and "variant – 2" (Figs. 16, 17), are more restricted to Costa Rica and to Colombia-Ecuador, respectively. These variants slightly differ from *N. bugabensis* in the form of the head, petiolar node, pilosity and color. Difference in scape length between *N. bugabensis* and its variant – 2 was also noticed, but it was not consistent across all individuals. Despite this, they are not described as new in this work since such traits, except for scape length, show some degree of plasticity in other species of the genus, for example, in *N. crenata* (Roger), *N. curvinodis* (Forel), *N. oberthueri* (Emery), *N. rugosula* Emery. On the other hand, the current specimen-set available for each variant: 5 specimens from Costa Rica belonging to variant – 1, and 5 specimens from

Colombia-Ecuador belonging to variant – 2, is not representative enough to detect a putative case of lineage divergence as judged from a pattern of morphological discontinuities departing from the traits characterizing *N. bugabensis*.

No doubt, this is a "tricky species", it may just be a highly variable form composed of ecotypes which are in process of adaptive speciation, or it may be a multi-species-in-one case for which morphological analysis alone is insufficiently informative. DNA sequencing may aid, but also increasing the specimen-set representing the whole known distribution is required. In *Neoponera*, a similar example occurring in this transitional region, i.e. southern Central America and northern South America, is possibly depicted by the gradation of striae on the petiolar node in *N. mashpi* Troya and Lattke populations: those from Central America show a tenuous nodal sculpture which is more clearly impressed in populations from South America (Troya and Lattke 2022).

The reader may use the following characters to distinguish these two variants from *N. bugabensis*. In parentheses are given the differential traits for the latter.

Variant – 1: 1) Head longer than broad in frontal view (vs. quadrate to subquadrate). 2) Antennal scape, when pulled posterad, exceeding posterior head margin by 2 – 2.5 times apical scape width (vs. 1.5 – 2 times). In a specimen from Valle del Cauca, Colombia (MUSENUV22595) the scape is even longer, exceeding said head margin by ca. 3 times apical scape width. 3) Petiolar node longer than high in lateral view (vs. relatively more symmetric). 4) Most erect hairs on body dorsum longer than maximum eye length (vs. mostly shorter).

Variant – 2. This form is very similar to variant – 1, including the head shape, antennal scape length, and length of erect hairs. The following characters, however, distinguish it from *N. bugabensis*: 1) Appressed pilosity pale yellowish, and that of gastral dorsum not entirely covering the integument (vs. intense golden and usually completely covering gastral integument). 2) Carina of dorsolateral margin of petiolar node relatively acute, somewhat similar to that in *N. insignis* (vs. blunt carina on dorsolateral nodal margin).

Neoponera bugabensis could be confused with the following five species in the *N. foetida* group: *N. insignis* (including the variant "*villosa*_cf2"), *N. lineaticeps*, *N. theresiae*, *N. prasiosomis* sp. nov., *N. villosa*. Of these, arguably *N. insignis* is very close phylogenetically to *N. bugabensis* (Troya et al. unpublished). *Neoponera insignis* and *N. bugabensis* occur in sympatry, at least in

Costa Rica (Longino 2010), and *N. villosa*_cf2 is known from a single specimen from Darien, Panama. According to Longino (2010), and Mackay and Mackay (2010), *N. insignis* is identical to *N. bugabensis*, and these differ in the striae orientation of the mid clypeus: transverse on the former, and longitudinal in the latter. However, among the material examined, three specimens of *N. insignis*, a worker and queen from Parque Nacional Katios, Colombia (LACMENT142417), and a worker from Darién, Panama (JTL9077-1), carry longitudinal striae on the mid clypeus. This is another evidence supporting the hypothesis that clypeal striae are a plastic trait in *Neoponera* and should not be used in species diagnoses. Further evidence is presented under the treatment of *N. curvinodis* (see below), where more examples of clypeal striae variations are brought together for other species in the genus. *Neoponera insignis* is indeed nearly indistinguishable from *N. bugabensis*. The following features are helpful: 1) The head of *N. insignis*, as measured horizontally from eye to eye, is slightly broader than that of *N. bugabensis*, and apparently, as inferred from the few specimens examined ($n = 4$ ☿, 2♀) from Colombia, Costa Rica, and Panama, the eye does not break- but just reaches, or at most feebly exceeds the lateral head margin. In *N. bugabensis* the eye always exceeds such margin. 2) The antennal scape of *N. insignis*, when pulled posterad, exceeds the posterior head margin by one- or at most 1.5 times the apical scape width, while in *N. bugabensis* it always exceeds that margin by 1.5 up to 3 times the apical scape width. 3) The dorsoposterior nodal margin in *N. insignis* is carinate, with the carina relatively acute. In *N. bugabensis* that margin is *usually* blunt, especially in the Central American specimens, but apparently this is not always the case in populations from South America. Two queens from Ecuador, for example, one from Esmeraldas (MEPN38311), a site from the Chocó-Darién, and another from the Amazonian Parque Nacional Yasuní (MEPN34643) show a slightly acute nodal margin, less so however, than in *N. insignis*.

Neoponera lineaticeps is easily distinguishable from *N. bugabensis* just by examining the dorsum of head and the dorsoposterior nodal face which carry well-impressed longitudinal striae, especially those on head (Fig. 4a) which may also be referred as costae since these are thicker than those on the node. These striae (or costae) are absent in *N. bugabensis*.

Neoponera theresiae is distinguished from *N. bugabensis* in: 1) Showing longitudinally divergent striae on the proximal region of the mandibular dorsum (Fig. 6a). *Neoponera bugabensis* also bears striae on such region but these are significantly more attenuated. 2) Well-impressed

striae are also present in *N. theresiae* laterally on the propodeum and petiolar node, as well as longitudinal, and irregularly shaped on the posterior nodal face. The body dorsum, of *N. bugabensis*, on the other hand, is virtually striae-less. 3) The head of *N. insignis* is somewhat circular-shaped rather than subquadrate as in *N. bugabensis*. This latter trait is perhaps the easiest way to separate both forms.

Neoponera prasiosomis sp. nov. has the following differing features as compared to *N. bugabensis*: 1) The eye is large as compared to head length, it represents at least 29% of that measure, while in *N. bugabensis* the eye mostly represents 27% or slightly less. 2) The cuticle of *N. prasiosomis* is greenish (holotype from Panama) or brownish (paratype from Ecuador), while the cuticle of *N. bugabensis* is *usually* black, or rarely castaneous in one specimen from Coclé, Panama (CASENT0632922). 3) Appressed hairs in *N. prasiosomis* are pale yellowish and less abundant, especially on the gastral dorsum, than those in *N. bugabensis* which are bright golden and abundant, so that the gastral cuticle is not easily discernible. 4) *Neoponera prasiosomis* is smaller than *N. bugabensis* (Fig. 12).

Neoponera villosa is larger than *N. bugabensis* (Fig. 12) and has a tumulus on the posterior petiolar node face. This structure is absent in *N. bugabensis*.

Neoponera insignis variant *N. villosa*_cf2 (Fig. 26) differs in the following from *N. bugabensis*: 1) The petiolar node is higher than long in lateral view, while in *N. bugabensis* is approximately symmetric. 2) The head and mesosomal cuticle are violaceous-black (see previous comment above about the cuticle of *N. bugabensis*). 3) The gaster is covered by abundant, relatively opaque, yellow hairs, so that the cuticle is virtually invisible (Fig. 26). Gastral hairs of *N. bugabensis* are golden bright and the cuticle is slightly discernible. 4) This is a small form (TLa = 8 mm), clearly smaller than *N. bugabensis* (TLa: 8.5 – 10.3, Fig. 12).

The elevational range of *N. bugabensis* spans from nearly the sea level, mostly in lowland rain forests, up to about 2300 m in mountainous Andean humid forests. Examined records belong from a number sites in Central America and northwestern South America. Mackay and Mackay (2010) report also a site near Puerto Maldonado, southeastern Peruvian Amazon. *Neoponera bugabensis* has been collected in various ecosystem types, from the Oaxacan montane humid forests near the Gulf of Mexico, to the Talamancan montane, Isthmian Atlantic and Pacific forests

in Central America, to the Colombian and Ecuadorian Chocó-Darien, and the Napo moist forests (Amazonian) Ecuador.

Natural history notes. See Mackay and Mackay (2010) and Longino (2010). From the present material: this arboreal species has been collected mostly in mature, well-preserved forests, using several techniques like fogging, pitfall, arboreal pitfall, and directly by hand, either in daylight or at night, this latter though through insecticidal canopy knockdown.

Material examined. 22☿, 3♀. **COLOMBIA – Nariño:** • 1☿; Altaquér, Reserva Natural Río Ñambí; 1.3, -78.0833; alt. 1351m; 2010-04-08; Flores, E. leg.; hand collected; (MEPN). – **Risaralda:** • 6☿; Puerto de Oro; 5.2995, -75.8869; alt. 1500m; 1991-09-01; Fernández, F. leg.; (ICN). – **Valle del Cauca:** • 1☿; Guandal; 3.893, -77.069; alt. 6m; 1998-02-03; Riascos, Y. leg.; (ICN). • 1☿; Km 18; 3.4, -76.5; (MUSENUV). • 1☿; Vereda Campo Alegre, R. Bravo; 3.8167, -76.5167; alt. 1413m; 1984-02-05; Cepeda, O. leg.; (ICN). **COSTA RICA – Heredia:** • 1☿; 16km SE La Virgen; 10.2682, -84.0842; alt. 500m; 2001-04-11; ALAS leg.; (JTLC). • 1☿; La Selva Biological Station; 10.4333, -84.0167; alt. 50m; 1991-10-15; Longino, J. leg.; (INBC). – **Limón:** • 1☿; Res. Biol. Hitoy Cerere; 9.6531, -83.0229; alt. 650m; 2015-06-11; Longino, J. leg.; (MUCR). **ECUADOR – Esmeraldas:** • 1♀; Reserva Ecológica Mache Chindul, Laguna de Cube; 0.3875, -79.65; alt. 434m; 2016/11; Troya, A. leg.; fogging; (MEPN). – **Orellana:** • 1♀; Parque Nacional Yasuní, Tiputini Biodiversity Station, 288 km SE Quito; -0.6319, -76.1442; alt. 230m; 2002-07-21; Erwin, T.; et al. leg.; fogging; (MEPN). • 2☿; Parque Nacional Yasuní, Tiputini Biodiversity Station, 288 km SE Quito; -0.6167, -76.1333; alt. 240m; 2002-07-21; Erwin, T.; et al. leg.; fogging; (MEPN). – **Pichincha:** • 1☿; Puerto Quito; -0.1, -79.2667; 1984/07; Ponce, P. leg.; (QCAZ). **HONDURAS – Comayagua:** • 1♀; PN Cerro Azul Meámbar; 14.8693, -87.8979; alt. 1170m; 2010-05-22; LLAMA leg.; (JTLC). • 1☿; Parque Nacional Cerro Azul Meámbar; 14.8698, -87.8987; alt. 1120m; 2010-05-20; LLAMA leg.; (JTLC). **MEXICO – Puebla:** • 1☿; 4km WNW Hueytamalco; 19.9567, -97.327; alt. 790m; 2019-06-15; Longino, J. leg.; (JTLC). **NICARAGUA – Chontales:** • 4km NE Cuapa; 12.2888, -85.3535; alt. 850m; 2011-04-20; Longino, J. leg.; hand collected; (JTLC). • 1☿; 4km NE Cuapa; 12.2888, -85.3535; alt. 850m; 2011-04-20; Longino, J. leg.; hand collected; (JTLC). **PANAMA – Chiriqui:** • 1☿; Bugaba; 8.4833, -82.6167; alt. 350m;

Champion leg.; (MHNG). – **Coclé:** • 1☿; 6 km NNW El Copé, Parque Nacional Omar Torrijos; 8.6669, -80.5887; alt. 790m; Longino, J. leg.; hand collected; (JTLC). – **Panamá:** • 1☿; Cerro Azul, Los Altos; 9.22, -79.41; alt. 838m; 1994-05-24; Smith, N.; Kassabian, R. leg.; (UCDC).

Geographic range. Southern Mexico: Puebla, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Southern Peru*. *: Literature record.

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***Neoponera curvinodis* (Forel 1899)**

Figures. 7c (pronotum ☿); 8b, c (petiole ♀); 11a (propodeum♀); 18: a – e (☿); 30b (distribution).

Pachycondyla villosa curvinodis Forel, 1899:15. ☿ syntype, Guatemala, [Quetzaltenango province], Las Mercedes, Torola, Champion [leg.], MHNG [absent from collection]; ☿ syntype, Panama, [Chiriquí province] Bugaba, Volcan de Chiriqui, Champion, [leg.], (MHNG) [absent from collection].

Neoponera bactronica Fernandes et al. 2014: 136. Figs. 1 – 14, 106, 107 (☿, ♂). ☿ holotype, Brazil, Bahia, Ilhéus, CEPEC Genética, PI24 bis Phenotype 2, XI.1998, leg. D. Fresneau, (MZSP) [examined]; 5 ☿, 3 ♂ paratypes: ☿, same data as for the holotype, (INPA: INPA–HYM033260) [examined]; ☿, same data as for the holotype, except: #4905, 17.I.1995, leg. Arouca J., (NHMW) [not examined]; ♂, same data as for the holotype, except: CEPEC#4587, 15.X.1986, leg. P. Terra, (MZSP) [examined]; ♂, same data as for the holotype, except: CEPEC#4587, 23.II.1988, leg. P. Terra, (INPA: INPA–HYM033261) [examined]; ♂, same data as for the holotype, (CPDC) [not examined]; 2 ☿, same data as for the holotype, (CPDC) [not examined]; ☿, same data as for the holotype, except: CEPEC, 6.XI.2007, leg. A.F.R. Carmo & I. C. Nascimento, (MPEG) [not examined]. **Syn. nov.**

Neoponera billemma Fernandes et al. 2014: 140. Figs. 15 – 29 (☿, ♀). ☿ holotype, Brazil, Pará, Benevides, Morelândia, 16.VI.1988, leg. Bittencourt, (MZSP) [examined]; 1 ☿, 2 ♀ paratypes: ☿ Brazil, Goiás, 1980, leg. Kent Redford, #124, (INPA: INPA–HYM033262) [examined]; ♀, same data as preceding, (NHMW) [not examined]; ♀, Brail, São Paulo, Rio Claro, 22.VIII.2000, leg. D. Fresnau, (CPDC) [not examined]. **Syn. nov.**

Neoponera subversa Lucas et al. 2002: 256. Fig. 1c (☿). (*nomen nudum*, unavailable). **Syn. nov.**

☿ **neotype** [present designation], Guatemala, Patulul [information on label hand written by A. Forel] (MHNG: MHNGENTO00097877) [image examined]. Note: material from A. Forel collection at MHNG; misidentified by him as *N. villosa*].

Combinations. In *Neoponera*: Emery, 1901: 47; in *Pachycondyla*: MacKay & MacKay, 2010: 297

Subspecies of *Neoponera villosa*: Forel, 1901: 45.

Status as species. MacKay & MacKay, 2010: 297 [redescription].

Senior synonym of *Neoponera inversa*: Emery, 1911: 73

Worker and queen diagnosis. Head rectangular, longer than broad, lateral head margin moderately straight, posterior head margin concave (Fig. 18a); antennal scape, when pulled posterad, exceeding posterior head margin by two times apical scape width, usually slightly more (Fig. 18b); posterolateral propodeal margin with raised carina, feebly crenulate (Fig. 18a, 11a), posterior propodeal face usually slightly concave dorsally, just in between propodeal carinae; in lateral view, anterior margin of petiolar node straight, inclined posterad, distal portion usually slightly curved anterad (Fig. 8b, 18a); in lateral view, posterior nodal margin convex, meeting anterodorsally with anterior margin in acute angle, ca. 45° (Fig. 8b); anterolateral nodal face usually feebly deflate, this is better discernible on the distal nodal portion (Fig. 8b, 18d).

Worker. Measurements (*n* = 64): HW: 2.12-2.91; HL: 2.38-3.28; EL: 0.56-0.85; SL: 2.44-3.25; WL: 3.94-5.03; PrW: 1.56-2.19; MsW: 1.0-1.44; MsL: 0.75-1.22; PW: 1.12-1.56; PH: 1.25-1.72; PL: 1.08-1.62; GL: 3.69-6.0; A3L: 1.47-2.09; A4L: 1.56-2.16; A3W: 1.81-2.31; A4W: 1.94-2.5; TLa: 10.79-13.91; TLr: 11.5-15.31. **Indices.** CI: 75.56-118.42; OI: 23.92-32.35; SI: 97.78-129.41; MsI: 108.57-140.74; LPI: 83.7-113.08; DPI: 85.42-115.79.

Queen. Measurements (*n* = 16): HW: 2.62-3.12; HL: 2.94-3.44; EL: 0.72-0.91; SL: 2.56-3.25; WL: 4.75-5.56; PrW: 2.0-2.56; MsW: 1.81-2.06; MsL: 1.65-2.62; PW: 1.38-1.75; PH: 1.45-1.88; PL: 1.25-1.69; GL: 4.81-6.69; A3L: 2.0-2.38; A4L: 2.0-2.41; A3W: 2.31-2.69; A4W: 2.44-2.84; TLa: 13.31-15.38; TLr: 13.94-17.12. **Indices.** CI: 88.24-97.87; OI: 24.47-31.82; SI: 93.18-107.14; MsI: 76.54-112.12; LPI: 80.7-98.11; DPI: 83.02-120.0.

Male. Described by Fernandes et al. (2014). The following is added to their diagnosis: notauli not touching posteriorly; shallow to absent anteromedian dorsal groove on propodeum, showing horizontal rugae; propodeum posterolaterally with blunt carina which does not reach dorsum; in lateral view, anterior margin of petiolar node mostly straight (it does not show the typical distally curved projection of workers and queens); lateral nodal margin feebly angulate, but this is hardly discernible since it bears abundant, slightly raised piligerous punctae; abundant yellow subappressed pilosity, most of which is arranged in groups of stacked hairs, like if they were combed; abdominal sternum VII flat to feebly concave, bearing appressed hairs though not abundant.

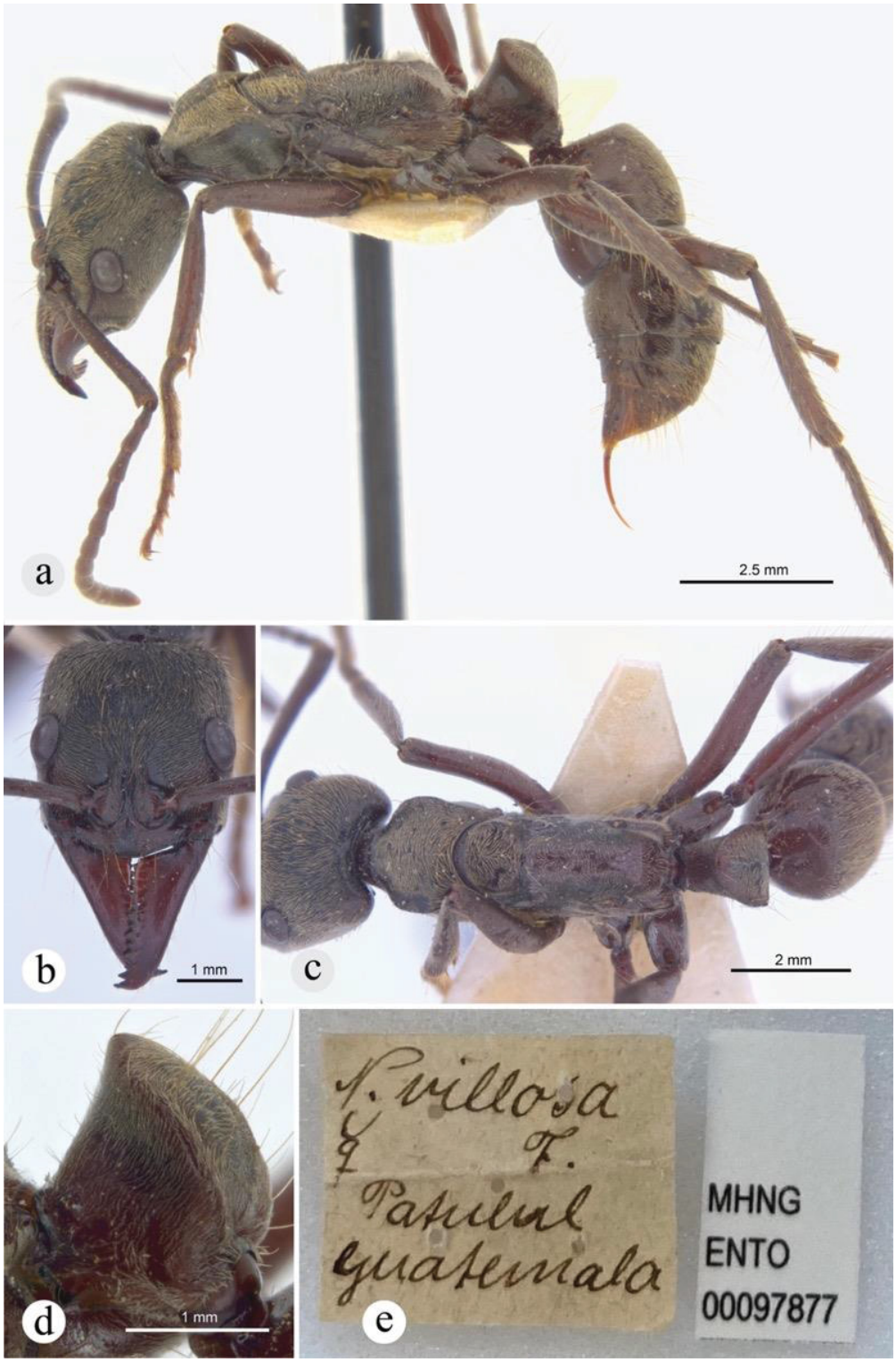


Fig. 18. *Neoponera curvinodis* neotype. ☿ (MHNG: MHNGENTO00097877), Guatemala. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view; **d.** Petiole in anterolateral view; e. Collection labels. Note: A. Forel misidentified this specimen as *N. villosa*. Images by Bernard Landry, MHNG.

Male. Measurements (n = 4): HW: 1.38-1.72; HL: 1.44-1.69; EL: 0.84-0.89; SL: 0.31-0.38; WL: 4.06-4.5; PrW: 1.62-1.75; MsW: 1.84-2.09; MsL: 2.31-2.5; PW: 0.78-0.88; PH: 0.94-1.09; PL: 1.06-1.19; GL: 5.0-5.62; A3L: 1.44-1.72; A4L: 1.56-1.81; A3W: 1.31-1.59; A4W: 1.81-2.0; TLa: 9.69-10.78; TLr: 12.0-12.88. **Indices.** CI: 92.59-105.77; OI: 50.91-61.36; SI: 20.0-22.73; MsI: 74.68-90.54; LPI: 103.03-120.0; DPI: 69.44-82.35.

Comments. *Neoponera curvinodis* is the largest species in the *N. foetida* group (Fig. 12; ☿ TLa = 10.8 – 13.9 mm; ♀TLa = 13.3 – 15.4 mm), and is the second largest in the genus after *N. commutata* Roger. Size variation in the worker caste is relatively large (SD = 0.69), and it is assumed something similar occurs in the queen, but few specimens were gathered and measured so as to reach a more solid conclusion.

Neoponera zuparkoi, *N. villosa*, and in particular *N. inversa* are morphologically most similar to *N. curvinodis* (see comparison further below). Their distinction can be daunting if diagnostic features are not carefully examined. Plasticity is prevalent in both *N. curvinodis* and *N. inversa*. Some variations like the shape and orientation of the mid clypeal striae, or the shape of the humeral carina and of the petiolar node can certainly obscure their taxonomic distinction. For example, the humeral carina can be well-developed and salient (Fig. 7c, 18c), or just feebly emerging from the cuticle.

The following three body regions are considered plastic in both workers and queens in *Neoponera curvinodis*, none of these variations are geographically correlated: the head lateral margin, the carina at the propodeal posterolateral margin, and the anterior margin of the petiolar node. The first two are less variable than the third. As for the lateral head margin, a “moderately straight” form (Fig. 18b) is dominant over a “somewhat curved” form (link). Both variations are usually imperceptible and can be detected only when examining numerous specimens representing a broad geographic range. The propodeal carina, on the other hand, is easier to distinguish, it may be clearly raised with weak crenulae (Fig. 11a, 18a), which is the most common form, or it may be just slightly raised with almost no signs of crenulae (Fig. 11b). The distal region of the anterior nodal margin may be curved anterad (Fig. 8b), or the margin is just slightly concave to straight distally (Fig. 8c). When the first state is present, the anterolateral nodal face is usually deflate. Both forms, concave or straight nodal margin, can be present in specimens obtained from the same collection events, and even from the same nest series (Fig. 8b, c). The degree to which the cuticle

of the petiolar node is deflate or contracted is perhaps the clearest example of plasticity in this species, but also in *N. inversa*. I hypothesize this could be the result of a physiological condition since it is present even among nestmates. I assume it could be due to variations in individual development, maybe linked to factors like diet (Thompson 1999, West-Eberhard 2005). If this hypothesis is further tested and potentially supported, then the question would be ¿Why it is present only in these lineages, i.e., *N. curvinodis* and *N. inversa*, and not in, for example, *N. villosa* and *N. zuparkoi* which are closely related to them? If this is not supported and physiology does not play a role here, another potential explanation would come from evolution itself, by considering instead these changes in morphology, especially on the node, an adaptive response over (unknown) selection pressures of the environment. However, since both species occur in sympatry, especially in several South American regions (Fig. 30b), interspecific gene flow may also play a part here. If this is the case, then populational analyses, using for example maternally-inherited genetic material, would be useful for identifying first-generation hybrids, also called F1. A recent study by Weyna et al. (2022), showed that ultraconserved elements can also be used to unveil hybridization history in non-model organisms. They also found that amongst a number of tested organisms, ants showed the highest number of F1 hybrids, which suggests higher rates of recent hybridization.

Whatever the causes involved for explaining this phenomenon in both species, such phenotypic plasticity likely was the source of confusion while identifying *N. curvinodis* from its very similar congeners, in particular with *N. inversa*. The following features of *N. curvinodis*, in combination with the taxonomic key, make easier their distinction: 1) The lateral head margin is moderately straight, so that the head outline is typically rectangular-shaped (slightly convex in *N. inversa*); 2) The posterolateral propodeal margin usually has a crenulate, raised carina (absent or weakly developed in *N. inversa*); 3) The petiolar node is relatively broad in lateral view: ☿ PL = 1.1 – 1.63 mm, with the dorsoposterior margin meeting with the anterior margin in 45° angle. In *N. inversa* the node is narrower: ☿ PL = 1 – 1.25 mm, with its dorsoposterior margin *usually* meeting with the anterior margin in 30° – 35° angle; 4) The anterolateral distal nodal face is deflate (frequently), or not deflate at all (rarely), while in *N. inversa* is always deflate, so that the nodal top seems more curved anterodorsad than in *N. curvinodis*; 5) *Neoponera curvinodis* is bigger (☿ TLa = 10.8 – 13.9 mm) than *N. inversa* (☿ TLa = 10.2 – 12.2 mm). **Notes**: 1. While identifying

these two taxa it is recommended making a final decision based on these five characters together; 2. Although the range cited for the variables Petiolar Length (PL) and Total Length accurate (TLa) was obtained from a number of specimens and localities in the Neotropics, the reader may expect these limits to fall out of such ranges.

Both *N. curvinodis* and *N. inversa* are distinguishable from *N. villosa* by examining the shape of the petiolar node: In *N. villosa* the anterior margin is vertically straight or nearly so, and the convex dorsoposterior face has a tumulus, better discernible in lateral view (Fig. 2b). This tumulus is absent in *N. curvinodis* and *N. inversa*. Also, the anterior half of the nodal dorsal margin is almost horizontally straight in *N. villosa*, it meets in ca. 90° angle with its anterior margin, and the nodal top is convex, in lateral view. In *N. curvinodis* and *N. inversa* the nodal dorsal margin is always inclined posterad, and the nodal top is relatively acute.

Neoponera curvinodis is also very similar to *N. zuparkoi*, whose nodal shape is virtually identical to that of *N. villosa*, therefore, different from the node of *N. curvinodis*. The humeral carina of *N. zuparkoi* is not salient, while in *N. curvinodis* is either strongly or feebly salient. The anterior mesopleural margin of *N. zuparkoi* has a protruding, anteroventrally directed cuticular lobe. Such region in *N. curvinodis* is only carinate as in all other members of the *N. foetida* group.

Justification for the neotype designation. The primary type material, which should be located in MHNG in Geneve, is absent from collection (Bernard Landry, pers. comm.). Since the worker syntype was collected by Mr. Champion, the other possible repositories for this specimen are the BMNH in London, or the USNM in Washington D.C. Information on this subject was requested to the BMNH and their online collections database was searched. The USNM ant collection was also examined. The type material is not vouchered in those institutions. Brian Fisher's imaging team could not locate this type in other relevant insect collections either. Designation of a neotype is necessary since this form is virtually impossible to distinguish from its highly similar congeners, *N. inversa* and *N. zuparkoi*. The chosen neotype is a worker from Patulul in Guatemala, a site approximately 230 Km west Las Mercedes, the type locality for this species. This specimen was misidentified by Auguste Forel as *N. villosa* (hand written on original label, Fig. 18e), and its morphology matches that of other specimens collected in Costa Rica, which are part of his collection preserved in MHNG, and identified by him as *N. villosa* var. *curvinodis*. The newly designated neotype is well-preserved and potentially suitable for molecular analyses.

***Neoponera bactronica* and *N. billemma* as junior synonyms of *N. curvinodis*.** The morphology of the examined type material of *N. bactronica* and *N. billemma* match the form of the presently designated neotype for *N. curvinodis*. The above shown variable body regions detected in *N. curvinodis* are also present in examined populations of the synonymized forms. Furthermore, the NMDS analysis based on 24 morphometric variables shows that specimens previously identified as *N. bactronica*, *N. billemma*, and *N. curvinodis* share almost all of their morphospace represented in the first two dimensions of the ordination with a strong stress value of 0.0893, thus indicating the observations are not randomly grouped (Fig. 19). These results are statistically supported by the pairwise contrast test which suggests these three forms are not different (*p* adjusted = 1). The global PERMANOVA analysis, on the other hand, rejected the null hypothesis that all observations are equal ($p < 0.000999$, 33% variance explained). This result is coherent with the taxa that share only some of their morphospace, this is, *N. inversa* and *N. villosa*, and does not apply to the other three forms which are grouped under the morphospace of a single species, here considered *N. curvinodis*.

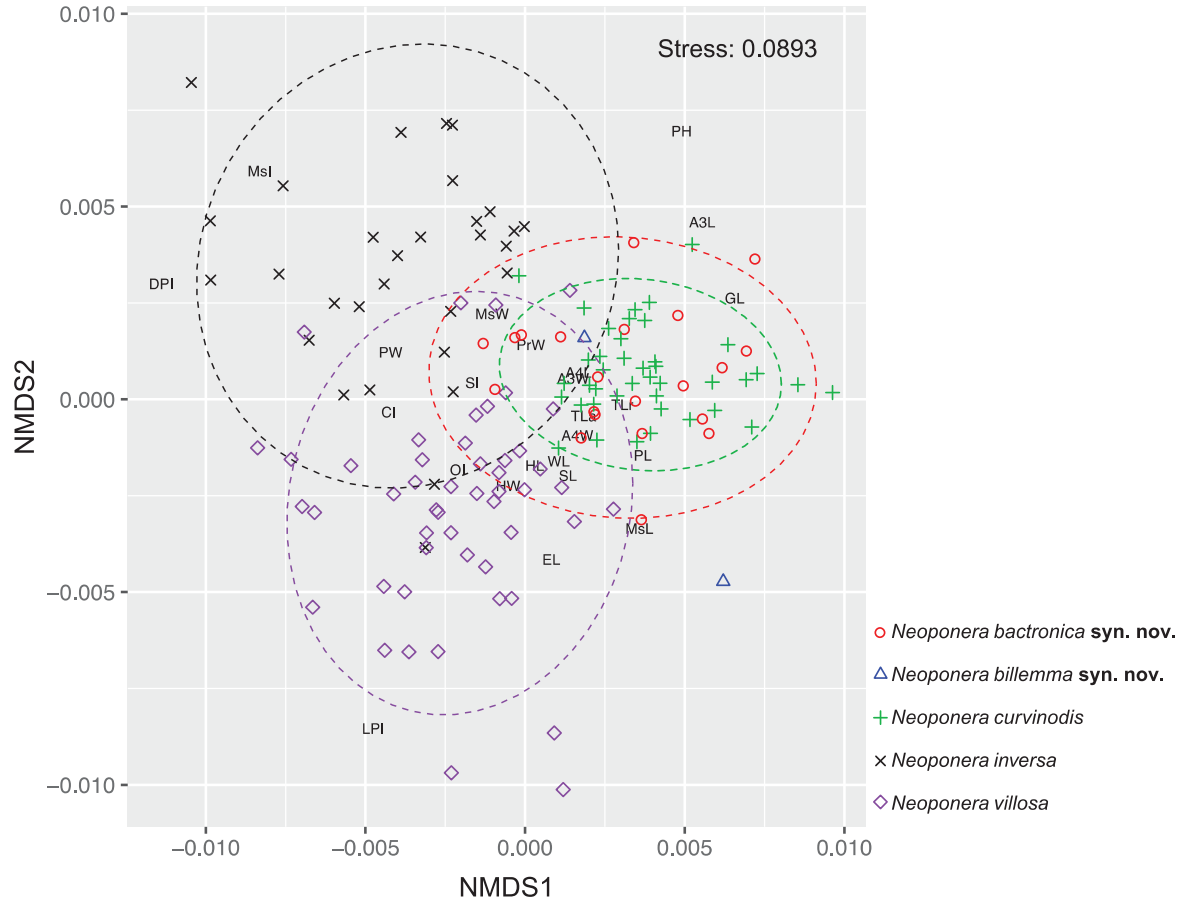


Fig. 19. Non-metric multidimensional scaling (NMDS) representing the distribution of specimens (icons) in the morphospace of some closely related species of the *N. foetida* group, two of which are here considered junior synonyms of *N. curvinodis*. Abbreviated letters represent the 24 morphometric variables involved in the analysis. The closer these are to the observations, the more relevant they are for explaining the observed ordination. Dashed circles represent the 95% confidence intervals.

In addition, the diagnostic characters of both *N. bactronica* and *N. billemma* do not support their specific status. As for *N. bactronica*, the first two characters, namely "head strongly punctate on frontal face; notopropodeal groove strongly marked on dorsum" (Fernandes et al. 2014, pg. 136) are also present in all lineages of the *N. foetida* group. The dorsal punctae on the head are usually shown in combination with striae of differing depth degree. In *Neoponera* this trait is highly homoplastic, thus not useful for species diagnoses in most cases, except for few species in the *N. aenescens* group, like *N. carbonaria* (Smith) where the head dorsum is typically micropunctate. The second trait, the notopropodeal groove, shows little interspecific variation and is considered apomorphic in the *N. foetida* group. This trait is absent in almost all species of the

N. crenata group, its siter clade, and is regained in the remaining *Neoponera* groups (Troya et al. unpublished). The third character "petiole without striae and longer than high in lateral view" (Fernandes et al. 2014, p. 136) is partially informative because the ratio of the nodal length vs its height is not intraspecifically constant. Also, most workers identified as *N. bactronica* have the node slightly higher than long as seen laterally, not longer than high as reported in Fernandes et al. (2014). Similar morphometric measurements were obtained in *N. curvinodis* and *N. inversa*. In *N. villosa*, the opposite pattern is found where the node is slightly longer than high, or rather symmetric. As for *N. billemma*, a pattern is impossible to discern since only two workers are known. However, the node of the paratype is also higher than long.

Current nodal morphometrics of *N. curvinodis*, *N. inversa*, and *N. villosa* match those of Lucas et al. (2002) for their morphospecies "Pvi2", "Pvi1", and "Pvv", respectively. Lucas et al. (2002) believed Pvi2 belonged to a new species and provisionally called it "*Pachycondyla subversa*" (currently *nomen nudum*). Based on Forel's (1899) illustration of *N. curvinodis*, specifically on the measurement of the petiolar node (height and length) and on the shape of the anterior margin, i.e., concave, Mackay and Mackay (2010) inferred that Pvi2 closely matches *N. curvinodis*. This is also supported here since the nodal shape of Pvi2 (Fig. 1c in Lucas et al. 2002) matches that of the neotype of *N. curvinodis*.

Therefore, if Pvi2 represents *N. curvinodis* (and not a new, but distinct species from *N. inversa* according to Mackay and Mackay 2010), then further erection of a new lineage (i.e. *N. bactronica*) was not required. Since *N. curvinodis* and *N. inversa* are so similar, commonly collected, and occur in sympatry in most regions for which I gathered specimens, it is crucial to first examine as much material as possible from their entire range. Examination of the type material is also very important, but also revising historical specimens identified by Forel.

Neoponera billemma, on the other hand, is diagnosed as a species with "Strong transverse striae on the [mid] clypeus; anterior face of petiole lightly striate below and concave" (Fernandes et al. 2014, p. 141). The first trait, the mid clypeal striae, is another plastic feature in *Neoponera*. Among the material thus far examined for the genus, these striae can vary intraspecifically with no detected geographical pattern. Although these striae are usually longitudinal in *Neoponera*, sometimes these are also: horizontal e.g., JTLC: INBIOCRI001281564 from Costa Rica (*N. insignis*); oblique, e.g., CPDC: AT570 from Bahia, Brazil (*N. villosa*); fingerprint-like, e.g.,

CPDC: AT922 from Distrito Federal, Brazil (*N. curvinodis*); mixed: horizontal and longitudinal, e.g., JTLC: CASENT0617097 from Honduras (*N. bugabensis*); or simply smooth, without striae, e.g., JTLC: JTL7597-S from Nicaragua (*N. villosa*). Out of the *N. foetida* group, the horizontally impressed striae also occur in for example, the *N. crenata* group: MZSP: AT511 from Santa Catarina, Brazil (*N. bra164*, undescribed). As for the second trait, "petiolar node lightly striate below", cited as diagnostic for *N. billemma* in Fernandes et al. (2014), many specimens from all species in the *N. foetida* group show them in variable depth degree. Finally, the nodal anterolateral concavity is another plastic feature of *N. curvinodis*, as previously commented.

Phylogenetic evidence. The phylogeny of the genus based on ultraconserved elements recovered with high support (100 % bootstrap) *N. curvinodis*, *N. inversa*, and *N. villosa* as distinct but closely related lineages (Troya et al., unpublished). *Neoponera zuparkoi* and the morphospecies *N.* ecu2923 (see details further below under that species), emerge as sister to *N. inversa*, with low support though. Santos et al. (2018) tested the specific status of the first three species and also included *N. bactronica*. Based on specimens from two regions of the Brazilian Atlantic Forest they sequenced two mitochondrial genes (CO1, 16S) and studied their karyotypes. They concluded these represent four distinct lineages. I agree with them except for *N. bactronica* which is grouped with *N. curvinodis* in the same clade (see their Fig. 2). Nonetheless, they suggested that *N. bactronica* and *N. curvinodis* diverged recently, and proposed further research on this issue. Mendoza-Ramírez et al. (2019) sequenced two mitochondrial genes (CO1, Cyt b) and eight nuclear microsatelites of the above species plus *N. solisi* and *N. bugabensis*. In their phylogeny *N. curvinodis* is sister to *N. bactronica* + *N. villosa* (Fig. 2 in their work). *Neoponera bactronica*, however, was represented by specimens from only two regions: a site in Mato Grosso (Brazil), and another from Colombia. *Neoponera curvinodis* was better represented by four specimens from: Chiapas (Mexico), Guatemala, Honduras, Nicaragua, and two from the same site in Mato Grosso. The authors showed that both *N. bactronica* and *N. curvinodis* have considerably high intraspecific genetic distances, up to 5.1% and 9.5 % for the CO1 and Cyt b, respectively, which is depicted in, for example, the long branch separating the Brazilian specimens from those of Colombia. They brought out two potential causes for this result: 1) A marked mitochondrial genetic structure which has been observed in other broadly ranged lineages, like *Solenopsis saevissima* (Smith), or 2) Each form could represent more than one species. Similarly, in the *Neoponera* phylogeny a *N. curvinodis* specimen (INPAHYM033801-2) from Santa Catarina,

southern Brazil showed a significantly larger branch than its conspecific (DZUP549372) from Sergipe, northeast Brazil. The observed plasticity of this species probably mirrors its high intraspecific genetic distance, in particular between geographically divergent populations.

In this revision I cannot confirm nor deny a multispecies hypothesis to further understand the systematics of *N. curvinodis*. Yet, the present data set does not seem to favor a cryptic status since this taxon is now re-diagnosed, although showing some level of intraspecific variation among the proposed characters. This new diagnosis fits well in the phylogeny of *Neoponera* allowing distinction from its putatively closest species, *N. inversa*, *N. villosa*, and *N. zuparkoi*. Nonetheless, the comparatively high genetic distances observed for this lineage (as represented by the long branches of two of the three sequenced specimens) is something to consider in future research including more specimens from its approximate distribution range. A model to follow is exemplified in Mendoza-Ramírez et al. (2019) for testing the genetic cohesiveness and geographic structure of *N. villosa* populations.

Natural history and distribution notes. See Mackay and Mackay (2010), and Fernandes et al. (2014). From the presently examined material: *Neoponera curvinodis* has been collected during daylight, in a variety of habitats from primary well-preserved, to second-growth, to relatively disturbed forests, using mostly canopy-aimed techniques like fogging, pitfall and arboreal Malaise, and less intensely through CDC, and mercury light trapping, Malaise, beating, sweeping, pan-trapping, Winkler, and hand collecting. Specimens and/or colonies have been found in *Cinnamomum chavarrianum* (Lauraceae), *Miconia cinerascens*, *Clidemia hirta* (Melastomataceae), *Qualea grandiflora* (Vochysiaceae), *Theobroma cacao* (Malvaceae) in agriculture systems, as well as in palms (e.g., *Bactris* spp.) and bromeliads. The elevational record extends from nearly the sea level up to 2300 m, this latter obtained in Cordillera del Cóndor, Ecuador. *Neoponera curvinodis* has been abundantly collected in the Atlantic Forest, and a number of records belong also from most Brazilian biomes except for the Pampa. Outside Brazil, records span from Amazonia, to the Venezuelan Cordillera de la Costa and Formación Lara-Falcón, to the Chocó-Darién and the Pacific and Atlantic lowland forests in Central America.

Material examined. 218☿, 22♀, 15♂. **BRAZIL – Acre:** • 1☿; Senador Guiomard; -10.0667, -67.6167; alt. 214m; 2014-05-31; Denicol, M. R.; Santos, A. M. leg.; arboreal pitfall; (DZUP). – **Amapá:** • 1♀; [no locality given]; 1.0, -52.0; 1978-10-22; Torres, M. leg.; (MPEG). •

1☿; [no locality given]; 1.0, -52.0; 1978-10-21; Torres, M. leg.; (CPDC). – **Amazonas:** • 1☿; Br. 174, Km 44; -2.724, -60.0472; alt. 72m; 1994-11-17; Harada, A. leg.; (INPA). • 1☿; Carabinaui river; -2.5307, -62.1502; alt. 146m; 1995-04-28; Motta; et al. leg.; light trap; (INPA). • 1♂; Liberdade river, Estirão da preta; -7.35, -71.8167; alt. 175m; 2011-05-11; Rafael, J.; et al. leg.; hand collected; (INPA). • 1☿; Manaus; -3.1167, -60.0167; alt. 65m; 1989-02-26; Vogh, R. leg.; (INPA). • 1♀; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9167, -59.9833; alt. 65m; 2010-05-16; Belmont, E. leg.; (INPA). – **Bahia:** • 2☿; 1.5 km E of Guaratinga; -16.5833, -39.7667; alt. 151m; 2002-12-06; Santos, J. R. M. leg.; baiting; (CPDC). • 1☿; 16 km N of Vitoria da Conquista; -15.0333, -49.9; alt. 752m; 2003-07-14; Carmo, J. C. S. leg.; (CPDC). • 1☿; 20 km E of Anadaraí; -12.7508, -41.1669; alt. 323m; 2001-03-16; Santos, J. R. M. leg.; (CPDC). • 1♂; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1986-10-15; Terra, P. leg.; (MZSP). • 1♂; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1988-02-23; Terra, P. leg.; (INPA). • 1♀; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.7659, -39.2159; alt. 53m; 1999-01-28; Delabie, J. H. C. leg.; (CPDC). • 1☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1998-11-01; Fresneau, D. leg.; (MZSP). • 3☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; (CPDC). • 1☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.7659, -39.2159; alt. 53m; 2017-08-01; Carvalho, E.; Queiroz, J. leg.; Malaise; (CPDC). • 1☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.7659, -39.2159; alt. 53m; 2012-05-17; Silva, J. A. leg.; (CPDC). • 1☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1998-11-01; Fresnau, D. leg.; (INPA). • 1☿; Andaraí; -12.8, -41.33; alt. 400m; 1993-01-01; Almeida, C. leg.; (CPDC). • 1☿; Andaraí; -12.758, -41.177; alt. 340m; 2001-03-16; Santos, J. R. M. leg.; (CPDC). • 1♂; Fazenda Bom Jesus; -7.1397, -45.3467; alt. 214m; 1992-04-11; Cardoso, P. leg.; (INPA). • 3☿; Fazenda Bom Jesus; -7.1397, -45.3467; alt. 214m; 1992-02-10; Cardoso, P. leg.; (CPDC). • 2☿; Fazenda Bom Jesus; -7.1397, -45.3467; alt. 214m; 1992-04-11; Cardoso, P. leg.; (INPA). • 3☿; Fazenda Silêncio ; -13.8585, -40.0838; alt. 214m; 1997-12-02; Argolo, J. S. leg.; (CPDC). • 1☿; Ilhéus; -14.7972, -39.035; alt. 23m; 1988-09-27;

Diniz leg.; hand collected; (DZUP). • 1☿; Indaiá; -14.52, -40.37; alt. 790m; 1988-02-04; Santos, J. R. M. leg.; (CPDC). • 1☿; Itabuna; -14.79, -39.28; alt. 60m; 2002-09-01; Santos, J. R. M. leg.; (CPDC). • 1☿; Itapebi; -15.9687, -39.5321; alt. 195m; 1980-04-11; Forbes; Benton leg.; (CPDC). • 1☿; Porto Seguro; -16.4455, -39.0658; alt. 3m; 1998-11-07; (CPDC). • 1☿; Porções; -14.52, -40.36; alt. 770m; 2004-01-25; Mariano, E. leg.; (CPDC). • 1♂; Reserva Biológica do Una; -15.1768, -39.1053; alt. 108m; 2011-11-01; Sena, D. U. leg.; (CPDC). • 1☿; São Domingos, Praia do Norte ; -14.7466, -39.0627; alt. 5m; 1995-05-07; Delabie, J. H. C. leg.; (CPDC). • 1☿; São José, Chapada Diamantina; -11.4408, -39.8778; alt. 392m; 2001-03-22; Santos, J. R. M. leg.; Winkler; (CPDC). – **Distrito Federal:** • 1☿; APA Gama Cabeça de Veado; -15.8667, -47.8333; alt. 1080m; (CPDC). • 1☿; Area de Proteção Ambiental Gama Cabeça de Veado; -15.8667, -47.8333; alt. 1080m; 2000-03-02; Mirelle, P. leg.; (DZUP). • 1☿; Area de Proteção Ambiental Gama Cabeça de Veado; -15.8667, -47.8333; alt. 1080m; 2000-02-01; Mirelle, P. leg.; (CPDC). • 2♀; Brasilia; -15.8261, -47.9207; alt. 1080m; 1976-07-06; Diniz, J. leg.; (DZUP). • 1☿; Brasilia; -15.8261, -47.9207; alt. 1080m; 1976-07-06; Diniz, J. leg.; (DZUP). • 1☿; Fazenda Agua Limpa; -15.9488, -47.9342; alt. 1085m; 2007-05-24; Maravalhas, J. leg.; (CPDC). • 1☿; Parque Nacional de Brasilia; -15.7293, -47.9613; alt. 1120m; 2014-01-18; Sendoya, S. leg.; (DZUP). • 1☿; RECOR IBGE; -15.9163, -47.8672; alt. 1161m; 2017-11-01; Lasmar, C. leg.; pitfall; (DZUP). – **Goiás:** • 1☿; 17 km NE of Jataí, Fazenda Rio Paraíso; -17.7333, -51.6167; alt. 891m; 2011-01-28; Diniz, J. leg.; pan trap; (DZUP). • 1☿; Açude; -17.8587, -51.727; alt. 788m; 2005-08-20; Paniago, G. leg.; (DZUP). • 1♀; Fazenda Luziana; -17.8715, -51.7309; alt. 831m; 2002-05-08; Diniz.; et al. leg.; (DZUP). • 1☿; Fazenda Santa Lucia; -17.0635, -51.6155; alt. 537m; 2008-10-10; Diniz, J. leg.; (DZUP). • 1☿; Goiás; -15.8257, -49.836; 1970-01-01.000001980; Redford, K. leg.; (INPA). • 1☿; Parque Nacional Chapada dos Veadeiros; -14.0388, -47.623; alt. 1287m; 2003-02-01; Ribas, C.; Madureira, M. leg.; arboreal pitfall; (DZUP). • 1♀; Parque Natural Municipal Mata Do Açude; -17.8605, -51.728; alt. 791m; 2005-11-12; Diniz, J. leg.; (DZUP). • 1☿; Parque Natural Municipal Mata Do Açude; -17.8605, -51.728; alt. 791m; 2005-12-21; (DZUP). • 1☿; Pequena Central Hidrelétrica (PCH) de Fazenda velha; -17.9706, -51.7627; alt. 623m; 2009-03-18; pan trap; (DZUP). – **Mato Grosso:** • 1☿; Chapada dos Guimarães; -15.45, -55.7333; alt. 726m; 1983-11-

27; (DZUP). • 1♂; Chapada dos Guimarães; -15.45, -55.7333; alt. 726m; 1983-07-08; (DZUP). • 1♂; Chapada dos Guimarães; -15.3, -55.9333; alt. 257m; 1983-12-04; (DZUP). • 1♀; Colégio Agricultura Buriti, Chapada dos Guimarães; -15.45, -55.7333; alt. 726m; 1982-11-12; Zanuto, M. leg.; (MPEG). • 1♂; Sesc. Pantanal; -16.5083, -56.4161; alt. 135m; 2017-04-01; Lasmar, C. leg.; pitfall; (DZUP). – **Mato Grosso do Sul:** • 1♀; 28 km E of Bataiporã; -22.35, -52.9333; alt. 294m; 2012-12-03; Savaris, M.; Lampert, S. leg.; (DZUP). • 1♂; Dourados Rodovia Itahum Km 2; -22.221, -54.8055; alt. 445m; 2019-07-14; Santos,P.; et al. leg.; (DZUP). – **Minas Gerais:** • 1♂; Boa Esperança; -21.0667, -45.6; alt. 845m; 2014-03-19; Queiroz; et al. leg.; pitfall; (DZUP). • 1♂; Chapada dos Guimarães; -15.3, -55.9333; alt. 308m; 1983-07-04; (DZUP). • 1♂; Fazenda Recife; -16.0167, -41.2667; 1989-07-21; Paiva, R. leg.; (MZSP). • 1♂; Itumirim; -21.2333, -44.8167; alt. 925m; 2014-02-19; Queiroz; et al. leg.; arboreal pitfall; (DZUP). • 1♂; Itumirim; -21.2167, -44.8333; alt. 925m; 2014-02-19; Queiroz; et al. leg.; arboreal pitfall; (DZUP). • 1♂; Itumirim; -21.2167, -44.8333; alt. 885m; 2014-02-19; Queiroz; et al. leg.; arboreal pitfall; (DZUP). • 1♂; Parque Estadual do Rio Preto; -18.1167, -43.3333; alt. 845m; 2017-11-01; Reis, A.; et al. leg.; pitfall; (DZUP). • 1♂; Pq. Floresta do Río Doce; -19.7, -42.7333; alt. 580m; 1989-09-23; Mel, G. A. R. leg.; (DZUP). • 1♀; UFU, Campus Santa Mônica; -19.5167, -52.2667; alt. 870m; 2013-12-23; Bueno, B. leg.; (DZUP). – **Paraná:** • 1♂; 7 km NW of Paranavaí, BR376 km 96; -23.0167, -52.5; alt. 486m; 2019-02-20; Azevedo, F.; Freitas, D. S. leg.; pitfall; (DZUP). • 1♀; Antonina; -25.3, -48.7667; alt. 114m; 2014-03-02; Calixto, J.; Feitosa, R. leg.; (DZUP). • 1♂; Antonina; -25.3, -48.6833; alt. 25m; 2009-09-14; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♀; Antonina centro; -25.4307, -48.7127; alt. 40m; 1966-01-19; Azevedo, M. leg.; (DZUP). • 1♂; Entorno do rio Brumado; -25.3402, -48.885; alt. 397m; 2017-10-18; Pinto, A.; et al. leg.; (DZUP). • 1♂; Foz do Iguaçu; -25.5, -54.5833; alt. 206m; 2000-08-20; Delabie, J. leg.; hand collected; (CPDC). • 1♀; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1984-12-06; Malaise; (DZUP). • 3♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-12-27; Malaise; (DZUP). • 2♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-05-13; Malaise; (DZUP). • 1♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1984-12-10; Malaise; (DZUP). • 1♂; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1984-12-03; Malaise; (DZUP). • 1♂;

Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-05-17; light trap; (DZUP). • 1♀; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-01-21; Malaise; (DZUP). • 1♀; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-02-04; Malaise; (DZUP). • 2♀; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-01-06; Malaise; (DZUP). • 2♀; Instituto Agronômico do Paraná; -25.4, -49.25; alt. 963m; 1985-01-28; Malaise; (DZUP). • 1♀; Morretes; -25.4, -49.25; alt. 963m; 1985-02-25; Malaise; (DZUP). • 1♀; Ourizona; -23.4167, -52.2; alt. 457m; 2005-07-23; Barbosa, A. C. leg.; (DZUP). • 5♀; Parque Nacional Iguaçu, 19 Km SE Foz do Iguaçu; -25.65, -54.4333; alt. 225m; 2017-10-01; Troya, A. leg.; hand collected; (MEPN). • 1♀; Reserva Guaricica, Sede SPVS; -25.3136, -48.6956; alt. 6m; 2019-03-23; (DZUP). • 1♀; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2010-01-14; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♀; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2009-12-09; Donatti, A. J.; Souza, J. M. T. leg.; (DZUP). • 1♀; Reserva Natural Guaricica; -25.3, -48.6833; alt. 25m; 2010-12-12; Souza, J. M. T. leg.; (DZUP). • 1♀; Reserva Natural Guaricica; -25.3, -48.6667; alt. 110m; (DZUP). – **Pará:** • 1♀; Benevides ; -1.35, -48.25; alt. 31m; 1988-06-16; Bittencourt, N. leg.; (MZSP). • 1♀; Fazenda Florentino; -7.1167, -55.3833; alt. 967m; 2010-12-12; Krinsk, D. leg.; pitfall; (DZUP). • 1♀; Floresta Nacional Caxiuanã; -1.7333, -51.45; alt. 21m; 2016-09-29; Silva, R.; et al. leg.; pitfall; (MPEG). – **Pernambuco:** • 1♀; Tapera; -9.3898, -40.5146; alt. 381m; 1929-01-26; Pickel, B. leg.; (INPA). – **Rio de Janeiro:** • 2♀; Ilha Grande; -23.1518, -44.2289; alt. 991m; 2013-11-18; Leponce, M.; Queiroz, J. leg.; (CPDC). • 1♀; [locality not given]; -22.9477, -43.212; alt. 280m; 1927-12-22; Conde, O. leg.; (INPA). – **Rondônia:** • 1♀; Ji-Paraná; -10.88, -61.95; 1984-07-15; Overal, W. leg.; hand collected; (MPEG). • 1♀; Reserva do INPA; -10.7, -62.2; 1985-03-29; Ramos, F. leg.; hand collected; (MPEG). – **Roraima:** • 1♀; Parque Nacional Serra da Mocidade; 1.6, -61.9; alt. 600m; 2016-01-15; Xivier, F.; et al. leg.; (INPA). – **Santa Catarina:** • 1♀; Unidade de Conservação Ambiental Desterro-UCAD; -27.5167, -48.5; alt. 241m; (CPDC). • 1♀; Unidade de Conservação Ambiental Desterro-UCAD; -27.5167, -48.5; alt. 241m; 2005-08-19; Zillikens, A. leg.; (INPA). • 1♀; Unidade de Conservação Ambiental Desterro-UCAD; -27.5833, -48.5333; alt. 22m; 2005-08-19; Schmid, V. leg.; (DZUP). • 3♀; Unidade de Conservação Ambiental Desterro-UCAD; -27.5167, -48.5; alt. 241m; 2005-08-19; Zillikens, A. leg.; (INPA). –

Sergipe: • 1☿; Santa Luzia do Itanhi; -11.4167, -37.4167; alt. 6m; 1993-10-05; Delabie, J. leg.; hand collected; (CPDC). • 1☿; São Cristovão; -10.9, -37.1833; alt. 21m; 1995-01-01; Feneron , R. leg.; (CPDC). • 1♀; UFS; -10.9167, -37.1; alt. 7m; 2015-06-16; Cruz, N. G. leg.; (DZUP). • 1☿; Universidade Federal de Sergipe, Campus São Cristóvão; -10.9264, -37.1026; alt. 9m; Feneron, R. leg.; (CPDC). – **São Paulo:** • 1♀; 33 km SW of José Bonifácio, Rio Tietê; -21.2199, -49.9575; alt. 359m; 1979-09-02; Diniz, J. leg.; (DZUP). • 3☿; Eng. Schmitt; -20.8669, -49.31; alt. 517m; 1970-11-16; Diniz, J. L. M.; Caballero leg.; (DZUP). • 1☿; Estação Ecologica de Itirapina; -22.2144, -47.9234; alt. 770m; 2014-03-06; Sendoya, S. leg.; (DZUP). • 1☿; Fazenda Campininha; -22.2167, -47.1167; alt. 722m; 1977-05-27; (DZUP). • 2☿; Ilha dos pescadores (Ilha da Vitória); -23.75, -45.0; alt. 33m; 1964-03-24; D. Zoologia leg.; (MZSP). • 2☿; Instituto de Biociências, Letras e Ciências Exatas (Ibilce), UNESP; -20.7852, -49.3598; alt. 533m; 1996-10-25; Izzo, T. J. leg.; (DZUP). • 1☿; Iporanga; -24.5859, -48.5945; alt. 96m; 1961-11-01; Lenko, K.; Reichardt leg.; (INPA). • 6♂; Mata de Santa Genebra; -22.8228, -47.1094; alt. 631m; 2009-11-01; Fernandes, I. leg.; (INPA). • 1♀; Mata de Santa Genebra; -22.8228, -47.1094; alt. 631m; 2009-11-01; Fernandes, I. leg.; (INPA). • 61☿; Mata de Santa Genebra; -22.8228, -47.1094; alt. 631m; 2009-11-01; Fernandes, I. leg.; (INPA). • 1☿; Pratânia; -22.7667, -48.7333; alt. 657m; 2015-02-01; Veiga, P. A. S. leg.; (DZUP). • 1♂; Ribeirão preto, Campos da USP; -21.166, -47.8499; alt. 605m; 2019-03-02; Glaser, S. leg.; (DZUP). • 1☿; Sete Barras; -24.3667, -47.9167; alt. 14m; 2004-07-11; Melo, G. leg.; Malaise; (DZUP). • 1☿; Sete Barras; -24.3667, -47.9167; alt. 14m; 2005-03-24; Melo, G. leg.; Malaise; (DZUP). • 2☿; Sete Barras; -24.3667, -47.9167; alt. 14m; 2005-01-08; Melo, G. leg.; Malaise; (DZUP). • 1☿; Severínia; -20.8062, -48.8092; alt. 579m; 1995-09-12; Fowler, H. G. leg.; (CPDC). • 1☿; Sitio Caranda; -22.0861, -48.1274; alt. 663m; 2016-12-01; Oliveira, J. leg.; CDC; (MPEG). • 1♂; UNESP - Campus; -22.397, -47.5478; alt. 628m; 1999-11-01; Fresneau, D. leg.; (CPDC). • 1☿; UNESP - Campus; -22.397, -47.5478; alt. 628m; 1999-11-01; Fresneau, D. leg.; (CPDC). **COLOMBIA – Chocó:** • 3☿; Estación Silvicultura al Bajo Atrato; 7.0406, -77.3378; alt. 149m; 1992-07-01; Mendoza, L. leg.; (MEPN). • 1☿; Estación Silvicultura al Bajo Atrato; 7.0406, -77.3378; alt. 149m; 1994-02-01; Ferro, L. leg.; (ICN). • 1☿; Parque Nacional Natural Los Katios, Centro administrativo Sautatá; 7.85, -77.1335; alt. 96m; 2003-05-

20; Cansia, A. leg.; pitfall; (IAvH). – **Nariño:** • 1☿; Tumaco; 1.7875, -78.7913; alt. 5m; 2015-09-16; (MEPN). – **Valle del Cauca:** • 1☿; Anchicaya ; 3.616, -76.909; alt. 350m; 1970-11-01; (MUSENUV). • 1♀; Bajo Anchicaya ; 3.689, -76.94; alt. 270m; 1983-03-01; Quintero, J. leg.; (MUSENUV). • 2☿; Bajo Anchicaya ; 3.689, -76.94; alt. 270m; 1983-03-01; Quintero, J. leg.; (MUSENUV). • 1♀; Cali; 3.4, -76.5; 1983-02-01; Manzano, M. leg.; (MUSENUV). • 1☿; San Cipriano, Buenaventura; 3.84, -76.898; alt. 80m; 2002-02-28; Gutiérrez, C. leg.; (MUSENUV). • 1☿; San Cipriano, Buenaventura; 3.84, -76.898; alt. 80m; 2002-06-08; Gutiérrez, C. leg.; (MUSENUV). **COSTA RICA – Limon:** • 2☿; Zent, 23 Km WNW Puerto Limón; 10.0167, -83.2667; alt. 21m; 1958-11-01; Lara, F. leg.; (MZSP). – **Puntarenas:** • 1☿; 14 km E Palmar Norte; 8.95, -83.3333; alt. 120m; 1985-08-01; Ward, P. S. leg.; (PSWC). • 1☿; Parque Nacional Corcovado, Sirena Station; 8.533, -83.533; 1992-06-03; McDonald, M. J. leg.; (AMNH). **ECUADOR – Manabi:** • 1☿; Estación Científica Río Palenque; -0.7333, -79.8; alt. 180m; 1980-12-29; Sandoval, S. leg.; (MZSP). – **Napo:** • 1☿; Limoncocha; -0.3998, -76.6001; alt. 280m; 1972-06-30; Kazan, P. leg.; (QCAZ). – **Zamora Chinchipe:** • 2☿; Paquisha alto, Hito 2, 15 Km SE Fruta del Norte, Cordillera del Cóndor; -3.9003, -78.4829; alt. 2325m; 2008-03-15; Troya, A. leg.; fogging; (MEPN). **FRENCH GUIANA – Cayenne:** • 1☿; Base Vie; 5.1667, -52.65; alt. 10m; (CPDC). • 1☿; Montagne dês Chevaux; 4.7333, -52.4333; alt. 75m; 2011-11-19; Team, S. E. A. G. leg.; (DZUP). **NICARAGUA – Región Autónoma del Atlántico Sur:** • 1☿; RN Kahka Creek; 12.671, -83.7175; alt. 30m; 2011-06-06; LLAMA leg.; Malaise; (JTLC). **PANAMA – Colón:** • 2♂; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2003-10-01; Dejean, A.; et al. leg.; (CPDC). • 1♀; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2004-03-08; Pizon, S. leg.; Malaise; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2522, -79.9894; alt. 96m; 2003-10-27; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2004-10-12; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2003-09-01; Schmidl, J. leg.; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2003-10-01; Dejean, A.; et al. leg.; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2004-02-17; Springae, N. D; Pizon, S leg.; Malaise; (CPDC). • 2☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt.

13m; 2003-04-01; (CPDC). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2003-10-05; Kitching, R. leg.; Light trap; (CPDC). **PERU – Cusco:** • 1☿; Quince Mil, km 8; -13.2167, -70.7167; alt. 633m; 2012-08-20; Cavichioli, R.; et al. leg.; Malaise; (DZUP).

Geographic range. Mexico (Chiapas)*, Guatemala, Honduras*, Nicaragua, Costa Rica, Panama, Colombia, Venezuela*, Guyana*, French Guiana, Ecuador, Peru, Bolivia*, Brazil (Acre, Amapá, Bahia, Distrito Federal, Espirito Santo*, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Piauí*, Rio de Janeiro, Rondônia, Roraima, Santa Catarina, São Paulo, Sergipe), Paraguay*, Argentina (Misiones)*. *: record from literature.

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***Neoponera dismarginata* (Mackay & Mackay 2010)**

Figures. 2a (petiole ♀); 20: a – e (☿); 31a (distribution).

Pachycondyla dismarginata MacKay & MacKay, 2010: 301, Figs. 111, 256, 257. ☿ holotype, Costa Rica, Heredia Prov., 16 km. N Vol. (Volcán) Barba, 10°17'N, 84 05'W, 950 m., 4-14.vii.1986, J. Longino (leg.) #1380-S, wet forest, workers on vegetation, (MCZC: MCZ-ENT00036273) [image examined, link]. Paratypes: 3 ☿ [same data as for holotype], (INBC, MCZC, WEMC) [not examined]. Note: Collection data transcribed *ipsis litteris* directly from holotype label.

Combination in *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species: Fernandes et al., 2014: 134.

Worker (and probably queen) diagnosis. Head longer than broad in frontal view; malar carina virtually absent, though a tiny longitudinal swelling combined with well-impressed rugae is present anteriorly (Fig. 20e); antennal scape very long, when pulled posterad exceeding posterior head margin by about four times apical scape width (Fig. 20c); eye relatively small (as compared to head length), distance from anterior eye margin to mandibular insertion slightly longer than maximum eye length (Fig. 20e); clypeus bearing well-impressed, irregular longitudinal striae, mid clypeus convex, relatively acute (Fig. 20c); humeral carina present, slightly acute anteriorly, not salient; mesosternal process highly reduced, stump-shaped; metasternal process well-developed as in all congeners of the *N. foetida* group, dorsally with longitudinal well-impressed striae;

posterolateral propodeal margin convex, not carinate (Fig. 20a); petiolar node subtriangular in lateral view, anterior and posterior margins irregularly straight, posterior face convex, nodal top slightly anterior to vertical midline (Fig. 2a, 20a); lateral nodal carina completely absent (Fig. 2a); subpetiolar process with well-developed, acute cusp and relatively flat dome (Fig. 2a); prora very small, slightly discerned laterally, anteriorly blunt (Fig. 2a); appressed pilosity white-brownish, not abundant and composed of tiny hairs (in contrast to most other congeners of the group where these hairs are longer and abundant); cuticle light castaneous.

Worker. Measurements (n = 3): HW: 2.25-2.3; HL: 2.6-2.85; EL: 0.6-0.72; SL: 3.25-3.3; WL: 4.3-4.5; PrW: 1.5-1.75; MsW: 1.0-1.2; MsL: 0.85-0.95; PW: 1.1-1.15; PH: 1.3-1.4; PL: 1.25-1.3; GL: 4.25-4.9; A3L: 1.5-1.75; A4L: 1.75-1.9; A3W: 1.9-2.05; A4W: 2.0-2.05; TLa: 11.7-11.98; TLr: 12.65-13.2. **Indices.** CI: 80.7-86.54; OI: 26.67-31.09; SI: 141.3-146.67; MsI: 117.65-129.41; LPI: 89.29-100.0; DPI: 88.0-88.46.

Queen and male. Unknown.

Comments. In the *N. foetida* group, *N. dismarginata* is the second largest species after *N. curvinodis* (Fig. 12; ☿ TLa = 11.7 – 12 mm). Since only four specimens were examined, all of them basically equal, no inference about morphological variation is possible for this Costa Rican endemic. Some body features like the long antennal scape, the tiny feebly impressed malar carina, the shape of the node, among others, make this taxon very singular among its congeners in this species-group, but also among species in the genus. Thus, it is unlikely for it to be misidentified with other *Neoponera*. Only *N. apicalis* (Latreille) and *N. obscuricornis* (Emery) show a relatively similar node, but their integument is dull black and the head has large eyes, clearly larger than *N. dismarginata*. Mackay and Mackay (2010) point out that *N. bugabensis* and *N. insignis* show malar carinae which do not reach the anterior eye margin, and because of that they are "placed" with *N. dismarginata*. Nevertheless, the malar carina of the latter is so poorly developed that it hardly would be closely related to those species based just on this single trait. Longino (2010) mentions that the "cheeks" (= malar region) have distinct carinae which reach the anterior eye margin. This is a typo, however, since the image of a specimen (INBIOCRI002278957) shown just above Longino's text depicts otherwise.

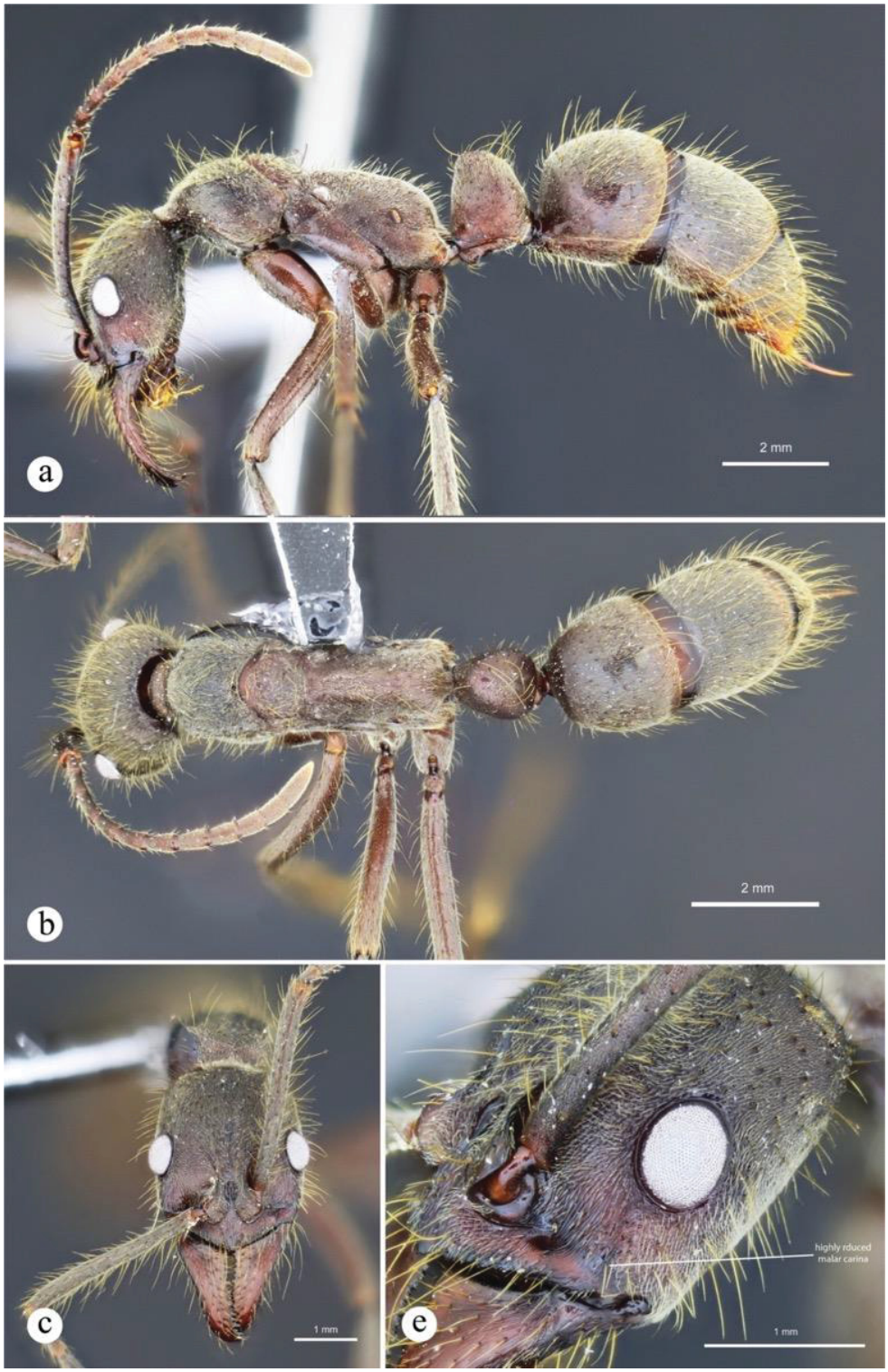


Fig. 20. *Neoponera dismarginata*. ☿ (JTL: JTL9295). **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Close-up of head in anterolateral view.

Neoponera dismarginata is the putative sister lineage of *N. solisi* (Troya et al. unpublished), but it is quite different to it. The petiolar node of *N. solisi* is somewhat block-shaped in lateral view with scarce appressed pubescence and the posterior face is glabrous, while the node of *N. dismarginata* is subtriangular in lateral view and carries relatively abundant appressed pilosity.

Populations of *N. dismarginata* apparently are not rare in Costa Rica from where it has been collected in a number of sites since 1984 up to 2015 according to AntWeb.org. It appears though that this is a true endemic for that region since no other records have been found in several other Central American countries where some sampling campaigns have been carried out (see for example the LLAMA and ADMAC projects led by J. Longino)

Natural history notes. See Longino (2010).

Material examined. 4☿. **COSTA RICA – Heredia:** • 1☿; 16km N Vol. Barba; 10.2833, -84.0833; alt. 950m; 1986-07-09; (MCZC). – **Limón:** • Cerro Platano, 26km WSW Limón; 9.8682, -83.2408; alt. 1140m; 2015-06-16; Longino, J. leg.; hand collected; (MUCR). • 1☿; Cerro Platano, 26km WSW Limón; 9.8682, -83.2408; alt. 1140m; 2015-06-16; Longino, J. leg.; hand collected; (MUCR). – **Puntarenas:** • 2☿; Wilson Botanical Garden, 4km S San Vito; 8.7833, -82.9667; alt. 1200m; 1990-03-22; Longino, J. leg.; (JTLC).

Geographic range. Costa Rica.

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***Neoponera fisheri* (Mackay & Mackay 2010)**

Figures. 1a (head ♀); 21: a – c (♀); 31a (distribution).

Pachycondyla fisheri MacKay & MacKay, 2010: 328, Figs. 30, 32, 34, 278, 279, 293, 451- 454. ☿ holotype, Panama, Colon Prov., Santa Rita Ridge, 9°21'N, 79°47'W, 250 m., 24.iii.189, B.L. Fisher (leg.), rain forest ex *Cecropia hispidissima*, (CASC: CASENT092338) [image examined, link]. Paratypes: 9 ☿, 6♀, 2 ♂, [same data as for holotype], (CASC, GFMP, IAVH, MCZC, USNM, WEMC) [not examined]. Note: Paratype from IAVH absent from collection.

Combination in *Neoponera*: Schmidt & Shattuck, 2014: 151.

Worker and queen diagnosis. Head subtrapezoidal, narrowed anteriorly; masticatory margin of mandible with eight to nine teeth, gradually decreasing in size, denticles absent, except for one proximal (Fig. 21b); eye, especially on workers, less globose than in all other congeners in the *N. foetida* group, and placed slightly anteriorly on head; mid clypeus strongly concave, somewhat like harelip (Fig. 21b); antennal scape, when pulled posterad, fails to reach posterior head margin by about one apical scape width (Fig. 1a, 21b); malar carina present but tiny, feebly protuberant anteriorly (Fig. 1a, 21b); humerus weakly marginate anteriorly, particularly on worker, but a true carina is absent; notopropodeal groove cross ribbed in workers only; mesopleural groove tenuously impressed on workers, and vestigial on queens (Fig. 21a); meso- and metasternal processes well-developed, fang-shaped; in lateral view, petiolar node somewhat block-shaped with broadly curving margin posteriorly in workers (link), and subtriangular in queens, with convex top (Fig. 21a); posterolateral nodal margin lacking carina (Fig. 21a); posterior nodal face glabrous (Fig. 5a); subpetiolar process smooth, lacking horizontal striae, instead bearing one or two longitudinal carinae; pale yellowish appressed pilosity although covering body surface, formed by fine, thin hairs, so that cuticle is clearly discerned.

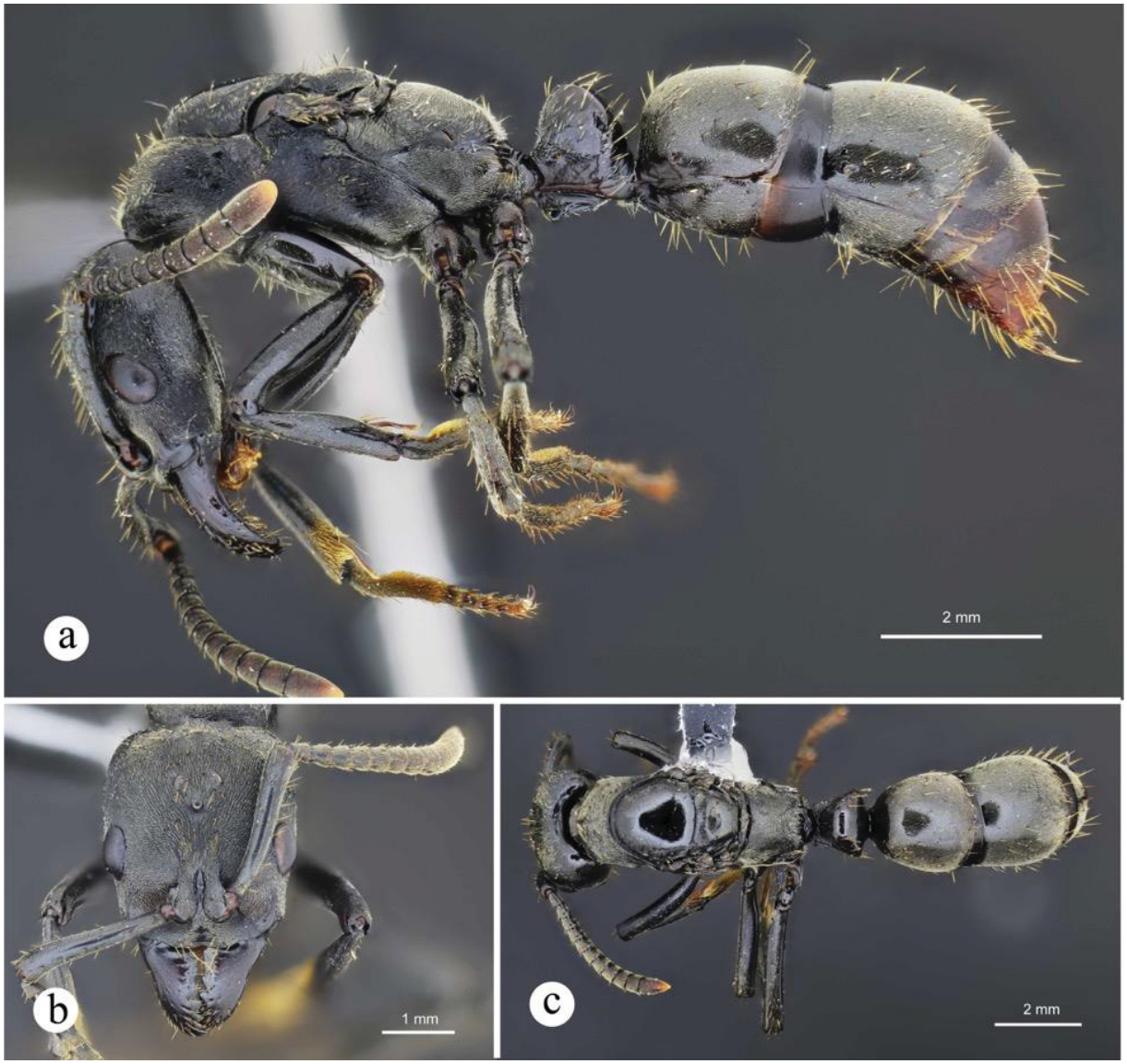


Fig. 21. *Neoponera fisheri*. ♀ (PSWC: CASENT0843089), Panama, Coclé. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Worker. Measurements (*n* = 1): HW: 2.6; HL: 2.75; EL: 0.65; SL: 1.9; WL: 4.25; PrW: 1.6; MsW: 1.3; MsL: 1.1; PW: 1.35; PH: 1.15; PL: 1.2; GL: 5.09; A3L: 1.65; A4L: 1.95; A3W: 1.95; A4W: 2.25; TLa: 11.8; TLr: 13.29. **Indices.** CI: 94.55; OI: 25; SI: 73.08; MsI: 118.18; LPI: 104.35; DPI: 112.5.

Queen. Measurements (*n* = 1): HW: 2.75; HL: 2.85; EL: 0.8; SL: 2.1; WL: 4.55; PrW: 2.2; MsW: 1.2; MsL: 0.8; PW: 1.5; PH: 1.2; PL: 1.2; GL: 5.66; A3L: 2.0; A4L: 2.15; A3W: 2.15;

A4W: 2.5; TLa: 12.75; TLr: 14.26. **Indices.** CI: 96.49; OI: 29.09; SI: 76.36; MsI: 150; LPI: 100; DPI: 125.

Male. Described by Mackay and Mackay (2010).

Comments. *Neoponera fisheri* is a relatively large species in the *N. foetida* group (Fig. 12). Few specimens are known, all of them collected in three sites from Panama (AntWeb.org), their body color varies from castaneous to black. Besides this, the overall morphology seems to be quite similar among the scant material available. Nevertheless, a queen from Coclé (CASENT0843089) shows a mid-clypeal triangular-shaped concavity carrying horizontal striae in frontal view, which is different from the equivalent structure in a worker from Nusagandi (MZSP) where this concavity is subrectangular and lacks striae. In addition, this same worker shows an anterior tiny ocellus (about two times smaller than those of the queen) and two posterior ocellar pits (see below a discussion about this).

Neoponera fisheri is another peculiar species in terms of morphology in the *N. foetida* group. Mackay and Mackay (2010) believed this as a possible link between species in the *N. aenescens* and the *N. foetida* groups. They placed *N. fisheri* in the former although without certainty, and further suggested that it may deserve its own complex. Mackay and Mackay's view about this species was in some way accurate because it is "almost" a link between two species-groups, but these are the *N. crenata* and the *N. foetida* groups. In the phylogeny of the genus, *N. fisheri* is placed at the base of the latter clade, and sister to all species in it (Troya et al., unpublished). From an evolutionary perspective, this placement makes sense since this lineage shares scant traits with its clade partners, namely the shape of head sculpture, and the fang-shaped metasternal process with broad lobes. Of these, only the latter is considered apomorphic between all species in the *N. foetida* group. Nevertheless, even with a well-supported phylogeny at hand I would refrain to suggest that the morphology of *N. fisheri* depicts the ancestral features of the remaining clade members. Whether these unusual features, like the short antennal scapes (unique among species in the genus), the strongly concave mid clypeus, the fused mesopleural plates of the queen, among others, represent ancestral states which have been lost in all other species of the group, or may these traits be independently gained as a function of the environment, for example through adaptive speciation, is a topic which warrants further research.

Out of the *N. foetida* group, another species with unique morphology features (among its clade partners) is *N. luteola* which belongs to the *N. crenata* group. Interestingly, some body regions of both *N. fisheri* and *N. luteola* are similar, like the outline of the head bearing somewhat flat eyes (less globose than in most other *Neoponera* belonging to these two sister clades), the shape and sculpture of the node, and the shape of the mesosoma. Current evidence supports a potential partnership between *Neoponera luteola* and some *Cecropia* plants in South America (Gutiérrez-Valencia et al. 2017). No (sufficient) evidence is still available for *N. fisheri* but it could well represent a similar case since specimens were collected inside *Cecropia* plants in different sites and years in Panama.

Natural history notes. Almost nothing is known about the biology and ecology of *N. fisheri*. The labels of the two examined specimens show that the worker and other nestmates (queen and larva) were collected by Phil Ward in three adjacent internodes of a *Cecropia insignis* (Urticaceae). The other group of individuals, consisting of the type material which was not physically examined here, was collected by Brian Fisher inside a *C. hispidissima*.

In regards to the ocellus observed in the worker from Nusagandi: ocelli-bearing workers is a relatively rare condition in *Neoponera*, but it has been seen in for example, members of the *N. apicalis* (*N. apicalis*, *N. cooki*), and *N. aenescens* groups (*N. aenescens*, *N. carbonaria*), being more frequent in *N. cooki*. Ocelli are usually found in worker ants which show crepuscular and night foraging behavior; these allow them capturing more light in dimly lit conditions (Narendra and Ribi 2017). In contrast to members of the *N. apicalis* and *N. aenescens* groups which are predominantly epigeic, where light incidence on the forest floor is reduced as compared to upper forest strata, most species in the *N. foetida* group, including *N. fisheri*, are arboreal. Apparently, the ocelli in workers of this group are quite rare, and thus far, has not been seen in workers of the arboreal *N. crenata* group, except for few specimens of *N. goeldii* (pers. obs.). *Neoponera goeldii* is arguably a nocturnal arboreal forager (Orivel et al. 2000). Perhaps, some *N. fisheri* workers forage at dawn or during the night, more frequently though than others with different schedule in their foraging behavior. Longino (2010) observed *N. dismarginata* workers in Costa Rica foraging at night. However, ocelli are thus far apparently absent from workers of this latter species.

Material examined. 3☿, 2♀, 1♂. **PANAMA – Coclé: •** 1♀; 6 km NNW El Copé, Parque Nacional Omar Torrijos; 8.6719, -80.595; alt. 840m; 2015-01-22; Ward, P. S. leg.; hand collected;

(PSWC). • 1☿; 6 km NNW El Copé, Parque Nacional Omar Torrijos; 8.6719, -80.595; alt. 840m; 2015-01-22; Ward, P. S. leg.; hand collected; (DZUP). • 6 km NNW El Copé, Parque Nacional Omar Torrijos; 8.6719, -80.595; alt. 840m; 2015-01-22; Ward, P. S. leg.; hand collected; (DZUP). **– Panama:** • 1☿; 42km W of Tupile, Reserva Nusagandi; 9.3489, -78.966; alt. 346m; 1989-10-26; Fisher, B. leg.; hand collected; (MZSP). • 1♂; Puerto Colón, Santa Rita ridge; 9.35, -79.7833; alt. 250m; 1989-03-24; Fisher, B. leg.; hand collected; (UTEP) [image from AntWeb]. • 1♀; Puerto Colón, Santa Rita ridge; 9.35, -79.7833; alt. 250m; 1989-03-24; Fisher, B. leg.; hand collected; (UTEP). • 1☿; Puerto Colón, Santa Rita ridge; 9.35, -79.7833; alt. 250m; 1989-03-24; Fisher, B. leg.; hand collected; (CAS).

Geographic range. Panama.

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***Neoponera foetida* (Linnaeus, 1758)**

Figures. 3a (petiole ☿); 22: a – c (♀); 31b (distribution)

Formica foetida Linnaeus, 1758: 582 ♀ "America meridionali" [no locality given], Rolander [leg.], (ZMLS) [absent from collection].

Combinations. In *Ponera*: Smith, 1858: 95; in *Pachycondyla*: Roger, 1863: 18; Brown, 1995: 305; in *Neoponera*: Emery, 1901: 47; Schmidt & Shattuck, 2014: 151.

Status as species. Linnaeus, 1767: 965; Roger, 1860: 312 [redescription]; MacKay & MacKay, 2010: 332 [redescription].

Neoponera pedunculata Smith, 1858: 96. **Syn. nov.**

Senior synonym of *Neoponera lobata*: Retzius 1783: 75.

Worker and queen diagnosis. Head subrectangular; antennal scapes, when pulled posterad, exceeding posterior head margin by about 1.5 times apical scape width; humeral carina salient, shelf-like (Figs. 7c, 22a); petiolar node block-shaped, with dorsal margin horizontally straight up to about the mid region and immediately broadly curving posterad, anterior margin mostly straight (Figs. 3a, 22a); node covered by usually gross horizontal striae, except by mid ventral region on lateral face (Fig. 3a); prora keel-shaped, tip usually acute, directed ventrad.

Worker. Measurements (*n* = 12): HW: 2.0-2.45; HL: 2.2-2.75; EL: 0.6-0.75; SL: 1.9-2.55; WL: 3.45-4.45; PrW: 1.5-1.9; MsW: 0.8-1.1; MsL: 0.75-0.97; PW: 1.1-1.5; PH: 0.9-1.46; PL: 0.95-1.19; GL: 3.7-4.44; A3L: 1.25-1.75; A4L: 1.35-1.85; A3W: 1.35-2.15; A4W: 1.5-2.2; TLa: 9.2-11.75; TLr: 10.3-12.46. **Indices.** CI: 86.96-98.0; OI: 25.53-35.0; SI: 95.0-107.5; MsI: 94.12-122.22; LPI: 79.4-127.78; DPI: 100.0-136.36.

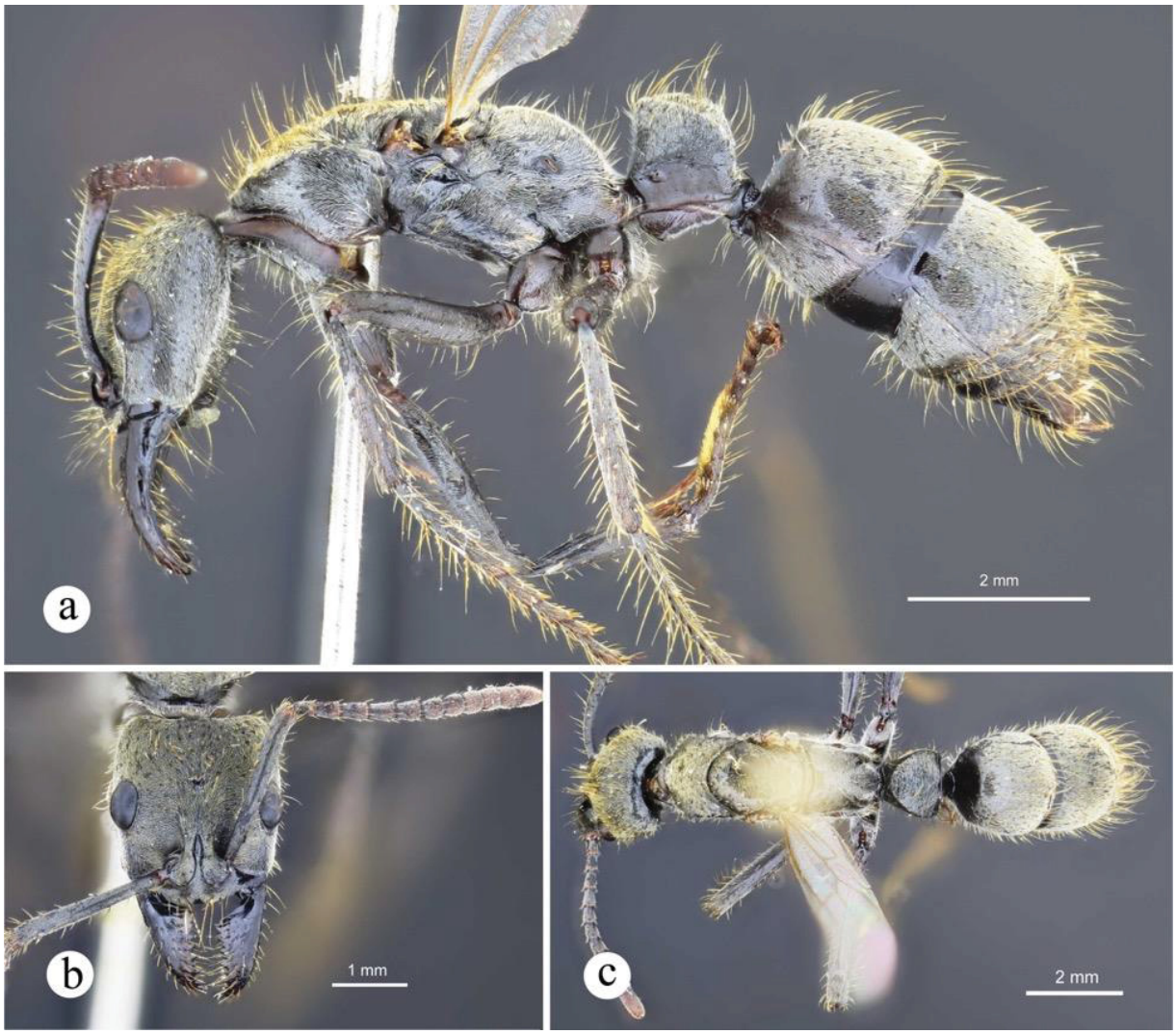


Fig. 22. *Neoponera foetida*. ♀ (MPEG: ATPFOR1848), Brazil, Amazonas. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Queen. Measurements (*n* = 2): HW: 2.2-2.75; HL: 2.45-2.8; EL: 0.6-0.7; SL: 2.25-2.75; WL: 4.25-5.09; PrW: 1.75-2.2; MsW: 1.0-1.65; MsL: 0.7-1.75; PW: 1.4-1.55; PH: 1.15-1.2; PL: 1.25-1.25; GL: 4.3-5.66; A3L: 1.5-1.95; A4L: 1.6-2.2; A3W: 2.1-2.3; A4W: 2.2-2.45; TLa: 11.05-13.29; TLr: 12.25-14.8. **Indices.** CI: 89.8-98.21; OI: 25.45-27.27; SI: 100.0-102.27; MsI: 94.29-142.86; LPI: 104.17-108.7; DPI: 112.0-124.0.

Male. Unknown.

Comments. *Neoponera foetida* is a medium-sized taxon in the *N. foetida* group (Fig 12; (☿ TLa = 9.2 – 11.75 mm; ♀TLa = 11 – 13.29 mm). Because of the coarse striae covering most of the petiolar node, this species is fairly easy to distinguish from all others in the group. Another potentially apomorphic populational trait is the salient humeral carina, which is slightly less protruding in specimens from Central America than those from South America. Other than that, the overall morphology of *N. foetida* is typical of this group, and it shows closer resemblance to the morphology of *N. villosa*, *N. curvinodis*, *N. inversa*, and *N. zuparkoi*, with which it forms a clade (Troya et al., unpublished).

This is the only species in the *N. foetida* group for which, thus far there are no clues about the location of the primary type material for any caste, except for the male which is still unknown. The highest possibility is the ZMLS collection in Sweden, but it has been confirmed it is not there either (pers. comm with ZMLS staff). Roger (1860) redescribed this species based on a queen but this is also apparently lost since it is not vouchered at the MNHU collection. Despite the nodal striae being conspicuous in *N. foetida*, these are almost identically displayed on the node of at least two other *Neoponera*: *N. striatinodis* (Emery) and *N. yasuni* Troya, which belong to the *N. crenata* group. *Neoponera foetida* is today relatively easy to identify, but probably this was not the case in the past due to the scarcity of reference specimens in collections. It is thanks to Roger's (1860) redescription and to De Geer's (1773) illustration of the nodal striae of *N. lobata* (currently senior synonym of *N. foetida*) that this species is now identifiable, and most importantly, diagnosable. For this reason, no attempt is made here to designate a neotype. The reader can use the present diagnosis and taxonomic key to recognize this species. Fernandes et al. (2014), Mackay and Mackay (2010), and AntWeb.org images (link) are also useful resources.

Natural history notes. See Longino (2010), and Mackay and Mackay (2010). Although some of the examined records suggest this species could be adapting to relatively anthropized

environments, for example, grasslands, near pasture zones, and even in major cities, the frequency of these captures is still relatively low. Well-preserved, mature, and second-growd forests seem to host more populations of *N. foetida* than those impacted by humans. This is more apparent in southern Central America, and in northern and central South America. Thus far, the last trace for this species in South America is central Mato Grosso (Fig. 31b). Surprisingly, while writing this manuscript, I noted that the holotype of *N. pedunculata* Smith, 1858, which here is designated as junior synonym of *N. foetida*, is a very old specimen from Rio de Janeiro, Brazil, presumably collected before the 20th Century; this specimen is vouchered at the BMNH collection. According to AntCat.org (2022) there is another, also very old specimen preserved in OXUM, in London, which matches the traits of *N. pedunculata*. However, no collection data is provided on the label of that specimen, only the word "*pedunculata*". Current specimen records of *N. foetida* represented in those directly examined here, which were also validated from AntWeb, and Antmaps, and from other confident literature sources that were used to represent the distribution of this species (see under references and map), suggest that populations of *N. foetida* are no longer encountered in nature in the Atlantic Forest, where they hypothetically used to inhabit in the past. I consulted a number of researchers in ant taxonomy and ecology, most of them Brazilians who have spent years collecting in various regions of the Atlantic Forest. They confirmed being unaware of no recent, nor past collections or sightings of this species in such biome. From any species in *Neoponera*, this could be the first confirmed case for a local extinction in the continent. Future field campaigns in this major Brazilian ecoregion may further inform about this concern.

Material examined. 40☿, 6♀. **BRAZIL – Amazonas:** • 1☿; 5 Km SW Alvarães; -3.2695, -64.823; alt. 70m; 1993-09-23; Gorayeb, I.; Silveira, O. leg.; Malaise; (MPEG). • 1☿; Fazenda Universidade Federal do Amazonas - UFAM; -2.6458, -60.0408; alt. 91m; 2011-08-02; Fernandes, I. leg.; (INPA). • 1♀; Mamirauá; -3.0333, -64.85; alt. 51m; 1993-09-25; Gorayeb, I.; Silveira, O. leg.; arboreal Malaise; (MPEG). • 1☿; Mamirauá; -3.0333, -64.85; alt. 51m; 1994-06-14; Gorayeb, I.; Silveira, O. leg.; arboreal Malaise; (MPEG). – **Mato Grosso:** • 1☿; 65 Km S Sinop; -12.5167, -55.6167; alt. 430m; 1974/10; Alvarenga, M.; Roppa leg.; (MPEG). • 1☿; Sapezal, Fazenda Tupanci; -13.5479, -58.8161; alt. 560m; 2017-12-11; Ferreira, J. leg.; pitfall; (DZUP). – **Pará:** • 1♀; Belém; -1.45, -48.4833; alt. 26m; 1992-01-08; Torres, M. leg.; (MPEG). • 1☿; Cuiú-Cuiú; -5.9167, -56.5667; alt. 160m; 2018-06-18; Siqueira, E. leg.; arboreal pitfall; (MPEG). • 1☿;

Mocambo Reserve; -1.4333, -48.4; alt. 29m; 1977-09-15; Torres, M. leg.; (MPEG). • 1♂; Tucuruí; -3.7655, -49.6702; alt. 35m; 1929-03-02; Overal, W. leg.; (MPEG). • 1♂; Xingu river, right shore; -3.8519, -51.8523; alt. 173m; 2001-03-03; Santos, R.; Dias, J. leg.; (MPEG). • 1♂; Xingu river, right shore; -3.8519, -51.8523; alt. 173m; 2001-03-11; Maciel, C..; Dias, J. leg.; arboreal Malaise; (MPEG). – **Rio de Janeiro:** • 1♂; Constancia; -22.9, -43.2; (BMNH). – **Rondônia:** • 1♀; St. Elena River, left shore; -10.9023, -62.168; alt. 230m; 1985-03-20; Torres, M. leg.; (MPEG). **COLOMBIA** • 1♀; Leticia; 4.2, -69.93; alt. 80m; (ICN). – **Antioquia:** • 1♂; Parque Nacional Natural Las Orquídeas; 6.549, -76.283; alt. 985m; 1976-10-21; Amat, G. leg.; (IAvH). – **Caqueta:** • 1♂; Araracuara; 2.399, -72.282; alt. 140m; 1988-11-15; Fernández, F. leg.; (IAvH). – **Cauca:** • 1♂; Parque Nacional Natural Gorgona; 2.966, -78.183; alt. 30m; 25/5/2001; Duque, R. leg.; (IAvH). • 1♂; Parque Nacional Natural Gorgona, Alto El Mirador; 2.9667, -77.1833; alt. 180m; 2000-03-01; Sharkey, M. leg.; Malaise; (IAvH). – **Valle del Cauca:** • 1♂; Bajo Calima; 3.998, -76.975; alt. 30m; 1996-05-17; hand collected; (MUSENUV). • 1♂; Cali, km 18; 3.4, -76.5; 2003-02-08; Mazo, A. leg.; (MUSENUV). • 1♂; Córdoba, San Cipriano; 3.84, -76.898; alt. 80m; Chacón, P. leg.; (MUSENUV). • 1♂; Guandal, R. Yurumangui; 3.265, -77.12; alt. 6m; 1998-01-28; Riascos, F. leg.; (IAvH). • 1♀; Laguna de Sonso; 3.861, -76.349; alt. 930m; 2000-10-07; Mogollon, J. leg.; (MUSENUV). **ECUADOR – Guayas:** • 1♂; Bosque Protector Cerro Blanco, Quebrada Condor; -2.1333, -80.0833; alt. 223m; 2016/11; Troya, A. leg.; pitfall; (MEPN). • 1♂; Bosque Protector Cerro Blanco, Quebrada Condor; -2.1333, -80.0833; alt. 223m; 2016/11; Troya, A. leg.; fogging; (MEPN). – **Los Rios:** • 1♂; C. R. R. Palenque; -1.432, -79.752; alt. 27m; 1977-03-02; De Vries, T. leg.; (QCAZ). – **Morona Santiago:** • 1♂; Reserva Wisui, Cordillera del Cutucú; -2.1, -77.7333; alt. 657m; 2008-02-28; Simbaña, M. leg.; Malaise; (MEPN). – **Orellana:** • 1♂; Estación Chiruisla; -0.6139, -75.8761; alt. 200m; 2005-09-15; Donoso, D. leg.; fogging; (QCAZ). • 1♂; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-07-03; Erwin, T.; et al. leg.; fogging; (MEPN). • 1♂; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1994-06-21; Erwin, T.; et al. leg.; fogging; (MEPN). **FRENCH GUIANA – Cayenne:** • 2♂; 12km East from the village of Sinnamary. Paracou Station; 5.2667, -52.9167; alt. 50m; 1996/11; Corbara, B.; et al.

leg.; (CPDC). • 1☿; Mont Kaw, Relais de Patawa; 4.55, -52.6667; alt. 300m; 2005/11; Cerda, J. A. leg.; Malaise; (CPDC). – **Saint-Laurent-du-Maroni:** • 1♀; Belvedere de Saul; 3.6167, -53.2; alt. 326m; 2011-05-20; Team, S. E. A. G. leg.; (DZUP). • 1☿; Belvedere de Saul; 3.6167, -53.2; alt. 326m; 2011-10-23; Team, S. E. A. G. leg.; (DZUP). • 1☿; Itoupe, P6; 3.1222, -53.9932; alt. 600m; 2014-11-15; Orivel, J.; Fichaux, M. leg.; Pitfall72h; (EcoFoG). **PANAMA – Colón:** • 1☿; Bosque Protector San Lorenzo; 9.3167, -80.0; alt. 20m; 2005-09-05; (DZUP). • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; (CPDC). • 3☿; Bosque Protector San Lorenzo; 9.283, -79.966; alt. 16m; 2003-10-01; Dejean, A.; et al. leg.; (CPDC). • 2☿; Bosque Protector San Lorenzo; 9.283, -79.966; alt. 16m; 2004-02-28; Springae, N.; Pinzon, S. leg.; Malaise; (CPDC). – **Darién:** • 1☿; 7 km SW Platanilla; 8.7769, -78.4341; alt. 440m; 2015-01-20; Longino, J. leg.; hand collected; (JTLC). **PERU – Loreto:** • 1☿; ACEER Lab; -3.1167, -72.9167; alt. 150m; 1994-08-05; Olson, D. M. leg.; (PSWC).

Geographic range. Costa Rica, Panama, Colombia, Trinidad and Tobago*, Venezuela, Guyana*, Suriname*, French Guiana, Ecuador, Peru*, Brazil: Acre*, Amapá*, Amazonas, Rondônia, Mato Grosso, Pará. *: record from literature.

***Neoponera insignis* (Mackay & Mackay 2010)**

Figures. 10a (petiole ☿); 23: a – d (☿); 24: a – c (♀); 25: a – e (♂); 30a (distribution).

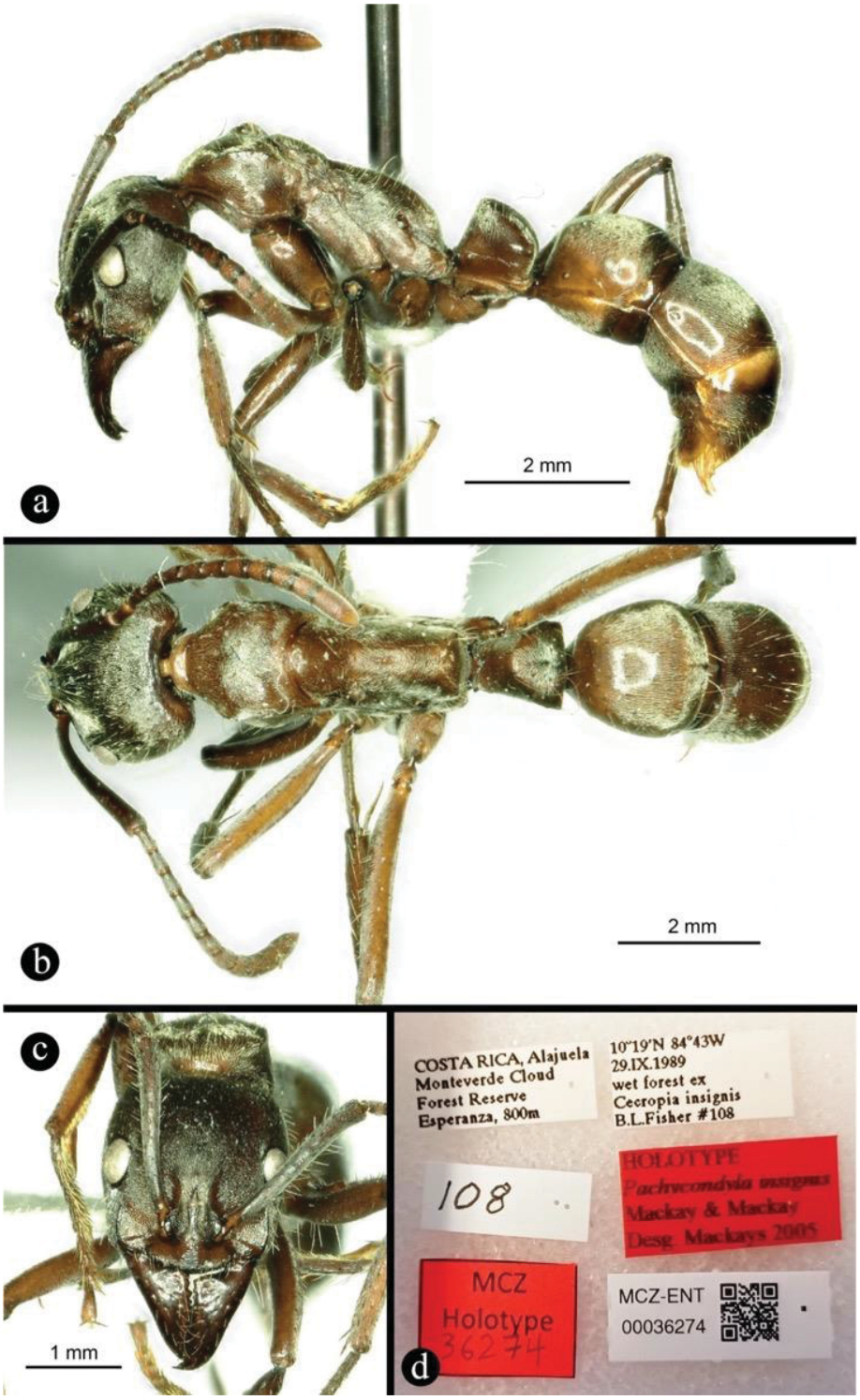


Fig. 23. *Neoponera insignis*. ☿ (MCZC: MCZ-ENT00036274), Costa Rica, Alajuela. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Collection labels. Images credit: Museum of Comparative Zoology, Harvard University, ©President and Fellows of Harvard College.

Pachycondyla insignis MacKay & MacKay, 2010: 405. Figs. 112, 269, 530-532. ☿ holotype, Costa Rica, Alajuela, Monteverde Cloud Forest Reserve, Esperanza, 800 m., 10°19'N, 84°43'W, 29.ix.1989, wet forest, ex *Cecropia insignis*, B.L. Fisher (leg.) # 108, (MCZC: MCZ-ENT00036274) [image examined]; Paratypes: ☿, ♀, [same data as for holotype], (MCZC, WEMC) [not examined].

Combination in *Neoponera*: Schmidt & Shattuck: 151

Status as species: Fernandes et al., 2014: 135.

Worker and queen diagnosis. Head subquadrate, sometimes slightly broadened at mid length in frontal view; eye slightly exceeding lateral head margin, sometimes just reaching it (Fig. 23c); antennal scape, when pulled posterad, exceeding posterior head margin by about one apical scape width (Figs. 9b, 23c); humeral carina weakly salient; posterolateral margin of petiolar node broadly convex and carinate, dorsal margin meeting with anterior margin in 80° angle approximately (Figs. 10a, 23a, 24a); subpetiolar process with acute cusp and inclined dome, the latter sometimes with acute longitudinal carina and feebly impressed longitudinal striae laterally (Figs. 10a, 24a), instead of the usually horizontal; anterior margin straight to slightly concave (Figs. 10a, 23a, 24a).

Worker. Measurements (*n* = 3): HW: 2.0-2.05; HL: 2.2-2.35; EL: 0.55-0.6; SL: 1.75-2.05; WL: 3.5-3.65; PrW: 1.4-1.5; MsW: 0.9-1.0; MsL: 0.75-0.85; PW: 1.1-1.15; PH: 0.7-1.0; PL: 0.9-0.95; GL: 4.2-4.55; A3L: 1.25-1.5; A4L: 1.4-1.6; A3W: 1.55-1.65; A4W: 1.65-1.75; TLa: 9.25-9.95; TLr: 10.8-11.5. **Indices.** CI: 85.11-90.91; OI: 27.5-29.27; SI: 87.5-100.0; MsI: 105.88-133.33; LPI: 94.74-135.71; DPI: 115.79-122.22.

Queen. Measurements (*n* = 2): HW: 2.2-2.2; HL: 2.35-2.4; EL: 0.55-0.6; SL: 1.95-1.95; WL: 3.95-3.95; PrW: 1.6-1.75; MsW: 1.3-1.65; MsL: 0.75-1.35; PW: 1.25-1.25; PH: 1.0-1.0; PL: 1.0-1.0; GL: 4.05-4.75; A3L: 1.7-1.85; A4L: 1.75-1.95; A3W: 1.5-1.95; A4W: 1.8-2.0; TLa: 10.75-11.15; TLr: 11.4-12.05. **Indices.** CI: 91.67-93.62; OI: 25.0-27.27; SI: 88.64-88.64; MsI: 122.22-173.33; LPI: 100.0-100.0; DPI: 125.0-125.0.

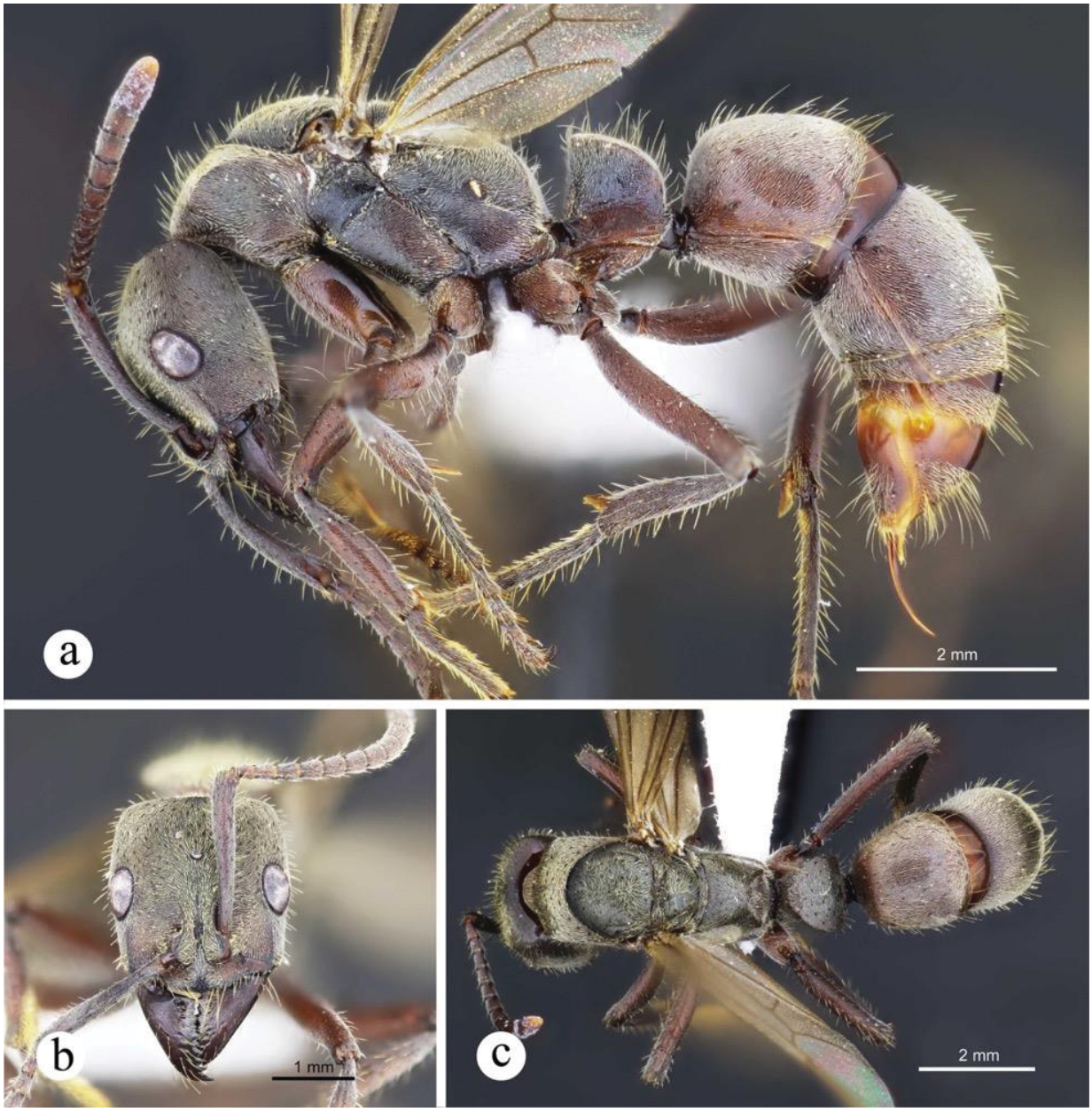


Fig. 24. *Neoponera insignis*. ♀ (JTLC: LACM-ENT142417), Colombia, Chocó. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

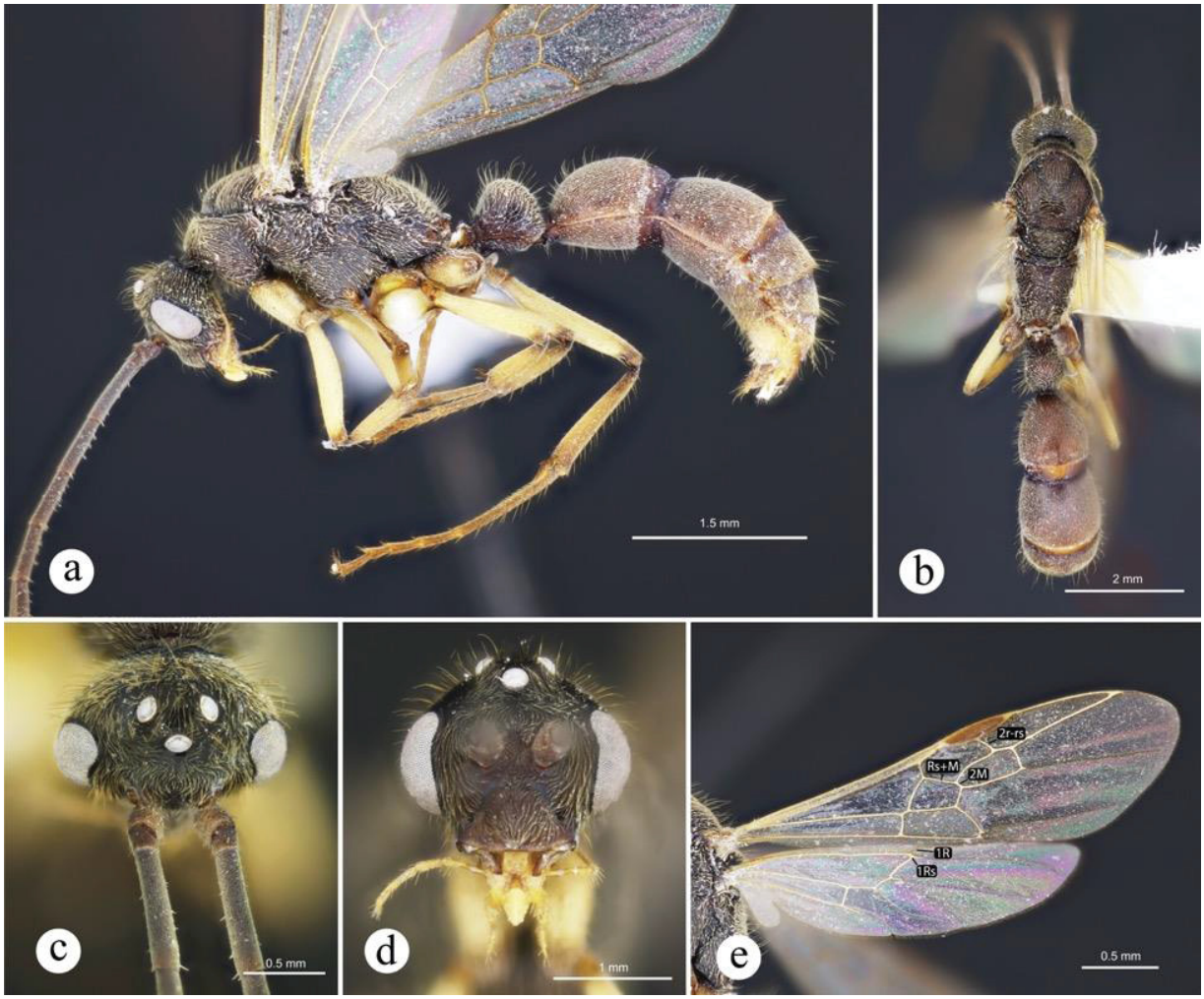


Fig. 25. *Neoponera insignis*. ♂ (JTLC: INBIOCRI002278907), Costa Rica, Alajuela. **a.** Lateral view; **b.** Dorsal view; Ocelli in dorsal view; **d.** Head in frontal view; **e.** Fore and hind wings.

Male diagnosis. Notauli well-impressed, not touching posteriorly (Fig. 25b); mesopleural sulcus well-impressed, cross ribbed; metanotum without tumulus or carina; in lateral view, petiolar node slightly longer than high, lacking posterolateral carina (Fig. 25a); hind wing bearing 10-12 notauli.

Male (first description). Measurements (n = 2): HW: 1.25-1.25; HL: 1.3-1.35; EL: 0.7-0.75; SL: 0.2-0.25; WL: 3.15-3.5; PrW: 1.35-1.4; MsW: 0.85-0.9; MsL: 0.65-0.65; PW: 0.7-0.7; PH: 0.5-0.65; PL: 0.8-0.85; GL: 3.75-3.8; A3L: 1.1-1.15; A4L: 1.25-1.3; A3W: 1.15-1.25; A4W: 1.15-1.5; TLa: 7.75-8.0; TLr: 9.05-9.45. **Indices.** CI: 92.59-96.15; OI: 56.0-60.0; SI: 16.0-20.0; MsI: 130.77-138.46; LPI: 130.77-160.0; DPI: 82.35-87.5.

Head. *Frontal view*: subrhomboid. Mandible spatulate, longer than wide, blunt apically. About two mandalus (maximum length) fit on mandibular dorsum, mandibular apex, when mandible is closed, barely touches lateral margin of labrum. Prementum with well-developed dome placed proximally. Palp formula: 6,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially straight to slightly concave, somewhat globular-shaped in lateral view, covering anteclypeus. Area between posterior margin of clypeus and supraclypeal area weakly concave. Posterior supraclypeal area round. Supraclypeal area slightly protruding from cuticule. Distance between internal margins of antennal sockets approximately one socket diameter. Torular lobe strongly reduced. Eye suboval, slightly notched in the dorsal third, maximum length slightly less than half head length, convex, globose, placed at cephalic mid-length. Ocellar area not protruding from cuticle. Ocellar area placed slightly posterad to vertex. Anterior ocellus maximum length subequal to that of posterior ocelli. Ocelli not equidistant to each other, distance between anterior ocellus to posterior ocelli slightly shorter than interposterior ocellar distance. Distance from posterior ocellar margin to posterior margin of head roughly one apical scape width. Distance between anterior and posterior ocelli about one anterior ocellus maximum length. Occipital carina present, well-developed. Scape subquadrate, about twice as long as pedicel. Length of first flagellomere longer than second flagellomere. **Mesosoma**. *Lateral view*: Dorsal margin convex. Pronotum lacking humeral carina, completely rounded. Anterior subalar area approximately as broad as tegular maximum width. Anapleural sulcus well-developed, running laterally only on mesopleuron, not reaching ventral mesopleural region. Metanotal trough deeply impressed. Metapleuropropodeal suture relatively shallow. Posterolateral margin of propodeal declivity with feeble, blunt carina, without crenulae. Anterolateral propodeal corner rounded. Propodeal spiracle slit-shaped. Posteroventral cuticular flap at metapleural gland opening reduced, weakly projecting dorsad, gland orifice completely discernible laterally. *Dorsal view*: mesoscutum about as long as broad, slightly more than two times length of mesoscutellum. Mesoscutum anterior triangular impression present, strongly impressed. Parapsidal lines evident, slightly divergent. Notauli present, strongly impressed, weakly cross ribbed, not meeting posteriorly, but close to do so, not extending to transscutal line. Transscutal sulcus well-developed. Scutoscutellar sulcus present, straight, strongly impressed, cross ribbed, not completely separating mesoscutum from mesoscutellum. Mesoscutellum subtrapezoid, domed. Metascutellum well-developed, clearly discernible dorsally, surface with slightly salient longitudinal carina.

Anterodorsal median propodeal sulcus present or absent, when present weakly impressed. Posterior face of propodeal declivity feebly convex. Propodeal lateral margins subparallel, not converging dorsomedially. *Ventral view*: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process well-developed, tooth-shaped, internal margins of lobes convergent, relatively flattened anteroposteriorly, space between lobes approximately equal to width of each. Metasternal process well-developed, triangular-shaped, flattened anteroposteriorly, apex shorter than half height of metacoxal internal margin, space between lobes narrower than width of each, internal margins running parallel. **Wings**. Hyaline. Weakly infuscated. Forewing venation Ogata type Ia: submarginal cells 1, 2 and discoidal present, vein 2M present, reduced, 2r-rs offset from Rs+m, Rs+M ca. three times longer than 2M, setose layer evenly covering surface. Hindwing venation Cantone and Von Zuben Type I: basal and subbasal cells and vein 2M present, 1R well-developed, 1Rs poorly developed. Jugal lobe present. Hindwing bearing 10–12 hamuli. **Legs**. Mesofemur slightly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora flattened roughly on distad half, surface even without groove. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur half-length of posterior spur. Pretarsal claw arched, with well-developed median tooth. Arolium present, roughly 0.5 times length of pretarsal claw. **Petiole**. *Lateral view*: Petiolar node anterior margin straight, inclined ca. 30° posterad; posterior margin straight, inclined ca. 30° anterad, anterior and posterior margins reaching approximately same level dorsally, middorsal margin convex, highest point at nodal longitudinal midline, posterior face slightly convex. Subpetiolar process subtriangular, with blunt, keel-shaped, grooved anterior cusp, followed posteriorly by relatively flat region bordered by longitudinal carinae, mostly smooth, with two weakly raised longitudinal carinae medially. Lateral projection of anteroventral nodal carina well-developed, with blunt tip feebly projecting dorsad. Lateral nodal carina vestigial. Anteroventral nodal carina incomplete, strongly concave medially. **Gaster**. *Lateral view*: Prora well-developed, with blunt tip projecting anteroventrad; posterior region slightly flattened and broadened. Anterior margin of tergum of A3 convex. Cinctus moderate. *Dorsal view*: Tergum of A3 equal in length to A4. Abdominal sternum 7 with concave surface, bearing scattered erect and suberect hairs. Spine at posterior margin of tergum of A8 well-developed, tip not surpassing posterior magin of sternum of A9, acute, slightly flattened laterally. Sternum of A9 longer than broad, posterior margin convex. Pygostyles present, about three times longer than broad. **Color**.

Mandibles and legs yellowish brownish or dark brown, antennae ferruginous brown. **Pilosity**. Body with moderately abundant, flexuous, golden to dark golden, erect and suberect hairs. Appressed pubescence abundant. Meso- and metatarsi bearing scant spine-like setate and abundant finer setae. **Sculpture**. Integument polished, with abundant, shallowly impressed piligerous punctures. Striae on head absent, mesosoma lacking striae, except for axilar areas and few feebly impressed anterolaterally on propodeum. Striae on petiolar node absent.

Comments. *Neoponera insignis* is a relatively small to medium-sized species in the *N. foetida* group (Fig. 12, ☿ TLa = 9.20 – 9.95 mm; ♀: 10.75 – 11.15 mm). Since only few workers and queens were here examined (n = 6), no profound inferences are possible in regards to morphology variations across its range. Nevertheless, specimens from Alajuela, Costa Rica (northernmost range) differ little from those of Chocó, Colombia (southernmost range) in the form of the petiolar node: the anterior margin is slightly concave in a queen from the latter site, while in those from Costa Rica the margin is straight.

Mackay and Mackay (2010) and Longino (2010) noted that *N. insignis* is essentially identical to *N. bugabensis*. They claimed that transverse clypeal striae of *N. insignis* differentiate it from *N. bugabensis* where this sculpture is longitudinal or absent. However, the clypeal striae are a plastic feature, sometimes transverse or horizontal, and sometimes longitudinal in this species (see also comments on *Neoponera* clypeal striae under *N. curvinodis*). Nonetheless, I certainly agree with Longino and Mackay and Mackay in considering both species morphologically identical. These two forms live in sympatry in Central America, use similar resources for housing their nests on the canopy (although Longino 2010 note that *N. bugabensis* is a general forager and opportunistic nester), and are closely related according to recent phylogenomic evidence (Troya et al., unpublished). It would be no surprise one lineage diverged from the other very recently.

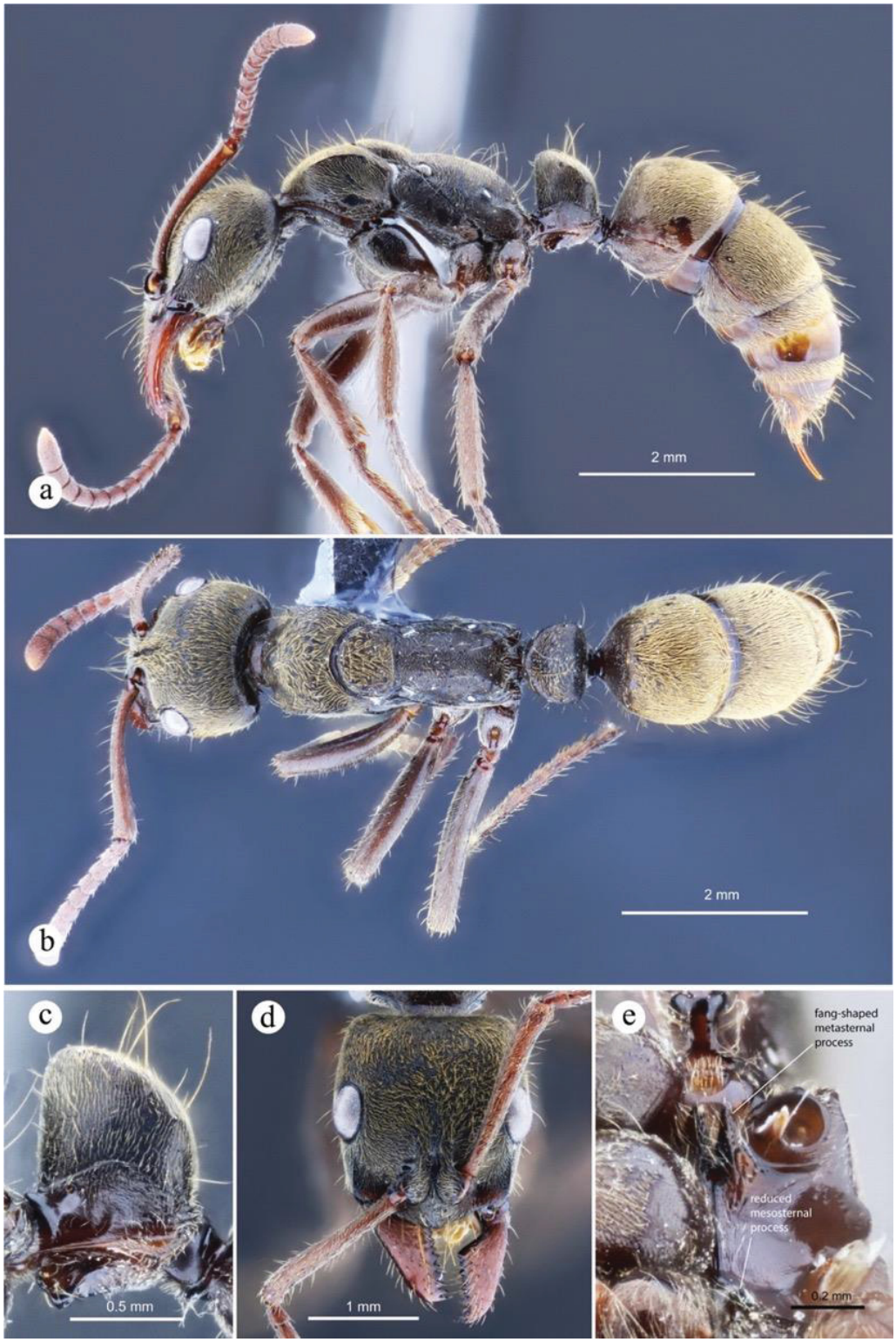


Fig. 26. *Neoponera insignis* (variant, referred in text as *N. villosa*_cf2). ☿ (PSWC: CASENT0249167), Panama, Darién. **a.** Lateral view; **b.** Dorsal view; **c.** Petiole in lateral view; **d.** Head in frontal view; **e.** Mesosternum in anteroventral view, showing the fang-shaped metasternal process, and the right lobe of the mesosternal process.

As hypothesized by Longino (2010), who observed the behavior of *N. insignis* in Costa Rica, it could have evolved through sympatric speciation from *N. bugabensis*, *N. villosa* or some ancestral version of them. Note that Longino also considered *N. villosa* highly similar to *N. insignis*, but these two species are easily distinguished from each other since *N. villosa* is larger and bears a tumulus on the posterior nodal face, which is absent in *N. insignis*. The reader may use the traits commented previously under the treatment of *N. bugabensis* to separate both species.

Neoponera insignis is also similar to *N. lineaticeps*, *N. theresiae*, *N. prasiosomis* sp. nov., and the morphospecies *N. villosa*_cf2 (see notes below about this latter). Some differing traits between these species and *N. bugabensis* were previously referred. These traits also apply to *N. insignis* since this is virtually identical to *N. bugabensis*.

Previously considered a Costa Rican endemic (Longino 2010, Mackay and Mackay 2010), now it is known that *N. insignis* reaches the northern lowland rain forests of the Colombian Chocó-Darién, and since many *Cecropia* ant-plants reach further southern regions in the continent as for example, Ecuador, Peru, Brazil, it is likely this species be found there in future sampling events. Due to its high similarity with *N. bugabensis*, which has been found as far south to Peru, is also plausible that a proportion of specimens cited in the literature are misidentifications.

Neoponera villosa*_cf2 as variant of *N. insignis. The only known specimen of *N. villosa*_cf2, a worker, is sister to *N. insignis* and these two forms are closely related to *N. bugabensis* and *N. prasiosomis* sp. nov. (Troya et al., unpublished). *Neoponera villosa*_cf2 is very similar to *N. insignis* except for: 1) The petiolar node is shorter (PL = 0.75 mm vs. 0.9 – 1 mm), and the posterolateral nodal margin is less convex than in *N. insignis*, but relatively straight and more inclined, it meets the anterior margin in 50° – 60° angle vs. 70° – 80° angle in *N. insignis*; 2) The gastral dorsum carries more appressed hairs than in *N. insignis* so that the cuticle is poorly discernible, while in *N insignis* is always discernible; 3) It is smaller (TLa = 8 mm vs. 9.2 – 9 mm). At first sight, *N. villosa*_cf2 is easily distinguished from *N. insignis* just by looking at its yellowish, pilose gaster. This latter feature, together with the nodal shape and comparatively small body size would suffice to consider two hypothetical different lineages. Nonetheless, this case is similar to that between *N. lineaticeps* and its variant from Guatemala which, despite showing clear variations on the nodal sculpture, it seems that variant belongs to a *N. lineaticeps* population under ongoing differentiation since it shows a relatively short branch in the genus phylogeny (Troya et al.,

unpublished; see further comments under that species). I am here inclined to support the same hypothesis for *N. insignis* and *N. villosa*_cf2 since a similar picture is depicted in the phylogeny, both being sister and showing short branches. *Neoponera villosa*_cf2 apparently would still belong to an *N. insignis* population which is already showing signs of morphological differentiation. This specimen was collected by D. M. Olson in the southern side of the Panamanian Darién National Park; this collection site is ca. 50 km west from another collection site in the Colombian Katios National Park, where M. Aide found a worker and queen of *N. insignis* (JTLC: LACMENT142417).

Overall body size is subject to variation across all lineages in *Neoponera*, so the differences cited between both forms may not count as determinant traits for proposing *N. villosa*_cf2 as a new lineage. However, the nodal shape is an important variation, since it clearly differs from the general pattern observed in both *N. insignis* and in *N. bugabensis* (including its two variants) which share a very similar nodal shape. Still, I do not consider this single nodal deviation, as well as the more abundant gastral appressed pilosity, sufficiently informative so as to confidently erect a new species. Therefore, *N. villosa*_cf2 is here considered a variant of *N. insignis* until further material become available.

Natural history notes. See Longino (2010) who provides an extensive, fine-grain account of observations on Costa Rican *N. insignis*, based on which William Brown was planning a manuscript (comment from Longino 2010).

Material examined. 4☿, 2♀, 2♂. **COLOMBIA – Chocó:** • 1♀; Parque Nacional Natural Los Katios; 7.8167, -77.2; alt. 236m; 1990-06-14; Aide, M. leg.; (JTLC). • 1☿; Parque Nacional Natural Los Katios; 7.8167, -77.2; alt. 236m; 1990-06-14; Aide, M. leg.; (JTLC). **COSTA RICA – Alajuela:** • 1♂; north side Laguna Arenal; 10.5, -84.7167; alt. 500m; 1987-06-12; Longino, J. leg.; (JTLC). • 1☿; north side Laguna Arenal; 10.5, -84.7167; alt. 500m; 1987-06-12; Longino, J. leg.; (JTLC). – **Puntarenas:** • 1♀; Cerro Plano de Monteverde; 10.3, -84.8167; alt. 1300m; 1989-06-11; Longino, J. leg.; (JTLC). • 1☿; Cerro Plano de Monteverde; 10.3, -84.8167; alt. 1300m; 1989-06-11; Longino, J. leg.; (JTLC). **PANAMA – Darién:** • 1♂; 9 km WSW Platanilla; 8.7759, -78.4539; alt. 750m; 2015-01-20; Longino, J. leg.; hand collected; (JTLC). • 9 km WSW Platanilla; 8.7759, -78.4539; alt. 750m; 2015-01-20; Longino, J. leg.; hand collected; (JTLC). • 1☿; 9 km

WSW Platanilla; 8.7759, -78.4539; alt. 750m; 2015-01-20; Longino, J. leg.; hand collected; (JTLC).

Geographic range. Costa Rica, Panama, Colombia.

***Neoponera inversa* (Smith, 1858)**

Figures. 2c (petiole ☿); 30b (distribution).

Ponera inversa Smith, 1858: 96. ☿ lectotype [by designation of Fernandes et al. 2014: 149], Ecuador ["South America"], Napo, "51/70", (BMNH: BMNH1015556, AntWeb: CASENT0902512) [image examined, link].

Combinations: In *Pachycondyla*: Mayr, 1886: 358; Emery, 1901: 45: Brown, 1995:306. In *Neoponera*: Emery, 1904: 597; Schmidt & Shattuck, 2014: 151.

Subspecies of *Neoponera villosa*: Emery, 1904: 597.

Status as species. Mayr, 1863: 448; MacKay & MacKay, 2010: 409 [redescription]; Fernandes et al., 2014: 149 [redescription].

Worker and queen diagnosis. Same diagnostic features as for *N. curvinodis*, except: Head subquadrate, lateral margin posterior to eye *usually* convex (link); posterolateral propodeal margin carina-less or with blunt, not raised carina (Fig. 11b); in lateral view, anterior margin of petiolar node moderately to strongly concave, distal portion curved anterad (Fig. 2c); anterolateral nodal face deflate (Fig. 2c); in lateral view, dorsoposterior nodal margin *usually* meeting with anterior margin in 30° – 35° angle (Fig. 2c).

Worker. Measurements (*n* = 26): HW: 2.15-2.6; HL: 2.4-2.95; EL: 0.55-0.77; SL: 2.25-2.65; WL: 3.6-4.45; PrW: 1.55-1.9; MsW: 0.95-1.4; MsL: 0.7-1.0; PW: 1.2-1.5; PH: 1.0-1.5; PL: 0.95-1.31; GL: 2.8-4.95; A3L: 1.1-2.0; A4L: 1.3-2.0; A3W: 1.3-2.14; A4W: 1.55-2.15; TLa: 10.05-12.23; TLr: 10.35-13.48. **Indices.** CI: 81.13-96.15; OI: 23.4-29.57; SI: 93.88-113.95; MsI: 115.79-200.0; LPI: 71.43-115.0; DPI: 104.17-142.86.

Queen. Measurements (*n* = 6): HW: 2.55-2.85; HL: 2.4-3.0; EL: 0.6-0.75; SL: 2.3-2.7; WL: 4.35-4.75; PrW: 2.0-2.1; MsW: 1.5-1.8; MsL: 1.3-1.5; PW: 1.5-1.75; PH: 1.25-1.75; PL: 1.05-1.3; GL: 4.15-5.6; A3L: 1.7-2.0; A4L: 1.8-2.1; A3W: 2.15-2.45; A4W: 2.25-2.45; TLa: 11.7-

12.85; TLr: 12.8-14.45. **Indices.** CI: 91.38-118.75; OI: 21.05-27.45; SI: 80.7-101.89; MsI: 103.45-126.92; LPI: 68.57-96.15; DPI: 128.0-152.38.

Male. Described by Fernandes et al. (2014). The following is added to their diagnosis: ocelli comparatively small, maximum length of each shorter than diameter of antennal socket acetabulum; notauli well-impressed, touching posteriorly; mesopleural sulcus well-marked but not sculpted; metanotum with feebly raised median carina.

Comments. *Neoponera inversa* is a medium-sized species in the *N. foetida* group (Fig. 12; ☿ TLa = 10.2 – 12.18 mm; ♀TLa: 10.2 – 12.18 mm). Its external morphology is virtually identical to that of *N. curvinodis* which is closely related to it (Troya et al. unpublished). The reader can find a detailed discussion on how to distinguish these two lineages apart under the treatment of *N. curvinodis*. Besides *N. curvinodis*, only two species in the *N. foetida* group are morphologically most similar to *N. inversa*: *N. villosa*, and *N. zuparkoi*. The first has a nearly vertically straight anterior nodal margin, and a tumulus on the posterior nodal face, while in *N. inversa* the anterior nodal margin is concave and lacks a tumulus on the posterior nodal face. *Neoponera zuparkoi* differs from *N. inversa* in showing a reduced, not salient humeral carina, and a lobate anterior projection on the mesopleuron. In examined workers and queens of *N. inversa* the humeral carina is always slightly to moderately salient, and the mesopleuron lacks a lobate anterior projection. Fernandes et al. 2014 considered *N. inversa* smaller than *N. curvinodis*, but my measurements of scape length (SL) and scape index (SI) differ from those reported by them (*N. curvinodis* ☿ SL: 2.63 – 2.70 mm, SI: 104.24 – 105.2 mm; *N. inversa* ☿ SL: 2.3 – 2.38 mm; SI: 94.65 – 95.2 mm) as follows: *N. inversa* ☿ SL: 2.25 to 2.65 mm, SI: 94 to 114 mm (n = 30), and *N. curvinodis* ☿ SL: 2.5 to 3.25 mm, SI: 102.3 to 115 mm (n = 64).

As in *N. curvinodis*, *N. inversa* shows some variation in the following body regions which are not geographically correlated: the humeral carina can be feebly- to moderately salient; the propodeal posterolateral margin in most cases is carina-less, but sometimes can carry a weak, blunt carina, somewhat similar to the state present in some *N. curvinodis*; and the anterolateral nodal face which may vary from weakly- to moderately deflate. This latter is the most common state and it gives the node its characteristic concavity. As in *N. curvinodis*, these variations are continuous, and they are not associated with body size. In contrast to Fernandes et al. (2014), I did not detect

variations in color among specimens belonging to regions closer to the equator, as compared to others obtained from regions distantly separated from that zone.

Most records of *N. inversa* belong to lowland forests up to ca. 1000 m of elevation, with an extreme of 2300 m at Cordillera del Cóndor, a mountainous region in southern Ecuador. Populations of *N. inversa* apparently prefer well-preserved forests as most specimens were collected in national parks and/or poorly degraded regions. This species is broadly distributed in South America and part of Central America; it inhabits in all Brazilian biomes (except for Pantanal), in the Chaco Húmedo of Paraguay, north to Amazonia of Bolivia, Peru, Ecuador, and Colombia. On the northwestern side of the continent records reach the Chocó-Darién and the Caribbean region of Colombia and Venezuela. In regards to Central America, some authors like Kempf (1972), Mackay and Mackay (2010), Branstetter and Sáenz (2012), among others (see AntCat.org) include Mexico and Guatemala as the northernmost range for *N. inversa*. These authors based their records for this species on Forel (1899) who did not mention those countries as part of the distribution of *N. inversa*. Forel recorded Las Mercedes in Guatemala as one of the type localities for *N. curvinodis* which is extremely similar to *N. inversa*. Thus far, the present literature search and the material examined support only northern Honduras (at the Atlantic) as the northernmost range for this species.

Natural history notes. See Mackay and Mackay (2010), and Fernandes et al. (2014). From this study: *Neoponera inversa* seems to prefer foraging and nesting on the canopy strata, most specimen-records for which the collection method is known, have been obtained using fogging, pitfall and arboreal Malaise, and beating.

Material examined. 57☿, 9♀. **BOLIVIA – Santa Cruz:** • 1♀; 7.5 K NNE Villa Yapacaní, near Parque Nacional Amboró; -17.3436, -63.8372; alt. 290m; Kozue leg.; ([no museum voucher]). **BRAZIL – Acre:** • 1☿; Fazenda Experimental Catuaba; -10.0667, -67.6167; alt. 226m; 2014-03-11; Denicol, M. R.; Santos, A. M. leg.; pitfall; (DZUP). • 1☿; Humaita; -9.75, -67.6333; alt. 168m; 1992-06-15; Gorayeb, I.; Hernriques, E. leg.; (MPEG). – **Amazonas:** • 1☿; AM 170, Km 10; -3.0476, -59.9784; alt. 40m; 1982-08-07; Harada, A. leg.; hand collected; (INPA). • 1☿; Estirão do Equador; -4.5167, -71.6167; alt. 91m; 1979/10; Alvarenga, M. leg.; (MPEG). – **Bahia:** • 1☿; 3 km s of Guaratinga; -16.6167, -39.7833; alt. 220m; 2007-07-26; Santos, J. R. M. leg.;

(CPDC). • 1♂; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 2014-05-02; Feitosa, R. M. leg.; (DZUP). • 1♂; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 2012-12-19; Silva, J. A. leg.; (CPDC). • 1♂; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 2005-02-02; Watkins, K.; M. Cobb. leg.; (CPDC). • 1♂; 4k NW of Una; -15.2667, -39.0333; alt. 34m; 2005-10-27; Santos, J. R. M. leg.; (CPDC). • 1♀; Buerarema; -14.9843, -39.2583; alt. 132m; 2006-05-03; Maia, J. R.; et al. leg.; (CPDC). • 2♂; Buerarema; -14.9843, -39.2583; alt. 132m; 2006-05-03; Maia, J. R.; et al. leg.; (CPDC). • 1♂; Canavieiras; -15.6777, -38.9417; alt. 7m; 1988-04-21; do Carmo, J. leg.; (CPDC). • 1♀; Ilhéus; -14.7833, -39.05; alt. 36m; 2014-05-02; Feitosa, R. M. leg.; (DZUP). • 1♂; Ilhéus; -14.7833, -39.05; alt. 36m; 2014-05-02; Feitosa, R. M. leg.; (DZUP). • 1♀; Reserva Biológica do Una; -15.1768, -39.1053; alt. 108m; 2011/11; Sena, D. U. leg.; (CPDC). • 1♂; Reserva Biológica do Una; -15.1768, -39.1053; alt. 108m; 2011-11-01; Uzel-Sena, D. leg.; (CPDC). • 2♂; Serra da Jibólia; -12.7717, -39.522; alt. 219m; 2004-06-04; Rodrigues, R. M. leg.; (CPDC). – **Ceará:** • 1♂; 2km S of Pacoti; -4.25, -38.9167; alt. 700m; 2001; Hites, N. leg.; (CPDC). – **Distrito Federal:** • Aguas emendadas; -15.5, -47.55; alt. 992m; 2014-06-13; Guaraldo, A. leg.; (DZUP). – **Espírito Santo:** • 1♂; Floresta Nacional Goytacazes; -19.4353, -40.072; alt. 26m; 2013-02-01; Simon, S. leg.; pitfall; (UFVLABECOL). – **Goiás:** • 1♂; Chapadão do Céu, Parque Nacional das Esmas; -18.2889, -52.3672; alt. 619m; 2014-01-07; Pinto, A.; et al. leg.; (DZUP). – **Mato Grosso do Sul:** • 1♂; Dourados; -22.2186, -54.8325; alt. 442m; 2009-01-01; Silvestre R. leg.; hand collected; (MuBio-UFGD). – **Paraná:** • 1♂; Entorno do rio Brumado; -25.3402, -48.885; alt. 397m; 2017-10-18; Pinto, A.; et al. leg.; (DZUP). • 1♂; P. E. Pico do Marumbi; -25.4833, -48.9833; alt. 968m; 2014-07-15; Feitosa, R. M.; et al. leg.; (DZUP). • 1♂; Reserva Bicudinho do Brejo; -25.8833, -48.5667; alt. 7m; 2015-06-26; Oliveira, D. A. leg.; (DZUP). • 1♂; Reserva Natural Guaricica, Guaricica trail; -25.3667, -48.7667; alt. 9m; 2019-03-22; Feitosa, R.; et al. leg.; Malaise; (DZUP). • 1♂; Reserva Natural Guaricica, dos Fornos trail; -25.3, -48.65; alt. 36m; 2018-11-06; Troya, A. leg.; beating; (MEPN). – **Pará:** • 1♂; Alter do Chão; -2.5041, -54.9548; alt. 23m; 2002-04-30; Vilhena, J. leg.; (INPA). • 1♀; Bairro Marco, Dr. Freitas; -1.4167, -48.45; alt. 22m; 2018/07; Prado, L. leg.; hand collected; (MPEG). • 1♀; Tucuruí; -

3.7658, -49.6777; alt. 48m; 1980-08-04; Nunes de Mello leg.; (INPA). • 1♂; Tucuruí; -3.7655, -49.6702; alt. 35m; 1979/02; Alvarenga, M. leg.; (MPEG). • 1♂; Utinga State Park; -1.4258, -48.4442; alt. 15m; 1979-01-27; Tadeu, P. leg.; (MPEG). • 1♂; Xingu river, left shore; -2.8817, -52.0095; alt. 4m; 2000-11-20; Maciel, C.; Dias, J. leg.; Malaise; (MPEG). – **Rio de Janeiro:** • 1♂; Paineras; -11.8425, -45.1739; 1964-03-29; Ross, C. E.; Ross, E. S. leg.; (CAS). – **Rondônia:** • 1♂; Parque Estadual do Guajara-Mirim, 18 km SW of Nova Dimensão; -10.3167, -64.55; alt. 152m; 1998-03-02; Santos, J. R. M. leg.; Malaise; (CPDC). – **São Paulo:** • 1♀; Mirassol; -20.8161, -49.5042; alt. 572m; 1977-12-12; Diniz, J. leg.; (DZUP). • 1♂; Parque Estadual Turistico do Alto Ribeira, Gruta Alambari de Baixo; -24.5514, -48.6803; alt. 181m; 2012-10-02; (MPEG). **COLOMBIA – Chocó:** • 1♂; Estación Silvicultura al Bajo Atrato; 7.0406, -77.3378; alt. 149m; 1992/08; Mendoza, L. leg.; (ICN). – **Vaupes:** • 1♂; Estación Biológica Caparú; 1.0756, -69.5136; alt. 97m; 2003-04-26; Benavides, L. leg.; (ICN). **COSTA RICA – Limón:** • 1♀; Res. Biol. Hitoy-Cerere; 9.6716, -83.0243; alt. 160m; 2015-06-12; Krissy Dominguez leg.; beating; (MUCR). **ECUADOR – Esmeraldas:** • 1♂; Reserva Ecológica Cotacachi Cayapas, La Tabla, 7 km EES Playa de Oro; 0.845, -78.744; alt. 120m; 2001-04-01; Araujo, P.; et al. leg.; fogging; (MEPN). – **Napo:** • 1♂; 3km NNE Archidona; -0.8833, -77.8; alt. 650m; 2003-12-09; Wild, A.; Donoso, D. leg.; (UTIC). • 1♂; Jatun Sacha 7km ESE Pto. Misahualli; -1.0667, -77.6167; alt. 400m; 1991-08-04; Ward, P. S. leg.; (PSWC). • 1♂; [no locality given]; -0.99, -77.81; (BMNH). – **Orellana:** • 1♂; Parque Nacional Yasuní, Guacamayo saladero; -1.294, -76.06; alt. 215m; 2014-02-02; Troya, A.; Duque, P. leg.; fogging; (MEPN). – **Sucumbíos:** • 1♂; Reserva Ecológica Cofán Bermejo; 0.1667, -77.35; alt. 920m; 2005-12-27; Troya, A. leg.; fogging; (MEPN). – **Zamora Chinchipe:** • 1♂; Paquisha alto, Hito 2, 15 Km SE Fruta del Norte, Cordillera del Cóndor; -3.9003, -78.4829; alt. 2325m; 2008-03-15; Troya, A. leg.; fogging; (MEPN). **FRENCH GUIANA – Cayenne:** • 1♂; Base Vie; 5.1667, -52.65; alt. 10m; 2000-07-06; Durou, S.; et al. leg.; (DZUP). • 3♂; Base Vie; 5.1667, -52.65; alt. 7m; 2000-12-06; Durou, S. leg.; (CPDC). • 1♂; Base Vie; 5.1667, -52.65; alt. 7m; 2000-07-06; Durou, S.; et al. leg.; (CPDC). • 1♂; Montagne dês Chevaux; 4.7333, -52.4333; alt. 75m; 2011-08-07; Team, S. E. A. G. leg.; (DZUP). • 3♂; Petit Saut; 5.0667, -53.0333; alt. 67m; 2013-10-30; Lenoir, A. leg.; (CPDC). • 2♂; Petit Saut; 5.0667, -53.0333; alt. 67m; 2003-04-03;

Orivel, J. leg.; (CPDC). • 1☿; Petit Saut; 5.0667, -53.0333; alt. 67m; 1996-07-08; Dejean, A. leg.; (CPDC). • 1☿; Petit Saut; 5.0667, -53.0333; alt. 67m; 1997/05; Orivel, J.; Dejean, A. leg.; (CPDC). **– Saint-Laurent-du-Maroni:** • 1☿; Galbao, P500-3; 3.6008, -53.2668; alt. 465m; 2018-10-13; Fichaux, M.; Jackie, O.; Touchard, A. leg.; Winkler48h; (EcoFoG). • 1☿; Galbao, P700-1; 3.6036, -53.2807; alt. 688m; 2018-10-18; Fichaux, M.; Jackie, O.; Touchard, A. leg.; Pitfall48h; (EcoFoG). • 1☿; Maripasoula; 3.6333, -54.0333; alt. 97m; 1999-07-01; Durou, S.; et al. leg.; (CPDC). **PANAMA – Colón:** • 1♀; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2004-03-09; Springatte; Pizon, S leg.; Malaise; (CPDC).

Distribution. Honduras*, Costa Rica, Panama, Venezuela*, Colombia, Guyana*, French Guiana, Ecuador, Peru, Bolivia, Brazil (Acre, Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo*, Goiás, Mato Grosso*, Mato Grosso do Sul, Pará, Paraná, Rondônia, Rio de Janeiro*, Santa Catarina*, São Paulo), Paraguay*. *: Literature records.

***Neoponera lineaticeps* (Mayr, 1866)**

Figures. 4a (head ☿); 27: a – d (☿ variant); 31b (distribution).

Pachycondyla lineaticeps Mayr, 1866: 502. ☿ lectotype [by designation of MacKay & MacKay, 2010: 437], Mexico [no further data], (NHMW, AntWeb: CASENT0915667, link) [image examined]. Paralectotypes: 2 ☿, 1♀ [same data as for lectotype], (NHMW).

Combinations. In *Neoponera*: Emery, 1901: 47; Schmidt & Shattuck, 2014: 151. In *Pachycondyla*: Brown, 1995: 306.

Status as species. Emery, 1890: 73; MacKay & MacKay, 2010: 437 [redescription].

Worker and queen diagnosis. Head subquadrate, posterior margin concave in frontal view (Fig.27b) ; antennal scape, when pulled posterad, exceeding posterior head margin by about 1.5 times apical scape width (link); head vertex, including region near internal eye margin, costate (Fig. 27b); humeral carina salient; in lateral view, anterior margin of petiolar node straight, weakly inclined posterad, meeting dorsal margin in 85° to 90° angle, nodal top blunt (link); anterior and lateral nodal face with gross, irregularly shaped striae (link), sometimes feebly impressed (link); posterior face with patch of gross, longitudinal striae.

Worker. Measurements (n = 4): HW: 1.7-1.95; HL: 1.5-2.05; EL: 0.5-0.5; SL: 1.55-1.95; WL: 2.75-3.05; PrW: 1.25-1.3; MsW: 0.75-0.8; MsL: 0.6-0.7; PW: 0.85-1.05; PH: 0.8-1.02; PL: 0.75-0.9; GL: 3.6-4.1; A3L: 1.0-1.25; A4L: 1.1-1.25; A3W: 1.4-1.55; A4W: 1.5-1.65; TLa: 7.25-8.3; TLr: 8.75-9.73. **Indices.** CI: 94.87-113.33; OI: 25.64-29.41; SI: 91.18-105.41; MsI: 107.14-133.33; LPI: 88.67-100.0; DPI: 94.44-126.67.

Queen and male. Described by Mackay and Mackay (2010).

Comments. *Neoponera lineaticeps* is amongst the smallest species in the *N. foetida* group (Fig. 12; ☿ TLa = 7.25 – 8.3 mm). It shows a homogeneous external morphology across its range except for variations on the sculpture of the petiolar node which may either carry feebly impressed striae laterally (CASENT0249153, link, Puntarenas, Costa Rica) or gross, irregular striae (CASENT0217563, link, Chiapas, Mexico). Despite being irregular, the striae on the lateral nodal face are always horizontally oriented. In this respect, a variant of *N. lineaticeps* from El Petén, Guatemala (Fig. 27), hereafter referred as *N.* JTL021, differs from *N. lineaticeps* in bearing more abundant and brighter appressed pilosity; the striae on the lateral nodal face is not horizontally arranged but rather vertically curved (Fig. 27d); and the nodal top is convex, not blunt as usual in *N. lineaticeps* (Fig. 27d). This unique specimen was subjected to DNA extraction, and according to the UCE phylogeny (Troya et al. unpublished) it is sister to *N. lineaticeps*, but the branches of both specimens are relatively short, thus suggesting a recent divergence.

The variation of said characters between these two forms are evident, but as observed previously in other species in the *N. foetida* group, for example, *N. curvinodis*, *N. inversa*, several body regions are subject to plasticity. Either these variants in Central America are the product of hybridization between several sympatric forms, or *N.* JTL021 is perhaps a distinct lineage belonging to poorly known, possibly small populations. Since the evidence, both molecular and morphological, is currently insufficient to make further judgments, I leave *N.* JTL021 as a variant of *N. lineaticeps* until more material is available.

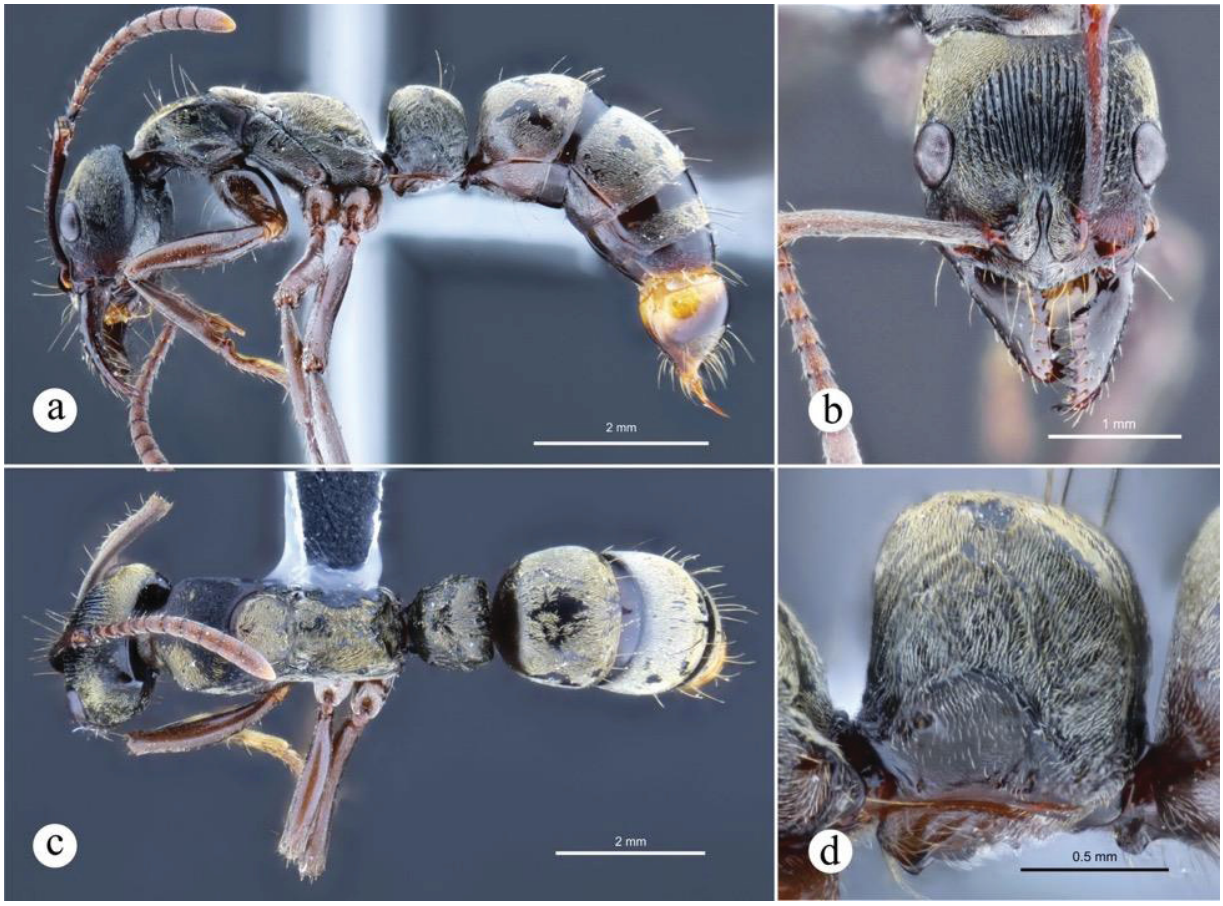


Fig. 27. *Neoponera lineaticeps* (variant, referred in text as *N.* JTL021). ☿ (JTLC: CASENT0610994), Guatemala, Petén. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view; **d.** Petiole in lateral view.

Because of its size, *N. lineaticeps* can only be confused with *N. bugabensis*, *N. insignis*, and *N. theresiae*, which have a very similar petiolar node. However, these species lack costae on the head dorsum. The node of *N. theresiae* is laterally striate but in no way similar to the usually gross striae of *N. lineaticeps*.

Neoponera lineaticeps inhabits in central – to southeastern Mexico and throughout Central America. Examined material originates from Central American moist and dry forests, as well as from Isthmian-Pacific moist forests, ranging from ca. 300 m up to ca. 1500 m elevation.

Fernandez and Palacio (1995) and Fernández et al. (1996) report this species for the Colombian departments of Cauca and Tolima, respectively. Later, however, Fernández in (Fernández and Guerrero 2019) report this species with the status “probably present in Colombia”

p. 532. Further sampling in northern Colombia may bring support to the hypothetical incursion of this species in South America.

Natural history notes. See Mackay and Mackay (2010), and Longino (2010).

Material examined. 8☿. **COSTA RICA – Alajuela:** • 1☿; Monteverde Cloud Forest Reserve; 10.2912, -84.8158; alt. 1220m; 2018-03-28; J. Longino leg.; beating; (JTLC). **– Heredia:** • 10km NE Vara Blanca; 10.2362, -84.1177; alt. 1500m; 2005-03-09; Longino, J. leg.; hand collected; (JTLC). • 1☿; 10km NE Vara Blanca; 10.2362, -84.1177; alt. 1500m; 2005-03-09; Longino, J. leg.; hand collected; (JTLC). **GUATEMALA – Petén:** • 1☿; Parque Nacional Tikal; 17.2436, -89.6217; alt. 270m; 2009-05-23; Longino, J. leg.; hand collected; (JTLC). **MEXICO – Chiapas:** • 1☿; Ocasinga, Laguna Ocotal Grande; 16.8, -91.4; alt. 971m; 1954/07; Dressler, R. L. leg.; (MZSP). • 1☿; [no locality given]; 23.0, -102.0; 1986-12-01; Sichel leg.; (NHMW). **NICARAGUA – Jinotega:** • 2☿; RN Cerro Kilambé; 13.5652, -85.6982; alt. 1290m; 2011-05-23; Prebus, M. leg.; hand collected; (MEPN). **– Matagalpa:** • 1☿; Hotel Selva Negra; 12.9989, -85.9092; alt. 1285m; 2003-07-07; Mackay, W.; Mackay, E. leg.; hand collected; (ICN).

Geographic range. Mexico (Chiapas, Querétaro*, Veracruz*), Guatemala, Honduras*, Nicaragua, Costa Rica, Panama. * Record from literature.

***Neoponera prasiosomis* sp. nov.**

Figures. 5c (petiolar node ☿); 28: a – g (☿); 30a (distribution).

Type material. ***Holotype*.** 1 ☿; **PANAMA**: **Colón**: S. Lorenzo forest, 9°17’ N, 79°58’ W, [October 2003], mosaic forest, [Dejean, A.; et al. leg.], (DZUP: ATPFOR2001).

Etymology. The specific epithet is derived from the Greek words πράσινος (prásinos), meaning green, and σῶμαsôma (sôma), meaning body, alluding to the tenuous greenish cuticle, especially discernible on the head and mesosoma of the holotype. The name is a noun in apposition, thus invariable.

Worker (and probably queen) diagnosis. Head rectangular, antennal scape, when pulled posterad, exceeding posterior head margin by 0.5 to 1 X apical scape width (Fig. 28e); anterior mid clypeal margin convex (Fig. 28e); humeral carina slightly salient; in lateral view,

anterior margin of petiolar node straight, meeting with posterior margin in ca. 80° angle, top of node relatively acute (Fig. 28a); posterior face of node either feebly striate (Figs. 5c, 28g) or punctate; integument of head, mesosoma and petiole slightly metallic greenish, gaster castaneous to dark brown.

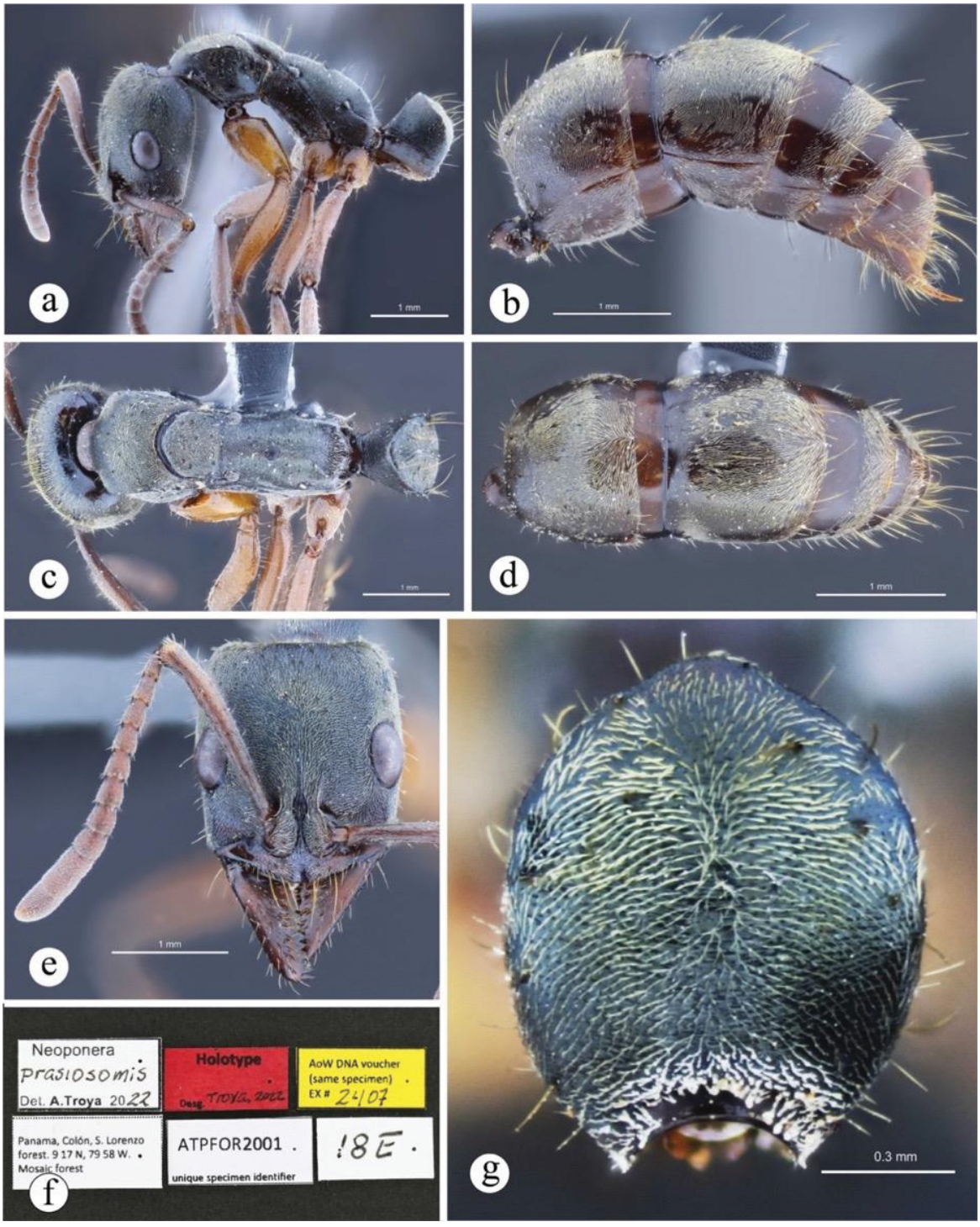


Fig. 28. *Neoponera prasiosomis* sp. nov. Holotype ☿ (ICN: ATPFOR2001). Panama, Colón. **a.** Head, mesosoma and petiole in lateral view; **b.** Gaster in lateral view; **c.** Head, mesosoma and petiole in dorsal view; **d.** Gaster in dorsal view; **e.** Head in frontal view; **f.** Collection labels; **g.** Posterior face of petiolar node showing weakly impressed horizontal striae.

Worker description. Measurements (*n* = 2; holotype in parenthesis): HW: 1.45-1.6 (1.45); HL: 1.7-1.95 (1.7); EL: 0.5-0.55 (0.5); SL: 1.5-1.7 (1.5); WL: 2.6-3.0 (2.6); PrW: 1.0-1.15 (1.0); MsW: 0.75-0.9 (0.75); MsL: 0.6-0.65 (0.6); PW: 0.7-0.9 (0.7); PH: 0.6-0.9 (0.6); PL: 0.7-0.75 (0.7); GL: 2.45-3.25 (2.45); A3L: 1.0-1.35 (1.0); A4L: 1.0-1.3 (1.0); A3W: 1.0-1.05 (1.0); A4W: 1.2-1.25 (1.25); TLa: 7.0-8.35 (7.0); TLr: 7.45-8.95 (7.45). **Indices.** CI: 82.05-85.29 (85.29); OI: 34.38-34.48 (34.48); SI: 103.45-106.25 (103.45); MsI: 125.0-138.46 (125.0); LPI: 83.33-116.67 (116.67); DPI: 100.0-120.0 (100.0).

Head. *Frontal view*: subrectangular. Mandible triangular, longer than wide, distal region slightly bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with eight to nine similarly sized teeth distally, and three smaller teeh proximally. Prementum with reduced transverse dome. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, with subtriangular-shaped, relatively acute extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina not reaching ocular mid-length. Torular lobe subtriangular, covering approximately 60% of acetabulum of antennal socket, posterolateral margin straight. Malar carina well-developed, not reaching anterointernal eye margin. Eye oval, maximum length ca. one-fourth head length, convex, slightly globose, reaching- to silghtly surpassing lateral margin of head, placed at cephalic mid-length. Posterior margin of head straight to slightly concave. Occipital carina vestigial. Scape, when pulled posterad, surpassing posterior margin of head by about one apical scape width. **Mesosoma**. *Lateral view*: Dorsal margin straight to slightly convex. Pronotum carinate, with carina slightly projecting from cuticle. Anapleural sulcus feebly developed, usually merged with surrounding striae. Posterolateral margin of propodeal declivity slightly marginated. Propodeal spiracle slit-shaped. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed. Notopropodeal suture present, forming shallow groove, mesonotum and propodeum separated. Posterior face of propodeal declivity flat. Propodeal lateral margins subparallel, not converging dorsomedially. *Ventral view*: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process well-developed, tooth-shaped, internal margins of lobes convergent, relatively flattened anteroposteriorly, inclined posterad ca. 20–30 degrees in lateral

view, space between lobes broader than width of each. Metasternal process well-developed, inclined posterad, 20°-30° in lateral view, triangular-shaped, flattened anteroposteriorly, apex higher than half height of metacoxal internal margin, space between lobes narrower than width of each, internal margins running parallel. Metasternal process external margins convergent. **Legs**. Mesofemur slightly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora flattened roughly on distad half, surface even without groove. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur about half-length of posterior spur. Anterior hind tibial spur about half-length of posterior spur. Pretarsal claw arched, unarmed (without accessory teeth on surface). Arolium present, roughly three times shorter than pretarsal claw. **Petiole**. *Lateral view*: Petiolar node with straight anterior margin and convex posterior margin, middorsal margin mostly flat, anterodorsal margin angulate, posterior face slightly convex. Subpetiolar process subtriangular, with acute, keel-shaped, slightly grooved anterior cusp, followed posteriorly by straight, slightly flat dome, dome devoid of- or with scant, feebly impressed striae. Lateral projection of anteroventral nodal carina well-developed, with acute to slightly blunt tip moderately bent dorsad. Lateral nodal carina weakly impressed. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. *Lateral view*: Prora poorly developed, similar to cuticular lip, slightly projected ventrad. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 nearly as high as maximum height of petiolar node margin. Anterodorsal margin of tergum of A3 convex. Cinctus moderate. *Dorsal view*: Tergum of A3 slightly shorter than A4. Posterior dorsum of epipygium completely smooth. **Color**. Appendages mandibles lighter than body integument, antennae dark brown to ferruginous brown, legs light brown. **Pilosity**. Body with flexuous, tenuously golden, erect and suberect hairs. Appressed pubescence moderately abundant, especially on gastral dorsum, though integument always discernible. Most erect hairs on body dorsum approximately equal to maximum eye length. Scape pilosity mostly composed of erect and suberect hairs and pruinose pubescence, erect hairs shorter than apical scape width. Meso- and metatarsi bearing moderately abundant spine-like setae interspersed with abundant suberect fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, shorter than eye maximum length. Posterior dorsum of epipygium surrounded by 20–30 long flexuous hairs, mostly longer than eye maximum length. **Sculpture**. Integument polished, with abundant, densely-packed piligerous punctures, most of which touch each other and form irregular, feebly impressed striae, especially on head dorsum where these are

more raised. Mandibles without striae dorsally. Striae on petiolar node mostly absent, except for few feebly impressed on anterior nodal face.

Queen and male. Unknown.

Comments. *Neoponera prasiosomis* is amongst the smallest taxa in the *N. foetida* group (Fig. 12, ☿ TLa = 7 – 8.35 mm), and the specimen from Esmeraldas, Ecuador (MEPN: MEPN4862) is the smallest specimen of this species-group. No strong inference is possible in regards to morphological variation since only two specimens are known. However, the specimen from Ecuador differs from the holotype in the following: the posterolateral margin of the petiolar node is almost horizontally straight, while that of the holotype is slightly inclined, meeting with the anterior margin in ca. 80° angle; the posterior nodal face is punctate, while that of the holotype has feebly impressed horizontal striae; the body integument is mostly castaneous (rather than greenish on the holotype) although a tenuous greenish hue is discernible.

Neoponera prasiosomis could be confused with *N. insignis*, *N. bugabensis*, *N. theresiae*, and *N. villosa*_cf2 (variant of *N. insignis*) in the *N. foetida* group. In particular, the first two species are very similar to it, the reader can use the following characters to separate them: *N. prasiosomis* has a rectangular head, clearly longer than broad, while the head of the other two species is mostly subquadrate; the antennal scape of *N. prasiosomis* exceeds the posterior head margin by mostly one apical scape width, while that of the other species is longer, surpassing the posterior head margin by one up to 2.5 times apical scape width; *N. prasiosomis* shows a greenish integument while that of the other species is mostly black, to brownish; in lateral view, the petiolar node of *N. prasiosomis* is shorter (☿ PL = 0.70 – 0.75 mm) than those of *N. insignis* (☿ PL = 0.9 – 1 mm), and *N. bugabensis* (☿ PL = 0.9 – 1.25 mm).

Neoponera theresiae, on the other hand, is more easily distinguished from *N. prasiosomis* since it has convex postocular head margins so that the overall head shaped in frontal view seems suboval, while in *N. prasiosomis* the postocular head margins are straighter. Also, *N. theresiae* has striae on the proximal mandibular region and laterally on the nodal face. *Neoponera prasiosomis* is striae-less on such regions.

Finally, *N. villosa*_cf2 (here considered variant of *N. insignis*) differs from *N. prasiosomis* in having a mostly quadrate head in frontal view; the posterolateral nodal margin is significantly

more inclined than in *N. prasiosomis*; and the gaster is abundantly covered with yellow appressed pilosity so that the integument is barely visible, while in *N. prasiosomis* the gaster is clearly less pilose allowing visibility of the integument.

Outside the *N. foetida* group, perhaps only *N. rugosula* and *N. unidentata* which belong to the *N. crenata* group, are similar. The easiest form to distinguish them is by examining the mesosomal dorsum where the notopropodeal suture is absent to vestigial, while in all species of the *N. foetida* group it is always present.

The elevational range of currently known specimens of *N. prasiosomis* spans from nearly the sea level up to 150 m. The Panamanian holotype was collected in the Isthmian-Atlantic moist forests, while the specimen from Ecuador belongs from the western Ecuadorian moist forests, which is part of the southern Chocó-Darién.

Natural history notes. Nothing is known about this species except that is probably arboreal, the specimen from Ecuador was collected using insecticidal knockdown, in a well-preserved, remote primary forest, about 20 years ago. Presently, the forests of this region are highly threatened by human activities, mainly wood extraction and mining (Rebolledo Monsalve et al. 2022).

Other material examined. 1☿. **ECUADOR – Esmeraldas:** • 1☿; Reserva Ecológica Cotacachi Cayapas, Pajonal, 4 km S Gualpi; 0.7584, -79.154; alt. 150m; 2001-04-01; Araujo, P.; et al. leg.; fogging; (MEPN).

Geographic range. Panama, northwestern Ecuador.

***Neoponera solisi* (Mackay & Mackay 2010)**

Figures. 3b, 5a (petiole ☿); 4b (head ☿); 29: a – c (♀); 31a (distribution).

Pachycondyla solisi MacKay & MacKay, 2010: 514, Figs. 113, 253, 635-638. ☿ holotype, Costa Rica, Heredia, Est. El Ceibo, P.N. Braulio Carrillo, 400-600 m., ii.1990, C. Chaves [leg,], (INBC, AntWeb: INBIOCRI000312327, link) [image examined]. Paratypes: 1 ☿, 1♀, [same data as for lectotype], (INBC, WEMC) [not examined].

Combination in *Neoponera*: Schmidt & Shattuck, 2014: 151

Status as species: Fernandes et al., 2014: 135.

Worker and queen diagnosis. Head subtrapezoid, posterior margin concave, with posterior corner slightly protruding in frontal view (Fig. 29a); anterior mid clypeal margin concave, with well-impressed longitudinal groove extending through supraclypeal area (Fig. 29a); malar carina present, weakly impressed; antennal scape, when pulled posterad, exceeding posterior head margin by about two times apical scape width; posterior head dorsum with gross longitudinal striae (Fig. 29a); humeral carina well-developed, salient anteriorly; posterolateral propodeal margin carinate; in lateral view, top of petiolar node convex, posterolateral margin carinate, ventral half of anterior face grossly striate (Fig. 3b); posterior nodal face mostly glabrous, except for some marginal long erect hairs (Fig. 5a); prora highly reduced to a feeble swelling (Fig. 3b); integument dark castaneous.

Worker. Measurements (*n* = 2): HW: 2.59-2.9; HL: 2.94-3.25; EL: 0.73-0.88; SL: 2.9-2.96; WL: 4.2-4.5; PrW: 1.8-2.3; MsW: 1.0-1.28; MsL: 0.9-1.15; PW: 1.1-1.29; PH: 1.28-1.48; PL: 1.28-1.39; GL: 4.5-5.1; A3L: 1.6-1.93; A4L: 1.72-1.8; A3W: 1.9-2.3; A4W: 2.3-2.3; TLa: 11.74-12.87; TLr: 12.92-14.24. **Indices.** CI: 88.1-89.23; OI: 28.19-30.34; SI: 102.07-111.97; MsI: 111.11-111.3; LPI: 93.92-100.0; DPI: 85.94-92.81.

Queen. Measurements (*n* = 1): HW: 3.5; HL: 3.7; EL: 1.0; SL: 3.2; WL: 5.5; PrW: 2.5; MsW: 2.0; MsL: 2.65; PW: 1.49; PH: 1.6; PL: 1.68; GL: 7.2; A3L: 2.45; A4L: 2.4; A3W: 2.65; A4W: 2.8; TLa: 15.73; TLr: 18.08. **Indices.** CI: 94.59; OI: 28.57-; SI: 91.43; MsI: 75.47; LPI: 105.0; DPI: 88.69.

Male. Unknown.

Comments. *Neoponera solisi* is a medium-sized to large species in the *N. foetida* group (Fig. 12; ☿ TLa = 11.7 – 12.9 mm; ♀TLa: 15.7 mm). Only three specimens were physically examined out of the scant collected through the ALAS project team in Parque Nacional Braulio Carrillo, in Heredia, Costa Rica, the only site in the Neotropics where this taxon is known from.

The morphology of this species, in particular the mid anterior clypeal region and the petiolar node, are very distinctive characters which make easier its distinction from any other species in this group, as well from any other in the genus. Mackay and Mackay (2010) point out it could be confused with *N. chyzeri* (which belongs to the *N. aenescens* group), and with *N. lineaticeps*. This is unlikely though, since both species have very different nodal shape. Also, *N. lineaticeps* has a black integument and is much smaller, while *N. chyzeri* is also black, lacks malar

carinae, and the body bears abundant, golden appressed hairs. *Neoponera solisi* inhabits in the Isthmian-Atlantic moist forests at ca. 500 m elevation.

Natural history notes. Nothing is known about this species. However, the morphology of its head, i.e., subtrapezoidal, is reminiscent of arboreal species like *N. fisheri* or *N. luteola* (Roger) which have been collected inside *Cecropia* spp. (Urticaceae) plants, in particular *N. luteola* which holds a mutualistic association with *C. membranacea* Trécul. in Peru (Gutiérrez-Valencia et al. 2017).

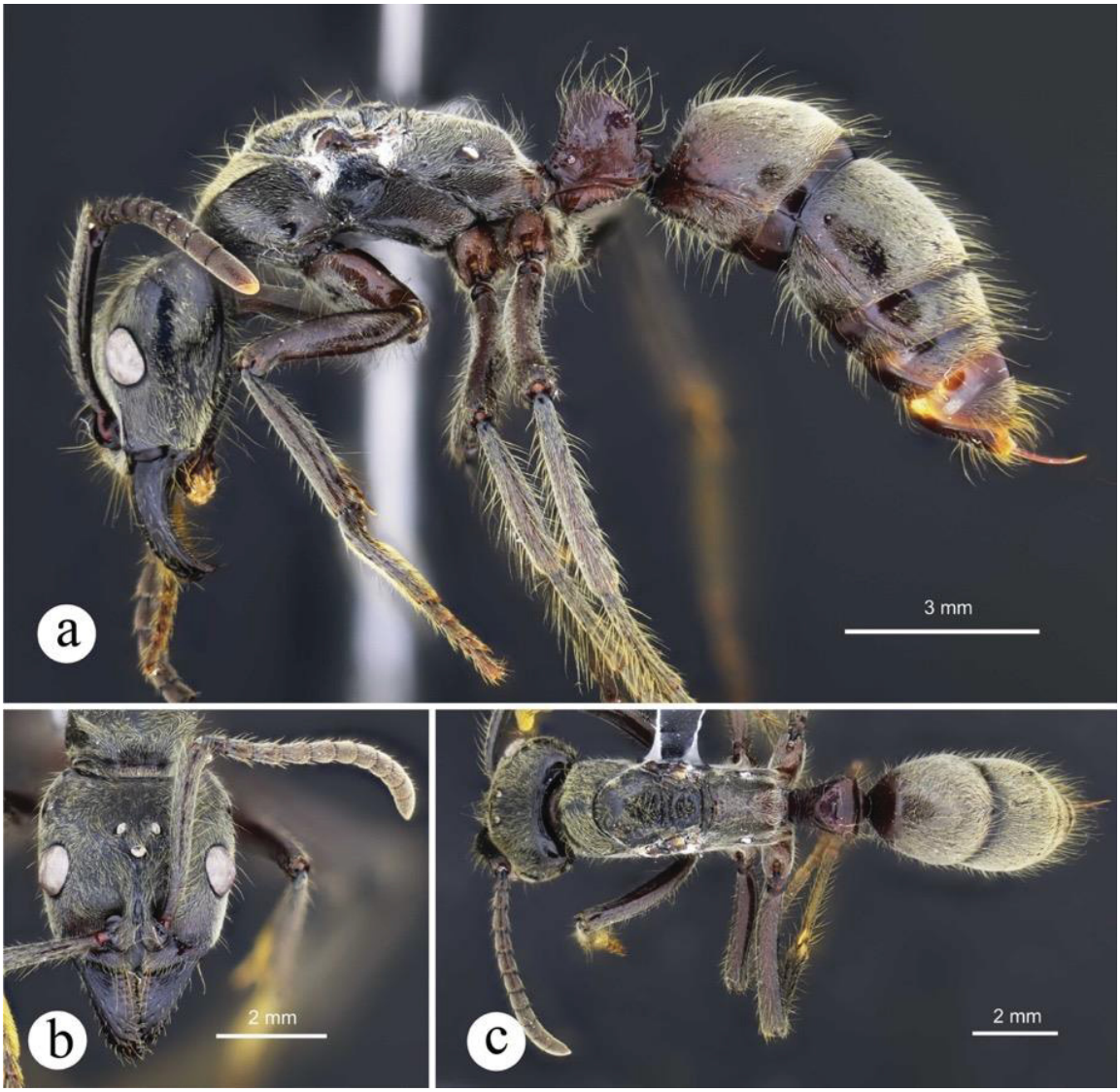


Fig. 29. *Neoponera solisi*. ♀ (INBC: INB0003662417), Costa Rica, Heredia. **a.** Lateral view; **b.** Head in frontal view; **c.** Dorsal view.

Material examined. 4☿, 1♀. **COSTA RICA – Heredia:** • 1☿; Estación El Ceibo; 10.328, -84.0804; alt. 400m; 1990-02-01; Chaves, C. leg.; (INBC). • 1☿; Estación El Ceibo; 10.328, -84.0804; alt. 400m; 1990-02-01; Chaves, C. leg.; (UTEP). • 1♀; Parque Nacional Braulio Carrillo, 11 km SE La Virgen; 10.3333, -84.0667; alt. 500m; 2003-02-12; ALAS leg.; Malaise; (INBC). • 2☿; Parque Nacional Braulio Carrillo, 11 km SE La Virgen; 10.3333, -84.0667; alt. 500m; 2003-02-12; ALAS leg.; Malaise; (INBC).

Geographic range. Northeastern Costa Rica.

***Neoponera theresiae* (Forel, 1899)**

Figures. 3c (petiole ☿); 6a (mandible ☿); 31a (distribution).

Pachycondyla theresiae Forel, 1899: 13, Plate 1, Fig. 11. ☿ lectotype [by designation of MacKay & MacKay, 2010: 549], Panama, Bugaba, Volcán de Chiriqui, Champion [leg.], (MHNG, AntWeb: CASENT0907241, link) [image examined].

Combinations. In *Pachycondyla*: Brown, 1995: 310; in *Neoponera*: Emery, 1901: 47; Schmidt & Shattuck, 2014: 152.

Status as species. Emery, 1911: 72; MacKay & MacKay, 2010: 549 [redescription].

Worker (and probably queen) diagnosis. Head subquadrate, lateral margin posterior to eye relatively round, posterior margin feebly concave to straight (link); anterior mid clypeal margin convex; proximal region of mandibular dorsum with well-impressed, divergent striae, distal region usually smooth (Fig. 6a); humeral carina present, slightly salient; posterolateral propodeal margin blunt; in lateral view, anterior margin of petiolar node straight, weakly inclined posterad, nodal top blunt to convex, posterolateral margin convex, carinate, meeting anterior margin in ca. 80° angle (link); posterior propodeal face, and anterolateral nodal face with well-marked horizontal striae (Fig. 3c).

Worker. Measurements (n = 2): HW: 1.9-2.08; HL: 2.05-2.09; EL: 0.45-0.5; SL: 2.0-2.0; WL: 2.8-3.0; PrW: 1.15-1.19; MsW: 0.74-0.75; MsL: 0.65-0.68; PW: 0.9-0.9; PH: 0.78-0.8; PL: 0.88-0.9; GL: 3.0-3.85; A3L: 1.15-1.2; A4L: 1.21-1.25; A3W: 1.4-1.45; A4W: 1.49-1.5; TLa: 8.18-8.35; TLr: 8.95-9.62. **Indices.** CI: 92.68-99.52; OI: 23.68-24.04; SI: 96.15-105.26; MsI: 108.82-115.38; LPI: 112.5-112.82; DPI: 100.0-102.27.

Queen and male. Unknown.

Comments. *Neoponera theresiae* is amongst the smallest species in the *N. foetida* group (Fig. 12; ☿ TLa = 8.18 – 8.35 mm). Although relatively few specimens were examined from Costa Rica, Panama and Colombia, no major deviations from the diagnostic limits of this species were detected. The nodal lateral striae of a Costa Rican specimen from San José (CASENT0843316) are slightly less impressed than those from two Colombian specimens from Valle del Cauca (MUSENUV16069). Besides this, the overall morphology of examined *N. theresiae* is quite homogeneous.

This species is somewhat hard to distinguish mainly due to the shape of the petiolar node which is very similar to that of *N. bugabensis*, *N. insignis*, *N. villosa, N. foetida*, and *N. lineaticeps*. In the first three, however, the node is striae-less, while the other two carry well-marked striae, more impressed than in *N. theresiae*. In *N. foetida* these striae cover most of the nodal surface, and in *N. lineaticeps* just a portion, but the striae are gross, clearly raised from cuticle. If doubts persist, the reader can look at the lateral head margins posterior to eyes which in *N. theresiae* are broadly convex, giving it the appearance of an ovoid shape, rather than subquadrate or rectangular. Another distinctive feature of *N. theresiae* are the divergent, well-marked striae on the mandibular dorsum. The other species all show striae on their mandibles but these are tenuously (e.g., *N. lineaticeps*) to moderately impressed (e.g., *N. villosa*), never strongly marked as in *N. theresiae*. An exception perhaps is *N. foetida*, where these striae are virtually absent, still some traces are distinguished.

Neoponera theresiae inhabits the Isthmian-Pacific moist forests in Central America, south to the Chocó-Darién, Cauca Valley montane forests, and Apure-Villavicencio dry forests in Colombia, spanning an elevation range from 300 m to ca. 1000 m. Wheeler (1923) cites "Cucuruzinho, Rio Autaz", p. 2. Rio Autaz is a river on the eastern side of the state of Amazonas, Brazil, while Cucuruzinho is not a site but a common name of an Amazonian frog. Emery (1911) cites Peru, without specific site though. Antmaps.org refers Gomes et al. (2010) to a supposed record in Alagoas; this is a probable misidentification, however, maybe with *N. foetida* which also carries striae in the lateral side of the node. I believe an Amazonian distribution for current *N. theresiae* populations is unlikely since not a single record for that Biome has been reported in past years.

Natural history notes. See Mackay and Mackay (2010), and Longino (2010).

Material examined. 8☿. **COLOMBIA – Meta:** • 1☿; San Juan de Arama; 3.34, -73.889; alt. 430m; 1995-06-08; Fernández, F. leg.; (MUSENUV). **– Valle del Cauca:** • 1☿; Central Hidroeléctrica Anchicayá; 3.61, -76.891; 1980-05-09; Reyes-Blanco, R. leg.; (MUSENUV). **COSTA RICA – Puntarenas:** • 1☿; 6 Km S San Vito; 8.7, -83.0; alt. 500m; 1967-03-13; OTS course leg.; (QCAZ). **– San José:** • 1☿; Ranchos Tinamú; 9.4857, -83.9572; alt. 870m; 2015-07-13; Mata, I. leg.; beating; (MUCR). • 1☿; Ranchos Tinamú; 9.4857, -83.9612; alt. 950m; 2015-07-04; Ward, P. S. leg.; beating; (PSWC). • 1☿; Ranchos Tinamú; 9.4858, -83.9544; alt. 760m; 2015-07-09; Ward, P. S. leg.; beating; (PSWC). • 1☿; Ranchos Tinamú; 9.4865, -83.9525; alt. 730m; 2015-07-11; ADMAC leg.; miniWinkler; (JTLC). **PANAMA – Chiriquí:** • 1☿; Bugaba; 8.4833, -82.6167; alt. 350m; Champion leg.; (MHNG).

Geographic range. Costa Rica, Panama, Colombia.

***Neoponera villosa* (Fabricius, 1804)**

Figures. 2a (petiole); 30b (distribution).

Formica villosa Fabricius, 1804: 409. ♀ lectotype [by designation of Fernandes et al. 2014: 155], Suriname, Essequibo, (ZMUC) [image from Fernandes et al. 2014, examined].

Combinations. In *Ponera*: Lepeletier de Saint-Fargeau, 1835: 192. In *Pachycondyla*: Mayr, 1862: 720; Brown, 1995: 311. In *Neoponera*: Emery, 1901: 43; Schmidt & Shattuck, 2014: 152.

Status as species. Lepeletier de Saint-Fargeau, 1835: 192; Roger, 1861: 1 [redescription]; Wheeler, 1908: 403 [redescription]; Gallardo, 1918: 56 [redescription]; MacKay & MacKay, 2010: 571 [redescription]; Fernandes et al., 2014: 154 [redescription].

Neoponera pilosa Smith, 1858: 95. [Junior synonym of *Pachycondyla crassinoda*. **Syn. nov.**]

Senior synonym of *Neoponera bicolor*: Roger, 1861: 1.

Worker and queen diagnosis. The following is added to the diagnosis of Fernandes et al. (2014): Head subquadrate, slightly longer than broad; humeral carina present, sometimes feebly salient; posterior propodeal margin carinate, carina feebly raised; posterolateral margin of petiolar node carinate; posterior face of node with tumulus; prora well developed, truncate anteriorly.

Worker. Measurements (*n* = 50): HW: 2.15-3.0; HL: 2.5-3.15; EL: 0.65-0.85; SL: 2.2-3.1; WL: 3.6-5.28; PrW: 1.45-2.0; MsW: 0.9-1.4; MsL: 0.75-1.15; PW: 1.15-1.6; PH: 1.0-1.5; PL: 1.0-1.5; GL: 3.5-5.28; A3L: 1.15-1.8; A4L: 1.45-1.95; A3W: 1.45-2.25; A4W: 1.65-2.35; TLa: 10.05-12.93; TLr: 11.1-14.69. **Indices.** CI: 84.75-98.36; OI: 23.64-30.23; SI: 81.82-109.8; MsI: 86.96-156.25; LPI: 83.33-125.0; DPI: 96.0-131.82.

Queen. Measurements (*n* = 13): HW: 2.1-3.1; HL: 2.2-3.25; EL: 0.6-0.9; SL: 2.25-3.35; WL: 1.85-5.35; PrW: 1.5-2.25; MsW: 1.15-2.15; MsL: 1.0-2.15; PW: 1.2-1.75; PH: 1.0-1.55; PL: 1.0-1.7; GL: 3.8-5.91; A3L: 1.45-2.1; A4L: 1.65-2.25; A3W: 2.05-2.55; A4W: 2.2-2.65; TLa: 9.55-14.34; TLr: 10.65-15.95. Indices. CI: 87.69-96.88; OI: 25.86-29.82; SI: 94.83-111.67; MsI: 76.74-143.33; LPI: 90.32-121.43; DPI: 102.94-136.0.

Male. Described by Mackay and Mackay (2010) and diagnosed by Fernandes et al (2014). The following is added to their diagnosis: notauli sometimes touching posteriorly, thus forming a Y shaped impression; mesopleural sulcus sculpted, slightly reaching ventral pleural surface; metanotum medially carinate; posterior propodeal margin sometimes with blunt carina, though mostly carina-less; posterior face of petiolar node with longitudinally oriented tumulus; node about as long as high in lateral view.

Male Measurements (*n* = 12): HW: 1.2-1.9; HL: 1.05-1.8; EL: 0.75-0.95; SL: 0.25-0.4; WL: 3.95-4.78; PrW: 1.25-1.8; MsW: 1.25-2.15; MsL: 0.75-1.8; PW: 0.75-1.25; PH: 0.95-1.1; PL: 0.75-1.2; GL: 4.5-6.1; A3L: 1.05-1.7; A4L: 0.65-1.9; A3W: 1.5-1.95; A4W: 1.8-2.15; TLa: 9.0-11.0; TLr: 10.85-13.22. **Indices.** CI: 82.76-147.62; OI: 47.37-75.0; SI: 13.16-33.33; MsI: 86.21-246.67; LPI: 75.0-121.05; DPI: 62.5-126.67.

Comments. *Neoponera villosa* is a medium-sized to relatively large species in the *N. foetida* group (Fig. 12; ☿ TLa = 10.05 – 12.93 mm; ♀TLa = 9.55 – 14.34 mm). *Neoponera bugabensis*, *N. curvinodis*, *N. insignis*, *N. inversa*, and *N. zuparkoi* are most similar to it. They can be distinguished from *N. villosa* by examining the following (differential traits indicated in parentheses): *N. bugabensis* and *N. insignis* have a convex (vs. concave) mid clypeus; *N. inversa* has a strongly to slightly concave (vs. straight) anterior nodal margin; and in *N. curvinodis* the anterior nodal margin may also be slightly concave to straight, but the nodal top is slightly curved anterad (vs. straight). The posterior nodal face of *N. curvinodis* is just convex, while in *N. villosa* besides being convex it has a tumulus (Fig. 2b). This latter feature is decisive for separating *N.*

villosa from all cited species, except *N. zuparkoi* which also has a tumulus on the same surface, but this species shows an anteriorly projected mesopleural margin, forming lobate or lamellate cuticular extension (Fig. 7a – b). In *N. villosa* the mesopleural anterior margin is only carinate or slightly lobate anteriorly (Fig 11a).

Neoponera villosa has a remarkably stable morphology across its distribution range, in comparison to other closely related congeners like *N. curvinodis* and *N. inversa* which show plasticity in some body regions, like the petiolar node (see comments under those species). The cuticular hue is the only detected variable trait in workers and queens of *N. villosa*, it can sometimes be dark brown combined with castaneous, particularly on the petiolar node (link), or simply dark brown to ferruginous brown (link). The morpho-stability in *N. villosa* is the only evident case known in the genus for a broadly-ranged lineage. Current observations converge with those of Mendoza-Ramírez et al. (2019) who demonstrated the existence of genetic (mitochondrial) cohesiveness between its populations, which in turn is reflected on their minimally variable external morphology. Arguably, this could be the result of a relatively young divergence from its most recent ancestor which, according to said authors, occurred during the late Pliocene to middle Pleistocene (3.03–1.26 mya), or even more recently in the late Pleistocene (0.75–0.3 mya).

Fernandes et al. (2014) noted that specimens from near the equator have darker mesosoma, gaster and legs, while Mendoza-Ramírez et al. (2019) detected that certain specimens from Peru and Colombia, which show slightly higher genetic distances than the rest in their specimen pool, have a more pilose mesosoma and gaster. In *Neoponera*, color and pilosity are usually variable traits not useful as species-level diagnostics, unless these clearly differ from those of other related lineages. In this treatment, no major external character variations were observed among the material examined. Thus, it appears that present genetic cohesiveness in *N. villosa* would be correlated with its morphological stability. Yet, this is a rare case in the genus and additional specimens from further South American regions and biomes need to be included in Mendoza-Ramírez et al.'s data set so as to confirm that hypothesis.

Within the *N. foetida* clade, *N. foetida* and *N. villosa* are ancestral to three described lineages: *N. curvinodis*, *N. inversa*, and *N. zuparkoi*, and also to the morphospecies *N.* ecu2923 (Troya et al. unpublished), the latter considered here a variation of *N. zuparkoi* (see comments

under that species). All being relatively young as their respective branches are comparatively short. Of these, populations of *N. inversa* and *N. curvinodis* show evident plasticity. As for the other two no inference is possible since scant specimens were examined. Is plasticity in those lineages a signature of ongoing speciation? Are these populations still in course of stablishing differentiated phenotypes? in contrast to what is seen in *N. villosa* and *N. foetida* whose morphology is significantly less variable. To tackle these questions more material and approaches are required rather than just morphology-driven inferences. Since *N. inversa* and *N. curvinodis* are so similar, and thus far, no evidence seems to indicate they occupy different ecological niches, they could even represent a single but highly variable species.

Neoponera villosa has the broadest latitudinal range of all species in the genus; it spans from central-eastern Texas to northern Argentina, and this taxon is also amongst the most commonly found. Only *N. apicalis*, and *N. verenae* Forel have a similar broad distribution. According to Antmaps.org, only three Brazilian states, Piauí, Alagoas and Sergipe lack records of this taxon. *Neoponera villosa* also inhabits a wide range of biomes and ecosystems, including: the Central and Southern mixed grasslands in central-southern Texas, the drylands of the Tamaulipan Mezquital in southern Texas and northeastern Mexico, the Mexican matorrales (xeric schrublands) of the Meseta Central, the Central American Isthmian Atlantic and Pacific moist forests, the Chocó-Darién, the Venezuelan xeric shrublands of the Cordillera de la Costa, a number of sites in Amazonia as well in all Brazilian biomes, the Bolivian Yungas, the dry and humid Chaco of Argentina and Paraguay, among others. This species mostly likes humid, lowland forests from near the sea level up to about 1400 m elevation, with a record extreme of 2500 m in the city of Bogotá, Colombia. This latter though may just be an interception and not a specimen from a truly established population.

Natural history notes. *Neoponera villosa* is a heavily studied species in several research lines, see for example, comments on biology and ecology in Perez et al. (1985), Dejean (1990), Longino (2010), Mackay and Mackay (2010), Fernandes et al. (2014), Pérez-Lachaud et al. (2021). Along with *N. apicalis* these are perhaps the most well-known lineages in the genus with respect to several fields of knowledge, but probably mostly in behavioral biology.

Material examined. 188☿, 14♀, 18♂. **ARGENTINA** • 1☿; Puerto Iguzú, Parque Nacional Iguazú; -25.6831, -54.4546; alt. 180m; 1905-07-08; Peres I. leg.; (DZUP). **BOLIVIA –**

La Paz: • 1☿; 30 km N Apolo; -14.48, -68.52; alt. 860m; 1993-09-08; Pease, G. leg.; (PSWC). – **La paz:** • 2☿; Sarampiuni; -15.4, -68.0833; alt. 754m; 2005-02-13; Rodriguez, J. leg.; Malaise; (DZUP). **BRAZIL – Acre:** • 1☿; 6 km E of Porto Walter; -8.25, -72.8; alt. 239m; 1997-02-05; Caldwell, J. P. leg.; (CPDC). – **Amapá:** • 1☿; Rod. Duque de Caixas, Km 9; 0.0361, -51.1322; alt. 21m; 1997-10-19; Vilhena, J. leg.; (INPA). – **Amazonas:** • 1♂; Amana lake; -2.6003, -64.6795; alt. 52m; 1979-09-28; Best, R. leg.; light trap; (INPA). • 1♂; Amana lake; -2.6003, -64.6795; alt. 52m; 1979-09-08; Best, R. leg.; light trap; (INPA). • 1☿; Balbina; -0.1918, -59.469; alt. 27m; 1992-07-04; Keiroz, M. leg.; (CPDC). • 1☿; Br. 174, Km 44; -2.724, -60.0472; alt. 72m; 1994-06-24; Harada, A. leg.; (INPA). • 1☿; Marchantaria island, Camaleão lake; -3.25, -59.9667; alt. 7m; 1992-09-02; Adis, J.; et al. leg.; fogging; (INPA). • 1☿; Marchantaria island, Camaleão lake; -3.25, -59.9667; alt. 7m; 2008-05-29; (INPA). • 1☿; Reserva Florestal Adolpho Ducke, Instituto Nacional de Pesquisas da Amazônia (INPA); -2.9333, -59.9667; alt. 106m; 1991-08-21; Adis, J.; et al. leg.; (INPA). • 3♂; São Francisco; -3.1227, -58.433; alt. 17m; 2009-10-02; Fernandes, I. leg.; (INPA). • 1♀; São Francisco; -3.1227, -58.433; alt. 17m; 2009-10-02; Fernandes, I. leg.; (INPA). • 23☿; São Francisco; -3.1227, -58.433; alt. 17m; 2009-10-02; Fernandes, I. leg.; (INPA). – **Bahia:** • 3♂; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 1997/09; Santos, J. R. M. leg.; (CPDC). • 1☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; (CPDC). • 1☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 2012-12-19; Silva, J. A. leg.; (CPDC). • 2☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 2004-05-04; pitfall; (CPDC). • 2☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 2014-05-04; baiting; (CPDC). • 1☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.75, -39.2167; alt. 61m; 2007-05-02; Santos, P. P. leg.; (CPDC). • 13☿; 3.3 Km N main entrance CEPLAC-CEPEC, Ilhéus-Itabuna road; -14.7659, -39.2159; alt. 53m; 2017/08; Carvalho, E.; Queiroz, J. leg.; Malaise; (CPDC). • 1☿; 6 km NW of Boa Nova; -14.3167, -40.25; alt. 844m; 2014-07-05; Silva, A. P. leg.; pitfall; (CPDC). • 2☿; Buerarema; -14.9844, -39.2583; alt. 130m; 2006-05-03; Maia, J. R.; et al. leg.; (CPDC). • 1☿; Ilhéus, CEPLAC; -14.7979, -39.0375; alt. 8m; 1988-09-27; Diniz.; et al. leg.; (DZUP). • 1☿;

Itamaraju; -17.0391, -39.5293; alt. 103m; 1994-01-21; Cardoso, I. leg.; (CPDC). • 2♀; Itororó; -15.1158, -40.0646; alt. 600m; 2007-06-02; Santos, J. R. M. leg.; (CPDC). • 1♀; Mutuípe; -13.228, -39.504; alt. 220m; 1988-06-21; Crispim, J. leg.; (CPDC). • 1♂; Teixeira de Freitas; -17.5403, -39.7431; alt. 119m; 2004-09-10; Santos, J. R. M. leg.; (CPDC). • 1♀; Teixeira de Freitas; -17.5403, -39.7431; alt. 119m; 2004-09-10; Santos, J. R. M. leg.; (CPDC). – **Ceará:** • 1♀; Chapada do Aroripe; -7.134, -39.594; alt. 770m; 1997-12-28; Almeida, A. leg.; (CPDC). • 1♀; Crato ; -7.23, -39.4123; alt. 430m; 2007-07-30; Tardim, T. leg.; (CPDC). – **Distrito Federal:** • 3♀; Area de Proteção Ambiental Gama Cabeça de Veado; -15.8667, -47.8333; alt. 1080m; 2000-03-02; Mirelle, P. leg.; (DZUP). • 1♀; Area de Proteção Ambiental Gama Cabeça de Veado; -15.8667, -47.8333; alt. 1080m; 2000-03-02; Mirelle, P. leg.; (CPDC). – **Espírito Santo:** • 2♂; 13 km SW of Linhares, Bonita; -19.4667, -39.9167; alt. 17m; 2007-07-14; Santos, J. R. M. leg.; (CPDC). • 1♀; 13 km SW of Linhares, Bonita; -19.4667, -39.9167; alt. 17m; 2007-07-14; Santos, J. R. M. leg.; (CPDC). • 1♀; Linhares; -19.3947, -40.0653; alt. 31m; 1966-10-11; Niella leg.; (CPDC). • 1♀; Linhares; -19.3947, -40.0653; alt. 31m; 1991-08-14; Araujo, C. leg.; (CPDC). • 1♀; Regência; -19.646, -39.826; alt. 6m; 1994-01-23; Delabie, J. leg.; (CPDC). – **Goiás:** • 1♀; 17 km NE of Jataí, Fazenda Rio Paraíso; -17.7333, -51.6333; alt. 869m; 2011-01-28; Diniz, J. leg.; pan trap; (DZUP). • 1♀; 24 km N of Serranópoli, fazenda São Cristóvão; -18.0833, -52.0333; alt. 817m; 2009-01-10; Santos, G. G. leg.; (DZUP). • 1♀; Fazenda Lageado; -17.8791, -51.7283; alt. 849m; 1998-09-09; Diniz leg.; (DZUP). • 1♀; Fazenda Lageado; -17.8791, -51.7283; alt. 849m; 2004-09-18; Gilmar leg.; (DZUP). • 1♀; Fazenda Mato; -17.8791, -51.7283; alt. 849m; 2001-08-31; Diniz, Baiano. leg.; (DZUP). • 1♀; Ipameri; -17.719, -48.159; alt. 760m; 2011-07-01; Rodrigues, C. leg.; (CPDC). • 1♀; Jataí; -17.8833, -51.7333; alt. 771m; 2008-04-23; Fachi, M. leg.; (DZUP). • 1♀; Mineiros, Fazenda Flores.; -17.458, -52.5988; alt. 868m; 2008-07-18; Rezende, F. leg.; (DZUP). • 1♀; Pequena Central Hidrelétrica (PCH) Retiro Velho; -18.8222, -52.174; alt. 565m; 2011-04-14; Gilmar; James leg.; (DZUP). • 1♀; Pousada dos Guardiões; -18.306, -51.958; alt. 746m; 2004-05-29; Souza, K. leg.; (DZUP). • 1♀; Quirinopolis; -18.4476, -50.4552; alt. 510m; 2012-08-05; Daiane leg.; pitfall; (DZUP). – **Mato Grosso:** • 1♂; 16 km N Chapada dos Guimarães; -15.1667, -55.7833; alt. 734m; 2013-01-17; Savaris, M.; Lampert, S. leg.; (DZUP). • 2♀; Barra da Garça; -15.8914, -

52.2619; alt. 313m; Negrett leg.; (DZUP). • 1♀; Chapada dos Guimarães; -15.45, -55.9; alt. 726m; 1983-12-01; (DZUP). • 1♀; Cuiabá; -15.6008, -56.0968; alt. 172m; 1985-02-19; Zanuto, M. leg.; Malaise; (MPEG). • 1♀; Fazenda Burití; -13.8333, -56.0667; alt. 459m; 1996-05-05; Ribeiro, G. C.; Mendes, H. F. leg.; (DZUP). • 2♀; Nhambiquara; -12.85, -59.3; alt. 464m; 1960-11-01; Alvarenga, M. leg.; (DZUP). • 1♀; Poxoréu, Ponte do Santo; -15.826, -54.4016; alt. 375m; 2005-07-23; Diniz.; et al. leg.; (DZUP). • 1♀; Sapezal, Fazenda Tupanci; -13.5479, -58.8161; alt. 560m; 2017-12-10; Ferreira, J. leg.; pitfall; (DZUP). • 2♀; Serra Roncador; -11.1667, -52.0833; alt. 303m; 1968-07-13; Laroca & Azevedo. leg.; (DZUP). • 1♀; Tangará da Serra; -14.6182, -57.4877; alt. 390m; 2008-05-30; Maria, P. R. leg.; (CPDC). • 1♀; UNEMAT- campus; -9.8833, -56.0833; alt. 287m; 2015-06-27; dos Santos, S. R. leg.; (DZUP). – **Mato Grosso do Sul:** • 1♀; 6km W of Jardim; -21.4833, -56.2167; alt. 316m; 2012-12-03; Savaris, M.; Lampert, S. leg.; (DZUP). • 1♂; 7 km NW of Bonito; -21.1, -56.55; alt. 362m; 2011-12-12; Savaris, M.; Lampert, S. leg.; Light trap; (DZUP). • 1♀; Corumbá; -19.0, -57.65; alt. 124m; 2016-01-13; Filho, R., et al. leg.; hand collected; (DZUP). • 1♀; Fazenda Nhumirim; -18.988, -56.619; alt. 106m; 2016-07-18; Filho, R., et al. leg.; pitfall; (DZUP). • 2♀; Fazenda olho d'agua; -19.6742, -51.1903; alt. 385m; 1972-07-12; Diniz, J. leg.; (DZUP). – **Minas Gerais:** • 1♀; Pandeiros; -15.4833, -44.75; alt. 510m; 2014-06-16; Santiago, et al. leg.; pitfall; (DZUP). • 2♀; Parque Estadual do Río Doce; -19.75, -42.6167; alt. 307m; 2015-10-14; Leponce, M, et al. leg.; (DZUP). • 1♀; Patrocínio; -19.1833, -47.0333; alt. 896m; 2011-06-06; Frizzo, T. leg.; (DZUP). • 1♀; Santana do Riacho; -19.1685, -43.7148; alt. 764m; 2001-02-19; Soares, S. M. leg.; (CPDC). – **Paraná:** • 1♀; 4 km SE Santa Terezinha de Itaipu; -25.4667, -54.35; alt. 296m; 2017-07-25; Filho, R., et al. leg.; pitfall; (DZUP). • 1♀; Foz do Iguaçu; -25.5, -54.5833; alt. 206m; 1966-12-03; (DZUP). • 1♀; Guairá; -24.0833, -54.2333; alt. 260m; 1982-09-01; Cordeirol, A. M. leg.; (DZUP). • 1♀; Guairá; -24.0833, -54.2333; alt. 260m; 1982-08-01; Cordeirol, A. M. leg.; (DZUP). • 1♀; Guairá; -24.0833, -54.2333; alt. 260m; 1982-09-01; Cordeirol, A. M. leg.; (DZUP). • 1♂; Reserva Natural Guaricica, Guaricica trail; -25.3, -48.65; alt. 36m; 2008/04; Feola, G. leg.; Malaise; (MEPN). • 2♀; São Camilo; -24.2667, -53.8333; alt. 335m; 2013-02-01; Gonçalves, R.; Artmann, N. leg.; Malaise; (DZUP). • 1♀; São Camilo; -24.3, -53.9167; alt. 330m; 2013-02-01; Gonçalves, R.; Artmann, N. leg.; Malaise; (DZUP). –

Paraíba: • 1☿; Universidade Federal do Paraíba; -7.143, -34.85; alt. 47m; 1995-04-02; Santos, M. leg.; (CPDC). – **Pará:** • 1♀; Bajurú; -1.51, -48.04; alt. 13m; 1978-01-12; França, W. leg.; (MPEG). • 1☿; Monte Dourado- área 75; -0.7, -52.7; alt. 50m; 2010-11-10; Marsh, C. J. leg.; (DZUP). • 1☿; Parque Nacional Amazonia; -4.3799, -56.781; alt. 99m; 1978-11-13; Overal, W. leg.; (MPEG). • 1☿; Xingu river, right shore; -2.8817, -52.0095; alt. 4m; 2000-12-12; Maciel, C.; Dias, J. leg.; Malaise; (MPEG). – **Rio Grande do Norte:** • 1☿; Parque do Jiqui; -5.9071, -35.1984; alt. 26m; 2008-11-04; Pinheiro, M. P. G. leg.; (CPDC). – **Rio de Janeiro:** • 1☿; Conceição de Malabu; -22.0839, -41.8723; alt. 51m; 1978/09; Alvarenga, M. leg.; (MPEG). • 1☿; Ilha da Gipóia; -23.0333, -44.35; alt. 113m; 1981-01-22; Rosado leg.; (DZUP). • 1☿; Maricá; -22.9194, -42.8187; alt. 32m; 2009-06-18; (DZUP). • 1☿; Universidade Federal Rural do Rio de Janeiro; -22.7713, -43.6863; alt. 23m; 2004-02-03; Delabie, J. H. C. leg.; (CPDC). • 1☿; Vila do Abraão; -23.1413, -44.1685; alt. 5m; 2012-08-29; Queiroz, J.; et al. leg.; (CPDC). – **Rondônia:** • 1☿; CEPLAC; -10.7167, -62.2333; alt. 359m; 2016-12-14; Silva, E. leg.; arboreal pitfall; (MPEG). • 1☿; Parque Estadual do Guajara-Mirim, 18 km SW of Nova Dimensão; -10.3167, -64.55; alt. 152m; 1998-02-12; Santos, J. R. M. leg.; hand collected; (CPDC). – **Roraima:** • 1☿; Estação Ecológica Caracaraí; 1.7764, -61.3049; alt. 71m; 1976-04-30; Nilu leg.; (INPA). • 1♀; Parque Nacional do Viruá; 1.4412, -61.0437; alt. 406m; 2017-12-06; Lattke, J.; et al. leg.; (DZUP). – **São Paulo:** • 1♂; Corumbataí; -22.222, -47.623; alt. 580m; 1963-09-01; (DZUP). • 1☿; Fazenda Boa Vista; -15.8947, -52.2624; alt. 308m; 2003-11-26; Diniz leg.; (DZUP). • 1☿; Fazenda Boa Vista; -15.8947, -52.2624; alt. 308m; 2003-11-26; Diniz.; et al. leg.; (DZUP). • 1☿; Ipaussu; -23.0552, -49.6237; alt. 575m; 1928-09-20; Pessoa, S. B. leg.; (DZUP). • 1☿; Itirapina; -22.2526, -47.8156; alt. 804m; 1990-04-10; Paiva, R. leg.; (DZUP). • 1☿; Itirapina-Cerrado; -22.25, -47.8167; alt. 762m; 2015-11-09; Martins, A. L.; Moericke, P. S. leg.; (DZUP). • 4♀; São José do Rio Preto; -22.1784, -42.966; alt. 601m; 1973-09-02; Taddei leg.; (DZUP). • 2♀; São José do Rio Preto; -22.1784, -42.966; alt. 601m; 1979-08-20; Latorre, J. R. leg.; (DZUP). • 1♀; São José do Rio Preto; -20.7851, -49.3599; alt. 533m; 1978-11-22; (DZUP). • 1♀; São Sebastião ; -23.8064, -45.4018; alt. 2m; 1978-09-04; Diniz, J. leg.; (DZUP). – **Tocantins:** • 1☿; Pium; -10.4433, -49.1794; alt. 275m; 2009; Leite, G. leg.; (CPDC). **COLOMBIA** • 1☿; Parque Nacional Natural Amacayacu, Matamata; 3.6833, -70.25; alt. 150m;

2001-02-02; Chota, D. leg.; Malaise; (IAvH). • 1♀; Parque Nacional Natural Serranía de La Macarena; 2.9692, -73.9006; alt. 1253m; 1986/10; (MUSENUV). • 1♀; Vía Tarapacá km 11; 2.9, -69.744; alt. 85m; 2002-05-27; (ICN). – **Chocó:** • 1♀; Estación Silvicultura al Bajo Atrato; 7.0406, -77.3378; alt. 149m; 1992-07-01; Mendoza, L. leg.; hand collected; (ICN). • 1♀; Parque Nacional Natural Los Katios, Centro administrativo Sautatá; 7.85, -77.1335; alt. 96m; 2001-05-01; Ramírez, D. leg.; Malaise; (IAvH). – **Cundinamarca:** • 1♀; Bogotá; 4.64, -74.086; alt. 2500m; 1985-05-24; Parada, C. leg.; (ICN). – **Magdalena:** • 1♀; Caribio; 10.76, -75.13; alt. 26m; 1982/10; Norberto, H. leg.; (MUSENUV). – **Meta:** • 1♀; La Virginia; 3.463, -73.622; alt. 300m; 1983-03-20; (ICN). • 1♀; Parque Nacional Natural Serranía de La Macarena; 2.9692, -73.9006; alt. 1253m; 1986/10; (MUSENUV). • 1♀; Parque Nacional Natural Serranía de La Macarena, Vereda Caño Curia; 3.4067, -73.9537; alt. 520m; 1992-07-18; Villalba, W. leg.; (ICN). • 1♀; Parque Nacional Natural Serranía de La Macarena, Vereda Caño Curia; 3.4067, -73.9537; alt. 100m; 2004-01-16; Villalba, W. leg.; Malaise; (IAvH). • 1♀; Puerto Gaitán; 4.312, -72.082; alt. 150m; 1975-12-22; Mackay, W.; Mackay, E. leg.; (ICN). – **Nariño:** • 1♀; Iscuande; 2.45, -77.979; alt. 6m; 1976/04; (MUSENUV). – **Putumayo:** • 1♀; Parque Nacional Natural La Paya; 0.1551, -75.2231; alt. 219m; 2008-02-20; Jiménez, L. leg.; (ICN). • 1♀; Parque Nacional Natural La Paya; 0.1551, -75.2231; alt. 219m; 2008-02-20; Jiménez, L. leg.; Malaise; (ICN). – **Risaralda:** • 1♀; Santa Cecilia; 5.238, -76.036; alt. 1300m; 1992-02-01; Fernández, F. leg.; (ICN). – **Valle del Cauca:** • 1♀; Vereda Campo Alegre; 3.8167, -76.5167; alt. 1413m; 1984-02-05; Cepeda, O. leg.; (ICN). **ECUADOR – Esmeraldas:** • 1♀; Reserva Ecológica Cotacachi Cayapas, La Tabla, 7 km EES Playa de Oro; 0.845, -78.744; alt. 120m; 2001-04-01; Araujo, P.; et al. leg.; fogging; (MEPN). – **Napo:** • 1♀; Limoncocha; -0.3998, -76.6001; alt. 280m; 1970-07-02; Kazan, P. leg.; (QCAZ). – **Orellana:** • 2♀; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-08; Erwin, T.; et al. leg.; fogging; (MEPN). – **Pastaza:** • 1♀; Parque Nacional Yasuní, Bameno, sendero Curaray 2; -1.301, -76.143; alt. 240m; 2014-01-13; Troya, A.; Duque, P. leg.; fogging; (MEPN). – **Sucumbíos:** • 1♀; Nuevo Sucumbíos; -0.229, -77.326; alt. 750m; 2005-12-27; Troya, A. leg.; fogging; (MEPN). • 1♀; Reserva de Producción Faunística Cuyabeno, Trocha Zábalo-Güepi; -0.26, -75.69; alt. 270m; 2000-08-08; Araujo, P. leg.; fogging;

(MEPN). **FRENCH GUIANA – Cayenne:** • 1☿; Campus, P2; 5.1728, -52.6552; alt. 2m; 2018-10-31; Petitclerc, F.; Jackie, O.; Fichaux, M.; Lepage, P. leg.; Winkler48h; (EcoFoG). • 1☿; Paracou Station; 5.2833, -52.9; alt. 72m; 2009/04; Groc, S. leg.; Winkler; (CPDC). • 1☿; Sinnamary; 5.3746, -52.9547; alt. 7m; 1999-08-15; Durou, S. leg.; (CPDC). – **Saint-Laurent-du-Maroni:** • 2☿; Awala-Yalimapo; 5.691, -53.9328; alt. 5m; 2008-05-17; Groc, S. leg.; (CPDC). • 1☿; Cayenne; 4.8228, -53.2764; alt. 126m; 2002/04; Orivel, J. leg.; (CPDC). **MEXICO – Chiapas:** • 1☿; Tapachula; 14.9, -92.26; alt. 173m; 1992-05-10; Fresnau, D. leg.; hand collected; (CPDC). – **Nuevo León:** • 1☿; Parque Natural La Estanzuela Monterrey; 25.5488, -100.2708; alt. 700m; Velasco, J. leg.; ([no museum voucher]). – **Oaxaca:** • 1☿; 2km E, La Grua, Chacahua; 15.7028, -96.6031; alt. 17m; 1985-11-30; Quiroz, L. leg.; (CPDC). – **Puebla:** • 1☿; Cascada Las Hamacas, 8km ENE Cuetzalán; 20.0343, -97.4512; alt. 280m; 2016-07-03; Longino, J. leg.; search; (JTLC). – **Quintana Roo:** • 2☿; Chetumal; 18.5009, -88.2961; alt. 6m; 2011/09; Poteauj, Ch. leg.; (CPDC). – **San Luís de Potosí:** • 1☿; Area Natural Protegida Parque Estatal Palma Larga; 21.8712, -99.9598; alt. 990m; 2021-06-25; Stevens, L. leg.; ([no museum voucher]). – **Veracruz:** • 3♂; La Mancha; 19.595, -96.3955; alt. 9m; 1998-05-06; Fresneau, D. leg.; (CPDC). • 1☿; La Mancha; 19.595, -96.3955; alt. 9m; 1997-06-10; Quiroz, L. leg.; (CPDC). • 1☿; Los Tuxtlas, 10km NNW Sontecomapan; 18.5833, -95.0833; alt. 200m; 1985-03-24; P.S. Ward leg.; (PSWC). • 3☿; Reserva de la Biosfera Los Tuxtlas; 18.4476, -95.2044; alt. 345m; (CPDC). – **Yucatán:** • 1☿; Chichén Itzá; 20.6833, -88.5667; alt. 33m; 2004-08-10; Zappi, I. leg.; hand collected; (MSNG). • 1☿; [no locality given]; 23.0, -102.0; (ZSBS). **NICARAGUA – Matagalpa:** • 3☿; RN Cerro Musún; 12.9549, -85.2303; alt. 620m; 2011-04-30; Prebus, M. leg.; hand collected; (MEPN). – **Región Autónoma del Atlántico Sur:** • 1♀; RN Kahka Creek; 12.6674, -83.7224; alt. 40m; 2011-06-06; Longino, J. leg.; hand collected; (JTLC). • 1☿; RN Kahka Creek; 12.6674, -83.7224; alt. 40m; 2011-06-06; Longino, J. leg.; hand collected; (JTLC). **PANAMA – Colón:** • 1☿; Bosque Protector San Lorenzo; 9.2833, -79.9667; alt. 13m; 2003/10; Dejean, A.; et al. leg.; (CPDC). – **Darién:** • 1☿; Cana; 7.7167, -77.7; alt. 500m; 1987-08-23; Olson, D. M. leg.; (PSWC). **PARAGUAY – Canindey√∫:** • 1☿; Reserva Natural del Bosque Mbaracayú, Lagunita; -24.1333, -55.4333; alt. 200m; 1996-09-20; A.L. Wild leg.; (ALWC). **PERU – Cusco:** • 1☿; Estación

Biológica Villa Carmen, 1.5 Km N Pillcopata; -12.8833, -71.4; alt. 521m; 2013-08-05; Ant course 2013 leg.; (DZUP). – **Loreto:** • 2☿; Jenaro Herrera; -4.9082, -73.6668; alt. 108m; 1989-10-22; Couturier, G. leg.; (CPDC). **UNITED STATES – Texas:** • 1☿; 9 km NE Sinton; 28.1026, -97.4561; alt. 17m; 1956/04; (MEPN). **VENEZUELA – Aragua:** • 1☿; La Toma. Rancho Grande; 10.0669, -67.5485; alt. 1100m; 1992-04-07; García, J. L.; Chacón, A. leg.; T. Intercep; (MIZA).

Geographic range. United States (central* and southern Texas), Mexico (Campeche*, Chiapas, Guerrero*, Hidalgo*, Jalisco*, Distrito Federal*, Michoacán*, Nayarit*, Nuevo León, San Luís Potosí, Oaxaca, Puebla*, Querétaro*, Quintana Roo, Sonora*, Sinaloa*, Tabasco*, Tamaulipas*, Veracruz, Yucatán), Belize*, Guatemala*, El Salvador*, Honduras*, Nicaragua, Costa Rica*, Panama, Puerto Rico*, Trinidad and Tobago*, Venezuela*, Colombia, Guyana*, Suriname*, French Guiana, Ecuador, Peru, Bolivia, Brazil (Acre, Amapá, Amazonas, Bahía, Ceará, DF, Espírito Santo, Maranhão*, Mato Grosso, Distrito Federal, Goiás, Minas Gerais, Espírito Santo, Mato Grosso, Mato Grosso Do Sul, Pará, Paraíba, Paraná, Rio de Janeiro, Rio Grande do Norte, Rondônia, Santa Catarina*, São Paulo, Tocantins), Paraguay*, Argentina (Chaco*, Formosa*, Jujuy*, Misiones, Salta*, Tucumán*). * Record from literature.

***Neoponera zuparkoi* (Mackay & Mackay 2010)**

Fig. 31b (distribution).

Pachycondyla zuparkoi MacKay & MacKay, 2010: 580, Figs. 114, 267, 685-687. ☿ holotype, Peru, Huánuco, Monson Valley, Tingo María, 15.x.1954, E.I. Schlinger & E.S. Ross (leg.), (CASC) [not examined].

Combination in *Neoponera*: Schmidt & Shattuck, 2014: 152.

Status as species. Fernandes et al., 2014: 134; Bezděčková et al., 2015: 124.

Worker (and probably queen) diagnosis. Antennal scape, when pulled posterad, exceeding posterior head margin by 1.5 to two times apical scape width; anterior mid clypeal margin straight to convex (link); humeral carina present, not salient (Fig. 7d); anterior mesopleural margin with anteroventrally directed lobate (Fig. 7b) or lamellate projection (Fig. 7a); posterolateral propodeal margin carinate, carina not raised, without crenulae (Fig. 11b); anterior

margin of petiolar node straight to feebly concave, posterolateral margin of node carinate, posterior nodal face with tumulus (Fig. 2b); prora well-developed with round tip (link).

Worker. Measurements (*n* = 5): HW: 2.5-2.75; HL: 2.4-3.06; EL: 0.65-0.75; SL: 2.4-2.62; WL: 3.95-4.53; PrW: 1.6-1.94; MsW: 1.15-1.38; MsL: 0.8-1.0; PW: 1.35-1.44; PH: 0.95-1.44; PL: 1.0-1.34; GL: 3.95-5.0; A3L: 1.3-1.75; A4L: 1.55-1.94; A3W: 1.95-2.19; A4W: 2.05-2.25; TLa: 10.75-12.56; TLr: 11.95-13.69. **Indices.** CI: 87.72-114.58; OI: 25.45-28.57; SI: 87.27-102.0; MsI: 129.03-150.0; LPI: 80.0-126.32; DPI: 106.98-140.0.

Queen and male. Unknown.

Comments. *Neoponera zuparkoi* is a medium-sized taxon in the *N. foetida* group (Fig. 12, ☿ TLa = 10.8 – 12.56 mm), and is very similar to *N. villosa*, *N. inversa*, *N. curvinodis*, and especially to the morphospecies *N.* ecu2923 (link) which I consider a variant of *N. zuparkoi* (see below), and hereafter refer to it as *N. zuparkoi*_var. These four lineages are closely related according to the phylogeny of the genus (Troya et al. unpublished). The lobate mesopleural projection of *N. zuparkoi* is the easiest form to separate it from those species. In *N. zuparkoi*_var the mesopleural lobe is expanded in the form of a lamella-shaped projection (Fig. 7a) which is significantly different from the common mesopleural carina present in all species of the *N. foetida* group, but also in all species of the genus. The humeral carina of *N. zuparkoi* is not absent, as stated by Mackay and Mackay (2010) and Fernandes et al. (2014), it is present but does not protrude laterally (salient) from the cuticle. Thus, this carina is somewhat poorly developed as compared to all other species in the *N. foetida* group. However, as previously observed in *N. curvinodis* and *N. inversa*, the humeral carina is subject to plasticity, and since just three specimens of this species were examined: two from southern Peru, and one from Rondônia, Brazil, no strong reliance on this character is possible, at least for this species. Likewise, the anterior nodal margin is variable in *N. zuparkoi* (concave to straight) as in said species. This leaves the putative autapomorphic lobate and/or lamella-shaped mesopleural projection as the only distinguishing feature, potentially useful to effectively separate it from all other species in the *N. foetida* group. Yet, this trait is apparently another body region which shows certain degree of plasticity in these related group of species, except for *N. villosa*. This margin is mostly carinate, not protruding, for example in *N. curvinodis* and *N. inversa*, but sometimes this carina is also slightly expanded in those species, never anteriorly protruding as in *N. zuparkoi*, however. Despite this, an untrained

eye may not find strong differences between a carinate, lobate, or lamella-shaped mesopleural margin. Differences become more obvious only after examining numerous specimens. The type locality of *N. zuparkoi* is the central Peruvian Amazonian locality of Tingo María; perhaps collecting more material in these biologically poorly known and vast region would shed further light on the morphology of this species which seems to represent a morphological link between *N. inversa* and *N. curvinodis* + *N. villosa*.

*Neoponera zuparkoi*_var is ancestral to *N. zuparkoi* in the *Neoponera* tree, but this relationship is poorly supported (Troya et al. unpublished). Since their morphology is highly similar with no strong, i.e., non-plastic morphological features justifying a potential taxonomic split, and given that scant specimens from both forms were examined (Mackay and Mackay 2010 erected *N. zuparkoi* based on a single specimen), I leave *N. zuparkoi*_var as a variant of *N. zuparkoi* until additional evidence become available.

Neoponera zuparkoi inhabits in well-preserved lowland forests in South America. The only four known records belong from the Peruvian Ucayali moist forests, the southern Peruvian Yungas, and the western Amazonian Madeira-Tapajós moist forests in Brazil. Whereas, *N. zuparkoi*_var is known from the Napo moist forests in Amazonian Ecuador, and from the Magdalena Valley montane forests in the Colombian Andean biome.

Natural history notes. Besides being collected using fogging, Malaise, and Winkler, nothing is known about this species.

Material examined. 5☿. **BRAZIL – Rondônia:** • 1☿; 18 Km SSE, St. Elena River station; -10.9023, -62.168; alt. 230m; 1985-03-23; Torres, M. leg.; (MPEG). **COLOMBIA – Cauca:** • 1☿; Parque Nacional Natural Serranía de los Churumbelos Auka-Wasi; 4.5709, -74.2973; alt. 2512m; 1998-07-02; Bustos, J. leg.; Winkler; (MUSENUV). **ECUADOR – Orellana:** • 1☿; Parque Nacional Yasuní, 32 Km SSE Limoncocha, Onkonegare Km 39 Pompeya Sur; -0.658, -76.452; alt. 216m; 1995-02-09; Erwin, T.; et al. leg.; fogging; (MEPN). **PERU – Cusco:** • 1☿; Quince Mil, km 8; -13.2167, -70.7167; alt. 633m; 2012-08-20; Cavichioli, R.; et al. leg.; Malaise; (DZUP). **– Madre de Dios:** • 1☿; Villa Carmen Biological Station; -12.8786, -71.4809; alt. 605m; 2013-08-08; Ward, P. S. leg.; (PSWC).

Geographic range. Peru, Brazil (Rondônia).

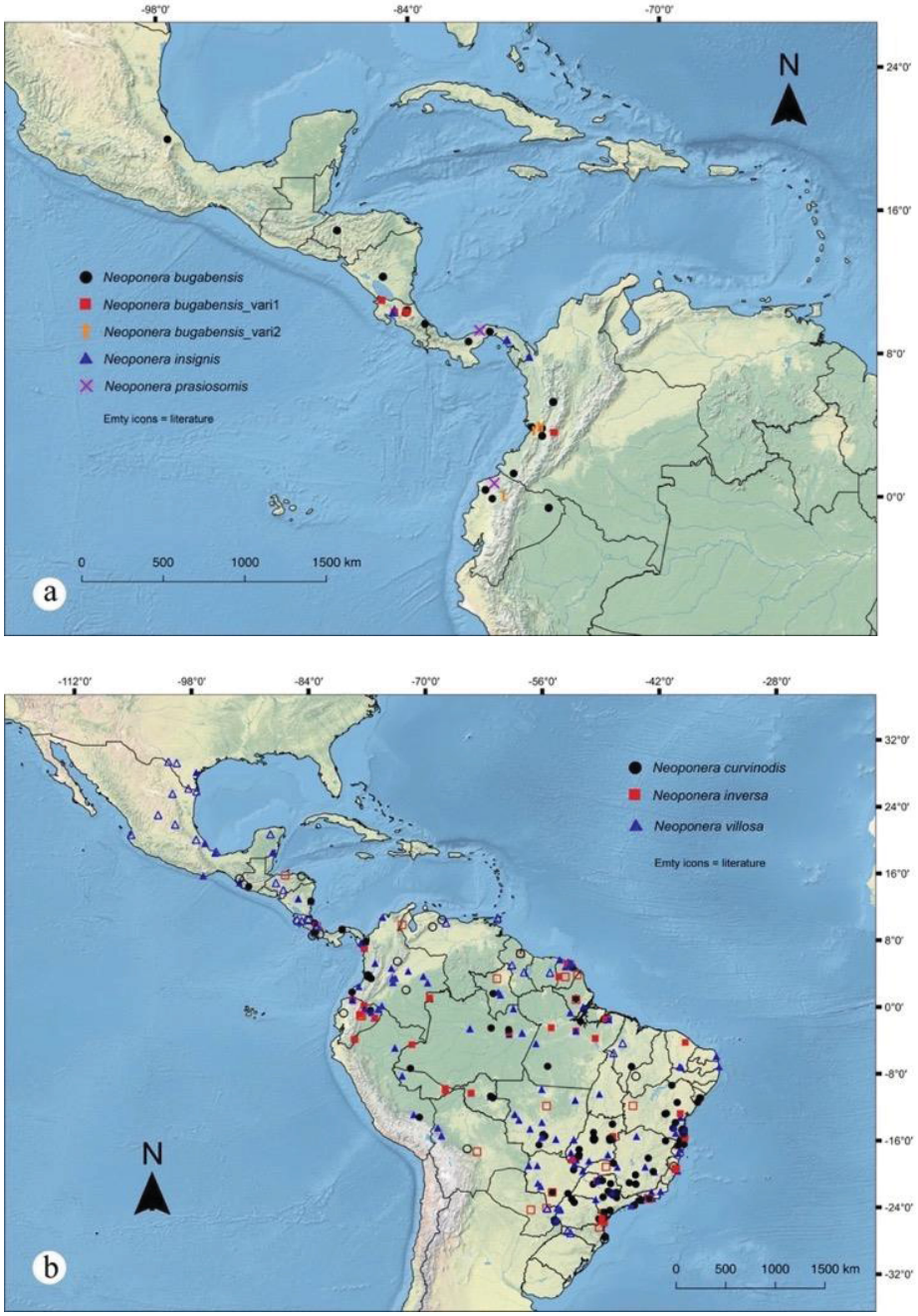


Fig. 30. Distribution of species in the *Neoponera foetida* group. **a.** *Neoponera bugabensis* (and its variants), *N. insignis*, *N. prasiosomis* sp. nov.; **b.** *Neoponera curvinodis*, *N. inversa*, *N. villosa*. Empty icons belong to the same species as those with filled icons in each figure, but these represent records obtained from the literature (see references below).

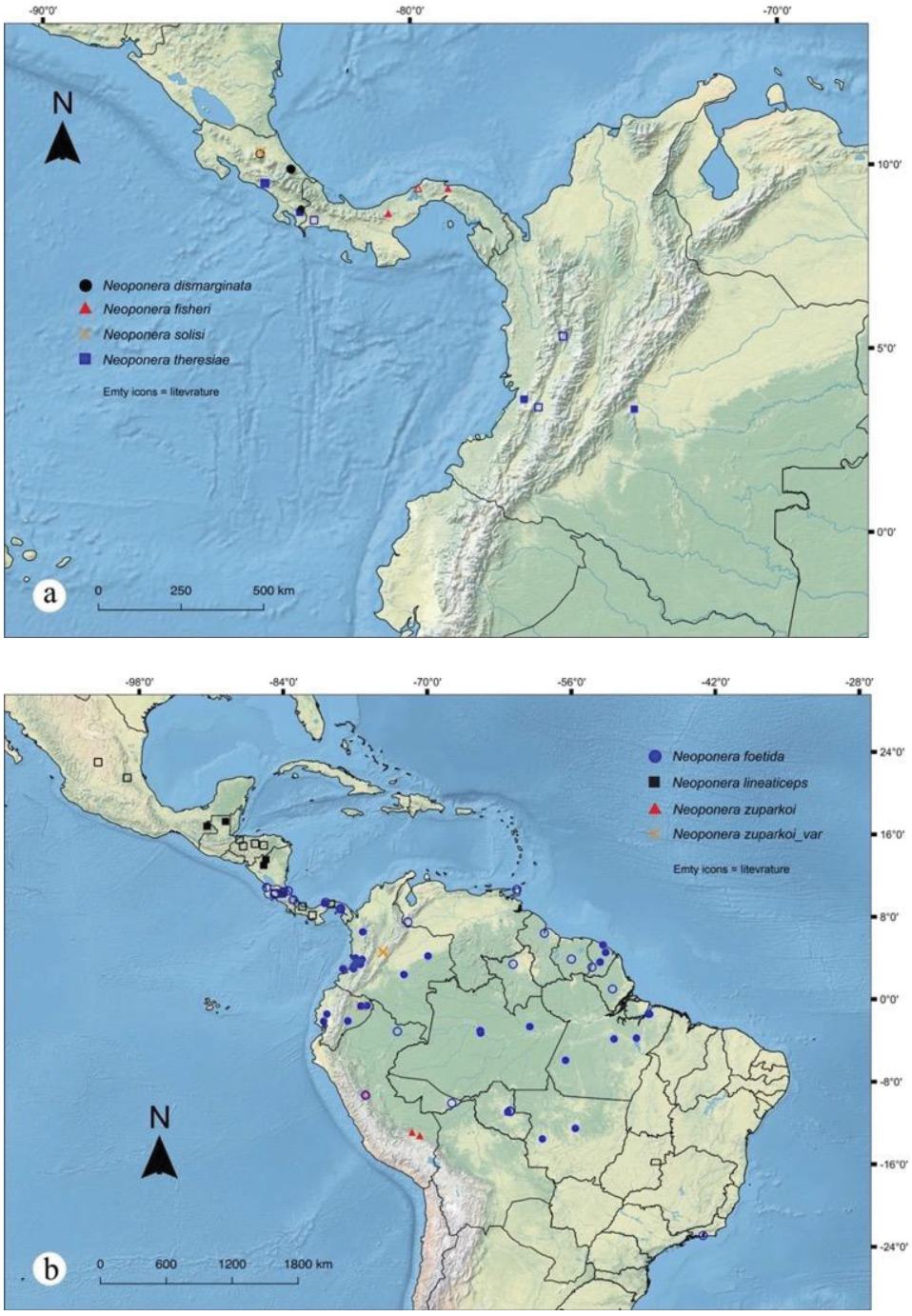


Fig. 31. Distribution of species in the *Neoponera foetida* group. **a.** *Neoponera dismarginata*, *N. fisheri*, *N. solisi, N. theresiae*; **b.** *Neoponera foetida*, *N. lineaticeps*, *N. zuparkoi* (and its variant). Empty icons belong to the same species as those with filled icons in each figure, but these represent records obtained from the literature (see references below).

The *N. emiliae* species-group

Worker-based key to species of the *N. emiliae* species-group

1 Dorsum of head and pronotum with mixture of punctae and striae (Fig. 1a, b); *N. emiliae* subclade …….. 2

Dorsum of head and pronotum costate (Fig. 1c); *N. magnifica* subclade ….. 3

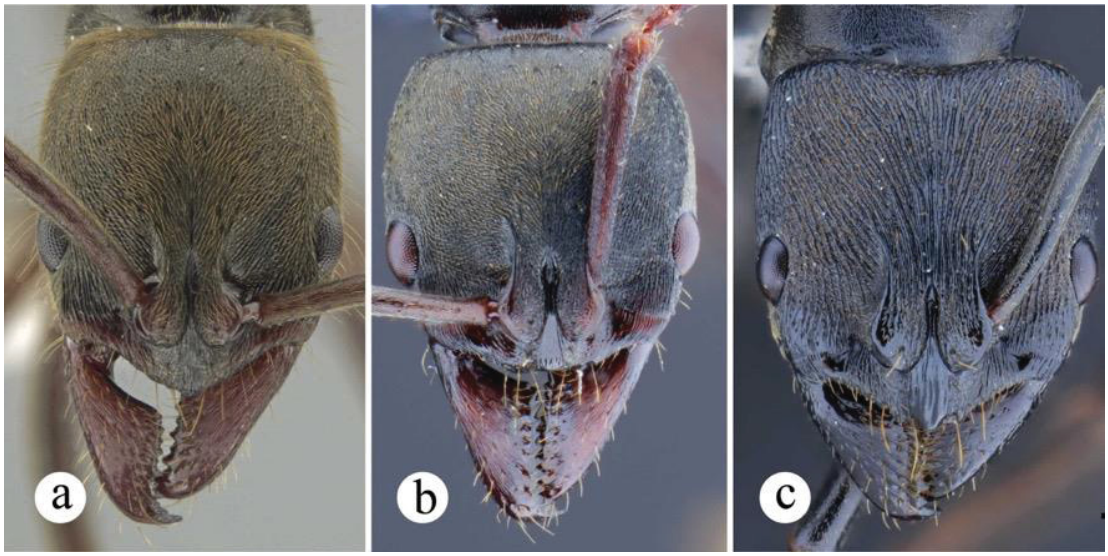


Fig. 1. Head sculpture variation. **a, b.** Punctate-striate: **a.** ☿ *N. emiliae* (JTLC: JTLC000015100), **b.** ☿ *N. metanotalis* (CPDC: ATPFOR1997); **c.** Costate (☿ *N. dropsy*, DZUP: ATPFOR1962).

2 (1) Anterior mid clypeal margin convex, relatively acute (Fig. 1a); body dorsum with abundant appressed copperish hairs (Fig. 1a, 2a); northwestern South America …….….. ***N. emiliae***

Anterior mid clypeal margin horizontally straight or weakly concave (Fig. 1b); body dorsum with pale golden appressed pilosity, significantly less abundant than in prior lead (Fig. 1b, 2b); eastern Brazil…….. ***N. metanotalis***

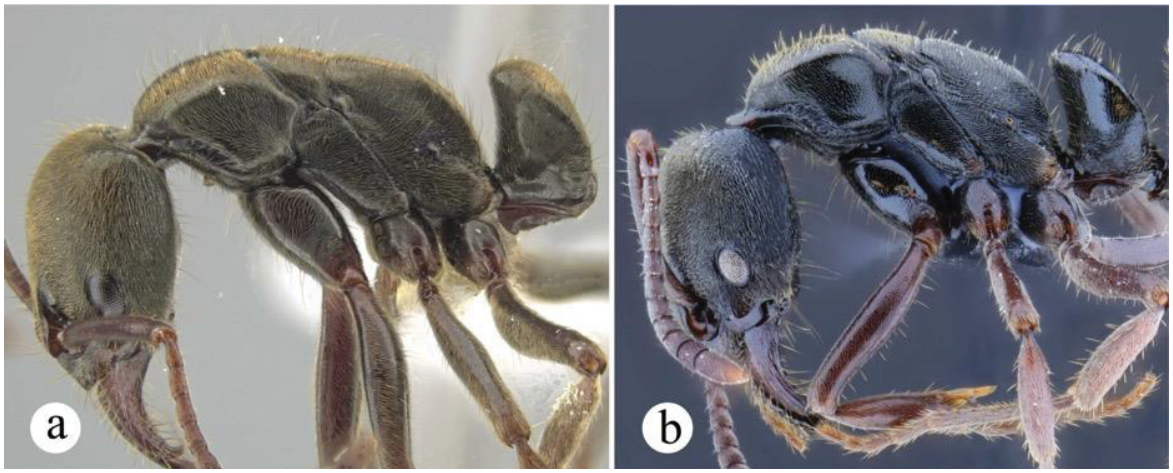


Fig. 2. Appressed pilosity. a. Abundant, copperish (☿ *N. emiliae*, JTLC: JTLC000015100); b. Less abundant, pale golden (☿ *N. metanotalis*, UFV: UFVLABECOL000625).

3 (1) Subpetiolar process notched (or concave) medially (Fig. 3a); head dorsum with two patches of appressed golden hairs (Fig. 13c); central Brazil ……..

…….. ***N. magnifica***

Subpetiolar process convex or straight medially (Fig. 3b, 12d); head dorsum with scant appressed golden pilosity (Fig. 1c), otherwise pilosity more abundant (Fig. 8c, e) but not as described in prior lead ……..…... **4**

4 (3) Posterior face of petiolar node glabrous (Fig. 4a); head dorsum with irregular, not continuous costae (Fig. 12d) better discernible on lateral side of head; eastern Brazil…….…….... ***N. glabra***

Posterior face of petiolar node striate, punctate or with mixture of both (Fig. 4b); costae on head dorsum less irregular than above, and continuous, without breaks (Fig. 8e) ……..... **5**

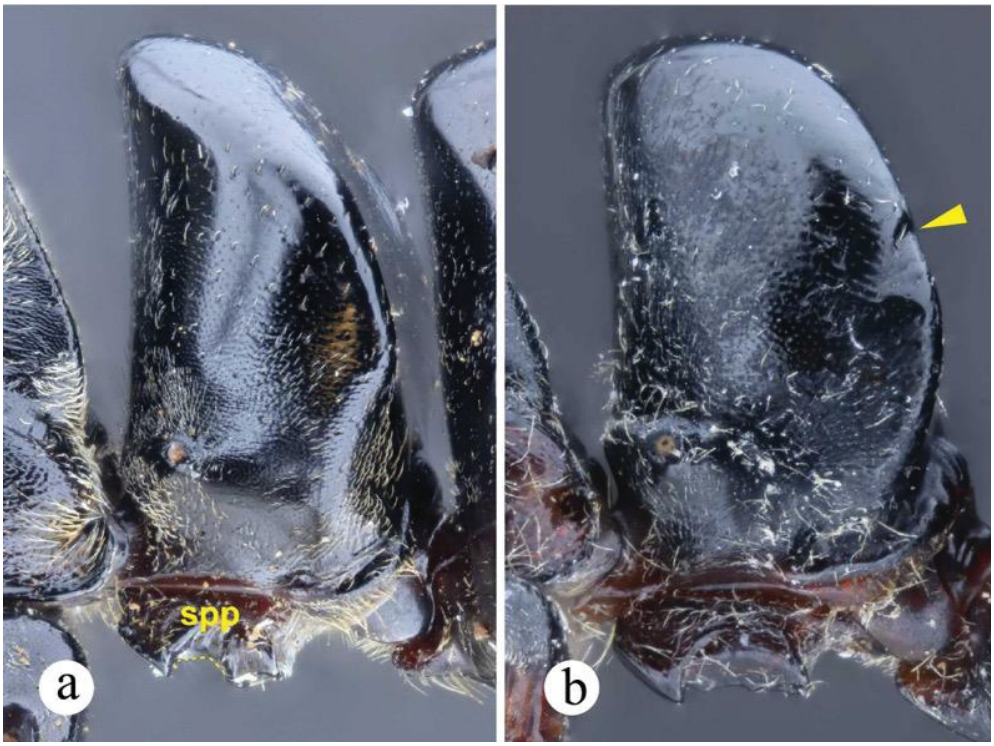


Fig. 3. Petiole in lateral view. a. Subpetiolar process notched medially (☿ *N. magnifica*, DZUP: DZUP549378); b. Subpetiolar process horizontally straight or feebly convex medially (*N. glabra*, CPDC: ATPFOR1993). **spp**: subpetiolar process. Arrowhead on **b.** shows an incision.

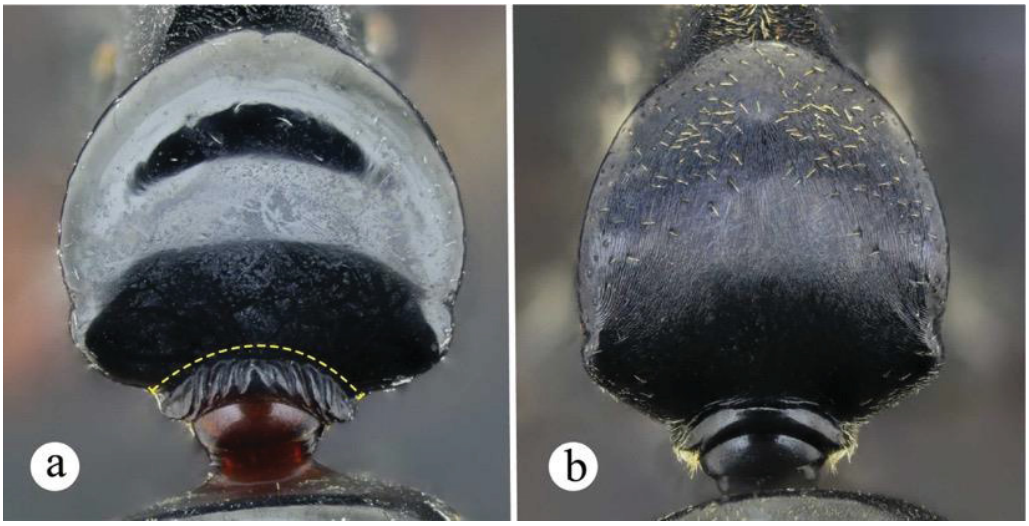


Fig. 4. Posterior face of petiolar node. **a.** Glabrous face, posteroventral nodal margin (in yellow dashed) showing scrobiculae (☿ *N. glabra*, CPDC: ATPFOR1993); **b.** Striate-punctate face, posteroventral nodal margin smooth (☿ *N. magnifica*, DZUP: DZUP549545).

5 (4) Posteroventral margin of petiolar node scrobiculate (Fig. 4a); mid-lateral margin of node with incision (Fig. 3b); meso and metapleuron mostly micropunctate (Fig. 8a); western and central Amazonia……... ***N. caxiuana***

Posteroventral margin of petiolar node smooth (Fig. 4b); mid-lateral margin of node without incision (Fig. 3a); meso and metapleuron costate (Fig. 12a) …….. 6

6 (5) Propodeum costate, except posterior face which has scattered piligerous punctae, costae on mesonotum are somewhat continued with those of propodeum (Fig. 5a, link); prora lip-shaped, comparatively small but well-discernible in lateral view (Fig. 9d); eastern Brazil……..……..... ***N. dorsilinea***

Propodeum mostly striate, dorsally with micro striae, and posteriorly with scattered piligerous punctate, costae of mesonotum reach only its posterior margin (Fig. 5b); prora tiny or vestigial, not discernible in lateral view (Fig. 10a); eastern Brazil ……..... ***N. dropsy***

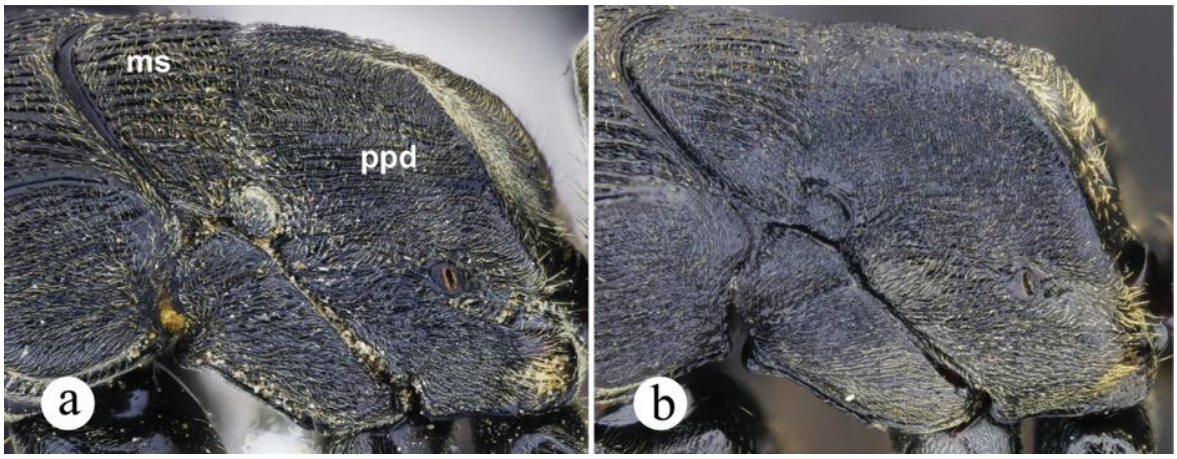


Fig. 5. Mesosoma in lateral view. **a.** Propodeum costate (☿ *N. dorsilinea*, CPDC: AT875); **b.** Propodeum striate (☿ *N. dropsy*, ATPFOR2060). **ms**: mesonotum; **ppd**: propodeum.

Taxonomy

Synoptic list

In parentheses the known castes per species: ☿ – worker; ♂ – male.

Neoponera caxiuana Troya, **sp. nov.** [Brazil: Pará; southern Colombia] (☿)

Neoponera dorsilinea Troya, **sp. nov.** [Brazil: Bahia] (☿)

Neoponera dropsy Troya, **sp. nov.** [Brazil: Bahia] (☿)

Neoponera emiliae Forel, 1901[Venezuela, Colombia, Ecuador] (☿)

Neoponera glabra Troya, **sp. nov.** [Brazil: Bahia] (☿)

Neoponera magnifica (Borgmeier, 1929) [Brazil: Goiás, Mato Grosso] (☿)

Neoponera metanotalis (Luederwaldt, 1918) [Brazil: São Paulo, Minas Gerais] (☿)

Neoponera emiliae species-group (unidentified ♂, *incertae sedis*) [Brazil: Rio de Janeiro]

Neoponera emiliae species-group differential diagnosis

For practical purpose only, and following the phylogenetic organization of *Neoponera* sensu Troya et al. (unpublished), the seven species belonging to this group can be subdivided in two subclades, both easily diagnosable because these show well-identified apomorphies: the first contains *N. emiliae* and *N. metanotalis*, while the second is composed by *N. magnifica* and four newly described species: *N. caxiuana, N. dorsilinea, N. dropsy*, *N. glabra*.

The first subclade, hereafter referred as *N. emiliae*, can be diagnosed as follows: basal (non-masticatory) mandibular margin longer than half length of internal (masticatory) margin; proximal corner of masticatory mandibular margin moderately acute, bearing at least one denticle; malar carina either present (*N. emiliae*), though not easily recognizable due to surrounding striae, or vestigial (*N. metanotalis*), here the carina is replaced by a longitudinal, shallow groove which is surrounded by striae; propodeal spiracle oval; subpetiolar process subtriangular with a straight inclined posterior region (also called dome, see further below). The second subclade, hereafter referred as *N. magnifica*, is diagnosed as follows: basal mandibular margin shorter than half length

of internal mandibular margin; proximal corner of masticatory mandibular margin round and unarmed; dorsum of head and pronotum costate; malar carina vestigial, replaced by swelling covered by surrounding costae; propodeal spiracle either oval or slit-shaped; subpetiolar process shovel-shaped (see below for extended details about this structure); epipygium medially coriaceous.

Worker (and probably queen). Species in this group are mostly dark-bodied, comparatively big-headed (in particular species of the *N. magnifica* subclade), rarely collected epigeic foragers. The ancestor of the *N. emiliae* group arguably displayed the least derived morphological and behavioral attributes of the *Neoponera* (Troya et al., unpublished). Some of these attributes related to, for example, foraging niche, and reproductive biology are possibly shared with the species allocated in the recently discovered, putative sister genus of *Neoponera*, "*N.* emiliae-2" (sensu Troya and Lattke 2022). The queen is unknown in this group though hypothetically it would be dealate ergatoid, a trait which is present in all species of "*N. emiliae*-2". The workers are overall large sized, as estimated by the variable total length accurate (TLa), when compared to workers of other species-groups (Fig. 6a); however, if only the head length (HL) or the head width (HW) are accounted for, this caste shows the largest morphospace among all *Neoponera* (Figs. 6b, c).

Workers of the *N. emiliae* group have at least two easily distinguished apomorphies: a well-marked, cross ribbed groove located on the ventrolateral pronotal margin (Fig. 10a), and a blunt, raised posterolateral propodeal carina (Fig. 10b). A third trait, the frontal carina posteriorly exceeding, or at least reaching posterior eye margin, is "almost" apomorphic because it is present in all examined specimens, except for one of *N. emiliae* from Meta, Colombia (ATPFOR2070), where this carina does not reach such eye margin. In *Neoponera*, the frontal carina is a stable feature, and the degree to which it is (apparently) extended posterad is measured by comparing their posterior limits relative to the position of the eyes on head. Therefore, another form of characterizing this last trait in species of this group is by stating that the eye is placed anteriorly on head, so that the frontal carina frequently surpasses its posterior margin. The combination of these traits plus those indicated in the key to *Neoponera* groups in Troya and Lattke (2022) should suffice to distinguish species in this group from any other in the genus.

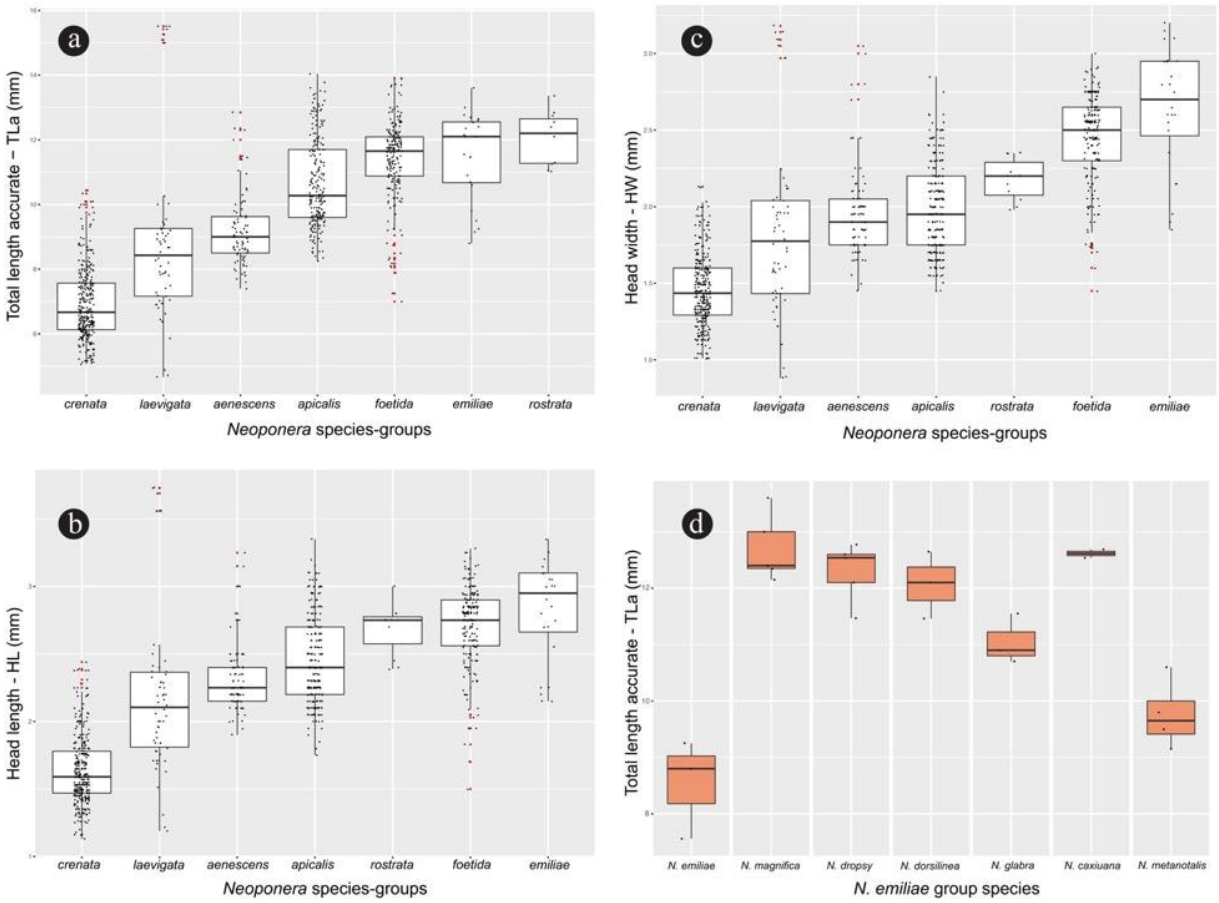


Fig. 6. Approximate size-range distribution among workers of *Neoponera* species-groups (a – c), and among species in the *N. emiliae* group (d), as estimated by the variables: Total length accurate (TLa), Head length (HL), and Head width (HW). Red dots are outliers.

The reader, however, can also use the following information to further compare specific body traits of species in this group with other *Neoponera* and even with other morphologically similar ponerines such as *Pachycondyla*, *Mayaponera*, *Rasopone*, and *N. emiliae*-2:

1) The mid clypeal margin is either convex or acute (Fig. 1a, c), or is straight to slightly concave (Fig. 1b), always projected anteriorly over the basal margin of mandible, when mandibles are closed. An acute and anteriorly projected clypeus is typically seen in most species of the *N. crenata* group, for example in *N. unidentata* (link), and in *N. concava* belonging to "*N. emiliae*-2", but in this latter species the projection is even more acute (link); the convex form, not necessarily acute, is present in many lineages across the six species-groups in the genus, plus *N.*

rostrata. The concave form, which in the *N. emiliae* group has been detected only in a variant of *N. metanotalis*, from Bahia, Brazil (ATPFOR1997), is less common in the genus, except for some species of the *N. aenescens* group where this trait is clearly displayed, for example, *N. aenescens* (link), *N. chyzeri*. Out of the genus, the concavity is found for example, in some species of *Pachycondyla*, like *P. impressa* (link), *P. crassinoda*, in *Rasopone*, like *R. ferruginea* (link).

2) Antennal scape comparatively short, either not reaching posterior head margin, when pulled posterad (only seen in *N. magnifica*, Fig.13), or exceeding such margin by one to 1.5 times apical scape width (Fig. 1b). The antennal scape is relatively long in almost all *Neoponera*, this is, exceeding posterior head margin by at least one apical scape width. Only in *N. fisheri* (link), from the *N. foetida* group, the scape is even shorter than in *N. magnifica*. In all species of "*N. emiliae*-2" the scape is very long, surpassing the posterior head margin by about 4 times apical scape width.

3) The eye is proportionally small, it occupies ca. 1/5 head length, and is placed slightly anteriorly on head (Fig. 1a – c). Except for most species in the *N. aenescens* (e.g., *N. eleonorae*, link) and *N. laevigata* (e.g., *N. marginata*, link) groups, where the eye is also placed anteriorly on head, the eye on the rest of *Neoponera* species is either placed medially on head (e.g., *N. globularia*, link), most species, or slightly posterior to head midlength (e.g., *N. apicalis*, link). In *Mayaponera*, *Rasopone* and *Pachycondyla*, the eye is always placed anteriorly on head, e.g., *P. crassinoda* (link), and occupies less than 1/5 head length. In "*N. emiliae*-2" the eye occupies ca. 1/4 (or less) of head length, and is slightly placed posterior to head midlength, for example in *N. venusta* (link).

4) The ventrolateral pronotal groove is almost exclusive for this group. Within *Neoponera*, it was regained few times, as in for example *N. goeldii*, from the *N. crenata* group; in all cases, however, the groove is not heavily sculpted (scrobiculate or cross ribbed).

5) The notopropodeal suture is present, sometimes feebly cross ribbed (only in the *N. emiliae* subclade), but does not form a groove (Fig. 11b). In many *Neoponera*, for example, *N. villosa* (link), *N. carbonaria* (link), *N. rostrata* (link), which belong to the *foetida*, *aenescens*, and the monotypic *rostrata* groups, respectively, such suture is well-marked on cuticle and grooved. In contrast, it is completely absent or vestigial in most *Pachycondyla*, feebly impressed in *Rasopone*, and usually well-marked and grooved in *Mayaponera* and in "*N. emiliae*-2".

6) The propodeal spiracle is either oval (Fig. 7f, 11a, 12a) in most species and only in two species, *N. magnifica*, and *N. maginifica*-5 it is slit-shaped (Fig. 8d), as in all other *Neoponera*. The oval form is arguably derived from the ancestral circular form which is an apomorphic trait in species of "*N. emiliae*-2". The form of the propodeal spiracle, circular/oval, or slit-shaped, is homoplastic in Ponerinae, the circular form is displayed in for example, *Mayaponera*, *Simopelta*, *Thaumatomyrmex*, which are part of the *Pachycondyla* genus-group sensu Schmidt and Shattuck (2014) where *Neoponera* belongs to, as well as in a number of other genera across that subfamily. Although these transformations are not significantly relevant in a phylogenetic context since they are frequently gained and lost across the Ponerinae (pers. obs.), these are useful for diagnosing clades and subclades in *Neoponera*.

7) The petiolar node is somewhat scale-shaped (Fig. 2a, b): higher than long in lateral view, and concave on the nodal posterior face (Fig. 3a), except for *N. emiliae* where this surface is just feebly concave to flat. This is a singular and distinctive trait of this species-group among the *Neoponera*, but is also shared with species in "*N. emiliae*-2", with some variations though. In the *Pachycondyla* group no other species shows a similar nodal shape, except perhaps for *P. procidua* (link), but the nodal posterior surface in that species is not concave but flat. In *Mayaponera*, the shape of the node could also be referred as scale-shaped, but it is evidently more triangular, as seen in lateral view, than in most species of the *N. emiliae* group.

8) The subpetiolar process is either shovel-shaped (Fig. 3a, b): posteriorly grooved, as seen in lateral view, present in species of the *N. magnifica* subclade, or subtriangular and without posterior groove, which is characteristic of the *N. emiliae* subclade). According to Troya and Lattke (unpublished revision of the *N. crenata* group) the subpetiolar process in *Neoponera* is formed by an anteriorly acute cusp or keel, and a posteriorly convex to relatively flat, sometimes inclined region, which is called "dome". A subtriangular subpetiolar process is commonly seen in most *Neoponera*, *Pachycondyla*, and *Mayaponera*, while in *Rasopone* the shovel-shaped form is the norm and potentially apomorphic (see Longino and Branstetter 2020). In "*N. emiliae*-2" both forms are present. The shovel-shaped form in the *N. emiliae* group may be straight (Fig. 3b) or concave (Fig. 3a) medially; and when the process is subtriangular the dome is either feebly convex (e.g., *N. metanotalis*, Fig. 2b), or straight (e.g., *N. emiliae*, Fig. 2a). The subtriangular form in most *Neoponera* shows a relatively high variation, for example, sometimes with a convex (e.g., some species in the *N. crenata* group – link), or relatively horizontal flat dome (e.g., *N. laevigata* – link,

N. donosoi – link), or sometimes inclined posteriorly and straight (e.g., *N. mashpi* – link) so that a true dome is not discernible.

9) The epipygium is either medially glabrous (members of the *N. emiliae* subclade), or coriaceous (members of the *N. magnifica* subclade, Fig. 9e). The glabrous surface is shared by all species in *Neoponera*, with certain modifications, for example, sometimes showing larger surfaces than others. In *Pachycondyla*, *Mayaponera* and Rasopone the epipygium is also medially glabrous.

Male. Until recently, the *N. emiliae* group was the only clade for which this caste was missing. Thanks to Julio Chaúl, from the Department of Entomology at Universidade Federal de Viçosa, who loaned to me an unidentified specimen represented on Fig. 7, the male is finally assigned to this group, although without affinities with currently known species. To put the morphology of this specimen in the genus context, the following unique and shared traits are provided so as to help distinguishing it from all *Neoponera* species, as well as from males of "*N. emiliae*-2" and *Pachycondyla*. The male caste in *Igaponera*, which is currently considered sister to *Neoponera* (Troya et al. 2022), is still unknown.

1) The clypeus is feebly convex in lateral view (Fig. 7a), and does not project anteriorly. Among *Neoponera* males, this trait is unique; the clypeus in remaining males can be: globular-shaped (broadly convex as seen laterally), either projecting anteriorly (e.g., members of the *N. laevigata* group), or not (e.g., members of the *N. foetida* and *N. crenata* groups, and *N. rostrata*); or, the clypeus is less convex than in the prior state but anteriorly projected (e.g., members of the *N. apicalis* group). The clypeus in most known males of *Pachycondyla* also have a similar shape in lateral view, but their ocelli are smaller than the antennal socket acetabulum, while in *N. emiliae* the ocelli are bigger than said structure. In "*N. emiliae*-2" the clypeus is not globular, nor feebly convex, it shows an intermediate state like in the *N. apicalis* group but it is not projected anteriorly; also, the ocelli in males of "*N. emiliae*-2" are tiny, approximately five times smaller than the antennal socket acetabulum.

2) The eye is relatively large, it occupies ca. 2/3 of head length (Fig. 7d). This is similar only to the known male of *N. rostrata*. In the remaining males in the genus the eye is smaller, its maximum length is either smaller than half head length, e.g., members of the *N. laevigata* group, or longer than half head length, e.g., members of the *N. apicalis* group, but never as indicated

above. The eye of all known *Pachycondyla* is smaller than half head length, while that of "*N. emilae*-2" is slightly longer, but not as long as in the male of the *N. emiliae* group.

3) The well-marked mesopleural sulcus reaches just a fraction of the ventral mesopleural plate. This feature is very similar to that found in the *crenata* and *foetida* groups, as well as in the two examined males of "*N. emiliae*-2". In contrast, in examined males of the *N. apicalis* group, and in *N. aenescens* (the sole examined male in the *aenescens* group), the sulcus clearly runs into the ventral mesopleural surface, almost reaching the pronotal posteroventral margin. In *N. rostrata*, the sulcus is deeply impressed on the cuticle, clearly deeper than most *Neoponera* males, and fades away just before reaching the mesopleural ventral region. In some *Pachycondyla*, the sulcus reaches the posteroventral pronotal margin, e.g., *P. crassinoda*, and in others do not, but in all examined males of that genus it exceeds the lateral mesopleural region.

4) The posterior propodeal face has a well-marked, raised carina (Fig. 7f) which runs across the entire posterolateral and posterodorsal propodeal border. A similar feature is found in males of *N. rostrata*, in *N. apicalis*, and in *N. commutata*. In all other *Neoponera* males this carina is either present but weakly raised, e.g., members of the *N. crenata* group; or entirely absent, members of the *N. foetida* group. In examined males of *Pachycondyla* the carina is also variable, it can be well-marked and raised dorsally, but vanishing ventrally, as in *P. impressa*, or well-marked and raised across the entire margin as in *P. crassinoda*. In "*N. emiliae*-2" this carina is completely absent.

5) The propodeal spiracle is oval (Fig. 7f). This is another unique feature amongst males in *Neoponera* and thus far the strongest evidence suggesting this specimen belongs to the *N. emiliae* group. In the remaining *Neoponera* species this spiracle is slit-shaped. Amongst examined workers of the *N. emiliae* group, only those belonging to the *N. emiliae* subclade show a very similar spiracular form; in workers of the *N. magnifica* subclade the spiracle is either oval, but comparatively longer than that in the *N. emiliae* subclade, or slit-shaped.

***Neoponera emiliae* group male description**. Measurements (n = 1): HW: 0.8; HL: 1.27; EL: 0.88; SL: 0.3; WL: 3; PrW: 1.22; MsW: 1.3; MsL: 1.2; PW: 0.75; PH: 1; PL: 0.85; GL: 3.5; A3L: 1.28; A4L: 1.3; A3W: 1.4; A4W: 1.56; TLa: 7.7; TLr: 8.62. Indices. CI: 62.99; OI: 110; SI: 152.5; MsI: 108.33; LPI: 85.0; DPI: 88.24.

Note: this specimen is still unassignable to any species; due to its oval spiracle, however, it may potentially fit under *N. emiliae* or *N. metanotalis*.

Head. *Frontal view*: subrhomboid. Mandible spatulate, longer than wide, acute apically. About 2.5 mandalus (maximum length) fit on mandibular dorsum, mandibular apex, when mandible is closed, slightly surpasses lateral margin of labrum; labrum small, about 4.5 times shorter than maximum clypeal width. Prementum with well-developed transverse dome. Palp formula: 6,4. Stipes mostly smooth; internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially straight to slightly concave; in lateral view, dorsal surface relatively straight to slightly convex, not inflated. Area between posterior margin of clypeus and supraclypeal area without depression. Posterior supraclypeal area acute. Supraclypeal area slightly protruding from cuticule, followed posteriorly by tenuously impressed inter-antennal socket carina. Distance between internal margins of antennal sockets less than one socket diameter. Torular lobe small but well-developed, not projecting over internal margin of antennal acetabulum. Malar carina absent. Eye suboval, notched near mid-length; maximum length slightly more than half head length, convex, globose, placed at cephalic mid-length. Ocellar area weakly protruding from cuticle, placed posterad to vertex. Anterior ocellus maximum length subequal to that of posterior ocelli. Ocelli approximately equidistant to each other; distance between anterior and posterior ocelli approximately 0.5 times anterior ocellus maximum length. Occipital carina present, well-developed. Scape cylindrical, one third longer than pedicel; first flagellomere longer than second. **Mesosoma.** *Lateral view*: Dorsal margin convex. Pronotum with weak, blunt, barely distinguishable humeral carina. Anterior subalar area approximately as broad as tegular maximum width. Mesopleural sulcus well-developed, slightly reaching ventral mesopleural region. Metanotal trough weakly impressed. Metapleuropropodeal suture relatively shallow. Posterolateral margin of propodeal declivity carinate, running along the posterodorsal propodeal margin. Anterolateral propodeal corner rounded. Propodeal spiracle oval. Posteroventral cuticular flap at metapleural gland opening well-developed, forming a vertically-oriented, salient carina; gland orifice completely visible in posterolateral view. Pheromone venting canal at metapleural gland opening absent. *Dorsal view*: mesoscutum about as long as broad, about two times length of mesoscutellum; anterior mesoscutal impression linear, well-marked. Parapsidal lines weakly impressed, slightly divergent. Notauli present, strongly impressed, cross ribbed, not meeting posteriorly. Transscutal sulcus well-developed. Scutoscutellar sulcus present, slightly arched

posterad, strongly impressed, cross ribbed, not separating mesoscutum from mesoscutellum. Mesoscutellum subrectangular, domed. Metascutellum well-developed, clearly discernible dorsally, surface with slightly salient longitudinal carina. Anterodorsal median propodeal sulcus present, weakly impressed. Posterior face of propodeal declivity mostly flat. Propodeal lateral margins subparallel in posterodorsal view. *Ventral view*: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process poorly developed. Metasternal process well-developed, inclined posterad, 20°-30° in lateral view, fang-shaped, flattened anteroposteriorly; apex about as long as mid height of metacoxal internal margin, space between lobes wider than width of each, internal margins divergent, external margins straight to slightly convergent. **Wings.** Hyaline. Slightly iridescent. Forewing venation Ogata type Ia: submarginal cells 1, 2 and discoidal present, vein 2M present, reduced, 2r-rs offset from Rs+M; Rs+M approximately three times longer than 2M, setose layer evenly covering surface. Hindwing venation Cantone and Von Zuben Type I: basal and subbasal cells and vein 2M present, 1R well-developed, 1Rs well-developed. Jugal lobe present. Hindwing bearing 10 hamuli. **Legs.** Mesofemur roughly equally thick as metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora convex from base to apex. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur about half-length of posterior spur. Anterior hind tibial spur about half-length of posterior spur. Pretarsal claw arched, with well-developed preapical tooth. Arolium present, roughly 0.5 times length of pretarsal claw. **Petiole.** *Lateral view*: Petiolar node anterior margin straight, inclined ca. 30° posterad; posterior margin straight, inclined ca. 30° anterad; anterior and posterior margins reaching approximately same level dorsally; middorsal margin convex, highest point at nodal longitudinal midline; posterior face mostly flat. Subpetiolar process subtriangular, with blunt, keel-shaped, grooved anterior cusp, followed posteriorly by relatively flat region bordered by longitudinal carinae, mostly smooth, with two weakly raised longitudinal carinae medially. Lateral projection of anteroventral nodal carina highly reduced. Lateral nodal carina well-impressed but short, not reaching nodal midlength. Anteroventral nodal carina incomplete, strongly concave medially. **Gaster.** *Lateral view*: Prora well-developed, small, projected anterad, not hidden by helcium laterally. Anterior margin of tergum of A3 convex. Cinctus well-impressed, cross ribbed. *Dorsal view*: Tergum of A3 slightly longer than A4. Abdominal sternum 7 with even surface, not concave, bearing scattered erect and suberect hairs. Spine at posterior margin of tergum of A8 well-developed, extending posterad, beyond posterior margin of sternum of A9,

acute, slightly flattened laterally. Sternum of A9 longer than broad, posterior margin acute. Pygostyles present, about three times longer than broad. **Pilosity.** Body with sparse, flexuous, brownish, erect and suberect hairs. Appressed pubescence moderately abundant, especially on gastral dorsum, though integument always discernible.

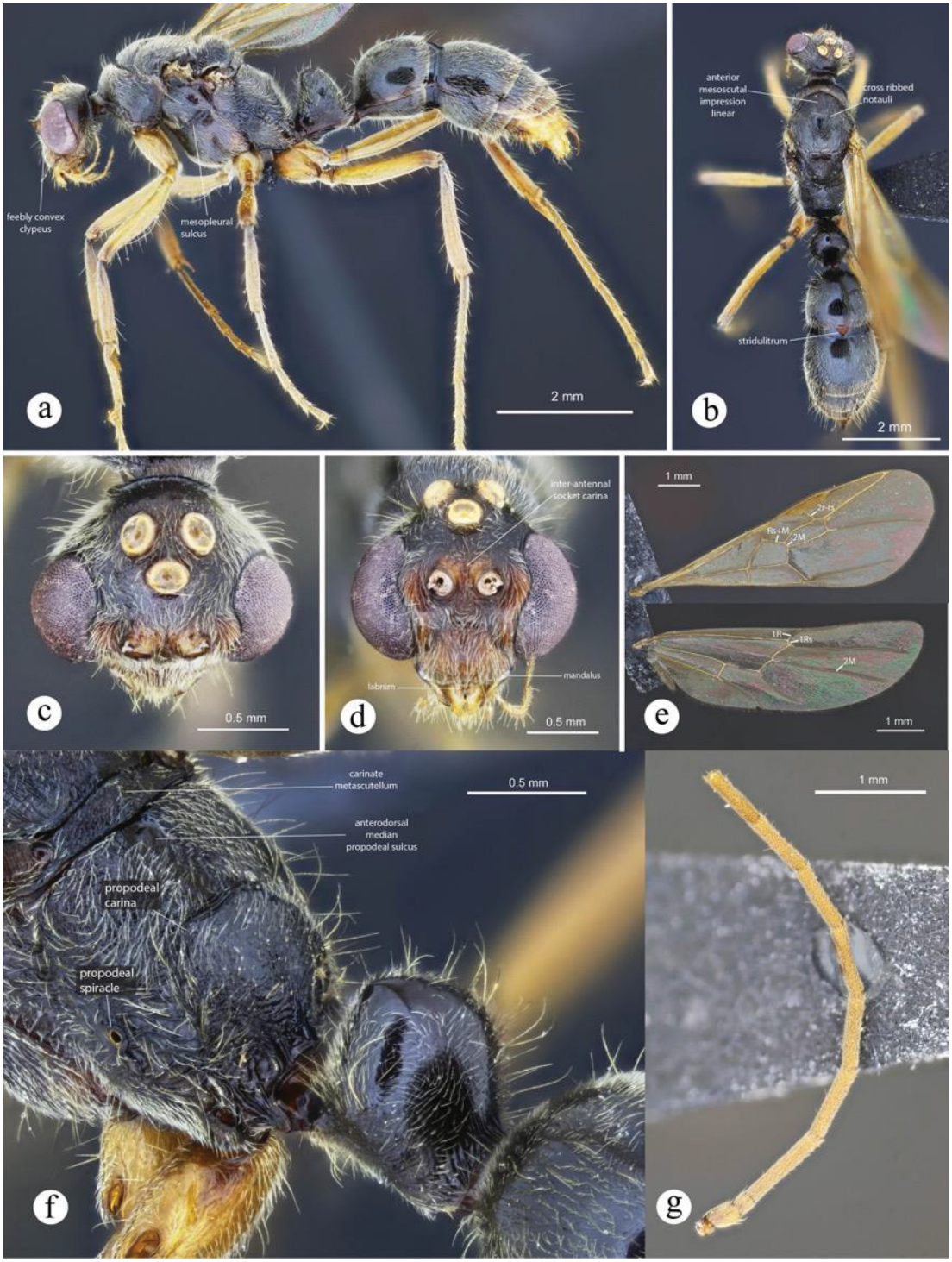


Fig. 7. *Neoponera emiliae* species-group, unidentified ♂ (*incertae sedis*). **a.** Lateral view; **b.** Dorsal view; **c.** Head in dorsal view; **d.** Head in frontal view; **e.** Fore and hind wings; **f.** Propodeum and node in posterodorsal view; **g.** Left antenna (broken, only nine antenommeres shown).

Most erect hairs on body dorsum approximately equal to scape length. Meso- and metatarsi bearing scant spine-like setae and abundant finer setae. **Color.** Overall body brownish black, brilliant. Antennae dark brown, mandibles yellowish. **Sculpture.** Integument polished, with mixture of abundant shallowly impressed punctae on gaster, and relatively more deeply impressed on rest of body. Striae on head absent; mesosoma bearing strong striae on axilar areas; propodeum with abundant coarse, irregular rugae. Striae on petiolar node absent.

Species accounts

The following species diagnoses include only the minimum features the reader will require to identify each species, in combination with the taxonomic key. Other useful diagnostic characters were mentioned above under the differential diagnosis for the present species-group. Although the queen is unknown, it likely is very similar to the worker as observed in all other *Neoponera* groups, thus all diagnoses may also apply to that caste as well.

***Neoponera caxiuana* sp. nov.**

Figures. 8: a – f (☿); 15: (distribution).

Type material. ***Holotype***. 1☿; **BRAZIL**: **Pará**: Melgaço, Caxiuanã [national preserve], Estação Científica Ferreira Penna, 1°45'S, 51°31'W, Plote IV Transecto 7-300, 28.x.2003, Pitfall 04, J. Souza & C. Moura leg., (INPA: INPAHYM034544).

Etymology. The specific epithet is a toponym after the well-preserved Amazonian Floresta Nacional de Caxiuanã, among the oldest reserves in Brazil, located in northern Pará state, and a source of future discoveries due to its high ant diversity (Harada 2016). The name is a noun in apposition, thus invariable.

Worker and queen diagnosis. Posterior head margin weakly concave (Fig. 8c); meso and metapleuron with shallow micropunctae (Fig. 8a); lateral propodeal side with scant well-impressed striae (Fig. 8a); in lateral view, petiolar node distinctly higher than long, anterior and posterior margins reaching nodal top at about same level (Fig. 8d); ventroposterior nodal margin scrobiculate (Fig. 8d); posterior nodal face with scattered micropunctae (Fig. 8b); prora well-developed, acute tip directed anterad (Fig. 8d).

Worker description. Measurements (*n* = 2; holotype in parenthesis): HW: 2.8-2.85 (2.85); HL: 3.05-3.1 (3.05); EL: 0.6-0.6 (0.6); SL: 2.31-2.4 (2.4); WL: 4.09-4.1 (4.09); PrW: 2.15-2.15 (2.15); MsW: 1.4-1.5 (1.4); MsL: 0.85-0.88 (0.85); PW: 1.9-2.1 (2.1); PH: 1.9-2.1 (1.9); PL: 1.05-1.05 (1.05); GL: 5.16-5.7 (5.16); A3L: 2.3-2.34 (2.3); A4L: 2.05-2.1 (2.05); A3W: 2.65-2.8 (2.8); A4W: 2.4-2.46 (2.4); TLa: 12.54-12.69 (12.54); TLr: 13.35-13.95 (13.35). **Indices**. CI: 90.32-93.44 (93.44); OI: 21.05-21.43 (21.05); SI: 82.5-84.21 (84.21); MsI: 164.71-170.45 (164.71); LPI: 50-55.26 (55.26); DPI: 180.95-200 (200).

Head. *Frontal view*: subquadrate. Mandible triangular, longer than wide, distal region moderately bent ventrad, dorsolateral margin weakly sinuous medially. Masticatory margin of mandible with four teeth distally followed by four to six denticles proximally. Prementum with well-developed transverse dome. Prementum and moderately impressed groove distally. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum mostly smooth, finely striated basally. Clypeus anteromedially convex, with truncate extension projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina surpassing ocular posterior margin, medially. Torular lobe subtriangular, almost completely covering acetabulum of antennal socket, posterolateral margin straight. Malar carina absent, though malar region is slightly raised. Eye suboval, maximum length ca. one-fifth head length, convex, surpassing lateral margin of head, placed slightly anterior to cephalic mid-length. Posterior margin of head concave. Occipital carina strongly reduced. Scape, when pulled posterad, surpassing posterior margin of head by half apical scape width. **Mesosoma**. *Lateral view*: Dorsal margin slightly convex. Pronotum carinate, with carina not projecting from cuticle. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum. Posterolateral margin of propodeal declivity with blunt, slightly salient carina. Propodeal spiracle slit-shaped. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Posterior face of propodeal declivity flat. Propodeal lateral margins parallel at base, convergent dorsad. *Ventral view*: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection acute. Mesosternal process well-developed, fang-shaped, internal margins of lobes slightly convergent, not parallel, relatively flattened anteroposteriorly, inclined posterad ca. 20–30 degrees in lateral view, space between lobes

approximately equal to width of each. Metasternal process well-developed, inclined posterad, 20°-30° in lateral view, triangular-shaped, flattened anteroposteriorly, apex about as long as mid height of metacoxal internal margin, space between lobes wider than width of each, internal margins running parallel. Metasternal process external margins straight to slightly convergent. **Legs**. Mesofemur slightly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora slightly flattened roughly on distad two thirds. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about 2.5 times shorter than posterior spur. Pretarsal claw arched, unarmed (without accessory teeth on surface). Arolium present, roughly three times shorter than pretarsal claw. **Petiole**. *Lateral view*: Petiolar node with straight anterior margin and convex posterior margin, posterior margin shorter than anterior margin, posterior face concave. Subpetiolar process shovel-shaped, with keel-shaped anterior cusp, followed by posterior horizontally straight region, dome and anterior cusp strongly rugose. Lateral projection of anteroventral nodal carina absent. Lateral nodal carina absent. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. *Lateral view*: Prora well-developed, small, with acute tip projected anterad, not hidden by helcium laterally. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin relatively angled. Anterodorsal margin of tergum of A3 convex. Cinctus weak. *Dorsal view*: Tergum of A3 slightly longer than A4. Posterior dorsum of epipygium coriaceous. **Color**. Mandibles feebly lighter than remaining body, legs ferruginous brown. **Pilosity**. Body with scant, flexuous, golden to dark golden, erect and suberect hairs which are mostly present ventrally. Appressed pubescence not abundant, mostly present on head, mesosoma and gaster, posterior face of petiole with significantly less piligerous punctae. Most erect hairs on body dorsum smaller than maximum eye length. Scape pilosity mostly pruinose but not abundant. Meso- and metatarsi bearing abundant spine-like setae and tiny appressed and suberect fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, shorter than eye maximum length. Posterior dorsum of epipygium surrounded by ca. 20 long flexuous hairs, longer than eye maximum length. **Sculpture**. Integument polished. Striae on head present as costae dorsally, and ventrally concentric, mandibles without striae dorsally, mesosoma, except for posterior propodeal face and most mesopleuron, completely covered by strong to moderately impressed costae. Striae on petiolar node absent.

Comments. *Neoponera caxiuana* is a relatively large species among those of the *N. emiliae* group (Fig. 6d). Within the species belonging to the *N. magnifica* subclade only *N. glabra* can be considered most similar to it since both share certain traits as the shape of the petiole bearing an incision on the lateral margin, and the scrobiculae on the nodal posteroventral margin. These two species, however, are easily separable since the posterior nodal face of *N. caxiuana* is punctate, and that of *N. glabra* is glabrous; in addition, the meso and metapleuron of *N. caxiuana* are mostly punctate, not costate as in *N. glabra*. This latter feature distinguishes *N. caxiuana* from the rest of species in the *N. magnifica* subclade, except for *N. magnifica* which also shows a similar sculpture, but this species has two patches of appressed golden pilosity and a medially notched petiolar node, both traits absent in *N. caxiuana*.

Out of the *N. magnifica* subclade, maybe *N. metanotalis* approximates its general shape, but the latter lacks costae and its clypeal anterior margin is medially straight to concave, not acute and convex.

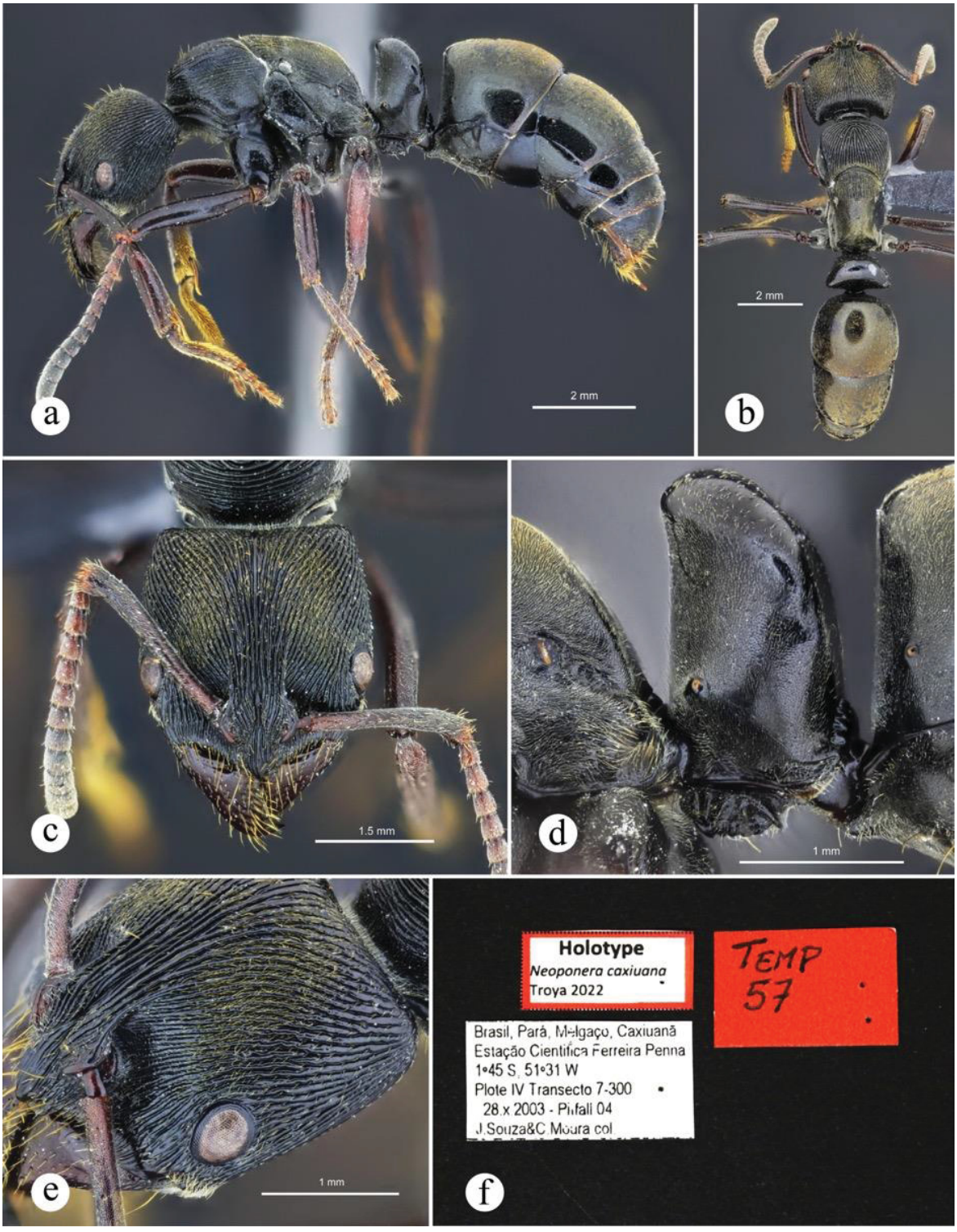


Fig. 8. *Neoponera caxiuana* sp. nov. Holotype ☿ (INPA: INPAHYM034544). Brazil: Pará. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Posterior region of propodeum and petiole in lateral view; **e.** Detail of costae on head; **f.** Collection labels.

The three examined specimens show very little variation in body size and shape; they only differ slightly on the amount of punctae on the posterior nodal face, and in the pleural sculpture, also with punctae, which if feebly more impressed on the holotype. Also, the tip of the prora in the holotype is slightly more acute than in the other two specimens.

I checked a fourth specimen record (IAvH-E-34321) identified as *N. magnifica* by Tania Arias (Arias 2003), which was collected in the Napo moist forests, in the southern Colombian department of Putumayo, northwestern Amazonia. Arias recognized some differences on the mesonotum and propodeal sculpture, as compared to the characters provided by Borgmeier (1929) in his description of *N. magnifica*. Arias sent to me two images of the specimen she studied; these images depict the body in lateral view, pronotum in dorsal view, and partially the head dorsum. This specimen is very similar to *N. caxiuana* mostly due to the shape of the petiolar node which is distinctly higher than long, and shows an incision on its margin; it also seems to show punctae on the mesonotum and propodeum, but these are definitely not costate. These three traits are diagnostic of *N. caxiuana*. However, this specimen shows two regions of golden, seemingly appressed hairs on the head dorsum; since the image is not clear enough, and the head is obliquely oriented (instead of fully frontally), it is not possible to accurately recognize if such regions actually represent the golden and dense hairy patches which, thus far, are diagnostic only for *N. magnifica*. The head dorsum of *N. caxiuana* has appressed golden pilosity laterally on head (Fig. 8c, e) but these hairs are much less dense than in *N. magnifica*. Arias deposited this specimen in IAVH, Villa de Leyva, Colombia. I revised the *Neoponera* in that collection but could not find it. Some other important characters defining the *N. emiliae* group, such as head sculpture, clypeal margin, details of the node, are not discernible in such images. Therefore, I leave this specimen as variant of *N. caxiuana* until someone finds it, and/or additional material from said region becomes available.

Neoponera caxiuana is known only from the Amazon biome: two records from northeastern Pará in the ecoregion of Xingu-Tocantins-Araguaia moist forests, and a single record from northwestern Mato Grosso, in a site between the Cerrado and the Mato Grosso seasonal forests.

Natural history notes. As with all its subclade partners, *N. caxiuana* is possibly an underground nester and/or chooses preformed cavities to grow its colonies. All examined specimens were collected through pitfall traps in well-preserved, mature forests.

Other material examined. 4☿. **BRAZIL – Mato Grosso:** • 1☿; Brasnorte, Fazenda Herminia; -12.1212, -58.0045; alt. 310m; 2017-12-01; Ferreira, J. leg.; pitfall; (DZUP). **– Pará:** • 1☿; Floresta Nacional Caxiuanã, Estação Científica Ferreira Pennna; -1.75, -51.5167; alt. 44m; 2003-10-28; Souza, J.; Moura, C. leg.; pitfall; (INPA). • 1☿; Serra dos Carajás, Floresta Nacional do Tapirapé-Aquiri; -6.2667, -50.5667; alt. 350m; 2018-10-16; Oliveira, D. E.; Siqueira, F. F. leg.; pitfall; (DZUP). **COLOMBIA – Putumayo:** • 1☿; Parque Nacional Natural La Paya, Cabaña la Paya; 0.1172, -74.9333; alt. 330m; 2002-04-15; Cobete, R. leg.; pitfall; (IAVH).

Geographic range. Southern Colombia, Brazil: Mato Grosso, Pará.

***Neoponera dorsilinea* sp. nov.**

Figures. 9: a – f (☿); 15: (distribution).

Type material. ***Holotype***. 1☿; **BRAZIL**: **Bahia**: Igrapiúna, Reserva da Michelín, 22-26.vii.2008 – 14.ix.2013, K. Benati et al. [leg.], 5747 [collector's code], (CPDC: ATPFOR1965).

Etymology. The name of the species is derived from the Latin words: *dorsum* meaning "back", and *līnea* meaning "line, thread", in allusion to the costae on the propodeum. The name is a noun in apposition, thus invariable.

Worker and queen diagnosis. Posterior head margin feebly concave (Fig. 9c), ventrally with gross, concentric striae; pleural and entire propodeal surface (except posterior face), with irregularly-shaped, well-impressed costae (Fig. 5a, 9a, link); posterior face of petiolar node mostly with longitudinal striae; prora small, lip-shaped, always discernible laterally (Fig. 9d).

Worker description. Measurements (n = 3; holotype in parenthesis): HW: 2.65-2.95 (2.8); HL: 2.9-3.2 (3); EL: 0.55-0.65 (0.6); SL: 2.1-2.45 (2.45); WL: 3.46-4.1 (3.9); PrW: 2.0-2.1 (2); MsW: 1.45-1.5 (1.5); MsL: 0.8-0.9 (0.8); PW: 1.75-2 (1.8); PH: 1.7-1.8 (1.7); PL: 1.0-1.1 (1); GL: 4.15-5.54 (5.54); A3L: 2.15-2.25 (2.2); A4L: 1.85-2.1 (2); A3W: 2.5-2.55 (2.55); A4W: 2.25-2.35 (2.3); TLa: 11.46-12.65 (12.1); TLr: 11.51-13.44 (13.44). **Indices.** CI: 91.38-93.33 (93.33);

OI: 20.75-22.03 (21.43); SI: 77.97-87.5 (87.5); MsI: 161.11-187.5 (187.5); LPI: 57.14-61.11 (58.82); DPI: 175.0-181.82 (180).

Head. *Frontal view*: subquadrate. Mandible triangular, longer than wide, distal region moderately bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with four teeth distally followed by four to five denticles proximally. Prementum with well-developed transverse dome. Prementum and strongly impressed transverse groove distally. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, with relatively acute extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina surpassing ocular posterior margin, medially. Torular lobe subtriangular, covering approximately 90% of acetabulum of antennal socket, posterolateral margin straight. Malar carina absent, though malar region is slightly raised. Eye suboval, maximum length ca. one-fifth head length, convex, surpassing lateral margin of head, placed slightly anterior to cephalic mid-length. Posterior margin of head concave. Occipital carina absent. Scape, when pulled posterad, surpassing posterior margin of head by half apical scape width. **Mesosoma**. *Lateral view*: Dorsal margin slightly convex. Pronotum carinate, with carina not projecting from cuticle. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum, masked by surrounding striae. Posterolateral margin of propodeal declivity with blunt, salient carina. Propodeal spiracle oval to suboval. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Notopropodeal suture vestigial. Posterior face of propodeal declivity flat. Propodeal lateral margins parallel at base, convergent dorsad. *Ventral view*: probasisternum triangular-shaped, bearing tiny groove medially. Probasisternal posterior projection with spine. Mesosternal process well-developed, tooth-shaped, internal margins of lobes running parallel, relatively flattened anteroposteriorly, inclined posterad ca. 10 degrees in lateral view, space between lobes approximately equal to width of each. Metasternal process well-developed, inclined posterad, ca. 10° in lateral view, triangular-shaped, flattened anteroposteriorly, apex about as long as mid height of metacoxal internal margin, space between lobes wider than width of each, internal margins divergent. Metasternal process external margins straight to slightly convergent. **Legs**. Mesofemur slightly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso-

and metafemora slightly flattened roughly on distad two thirds. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about 2.5 times shorter than posterior spur. Pretarsal claw arched, unarmed (without accessory teeth on surface). Arolium present, roughly three times shorter than pretarsal claw. **Petiole**. *Lateral view*: Petiolar node with slightly concave anterior margin and convex posterior margin, posterior margin shorter than anterior margin, posterior face concave. Subpetiolar process shovel-shaped, with mostly round anterior cusp, followed by posterior horizontally straight region, dome with transverse, strongly impressed striae. Lateral projection of anteroventral nodal carina highly reduced. Lateral nodal carina absent. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. *Lateral view*: Prora well-developed, small, projected anterad, not hidden by helcium laterally. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin acute. Anterodorsal margin of tergum of A3 slightly convex. Cinctus weak. *Dorsal view*: Tergum of A3 slightly longer than A4. Posterior dorsum of epipygium coriaceous. **Color**. Body black, mandibles feebly lighter than remaining body, legs ferruginous brown. **Pilosity**. Body with scant, flexuous, golden to dark golden, erect and suberect hairs which are mostly present ventrally. Appressed pubescence present, mostly fine small hairs distributed across integument which is easily discernible. Most erect hairs on body dorsum approximately equal to maximum eye length. Scape pilosity mostly pruinose but not abundant. Meso- and metatarsi bearing abundant spine-like setae and tiny appressed and suberect fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, usually longer than eye maximum length. Posterior dorsum of epipygium surrounded by ca. 20 long flexuous hairs, as long as maximum eye length. **Sculpture**. Integument polished. Striae on head present as costae dorsally, and ventrally concentric, mandibles without striae dorsally, mesosoma, except for posterior propodeal face, completely covered by strong to moderately impressed costae. Striae on petiolar node present, feebly impressed, slightly more discernible on posterior face.

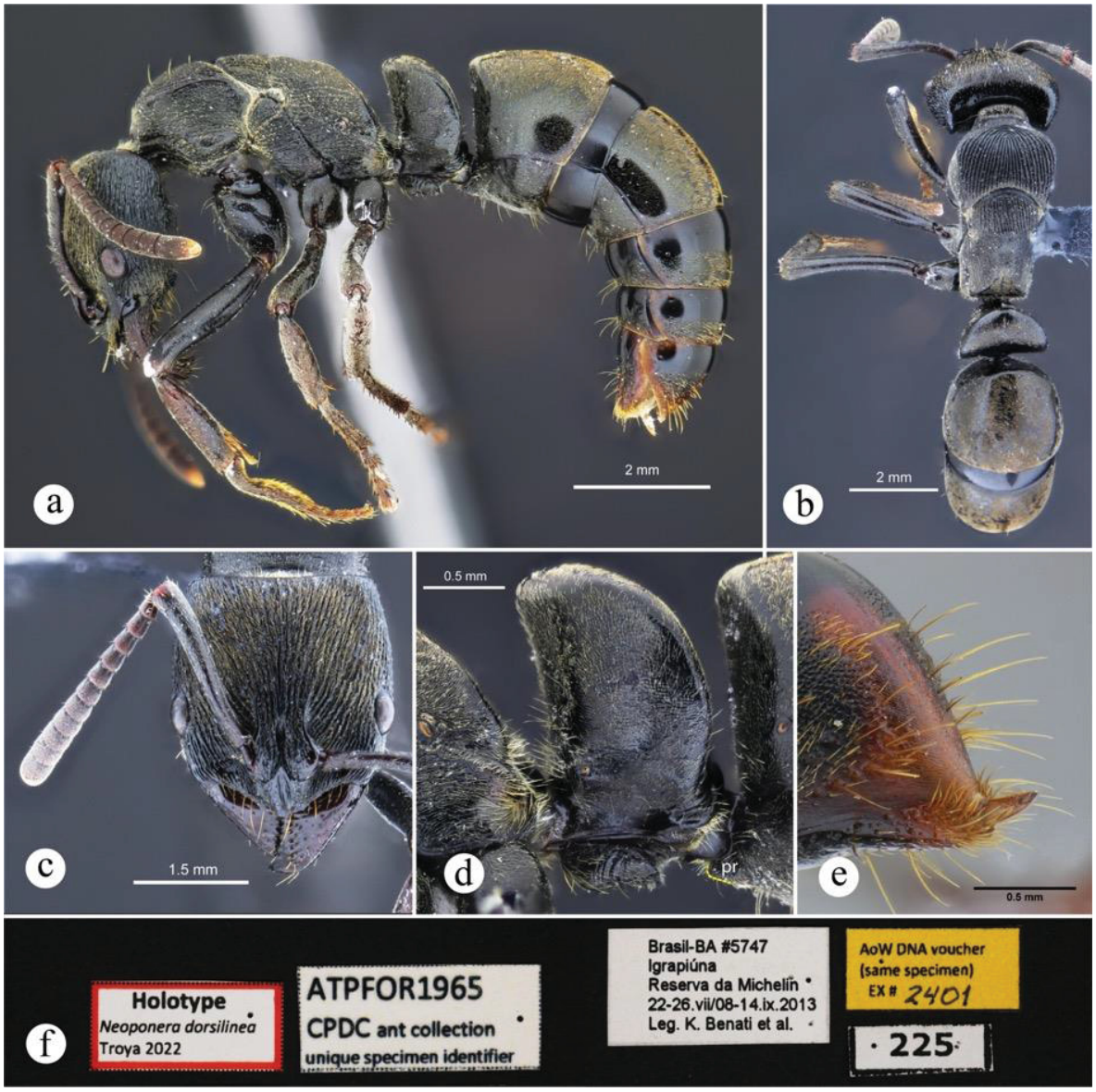


Fig. 9. *Neoponera dorsilinea* sp. nov. Holotype ☿ (CPDC: ATPFOR1965). Brazil: Bahia, except, **e.** ☿ from Brazil, Minas Gerais (UFVLABECOL000003). **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Petiolar node in lateral view; **e.** Epipygium in posterolateral view; **f.** Collection labels. **pr**: prora. Image in **e.** by Julio Chaúl.

Comments. *Neoponera dorsilinea* is a relatively large species among those in the *N. emiliae* group (Fig. 6d, TLa: 11.46 – 12.65 mm); this taxon is very similar to *N. dropsy*, and both are putative sisters (Troya et al., unpublished). The easiest way to separate them is by examining the prora, which is, at least from the material examined, always discernible laterally in *N. dorsilinea* (Fig. 9d), whereas the prora of the other is tiny, or in exceptional cases, vestigial so that

it is almost indistinguishable in lateral view (Fig. 10a). Other differences between these two taxa were cited under the *N. dropsy* treatment.

Neoponera glabra and *N. caxiuana* are also similar, thus potentially confusable with *N. dorsilinea*; the reader can examine the following features to distinguish them: the posteroventral head margin of *N. dorsilinea* has a ventrally-directed, feebly protruding tumulus (Fig. 9a, 10a) which is absent in *N. glabra* and *N. caxiuana*; the propodeum (except for its posterior face) is entirely costate; these costae, as seen laterally (mostly), are nearly continuous with those on the mesonotum (link), whereas in the other species the propodeum bears only few, shallow and weakly impressed costae, mixed with microstriae (Fig. 5b); the posteroventral margin of the petiolar node is smooth in *N. dorsilinea*, while that region is scrobiculate in the other two species (Fig. 4a).

Neoponera dorsilinea could also be confused with *N. magnifica*, in lesser degree though than those which preceded since this species has two well-noticeable patches of appressed golden hairs, and the subpetiolar process is notched medially. No other species in the *N. emiliae* group, nor in the genus has these peculiarities.

The specimens examined are virtually identical and differ only in the depth and shape of the propodeal costae on the anterodorsal median region, which are less impressed in the holotype. For reference, the reader can see in AntWeb.org one specimen from Samarco, Minas Gerais (link) which neatly depicts well-impressed propodeal costae.

The only four records known of *N. dorsilinea* belong from southeastern Bahia, where the holotype belongs from, and from eastern Minas Gerais; the elevational range spans from near the sea level up to about 800 m, and as *N. dropsy*, it lives in the ecoregions of Bahia Interior forests and Bahia Coastal forests.

Natural history notes. As hypothesized for its subclade partners, this epigeic species possibly nests underground or opportunistically inside preformed cavities on the soil surface, like tree roots, broken sticks, death stems. The scant records found which, thus far, reflects a reduced distribution for this species is a matter of concern. As hypothesized for *N. magnifica*, likely the populations of *N. dorsilinea* are small, with possibly small colony sizes. If this is supported in future research, the species would potentially fell under risk of extinction, in particular due to pervasive degradation of its natural habitat in eastern Bahia and Minas Gerais (Nemésio et al. 2016, Neves et al. 2021).

Other material examined. 3☿. **BRAZIL – Bahia:** • 1☿; Itororó; -15.1158, -40.0646; alt. 600m; 2000-03-01; Santos, J. R.; Campos, D. O. leg.; (CPDC). **– Minas Gerais:** • 1☿; 5 km NNE Ipaba; -19.3667, -42.4; alt. 277m; 2016-06-12; Santos, et al. leg.; pitfall; (DZUP). • 1☿; Samarco; -20.2306, -43.4497; alt. 750m; Paolucci, L. leg.; pitfall; (UFVLABECOL).

Geographic range. Eastern Brazil: Bahia, Minas Gerais.

***Neoponera dropsy* sp. nov.**

Figures. 10: a – d (☿); 15: (distribution).

Type material. ***Holotype***. 1☿; **BRAZIL**: **Bahia**: Vit. [Vitória] da Conquista, Poço Escuro [forest reserve], 40°50'28"S, 40°50'20"W, 9-17.i.2001, J.C.S. Carmo [leg.], 5309a [collector's code], (MEPN: ATPFOR2060). ***Paratypes***. 3☿ [same data as for holotype], (CPDC: ATPFOR2163, DZUP: ATPFOR1962, ICN: ATPFOR2139).

Etymology. The specific name is derived from the Greek ὕδωρ (húdōr, "water"), but here I consider the archaic synonym for "edema", which in new Latin means "swelling", in allusion to the feebly convex projection, or tumulus, on the posteroventral head corner.

Worker and queen diagnosis. Posterior head margin concave (Fig. 10c), ventrally with coarse, concentric striae; posteroventral head corner with ventrally directed tumulus (Fig. 10a); pleural surface and lateral propodeal side with shallowly impressed costae (Fig. 10a); posterior face of petiolar node with mixture of longitudinal and concentric striae; prora tiny or vestigial, hardly seen in lateral view (Fig. 10a).

Worker description. Measurements (n = 6; holotype in parentheses): HW: 2.75-3.2 (2.98); HL: 3.0-3.25 (3.2); EL: 0.5-0.65 (0.6); SL: 2.0-2.45 (2.38); WL: 3.7-4.0 (4); PrW: 1.85-2.25 (2.2); MsW: 1.3-1.51 (1.4); MsL: 0.8-1.3 (0.9); PW: 1.8-2 (1.99); PH: 1.5-2 (1.98); PL: 0.9-1.1 (1.08); GL: 4.3-5 (5); A3L: 1.6-2.52 (2.39); A4L: 2.05-2.15 (2.05); A3W: 2.05-2.75 (2.6); A4W: 1.95-2.5 (2.36); TLa: 11.47-12.77 (12.72); TLr: 11.9-13.28 (13.28). **Indices.** CI: 91.67-100 (93.12); OI: 18-22.03 (20.13); SI: 72.73-79.66 (79.8); MsI: 107.69-187.5 (155.56); LPI: 50.0-65.38 (54.55); DPI: 180.0-200.0 (184.26).

Head. *Frontal view*: subquadrate. Mandible triangular, longer than wide, distal region moderately bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with

four teeth distally followed by four to five denticles proximally. Prementum with well-developed transverse dome, and strongly impressed transverse groove distally. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum smooth. Clypeus anteromedially convex, with relatively acute extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina surpassing ocular posterior margin, medially. Torular lobe subtriangular, almost completely covering acetabulum of antennal socket, posterolateral margin straight. Malar carina absent, though malar region is slightly raised. Eye suboval, maximum length ca. one-fifth head length, convex, surpassing lateral margin of head, placed slightly anterior to cephalic mid-length. Posterior margin of head concave. Occipital carina absent. Scape, when pulled posterad, barely reaching posterior margin of head. **Mesosoma**. *Lateral view*: Dorsal margin slightly convex. Pronotum carinate, with carina not projecting from cuticle. Anapleural sulcus well-developed, usually completely dividing mesopleuron in anepisternum and katepisternum and, sometimes masked by surrounding striae. Posterolateral margin of propodeal declivity with blunt, salient carina. Propodeal spiracle oval to suboval. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Notopropodeal suture vestigial dorsally and shallowly impressed laterally, not forming groove though. Posterior face of propodeal declivity flat. Propodeal lateral margins parallel at base, convergent dorsad. *Ventral view*: probasisternum triangular-shaped, bearing tiny groove medially. Probasisternal posterior projection acute. Mesosternal process poorly developed, tooth-shaped, internal margins of lobes running parallel, subconical, space between lobes broader than width of each. Metasternal process well-developed, inclined posterad, 20°-30° in lateral view, triangular-shaped, slightly flattened anteroposteriorly, apex shorter than half height of metacoxal internal margin, space between lobes wider than width of each, internal margins divergent. Metasternal process external margins straight to slightly convergent. **Legs**. Mesofemur thickened medially, feebly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora slightly flattened roughly on distad two thirds. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur half-length of posterior spur. Anterior hind tibial spur about 2.5 times shorter than posterior spur. Pretarsal claw arched, unarmed (without accessory teeth on surface). Arolium present, roughly three times shorter than pretarsal claw.

Petiole. *Lateral view*: Petiolar node with slightly concave anterior margin and convex posterior margin, posterior margin shorter than anterior margin, posterior face concave. Subpetiolar process shovel-shaped, with keel-shaped anterior cusp, followed by posterior horizontally straight region, dome with transverse, strongly impressed striae. Lateral projection of anteroventral nodal carina highly reduced. Lateral nodal carina absent. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. *Lateral view*: Prora strongly reduced to tiny projection which is partially hidden by helcium. Anterior margin of tergum of A3 straight at base and slightly projected anterad at dorsum. Dorsalmost limit of anterior tergal margin of A3 slightly below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin acute. Anterodorsal margin of tergum of A3 slightly convex. Cinctus weak. *Dorsal view*: Tergum of A3 slightly longer than A4. Posterior dorsum of epipygium coriaceous. **Color**. Body with black cuticle, mandibles feebly lighter than remaining body, legs black blended with ferruginous brown. **Pilosity**. Body with scant, flexuous, golden to dark golden, erect and suberect hairs which are mostly present ventrally. Appressed pubescence present, mostly fine small hairs distributed across integument which is easily discernible. Most erect hairs on body dorsum approximately equal to maximum eye length. Scape pilosity mostly pruinose but not abundant. Meso- and metatarsi bearing abundant spine-like setae and tiny appressed and suberect fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, usually longer than eye maximum length. Posterior dorsum of epipygium surrounded by 20–40 long flexuous hairs, longer than eye maximum length. **Sculpture**. Integument polished. Striae on head present as costae dorsally, and ventrally concentric, mandibles usually finely striate dorsally, mesosoma bearing costae dorsally on pronotum and mesonotum, propodeum finely rugose. Striae on petiolar node present, feebly impressed, slightly more discernible on posterior face.

Comments. *Neoponera dropsy* is a relatively large form among those of the *N. emiliae* group (Fig. 6d, TLa: 11.47 – 12.77 mm); its most similar lineage is *N. dorsilinea* (Fig. 9), both apparently occurring in sympatry at least in their northern known distribution, mid-eastern Bahia (Fig. 15). They can be separated by examining the following two characters: 1) The lateral and dorsal side of the propodeum of *N. dropsy* show shallow striae which can also be seen as microrugosities (Fig. 10a), so that a notorious difference is evident as compared to the costae on the mesonotum (Fig. 10b); in *N. dorsilinea*, the propodeum is almost completely covered by costae, so that dorsally it appears these to form a continuum with the costae on the mesonotum

(link). 2) The prora is tiny to vestigial in *N. dropsy*; when tiny it is hardly discernible in lateral view, while in *N. dorsilinea* is lip-shaped and small, but easily discernible (Fig. 9d). A third trait, the subpetiolar process, in the holotype and paratypes of *N. dropsy* is slightly longer than that of *N. maginifica*-2, and it seems to have a slightly deeper groove posteriorly, which is only weakly grooved in the same structure of *N. maginifica*-2. However, these latter differences are not notorious and the reader may only rely on the two traits described above.

The other three species of the *N. magnifica* subclade are relatively less similar to *N. maginifica*-1 but still potentially confusable between every other; the user may focus on the traits mentioned under *N. magnifica* treatment, and also on the following: *N. dropsy* has a posteroventral, weakly protruding tumulus, which is only shared with *N. dorsilinea*; the mesosternal process is reduced so that the lobes slightly emerge from cuticle, their length is about one or at most two times their width, in contrast to all other species where these lobes are well-developed and longer, three (or more) times longer than broad.

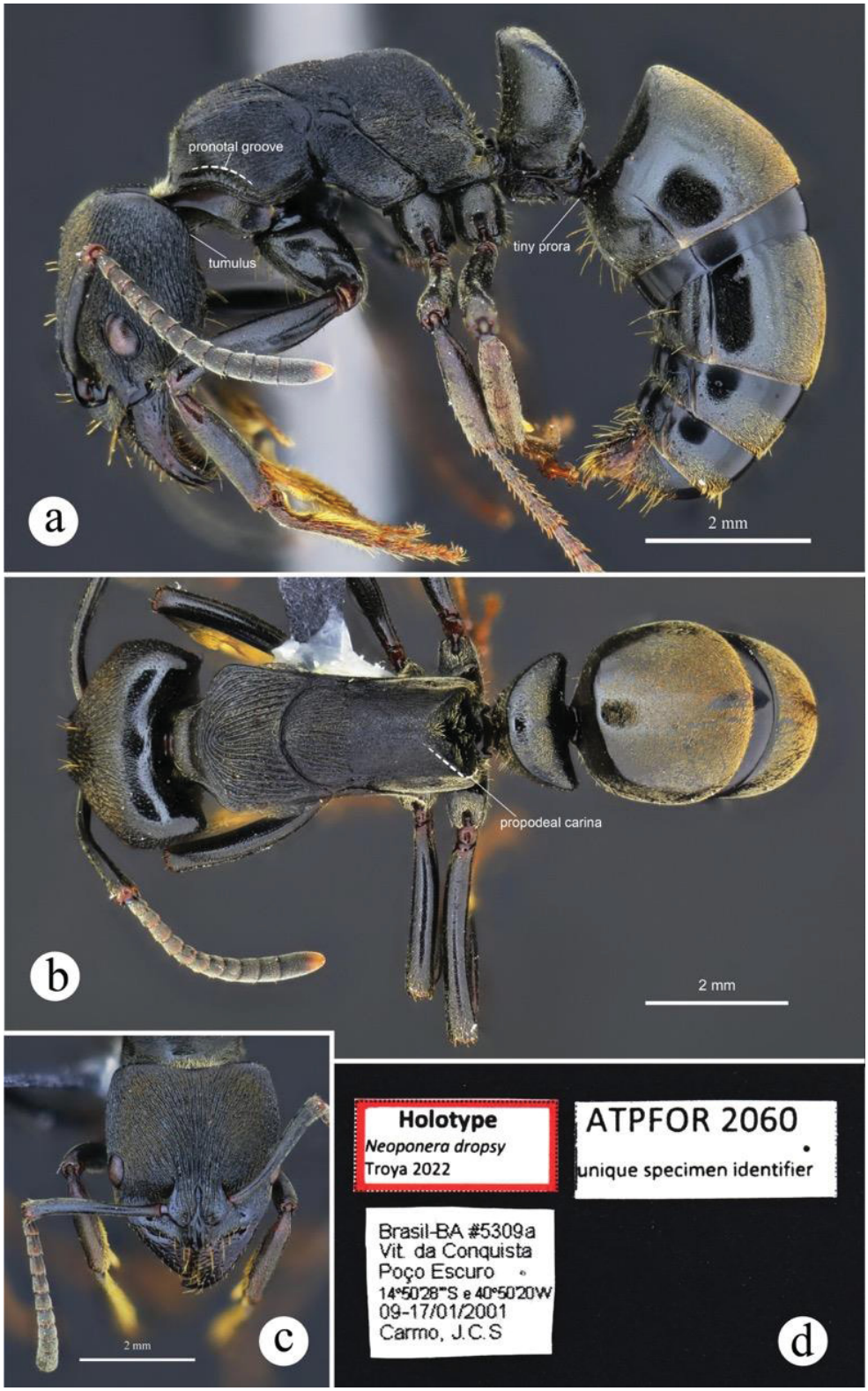


Fig 10. *Neoponera dropsy* sp. nov. Holotype ☿ (MEPN: ATPFOR2060). Brazil: Bahia. **a.** Lateral view; **b.** Lateral view; **c.** Head in frontal view; **d.** Collection labels.

Thus far, the only records found for *N. dropsy* belong from three sites in southeastern Bahia, spanning an elevational range between 800 m up to about 1100 m; these specimens, all collected in the early 2000's lie on the ecoregions of Bahia Coastal forests and Bahia Interior forests (da Silva 2018).

Natural history notes. Besides being a probable soil dweller and possibly predator, nothing is known about its behavior or biology. As noted in *N. magnifica*, however, this species may possibly nest underground or in cavities of e.g., sticks, stems, on soil surface, as some specimens had ground particles sticked to their bodies. The restricted known distribution of this species is a matter of concern, as stated previously for its group partners. The conservation risk of its populations increases since these live in arguably, the most human-threatened biome in South America (Zalles et al. 2021).

Other material examined. 5☿. **BRAZIL – Bahia:** • 1☿; 5 km NW of Jussari; -13.8333, -39.1667; alt. 41m; 1999-05-26; Carmo, J. C. S.; Santos, J. R. M. leg.; (CPDC). • 1☿; Barra do Choça; -14.6333, -40.9167; alt. 888m; 2005-01-08; Conceição E. S. leg.; (DZUP). • 1☿; Barra do Choça; -14.8659, -40.5778; alt. 873m; (CPDC). • 2☿; Barra do Choça; -14.8659, -40.5781; alt. 873m; 2001-01-08; Conceição, E. S. leg.; (CPDC).

Geographic range. Eastern Brazil: Bahia.

***Neoponera emiliae* Forel, 1901**

Figures.11: a – c (☿); 15: (distribution).

Neoponera emiliae Forel, 1901: 349. ☿ lectotype [by designation of MacKay & MacKay, 2010 311], Venezuela, Porto Cabello, A. Forel [leg.], (MHNG, AntWeb CASENT0907239) [image examined, link]. Paralectotypes: 2 ☿ [same data as for lectotype], (MHNG) [not examined].

Combinations. In *Pachycondyla*: Brown, 1995: 305; in *Neoponera*: Schmidt and Shattuck, 2014: 151.

Status as species. Emery, 1911: 72; MacKay & MacKay, 2010: 311 (redescription).

Worker (and probably queen) diagnosis. Head slightly longer than broad, densely punctate; antennal scape, when pulled posterad, exceeding posterior head margin by about 1 to 1.5

times apical scape width (Fig. 11c); anterior mid clypeal margin relatively acute (Fig. 1a); posterior face of petiolar node with piligerous punctae (Fig. b); prora well-developed, keel-shaped, either truncate (specimens from Venezuela, link), or acute with tip directed ventrad (specimens from Colombia, Fig.11a); body covered with abundant appressed, copperish hairs.

Worker. Measurements (*n* = 3): HW: 1.85-1.9; HL: 2.15-2.15; EL: 0.45-0.45; SL: 1.65-1.75; WL: 3-3.05; PrW: 1.3-1.45; MsW: 0.95-1; MsL: 0.6-0.65; PW: 1.3-1.35; PH: 1.2-1.25; PL: 0.8-1; GL: 3.15-3.55; A3L: 1.4-1.5; A4L: 1.45-1.55; A3W: 1.6-1.75; A4W: 1.7-1.7; TLa: 8.8-9.25; TLr: 9.1-9.75. Indices. CI: 86.05-88.37; OI: 23.68-24.32; SI: 89.19-92.11; MsI: 153.85-158.33; LPI: 64.0-83.33; DPI: 135.0-162.5.

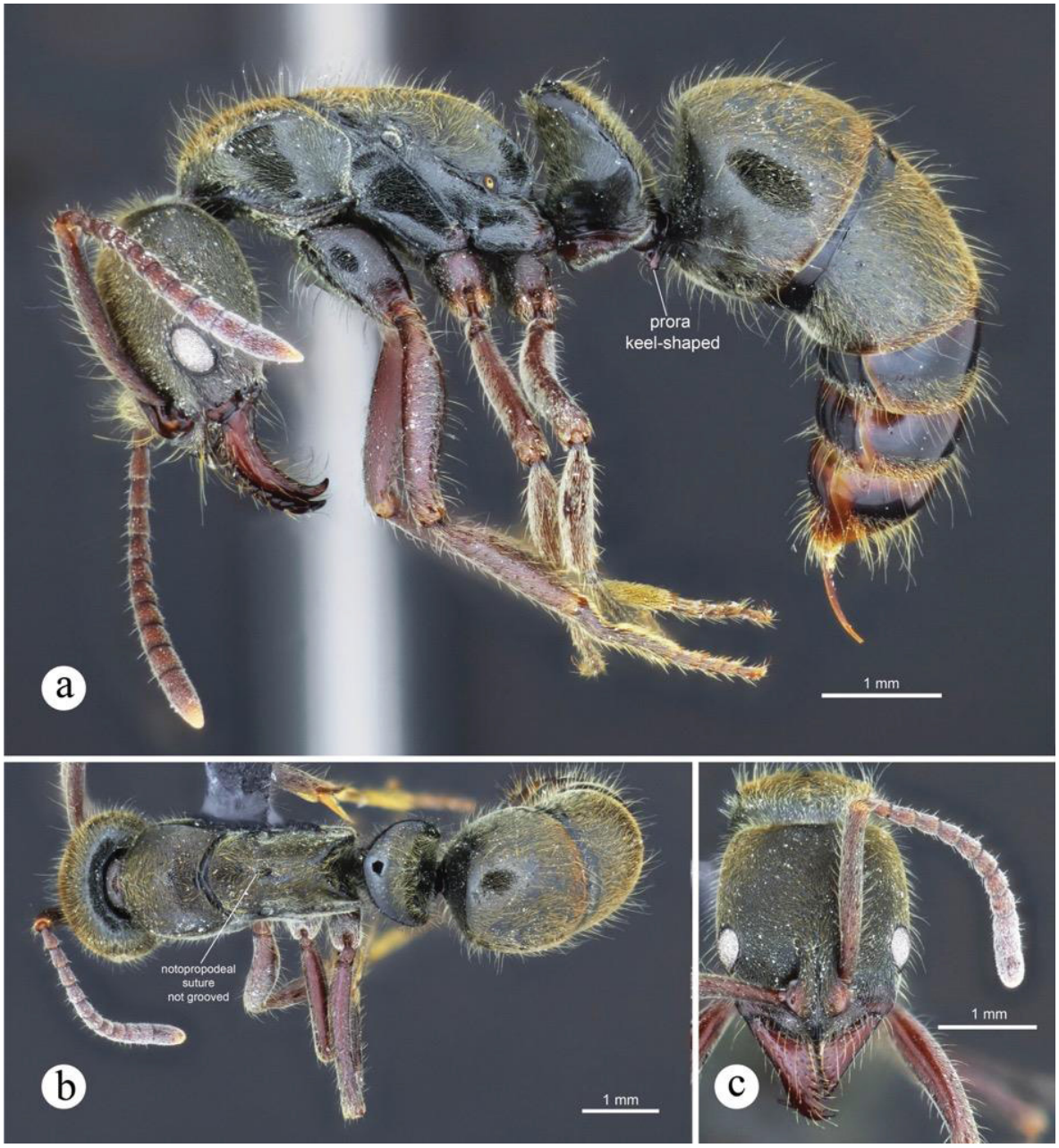


Fig. 11. *Neoponera emiliae* Forel, 1901. ☿ (MEPN: ATPFOR2070). Colombia: Meta. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view.

Comments. *Neoponera emiliae* is the smallest species of the *N. emiliae* group (Fig. 6d, ☿ TLa = 8.8 – 9.3 mm). Nine specimens were examined (two from images) from this rarely collected taxon, they belong from Colombia, Venezuela, and Ecuador; a single specimen was identified from this latter country but unfortunately it is lost, I could not compare it with the current specimen set, but I assume it is similar to those from Colombia. The following variations were detected between the material from Colombia vs. that from Venezuela: larger body size (TLa ≳ 9 mm), vs. smaller (TLa ≲ 7.5 mm); the antennal scape exceeds the posterior head margin by 0.5 times apical scape width, vs. 1.5 times said measurement; humeral carina blunt but evident, vs. reduced and poorly discernible; prora well-developed, keel-shaped with acute tip directed ventrad, vs. tiny, lip-shaped. Apparently, these differences would be enough evidence to propose two distinct lineages among these populations, being those from Venezuela the "true" *N. emiliae* since their morphology match that of the lectotype from Puerto Cabello, just 40 km west from Estación Biológica Rancho Grande in the state of Aragua. However, prior observations of some *Neoponera* belonging to other species groups suggest that morphological plasticity is more common in this genus than previously expected. Wild (2005) and Delabie et al. (2008) cite some notorious examples of populational variations in broadly-ranged and sympatric species like *N. apicalis* (Latreille) and some related to *N. villosa* (Fabricius). I confirmed their observations and detected other cases in for example, *N. bugabensis*, *N. curvinodis*, *N. inversa,* which belong to the *N. foetida* group, where body regions like the humeral and propodeal carina, and the shape of the petiolar node have certain degree of plasticity; or in *N. fiebrigi*, from the *N. crenata* group, for which marked body size differences were found between populations from the mid-southern Atlantic Forest vs. those from the southern Atlantic Forest and the Humid Chaco in Paraguay.

The Venezuelan and Colombian populations of *N. emiliae* are geographically broadly separated, and belong to different ecoregions, which is another factor potentially justifying its taxonomic split. Nonetheless, the scarcity of material prevents distinction of clear morphological discontinuities which would support absence of gene flow among these forms. At least three of the above said traits, namely, body size, the carinae, and the prora, are expected to show some level of intraspecific plasticity in other *Neoponera*, like *N. curvinodis* or *N. inversa*. Yet, despite being hard to diagnose, both are considered good species, which is also supported in the genus phylogeny (Troya et al., unpublished). Only one *N. emiliae* specimen, from the Venezuelan population, is represented in such tree. I expect that by including at least another from the Colombian region the

blurry be swept off around the hypothesis of whether these are species-specific variations, or represent changes mirroring true (recently?) separated lineages.

Neoponera emiliae can only be confused with its siter lineage, *N. metanotalis*; they differ though in two traits: the anterior mid clypeal margin is convex, relatively acute in *N. emiliae*, while in *N. metanotalis* is straight or even slightly concave; the body dorsum has abundant appressed, copperish pilosity in *N. emiliae*, while that of *N. metanotalis* is significantly less hairy, so that the cuticle seems polished, and also these hairs are pale golden.

Records of *N. emiliae* span from ca. 200 m to ca. 1200 m elevation, the latter found in the humid habitats of Cordillera de la Costa montane forests in Venezuela; whereas the Colombian specimens belong from the Los Llanos and Aguirre-Villavicencio dry forests, at the western side of the Cordillera Oriental. The specimen from Ecuador was collected in a private reserve located on the Northwestern Andean montane forests ecoregion.

Natural history notes. Almost nothing is known about the biology of this epigeic forager, but see Mackay and Mackay (2010).

Material examined. 8☿. **COLOMBIA – Meta:** • 2☿; Acacias, Araguaney ; 3.9518, -73.7002; alt. 490m; 2004-04-23; Florez, E. leg.; (ICN). • 1☿; Finca Versalles; 3.2727, -73.0879; alt. 206m; 2004-04-19; Flores, E. leg.; pitfall; (MEPN). • 1☿; La Esmeralda; 3.2727, -73.0879; alt. 206m; 2005-04-25; Flores, E. leg.; pitfall; (MEPN). • 1☿; Parque Nacional Natural Tinigua; 3.9899, -73.966; alt. 1800m; 1992-01-01; L. T.; C. E. leg.; (IAvH). • **ECUADOR – Pichincha:** • 1☿; Pichincha, Reserva Otongachi; -0.321, -78.951; alt. 770m; (MEPN?). • **VENEZUELA – Aragua:** • 1☿; Est. Biol. Rancho Grande; 10.3531, -67.6798; alt. 1200m; 2008-08-13; Longino, J. leg.; (JTLC). • 1☿; Est. Biol. Rancho Grande; 10.3531, -67.6798; alt. 1200m; 2008-08-13; J. Longino leg.; bait; (JTLC). – **Carabobo:** • 1☿; Puerto Cabello; 10.4731, -68.0125; (MHNG).

Geographic range. Venezuela, Colombia, Ecuador.

***Neoponera glabra* sp. nov.**

Figures. 12: a – f (☿); 15: (distribution).

Type material. ***Holotype***. 1☿; **BRAZIL**: **Bahia**: Esplanada, Baixio, 12 06 52 S, 37 41 49 W, 06.x.2010, M. L. O. Travassos [leg.], E763 [collector's code], (CPDC: ATPFOR1993).

Etymology. The specific epithet is derived from the singular Latin *glaber* meaning "hairless, smooth, bald". I am referring thus to the glabrous surface of the nodal posterior face.

Worker diagnosis. Posterior head margin feebly concave (Fig. 12c); ventrolateral head surface with concentric striae, progressively fading toward midcentral region; head dorsum with irregularly-shaped, not continuous costae (Fig. 12d); propodeum with shallowly-impressed, fused punctae (Fig. 12a, b); meso and metapleuron with irregular costae (Fig. 12a, e); posterior face of petiolar node glabrous (Fig. 4a); mid-lateral nodal margin with incision (Fig. 12e); ventroposterior nodal margin scrobiculate (Fig. 4a, 12e); prora well-developed, with blunt tip directed anterad (Fig. 12e).

Worker description. Measurements (n = 3, holotype in parenthesis): HW: 2.5-2.6 (2.55); HL: 2.7-2.8 (2.7); EL: 0.55-0.6 (0.55); SL: 2-2.25 (2); WL: 3.3-3.85 (3.4); PrW: 1.75-2.05 (1.75); MsW: 1.2-1.25 (1.2); MsL: 0.75-0.85 (0.75); PW: 1.7-2 (1.75); PH: 1.6-1.75 (1.6); PL: 0.9-1.05 (0.9); GL: 3.8-5 (4.7); A3L: 1.85-1.95 (1.95); A4L: 1.9-1.95 (1.95); A3W: 2.3-2.35 (2.3); A4W: 2.05-2.2 (2.05); TLa: 10.7-11.55 (10.9); TLr: 11.5-11.95 (11.7). **Indices**. CI: 92.59-94.44 (94.44); OI: 21.57-24 (21.57); SI: 78.43-86.54 (78.43); MsI: 147.06-160 (160); LPI: 55.88-60 (56.25); DPI: 178.95-194.44 (194.44).

Head. *Frontal view*: subquadrate. Mandible triangular, longer than wide, distal region moderately bent ventrad, dorsolateral margin mostly straight. Masticatory margin of mandible with four teeth distally followed by four to five denticles proximally. Prementum with well-developed transverse dome. Prementum and round groove distally. Palp formula: 4,4. Stipes mostly smooth, internal longitudinal groove present. Labrum dorsum mostly smooth, finely striated basally. Clypeus anteromedially convex, with relatively acute extension of the cuticle projecting anterad. Posterior margin of frontoclypeal sulcus not reaching ocular mid-length. Frontal carina surpassing ocular posterior margin, medially. Torular lobe subtriangular, almost completely covering acetabulum of antennal socket, posterolateral margin slightly convex. Malar carina absent, though

malar region is slightly raised. Eye suboval, maximum length between one-fourth and one-fifth head length, convex, surpassing lateral margin of head, placed slightly anterior to cephalic mid-length. Posterior margin of head concave. Occipital carina strongly reduced. Scape, when pulled posterad, surpassing posterior margin of head by half apical scape width. **Mesosoma**. *Lateral view*: Dorsal margin slightly convex. Pronotum carinate, with carina not projecting from cuticle. Anapleural sulcus well-developed, completely dividing mesopleuron in anepisternum and katepisternum. Posterolateral margin of propodeal declivity slightly marginated. Propodeal spiracle oval to suboval. Ventrolateral propodeal declivity without deep groove. Posteroventral cuticular flap at metapleural gland opening well-developed, slightly bent dorsad, gland orifice clearly visible in posterolateral view. Pheromone venting canal at metapleural gland opening present, well-developed, mostly smooth. Posterior face of propodeal declivity flat. Propodeal lateral margins parallel at base, convergent dorsad. *Ventral view*: probasisternum triangular-shaped, strongly grooved. Probasisternal posterior projection with spine. Mesosternal process well-developed, fang-shaped, internal margins of lobes running relatively parallel, relatively flattened anteroposteriorly, inclined posterad ca. 30–45 degrees in lateral view, space between lobes approximately equal to width of each. Metasternal process well-developed, inclined posterad, ca. 45° in lateral view, triangular-shaped, flattened anteroposteriorly, apex slightly higher than half height of metacoxal internal margin, space between lobes wider than width of each, internal margins divergent. Metasternal process external margins convergent. **Legs**. Mesofemur slightly thicker than metafemur, in dorsal or ventral view. Ventral surface of meso- and metafemora slightly flattened roughly on distad two thirds. Tibial spur formula 2(1s, 1p), 2(1s, 1p). Anterior mid tibial spur slightly longer than half-length of posterior spur. Anterior hind tibial spur about 2.5 times shorter than posterior spur. Pretarsal claw arched, unarmed (without accessory teeth on surface). Arolium present, roughly three times shorter than pretarsal claw. **Petiole**. *Lateral view*: Petiolar node with straight anterior margin and convex posterior margin, posterior margin shorter than anterior margin, posterior face concave. Subpetiolar process shovel-shaped, with keel-shaped anterior cusp, followed by posterior horizontally straight region, dome with transverse, feebly impressed striae. Lateral projection of anteroventral nodal carina well-developed, with blunt tip projecting dorsad. Lateral nodal carina absent. Anteroventral nodal carina incomplete, feebly concave medially. **Gaster**. *Lateral view*: Prora well-developed, small, projected anterad, not hidden by helcium laterally. Anterior margin of tergum of A3 straight. Dorsalmost limit of anterior

tergal margin of A3 below nodal dorsal margin. Meeting region of anterior margin of tergum of A3 with its dorsal margin relatively angled. Anterodorsal margin of tergum of A3 slightly convex. Cinctus weak. *Dorsal view*: Tergum of A3 slightly longer than A4. Posterior dorsum of epipygium coriaceous. **Color**. Appendages mostly ferruginous black, mandibles lighter than overall body. **Pilosity**. Body with scant, flexuous, golden to dark golden, erect and suberect hairs which are mostly present ventrally. Appressed pubescence not abundant, mostly present on head and mesosoma, petiole and gaster with significantly less piligerous punctae. Most erect hairs on body dorsum smaller than maximum eye length. Scape pilosity mostly pruinose but not abundant. Meso- and metatarsi bearing abundant spine-like setae and tiny appressed and suberect fine setae. Posterior ventrolateral margin of hypopygium (just next to the base of sting) bearing scattered flexuous hairs, shorter than eye maximum length. Posterior dorsum of epipygium surrounded by sparse, ca. 10 long flexuous hairs, longer than eye maximum length. **Sculpture**. Integument polished. Striae on head present as costae dorsally, and ventrally concentric, mandibles finely striate dorsally, mesosoma, except for posterior propodeal face, completely covered by strong to moderately impressed costae. Striae on petiolar node absent.

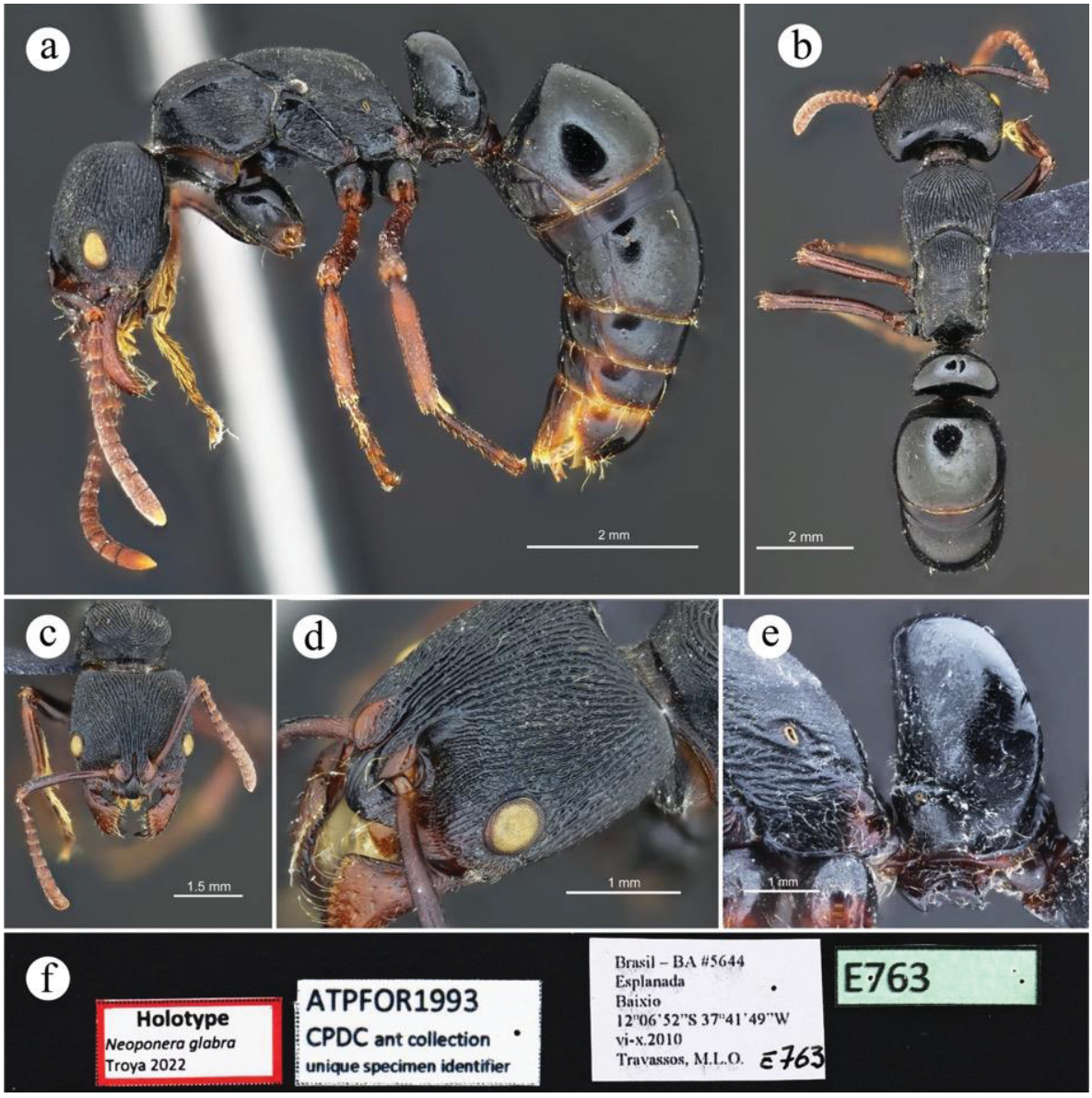


Fig. 12. *Neoponera glabra* sp. nov. Holotype ☿ (CPDC: ATPFOR1993). Brazil: Bahia. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.** Detail of striae on head; **e.** Posterior region of propodeum and petiole in lateral view (same individual with different hue); **f.** Collection labels.

Comments. *Neoponera glabra* is a medium-sized taxon among species in the *N. emiliae* group (Fig. 6d, TLa: 10.7 – 11.55 mm). The irregular-shaped costae on its head dorsum, some of which fuse with each other forming random variable patterns which are particularly noticeable on the lateral side over the internal eye margin (Fig. 12d), plus the glabrous posterior nodal face, are good defining characters which differentiates this species from every other in this species-group.

The costae on the head dorsum of all other species in the *N. magnifica* subclade are mostly straight, and the posterior nodal face is either punctate or striate, or with a mixture of both. Despite such unique features, only *N. caxiuana* could be confused with *N. glabra*, but the meso and metapleuron of the former are punctate, not costate as in *N. glabra*.

Since only three specimens are known, all from eastern Bahia (Fig. 15), no major conclusion about potential apomorphies is possible, nevertheless, the three specimens are mostly identical which may be no surprise since the sites where the collections sites are in relative proximity: two of these lie in the Bahia Coastal forests (where the holotype was found) at about the sea level, and are separated by about 70 km from each other; whereas the third specimen was collected from a contact zone between the Caatinga biome and the Bahia Interior forests, an ecoregion of the Atlantic Forest biome (da Silva 2018), at about 750 m elevation, located 200 km west from the other sites.

Current phylogenetic data suggest that *N. glabra* is the least derived lineage of the *N. magnifica* subclade (Troya et al., unpublished), and in terms of genetic divergence this lineage is about 2.5 % different from its closest lineage, *N. dropsy*. Since only three species were sequenced (one specimen/species) in the *N. magnifica* subclade, is almost impossible to infer potential ancestral states for these apparently not so related lineages, as judged by their relative long branches. Based exclusively on the morphology of all species in the *N. emiliae* group, however, it seems that, for example, the irregularly-shaped costae of *N. glabra* could illustrate part of the traits which putatively were present in the ancestor of this subclade.

Natural history notes. The examined specimens were collected through Winkler extractors and directly by hand, and as the other species in this group, *N. glabra* likely is an underground nester and/or uses preformed cavities like hollowed sticks or dead stems for colony founding.

Other material examined. 2☿. **BRAZIL – Bahia:** • 1☿; Mata de São João; -12.5311, -38.3013; alt. 42m; 2012/08; Melo, T. S. leg.; hand collected; (MEPN). • 1☿; Milagres; -12.9, -39.85; alt. 753m; 2010-10-23; Ulysséa, M. A.; Medina, A. M.; Campos, E. M. leg.; Winkler; (MZSP).

Geographic range. Brazil: eastern Bahia.

***Neoponera magnifica* (Borgmeier, 1929)**

Figures. 13: a – d (☿); 15: (distribution).

Pachycondyla magnifica Borgmeier, 1929: 196. 2 ☿ syntype, Brazil, Staat Goyaz [Goiás], Campinas [today a region in the city of Goiânia], ii.1928, P.J.S. Schwarzmaier, C. ss. R. leg., No. 3751 [Borgmeier's collection code], (MCZC, MZSP [examined]). Note: one ☿ at MZSP labeled as "lectotypus" by Borgmeier (Fig. 9) is in fact part of the syntype material.

Combinations. In *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species. Kempf, 1961: 198 (redescription); MacKay & MacKay, 2010: 451 (redescription).

Worker (and probably queen) diagnosis. Head with two patches of appressed, golden hairs (Fig. 13c); antennal scape, when pulled posterad barely reaching, or at most exceeding posterior head margin by less than half apical scape width (Fig. 13c); posterior head margin straight to weakly concave (Fig. 13c, link); mesonotum either with horizontal, vertical, or oblique well-impressed striae (Fig. 13b); propodeum and pleural regions with mixture of shallow microstriae and micropunctae; subpetiolar process medially notched (Fig. 3a); posterior nodal face with mixture of shallow striae and punctae.

Worker. Measurements (n = 5): HW: 2.6-3.1; HL: 2.85-3.35; EL: 0.5-0.6; SL: 1.95-2.25; WL: 3.65-4.25; PrW: 2.0-2.35; MsW: 1.25-1.4; MsL: 0.9-1; PW: 1.85-1.95; PH: 1.7-1.9; PL: 0.95-1.1; GL: 5.16-8; A3L: 2.4-2.7; A4L: 2.05-2.2; A3W: 2.65-2.8; A4W: 2.35-2.7; TLa: 12.15-13.6; TLr: 12.86-16.7. **Indices.** CI: 86.67-95.16; OI: 17.74-21.15; SI: 66.1-84.62; MsI: 131.58-150; LPI: 52.78-57.89; DPI: 177.27-200.

Comments. *Neoponera magnifica* is the largest taxon of the *N. emiliae* group (Fig. 6d, TLa = 12.15 – 13.6 mm). From the scant specimens examined, all belonging from the Cerrado biome in Brazil, almost no differences in their morphology were noted, except for the relative amount and depth of striae on the mesonotum and posterior face of the petiolar node. The syntype from Campinas (today a neighborhood of the city capital of Goiânia), state of Goiás, for example, has a mesonotum with oblique and concentric striae, while in specimens from Anápolis, Goiás (DZUP549378), and Ribas do Rio Pardo, Mato Grosso do Sul (DZUP549545), this structure shows concentric, and vertical striae, respectively. As for the nodal posterior face, the syntype shows

scattered, feebly impressed, vertical and concentric striae. A similar pattern is displayed on the specimen from Anápolis, while in the specimen from Mato Grosso do Sul the striae are vertical and well-marked on the whole nodal surface. As judged from other species in this subclade, it seems that the depth, amount and orientation of striae and punctae vary from site to site. This does not apply though to the material of *N. maginifica*-1 sp. nov. where all specimens were almost identical.

Neoponera magnifica is very similar to all its subclade partners, except for *N. glabra* which is smaller (TLa ≃ 11 mm), without pilose patches on head dorsum, and the subpetiolar process is horizontally straight medially. The following features of *N. magnifica* distinguish it from the rest of species in the subclade: the head dorsum has a pair of golden patches of pilosity (vs. absent in the other species); the subpetiolar process is notched or concave medially (vs. horizontally straight or feebly convex); and the propodeal spiracle is slit-shaped (vs. oval, except for *N. caxiuana* which also shows a slit-shaped spiracle).

Mackay and Mackay (2010) believed this species should be placed in its own species-complex (here considered species-group since this and its related lineages are diagnosable), due to its unusual morphology. They realized that in doing so all the other members of the *N. emiliae* group would require also their own group. M&M were correct, in part, because *N. magnifica*, and now its subclade partners, are sister to the species of the *N. emiliae* subclade, but unrelated to those of "*N. emiliae*-2", which they had placed in the *N. emiliae* group.

Species of the *N. magnifica* subclade may be considered unique among the *Neoponera*, mostly because of their costate sculpture, the comparatively small eyes placed anteriorly on a relatively large cranium, and the extravagant cephalic golden patches (though this is autapomorphic only for *N. magnifica*). Some of these traits are apparently plesiomorphic residues from closely related genera as *Pachycondyla* and *Igaponera* which show similar morphologies. Moreover, these traits, for example, the heavily costate cuticle which is thought to reduce wear and tear in epigeic scavengers, are among the few vestiges in the genus, and this is telling its very origins from the ground as commented by Schmidt and Shattuck (2014). This is also reflected in the tree topology of *Neoponera* as the ancestor of the lineages in the *N. emiliae* group is the first diverging node in the genus (Troya et al., unpublished).

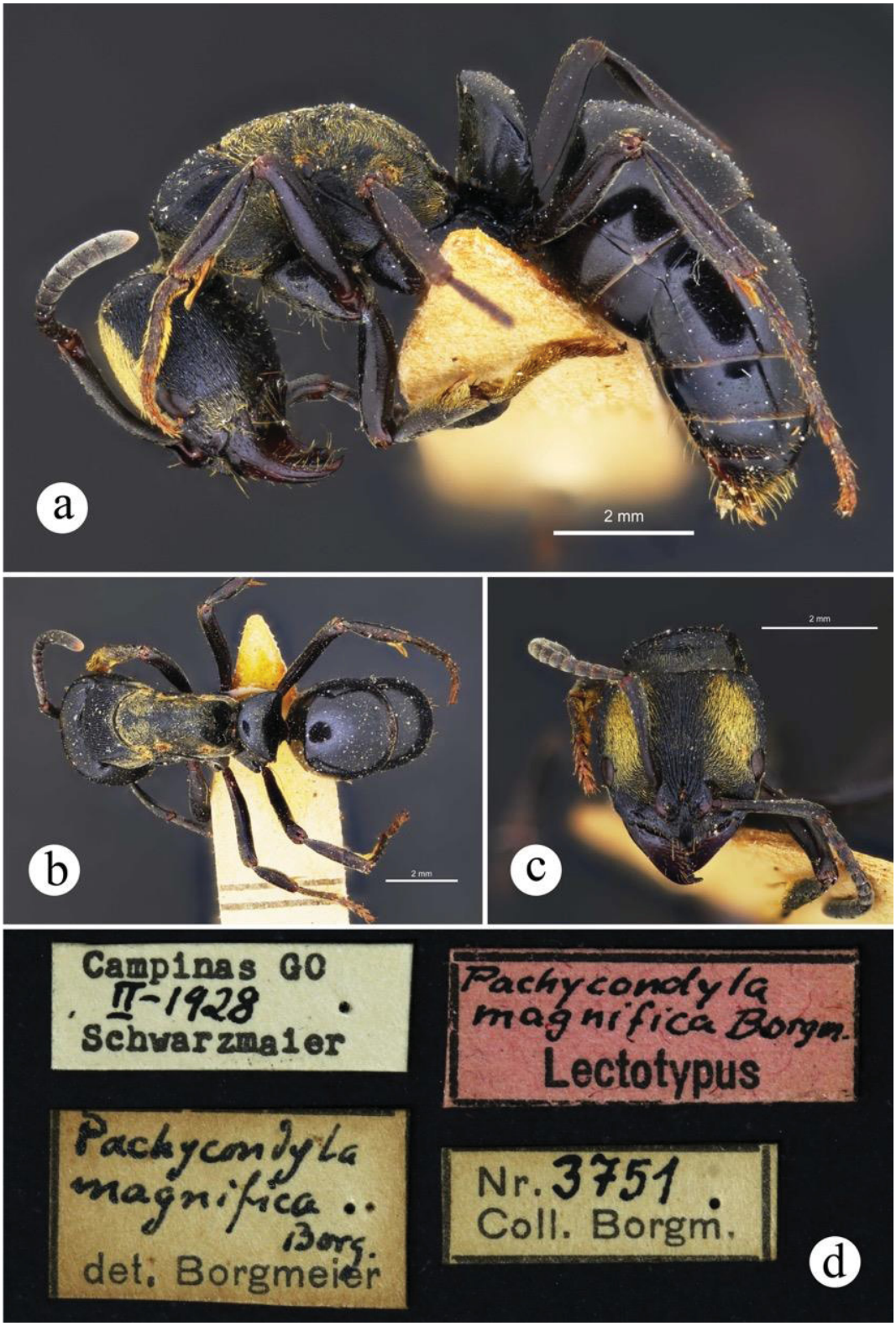


Fig. 13. *Neoponera magnifica* (Borgmeier, 1929). Syntype ☿ (MZSP). Brazil: Goiás. a. Lateral view; b. Dorsal view; c. Head in frontal view; d. Collection labels.

Current *N. magnifica* populations are restricted to a relatively small region of the Cerrado biome in Brazil; records belong from central Goiás and southern Mato Grosso do Sul, spanning an altitudinal range between ca. 700 m to ca. 1000 m.

Natural history & conservation notes. Almost nothing is known about the biology or behavior of this enigmatic species; it seems though they nest underground, or at least on cavities on the floor surface, since almost all examined specimens had their bodies coated with traces of ground. Although no information was provided on the specimen labels of the examined material, including the syntype, these specimens were likely collected randomly by hand or by pitfall traps. The two specimens from southern Mato Grosso do Sul were collected in 2017, while those from Goiás and Distrito Federal date back 50 – 90 years ago. Today, the original vegetation of these regions has been virtually entirely replaced by human-driven production zones where cattle ranching and agriculture dominate, and has increased in recent decades (Bell 2019, Vale et al. 2019, ForestWatch.org 2021). Maybe, the rarity of specimens of *N. magnifica* in natural history collections is not due to their putative cryptic behavior, but perhaps due to its reproductive behavior producing small colonies; if this is confirmed, then it would also be the case for all species in the *N. emiliae* group for which very low capture events are recorded as well. Whether this hypothesis is challenged or not in future research while collection efforts increase, the underlying conservation issue remains. Populations of *N. magnifica*, if still exist in the Cerrado regions of Goiás, are likely prone to extinction; the impact of human development coupled with intentional fire events in a number of sites in that state (Pivello et al. 2021, Zalles et al. 2021) can dramatically reduce the likelihood of survival of most organisms. The populations from Mato Grosso do Sul have perhaps a more promissory future, however, since the natural land cover to the south of that state is apparently increasing (ForestWatch.org 2021).

Material examined. 8♀. **BRAZIL – Goiás:** • 1♀; Anapolis; -16.3285, -48.9534; alt. 1000m; 1969-01-16; Kempf, W. leg.; (MZSP). • 1♀; Anápolis; -16.3285, -48.9534; alt. 1000m; 1969-01-16; Kempf, W. leg.; (DZUP). • 1♀; Campinas; -16.661, -49.2924; alt. 703m; 1928/02; Schwarzmaier leg.; (MZSP). • 1♀; Campinas; -16.661, -49.2924; alt. 703m; 1928-10-10; Schwarzmaier leg.; (MZSP). • 1♀; Campinas; -16.661, -49.2924; alt. 703m; Schwarzmaier leg.; (MZSP). • 1♀; Distrito Federal; -15.7, -47.8; alt. 1000m; 1961-10-01; Araujo, R. L. leg.; (MZSP). **– Mato Grosso do Sul:** • 1♀; Assentamento Lagoa Grande; -21.9833, -55.3167; alt. 430m; 2017-

01-01; Lopez, V. leg.; (MuBio-UFGD). • 1☿; Ribas do Rio Pardo; -21.0899, -53.7005; alt. 460m; 2017-08-14; Aranda, R. leg.; (ZSUP).

Geographic range. Brazil's central (?) and southern Cerrado.

***Neoponera metanotalis* (Luederwaldt, 1918)**

Figures. 14: a – d (☿); 15: (distribution).

Pachycondyla metanotalis Luederwaldt, 1918: 54. ☿ holotype, Brazil, Minas Gerais, Christina, H. Luederwaldt (leg.), 17.195 [Luederwaldt's collection code], (MZSP) [examined].

Combination in *Neoponera*: Schmidt & Shattuck, 2014: 151.

Status as species. Borgmeier, 1923: 70; Kempf, 1961: 200 (redescription); MacKay & MacKay, 2010: 460 (redescription).

Worker and queen diagnosis. Antennal scape, when pulled posterad, exceeding posterior head margin by about 0.5 to 1 X apical scape width (Fig. 1b); mid clypeal margin horizontally straight (Fig. 1b); mesosoma mostly punctate, with feebly to well-impressed striae dorsolaterally on propodeum (link); posterior face of petiolar node either glabrous (link), or with scattered to abundant piligerous punctae; prora well-developed, either lip-shaped (with round tip, link) or truncate (link).

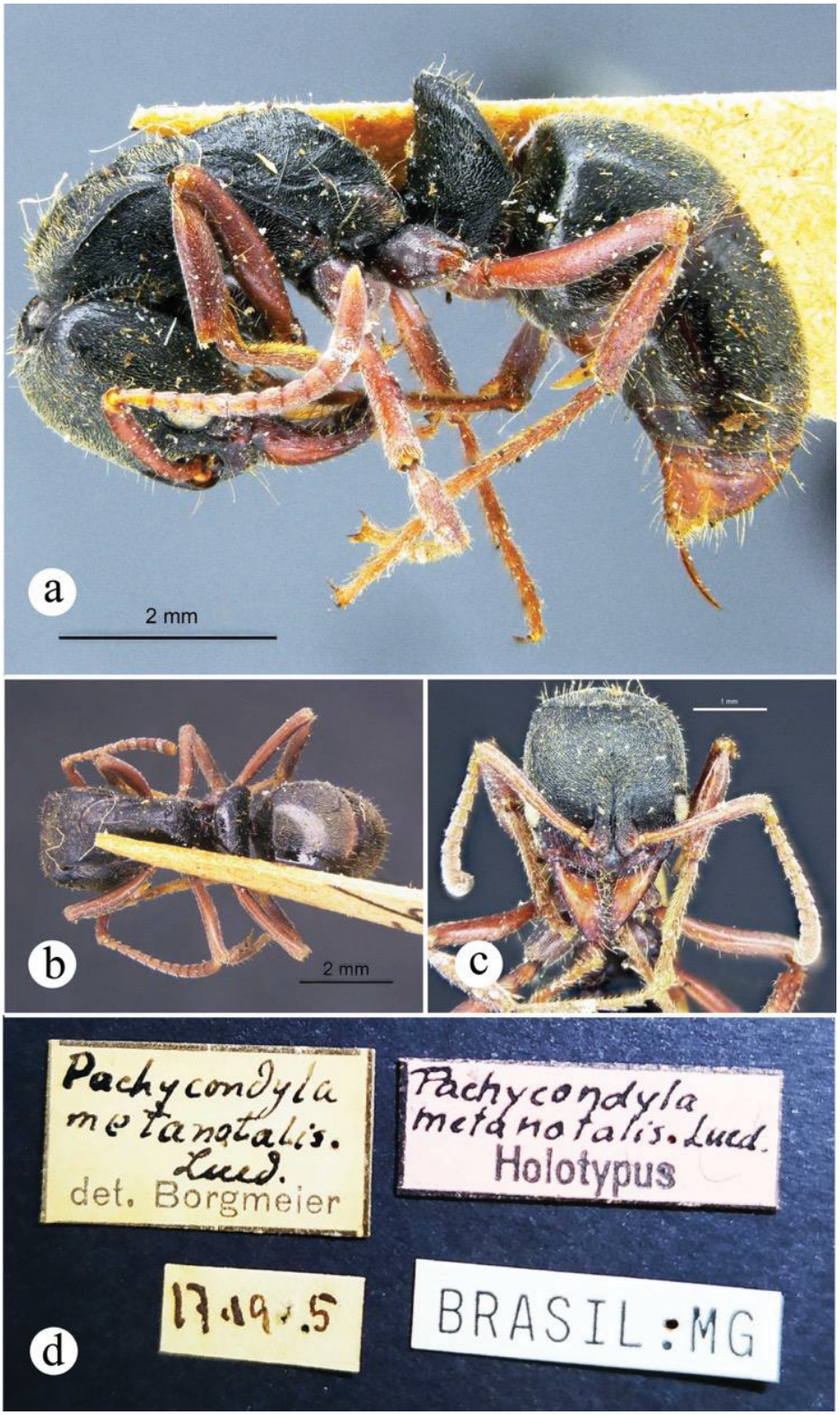


Fig. 14. *Neoponera metanotalis* (Luederwaldt, 1918). Holotype ☿ (MZSP). Brazil: Minas Gerais. **a.** Lateral view; **b.** Dorsal view; **c.** Head in frontal view; **d.**; Collection labels.

Worker. Measurements (n = 4): HW: 1.95-2.35; HL: 2.2-2.55; EL: 0.35-0.55; SL: 1.75-2.35; WL: 3-3.65; PrW: 1.4-1.6; MsW: 0.85-1.2; MsL: 0.65-0.75; PW: 1.35-1.55; PH: 1.2-1.5; PL: 0.75-1; GL: 2.8-4.45; A3L: 1.5-1.65; A4L: 1.55-1.75; A3W: 1.85-2.15; A4W: 1.75-2.1; TLa: 9.15-10.6; TLr: 8.9-10.95. **Indices**. CI: 88.64-95.56; OI: 16.28-23.4; SI: 87.23-109.3; MsI: 128.57-160; LPI: 53.33-70.83; DPI: 155.0-187.5.

Comments. *Neoponera metanotalis* is the second smallest species of the *N. emiliae* group (Fig. 6d, TLa = 9.2 – 10.6 mm). As *N. emiliae*, this is amongst the least commonly collected taxon of this species-group, but also amongst species in the genus. Interestingly, from the scant six workers known, all belonging from a central region of the Atlantic Forest in Brazil, eastern Bahia – BA, Minas Gerais – MG (the holotype is from this locality), and São Paulo – SP (Fig. 15), the following variations were detected: the antennal scape exceeds the posterior head margin by about one apical scape width in specimens from MG and SP, while the specimen from BA shows a smaller antennal scape, exceeding said margin by 0.5 times apical scape width; the posterior face of petiolar node has piligerous punctae, either scant to abundant in specimens from SP, or mostly glabrous in those from MG and BA; the node is shorter in specimens from SP and MG (PL = 0.75 – 0.85 mm) than that from BA (PL = 1 mm); the posterior nodal margin of the specimen from BA is clearly less inclined than the equivalent from those of SP and MG; the prora in all specimens is well-developed, but in specimens from SP and BA it is truncate, while in the rest it is lip-shaped; the specimen from BA is larger (TLa = 10.6 mm) than those from SP and MG (TLa = 9.15 – 9.80 mm). The morphology of the specimens from SP and MG mostly fits the morphology of the holotype, while the specimen from BA (link) likely represents a populational variant. Since these variations are not strongly diverging from the diagnostic features here considered, and given the scarcity of specimens involved, it seems prudent to leave it as such, while eventually additional material is found. In terms of genetic divergence, on the other hand, the *Neoponera* phylogeny depicts a relatively broad distance (1.68 %) of this variant with respect to a specimen representing the population of MG (Troya et al., unpublished). Since only two specimens were included in the analysis, however, is impossible to support any hypothesis of lineage split between these populations whose records belong from similar ecoregions (Serra do Mar coastal forests and Bahia Interior forests) in terms vegetation type, which is predominantly seasonal moist forest (da Silva 2018).

Neoponera metanotalis is most similar to its sister lineage *N. emiliae* among species in this group. Differences between these two lineages were cited already under the *N. emiliae* treatment (see above).

The elevational range of this species spans from ca. 600 m to ca. 1300 m.

Natural history notes. This is probably a terrestrial forager, maybe predatory species. The two records of SP were collected using Winkler extractors, while the other records from MG and BA were possibly obtained directly by hand. Besides this, nothing is known about its biology.

Material examined. 6☿. **BRAZIL – Bahia:** • 1☿; 18 km N of Itororò; -14.95, -40.0333; alt. 600m; 2000-08-08; Lacau, S. leg.; (CPDC). – **Minas Gerais:** • 1☿; Caparaó; -20.4193, -41.8514; alt. 1350m; 2011-12-05; Chaul, J. leg.; (DZUP). • 1☿; Christina; -22.21, -45.26; 1905-03-19; Luederwaldt, H. leg.; (MZSP). – **São Paulo:** • 2☿; Parque Estadual Serra do Mar, núcleo Cunha; -23.25, -45.0; alt. 1147m; 2001-04-21; Tavarés, A. A.; Silva, R. R. leg.; Winkler; (MZSP). • 1☿; REBIO do Alto da Serra de Paranapiacaba; -23.8067, -47.1233; alt. 919m; 1962-09-24; Werner, R. leg.; (DZUP).

Geographic range. Eastern Brazil.

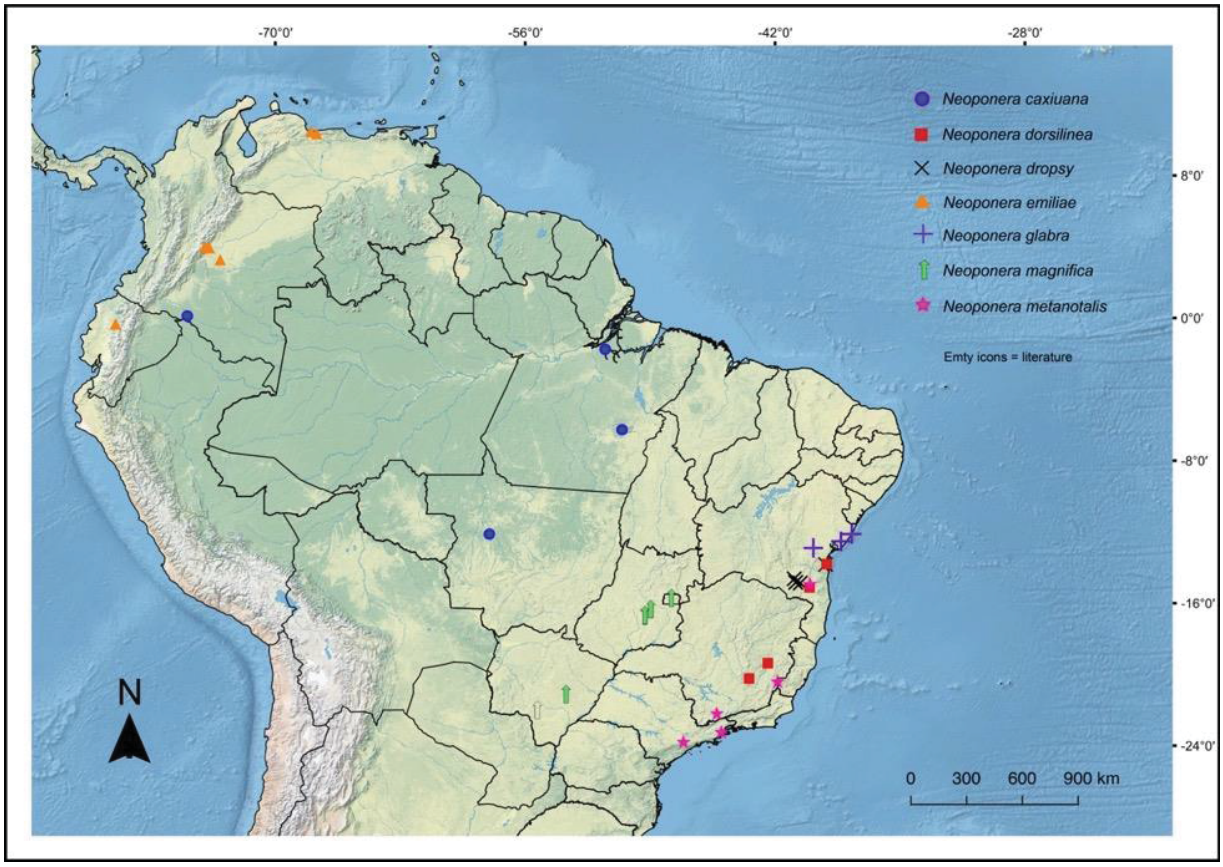


Fig. 15. Distribution of examined species records of the *N. emiliae* species group. Empty arrow belongs to *N. magnifica*, record from AntWeb.org.

REFERENCES

AntCat. **2022**. AntCat (2022) An online catalogue of the ants of the world by Barry Bolton. Available from https//www. antcat.org. (accessed Mar 2022).

Arias, T. 2003. Nuevos registros de especies de hormigas de la subfamilia Ponerinae (Hymenoptera: Formicidae) para Colombia. Caldasia. 25: 429–431.

Arnold, M. L. 1992. Natural hybridization as an evolutionary process. Annu. Rev. Ecol. Syst. 23: 237–261.

Bell, S. 2019. Cattle in the Backlands: Mato Grosso and the Evolution of Ranching in the Brazilian Tropics. AAG Rev. Books. 7: 235–237.

Bolton, B. 1994. Identification guide to the ant genera of the world, Harvard Univ. Press.

Bolton, B. 1995. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, Mass.

Borgmeier, T. 1923. Catalogo systematico e synonymico das formigas do Brasil. 1 parte. Subfam. Dorylinae, Cerapachyinae, Ponerinae, Dolichoderinae. Arch. do Mus. Nac. (Rio Janeiro). 22–103.

Borgmeier, T. 1929. Zur Kenntnis der brasilianischen Ameisen. Rev. Española Entomol. 195–214.

Boudinot, B. E. 2013. The male genitalia of ants: Musculature, homology, and functional morphology (Hymenoptera, Aculeata, Formicidae). J. Hymenopt. Res. 30: 29–49.

Boudinot, B. E. 2015. Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata): a new diagnosis of the family, the first global male-based key to subfamilies, and a treatment of early branching lineages. Eur. J. Taxon. 120: 1–62.

Branstetter, M. G., and J. T. Longino. **2022**. UCE Phylogenomics of New World Cryptopone (Hymenoptera: Formicidae) Elucidates Genus Boundaries, Species Boundaries, and the Vicariant History of a Temperate–Tropical Disjunction. Insect Syst. Divers. 6.

Branstetter, M. G., and L. Sáenz. **2012**. Las hormigas (Hymenoptera: Formicidae) de Guatemala, pp. 12–22. *In* Cano, B., Schuster, J.C. (eds.), Biodivers. Guatemala. Universidad del Valle de Guatemala, Guatemala.

Brown, W. 1973. A comparison of the Hylean and Congo-west African rain forest ants faunas, p. 350. *In* Meggers, B.J., Ayensu, E.S., Duckworth, W.D. (eds.), Trop. For. Ecosyst. Africa South Am. a Comp. Rev. Smithsonian Institution Press, Washington, D.C.

Brown, W. L. 1995. Untitled. Taxonomic changes in Pachycondyla and Neoponera attributed to Brown., pp. 302–311. *In* Bolton, B. (ed.), A New Gen. Cat. Ants World. Cambridge, Mass.: Harvard University Press, 504 pp., USA.

Cantone, S. 2017. Winged ants – The male. Dichotomous key to genera of winged male ants in the world. Behavioral ecology of mating flight. São Paulo: Autopubblicato.

Cantone, S., and C. J. Von Zuben. **2019**. The Hindwings of Ants: A Phylogenetic Analysis. Psyche (London). 2019.

Dallwitz, M. 1980. A general system for coding taxonomic descriptions. Taxon. 29: 41–46.

Dejean, A. 1990. Influence de l'environnement pré-imaginal et précoce dans le choix du site de nidification de Pachycondyla (= Neoponera) villosa (Fabr.)(Formicidae, Ponerinae). Behav. Processes. 21: 107–125.

Delabie, J. H. C., C. S. F. Mariano, L. F. Mendes, S. G. Pompolo, and D. Fresneau. **2008**. Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no gênero Pachycondyla na região neotropical: o caso do complexo apicalis, pp. 196–222. *In* Vilela, E.F., Santos, I.A., Schoereder, J.H., Lino Neto, J., Campos, L.A.O., Serrão, J.E. (eds.), Insetos Sociais Da Biol. à Apl. Editora da Univ. Federal de Viçosa, 442 p., Viçosa, MG.

Delsinne, T., F. J. Serna, M. Leponce, and B. E. Boudinot. **2019**. Capítulo 13. Glosario de morfología, pp. 387–457. *In* Fernández, F., Guerrero, R., Delsinne, T. (eds.), Hormigas Colomb. Universidad Nacional de Colombia, Bogotá.

Emery, C. 1890. Voyage de M. E. Simon au Venezuela (Décembre 1887 - Avril 1888). Formicides. Ann. la Société Entomol. Fr. 55–76.

Emery, C. 1901. Notes sur les sous-familles des dorylines et ponérines (famille des Formicides). Ann. la Société Entomol. Belgique. 45: 32–54.

Emery, C. 1904. Zur Kenntniss des Polymorphismus der Ameisen. Zool. Jahrbücher. Suppl. 587–610.

Emery, C. 1911. Hymenoptera. Fam. Formicidae. Subfam. Ponerinae, p. 124. *In* Wytsman, P. (ed.), Genera Insectorum. Bologne.

Fabricius, J. C. 1804. Systema Piezatorum secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus. Brunswick: C. Reichard.

Fernandes, I. O., M. L. De Oliveira, and J. H. C. Delabie. **2014**. Description of two new species in the Neotropical Pachycondyla foetida complex (Hymenoptera: Formicidae: Ponerinae) and taxonomic notes on the genus. Myrmecological News. 19: 133–163.

Fernández, F., and R. J. Guerrero. **2019**. Capítulo 17. Subfamilia Ponerinae, pp. 509–553. *In* Fernández, F., Guerrero, R.J., Delsinne, T. (eds.), Hormigas Colomb. Universidad Nacional de Colombia, Bogotá.

Fernandez, F., and E. E. Palacio. **1995**. Hormigas de Colombia IV: nuevos registros de géneros y especies. Caldasia. 17: 587–596.

Fernández, F., E. E. Palacio, W. P. MacKay, and E. S. MacKay. **1996**. Introducción al estudio de las hormigas (Hymenoptera: Formicidae) de Colombia, pp. 349–412. *In* Andrade, M.G., Amat García, G., Fernández, F. (eds.), Insectos Colomb. Estud. Escogidos. Academia Colombiana de Ciencias Exactas, Físicas y Naturales, 541 pp., Bogotá.

Field, D. L., D. J. Ayre, R. J. Whelan, and A. M. Young. **2011**. Patterns of hybridization and asymmetrical gene flow in hybrid zones of the rare Eucalyptus aggregata and common E. rubida. Heredity (Edinb). 106: 841–853.

Forel, A. 1899. Biologia Centrali-Americana; or, contributions to the knowledge of the fauna and flora of Mexico and Central America. In- secta. Hymenoptera. Vol. III. (Formicidae.), Biol. Cent. Hym. London.

Forel, A. 1901. Nouvelles espèces de Ponerinae. (Avec un nouveau sous-genre et une espèce nouvelle d'Eciton). Rev. Suisse Zool. 325–353.

ForestWatch.org. **2021**. Tree cover change Brazil. (www.globalforestwatch.org.).

Gallardo, A. 1918. Las hormigas de la República Argentina. Subfamilia Ponerinas. An. del Mus. Nac. Hist. Nat. Buenos Aires. 1–112.

De Geer, C. 1773. Mémoires pour servir à l'histoire des insectes. Tome troisième. Pierre Hesselberg, 696 pp., Stockholm.

Gomes, J. P., L. Iannuzzi, and I. R. Leal. **2010**. Response of the ant community to attributes of fragments and vegetation in a northeastern Atlantic rain forest area, Brazil. Neotrop. Entomol. 39: 898–905.

Google. **2022**. Google Earth. (https://earth.google.com.).

Gutiérrez-Valencia, J., G. Chomicki, and S. S. Renner. **2017**. Recurrent breakdowns of mutualisms with ants in the neotropical ant-plant genus Cecropia (Urticaceae). Mol. Phylogenet. Evol. 111: 196–205.

Harada, A. Y. 2016. State of Art of Ants (Hymenoptera: Formicidae) at Caxiuanã, Melgaco, Pará, Brazil. Adv. Entomol. 04: 115–132.

Harris, R. A. 1979. Glossary of surface sculpturing. Occas. Pap. Entomol. 32.

Keller, R. A. 2011. A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. Bull. Am. Museum Nat. Hist. 2011: 1–90.

Kempf, W. W. 1961. As formigas do gênero Pachycondyla Fr. Smith no Brasil (Hymenoptera: Formicidae). Rev. Bras. Entomol. 189–204.

Kempf, W. W. 1972. Catálogo Abreviado das formigas da Região Neotropical (Hymenoptera: Formicidae). Stud. Entomol.

Lepeletier de Saint-Fargeau, A. 1835. Histoire naturelle des insectes. Hyménoptères. Tome I. Paris: Roret, Paris.

Longino, J. 2010. Ants of Costa Rica. (https://ants.biology.utah.edu/AntsofCostaRica.html).

Longino, J. T., and M. G. Branstetter. **2020**. Phylogenomic Species Delimitation, Taxonomy, and 'Bird Guide' Identification for the Neotropical Ant Genus Rasopone (Hymenoptera: Formicidae), Insect Syst. Divers.

Lucas, C., D. Fresneau, K. Kolmer, J. Heinze, J. H. C. Delabie, and D. B. Pho. **2002**. A multidisciplinary approach to discriminating different taxa in the species complex Pachycondyla villosa (Formicidae). Biol. J. Linn. Soc. 75: 249–259.

Luederwaldt, H. 1918. Notas myrmecologicas. Rev. do Mus. Paul. 29–64.

MacKay, W., and E. Mackay. **2010**. The systematics and biology of the New World ants of the genus Pachycondyla (Hymenoptera: Formicidae). Edwin Mellen Press.

Mackay, W. P. 2008. Género Pachycondyla, pp. 170–200. *In* Jiménez, E., Fernández, F., Arias, T.M., Lozano-Zambrano, F.H. (eds.), Sist. Biogeogr. y Conserv. Las Hormigas Cazadoras Colomb. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, XIV + 609 pp., Bogotá.

Mayr, E. 1942. Systematics and the Origin of Species, 14th Editi. ed. Columbia University Press, New York.

Mayr, G. 1862. Myrmecologische Studien. Verhandlungen der Kais. Zool. Gesellschaft Wien. 649–776.

Mayr, G. 1863. Formicidarum index synonymicus. Verhandlungen der Kais. Zool. Gesellschaft Wien. 385–460.

Mayr, G. 1866. Myrmecologische Beiträge. Sitzungsberichte der Kais. Akad. der Wissenschaften Wien. Math. Classe. Abteilung I. 484–517.

Mayr, G. 1886. Notizen über die Formiciden-Sammlung des British Museum in London. Verhandlungen der Kais. Zool. Gesellschaft Wien. 353–368.

Mendoza-Ramírez, M., J. Gutiérrez-Rodríguez, C. Poteaux, P. Ornelas-García, and A. Zaldívar-Riverón. **2019**. Late Pleistocene genetic diversification and demographic expansion in the widely distributed neotropical ant Neoponera villosa (Ponerinae). Mitochondrial DNA Part A DNA Mapping, Seq. Anal. 30: 296–306.

Narendra, A., and W. A. Ribi. **2017**. Ocellar structure is driven by the mode of locomotion and activity time in Myrmecia ants. J. Exp. Biol. 220: 4383–4390.

Nemésio, A., D. P. Silva, J. C. Nabout, and S. Varela. **2016**. Effects of climate change and habitat loss on a forest-dependent bee species in a tropical fragmented landscape. Insect Conserv. Divers. 9: 149–160.

Neves, F. M., G. Alvarez, F. F. Corrêa, and J. B. L. Silva. **2021**. Drivers of vulnerability to climate change in the southernmost region of Bahia (Brazil). Soc. Nat. 34.

Ogata, K. 1991. A generic synopsis of the poneroid complex of the family Formicidae (Hymenoptera). Part II. Subfamily Myrmicinae. Bull. Inst. trop. Agric. Kyushu Univ. 14: 61–149.

Orivel, J., A. Souchal, P. Cerdan, and A. Dejean. **2000**. Prey capture behavior of the arboreal ponerine ant Pachycondyla goeldii.pdf. Sociobiology. 35: 131–140.

Pérez-Lachaud, G., F. H. Rocha, C. Pozo, L. A. Kaminski, N. Seraphim, and J. P. Lachaud. **2021**. A new ant-butterfly symbiosis in the forest canopy fills an evolutionary gap. Sci. Rep. 11: 1–11.

Perez, B., J. P. Lachaud, and D. Fresnau. **1985**. La division del trabajo en la hormiga primitiva Neoponera villosa. Folia Entomol. Mex. 65: 119–130.

Pivello, V. R., I. Vieira, A. V. Christianini, D. B. Ribeiro, L. da Silva Menezes, C. N. Berlinck,

F. P. L. Melo, J. A. Marengo, C. G. Tornquist, W. M. Tomas, and G. E. Overbeck. **2021**. Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. Perspect. Ecol. Conserv. 19: 233–255.

Rebolledo Monsalve, E., P. Jiménez Prado, J. Molinero Ortiz, and T. Toulkeridis. **2022**. Differences in Fish Abundance in Rivers under the Influence of Open-Pit Gold Mining in the Santiago-Cayapas Watershed, Esmeraldas, Ecuador. Water. 1–21.

Retzius, A. J. 1783. Caroli de Geer. Genera et species insectorum e generosissimi auctoris scriptis extraxit, digessit, Latine quoad partem reddidit, et terminologiam insectorum Linneanam addidit. Leipzig.

Roger, J. 1860. Die Ponera artigen ameisen. Berliner Entomol. Zeitschrift. 4: 278–312.

Roger, J. 1861. Die Ponera-artigen Ameisen (Schluss). Berliner Entomol. Zeitschrift. 1–54.

Roger, J. 1863. Verzeichniss der Formiciden-Gattungen und Arten. Berliner Entomol. Zeitschrift. 1–65.

Santos, R. P., C. S. F. Mariano, J. H. C. Delabie, M. A. Costa, K. M. Lima, S. G. Pompolo, I. O. Fernandes, E. A. Miranda, A. F. Carvalho, and J. G. Silva. **2018**. Genetic characterization of some Neoponera (Hymenoptera: Formicidae) Populations within the foetida Species Complex. J. Insect Sci. 18: 1–7.

Schmidt, C. 2013. Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). 3647: 201–250.

Schmidt, C. A., and S. O. Shattuck. **2014**. The Higher Classification of the Ant Subfamily Ponerinae (Hymenoptera: Formicidae), with a Review of Ponerine Ecology and Behavior.

Serna, F., and W. MacKay. **2010**. A descriptive morphology of the ant genus Procryptocerus (Hymenoptera: Formicidae). J. Insect Sci. 10.

da Silva, J. M. C. 2018. Bahia Interior Forest. (https://www.worldwildlife.org/ecoregions/nt0104).

Smith, F. 1858. Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. London: British Museum, London.

Thompson, D. B. 1999. Genotype-environment interaction and the ontogeny of diet-induced

phenotypic plasticity in size and shape of Melanoplus femurrubrum (Orthoptera: Acrididae). J. Evol. Biol. 12: 38–48.

Tozetto, L., and J. E. Lattke. **2020**. Revealing male genital morphology in the giant ant genus Dinoponera with geometric morphometrics. Arthropod Struct. Dev. 57: 100943.

Troya, A., and J. Lattke. **2022**. Neoponera Emery, 1901 (Hymenoptera: Formicidae) revisited: 1. The N. laevigata species-group. Insect Syst. Evol. 1901: 1–76.

Troya, A., F. Marcineiro, J. E. Lattke, and J. Longino. **2022**. Igaponera curiosa, a new ponerine genus (Hymenoptera: Formicidae) from the Amazon. Eur. J. Taxon. 823: 82–101.

Vale, P., H. Gibbs, R. Vale, J. Munger, A. Brandão, M. Christie, and E. Florence. **2019**. Mapping the cattle industry in Brazil's most dynamic cattle-ranching state: Slaughterhouses in Mato grosso, 1967-2016. PLoS One. 14: 1–25.

West-Eberhard, M. J. 2005. Phenotypic accommodation: Adaptive innovation due to developmental plasticity. J. Exp. Zool. 304: 610–618.

Weyna, A., L. Bourouina, N. Galtier, and J. Romiguier. **2022**. Detection of F1 Hybrids from Single-genome Data Reveals Frequent Hybridization in Hymenoptera and Particularly Ants. Mol. Biol. Evol. 39: 1–13.

Wheeler, W. M. 1908. The ants of Texas, New Mexico and Arizona. (Part I.). Bull. Am. Museum Nat. Hist. 399–485.

Wild, A. L. 2005. Taxonomic revision of the Pachycondyla apicalis species complex (Hymenoptera: Formicidae). 25: 1–25.

Wilson, E. O. 1955. A Monographic Revision of the Ant Genus Lasius. Bull. Mus. Comp. Zool.

Yoder, M. J., I. Mikó, K. C. Seltmann, M. A. Bertone, and A. R. Deans. **2010**. A gross anatomy ontology for hymenoptera. PLoS One. 5: e15991.

Zalles, V., M. C. Hansen, P. V. Potapov, D. Parker, S. V. Stehman, A. H. Pickens, L. L. Parente, L. G. Ferreira, X. P. Song, A. Hernandez-Serna, and I. Kommareddy. **2021**. Rapid expansion of human impact on natural land in South America since 1985. Sci. Adv. 7: 1–12.

REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle, pp. 267–281. *In* Petrov, B.N., Csaki, F. (eds.), 2nd Int. Symp. Inf. Theory. Springer, Akademia Kiado, Budapest.

Anisimova, M., M. Gil, J. F. Dufayard, C. Dessimoz, and O. Gascuel. **2011**. Survey of branch support methods demonstrates accuracy, power, and robustness of fast likelihood-based approximation schemes. Syst. Biol. 60: 685–699.

AntCat. **2022**. AntCat (2022) An online catalogue of the ants of the world by Barry Bolton. Available from https//www. antcat.org. (accessed Mar 2022).

AntWeb. **2022**. AntWeb. Calif. Acad. Sci. online https//www.antweb.org. Accessed 14 July 2022.

AntWiki.org. **2022**. AntWiki. (https://antwiki.org/wiki/Category:Neoponera_species).

Arias, T. 2003. Nuevos registros de especies de hormigas de la subfamilia Ponerinae (Hymenoptera: Formicidae) para Colombia. Caldasia. 25: 429–431.

Arnold, M. L. 1992. Natural hybridization as an evolutionary process. Annu. Rev. Ecol. Syst. 23: 237–261.

Auger, C. P. 1975. Use of reports literature. London: Buttelworths.

Bankevich, A., S. Nurk, D. Antipov, A. A. Gurevich, M. Dvorkin, A. S. Kulikov, V. M. Lesin, S. I. Nikolenko, S. Pham, A. D. Prjibelski, A. V. Pyshkin, A. V. Sirotkin, N. Vyahhi, G. Tesler, M. A. Alekseyev, and P. A. Pevzner. **2012**. SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. J. Comput. Biol. 19: 455–477.

Bell, S. 2019. Cattle in the Backlands: Mato Grosso and the Evolution of Ranching in the Brazilian Tropics. AAG Rev. Books. 7: 235–237.

Bezděčková, K., P. Bezděčka, and I. Machar. **2015**. A checklist of the ants (Hymenoptera: Formicidae) of Peru. Zootaxa. 4020: 101–133.

Blanchard, B. D., and C. S. Moreau. **2017**. Defensive traits exhibit an evolutionary trade-off and drive diversification in ants. Evolution (N. Y). 71: 315–328.

Bolger, A. M., M. Lohse, and B. Usadel. **2014**. Trimmomatic: A flexible trimmer for Illumina sequence data. Bioinformatics. 30: 2114–2120.

Bolton, B. 1994. Identification guide to the ant genera of the world, Harvard Univ. Press.

Bolton, B. 1995. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, Mass.

Borgmeier, T. 1923. Catalogo systematico e synonymico das formigas do Brasil. 1 parte. Subfam. Dorylinae, Cerapachyinae, Ponerinae, Dolichoderinae. Arch. do Mus. Nac. (Rio Janeiro). 22–103.

Borgmeier, T. 1929. Zur Kenntnis der brasilianischen Ameisen. Rev. Española Entomol. 195–214.

Borowiec, M. L., C. Rabeling, S. G. Brady, B. L. Fisher, T. R. Schultz, and P. S. Ward. **2019**. Compositional heterogeneity and outgroup choice influence the internal phylogeny of the ants. Mol. Phylogenet. Evol. 134: 111–121.

Boudinot, B. E. 2013. The male genitalia of ants: Musculature, homology, and functional morphology (Hymenoptera, Aculeata, Formicidae). J. Hymenopt. Res. 30: 29–49.

Boudinot, B. E. 2015. Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata): a new diagnosis of the family, the first global male-based key to subfamilies, and a treatment of early branching lineages. Eur. J. Taxon. 120: 1–62.

Branstetter, M. G. 2013. Revision of the Middle American clade of the ant genus Stenamma Westwood (Hymenoptera, Formicidae, Myrmicinae). Zookeys. 295: 1–277.

Branstetter, M. G., and J. T. Longino. **2022**. UCE Phylogenomics of New World Cryptopone (Hymenoptera: Formicidae) Elucidates Genus Boundaries, Species Boundaries, and the Vicariant History of a Temperate–Tropical Disjunction. Insect Syst. Divers. 6.

Branstetter, M. G., J. T. Longino, P. S. Ward, and B. C. Faircloth. **2017**. Enriching the ant tree of life: enhanced UCE bait set for genome-scale phylogenetics of ants and other Hymenoptera. Methods Ecol. Evol. 8: 768–776.

Branstetter, M. G., and L. Sáenz. **2012**. Las hormigas (Hymenoptera: Formicidae) de Guatemala, pp. 12–22. *In* Cano, B., Schuster, J.C. (eds.), Biodivers. Guatemala. Universidad

del Valle de Guatemala, Guatemala.

Brown, B. Y. W. L. 1957. Centrifugal speciation. Q. Rev. Biol. 32: 247–277.

Brown, W. 1973. A comparison of the Hylean and Congo-west African rain forest ants faunas, p. 350. *In* Meggers, B.J., Ayensu, E.S., Duckworth, W.D. (eds.), Trop. For. Ecosyst. Africa South Am. a Comp. Rev. Smithsonian Institution Press, Washington, D.C.

Brown, W. L. 1995. Untitled. Taxonomic changes in Pachycondyla and Neoponera attributed to Brown., pp. 302–311. *In* Bolton, B. (ed.), A New Gen. Cat. Ants World. Cambridge, Mass.: Harvard University Press, 504 pp., USA.

Camacho, G. P., W. Franco, M. G. Branstetter, M. R. Pie, J. T. Longino, T. R. Schultz, and R. M. Feitosa. **2022**. UCE Phylogenomics Resolves Major Relationships Among Ectaheteromorph Ants (Hymenoptera: Formicidae: Ectatomminae, Heteroponerinae): A New Classification For the Subfamilies and the Description of a New Genus. Insect Syst. Divers. 6.

Cantone, S. 2017. Winged ants – The male. Dichotomous key to genera of winged male ants in the world. Behavioral ecology of mating flight. São Paulo: Autopubblicato.

Cantone, S., and C. J. Von Zuben. **2019**. The Hindwings of Ants: A Phylogenetic Analysis. Psyche (London). 2019.

Colinvaux, P. A., P. E. De Oliveira, and M. B. Bush. **2000**. Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. Quat. Sci. Rev. 19: 141–169.

Dallwitz, M. 1980. A general system for coding taxonomic descriptions. Taxon. 29: 41–46.

Davidson, D., S. Cook, R. Snelling, and T. Chua. **2010**. Explaining the Abundance of Ants in Lowland Tropical Rainforest Canopies. ScienceScience. 300: 969–972.

Dejean, A. 1990. Influence de l'environnement pré-imaginal et précoce dans le choix du site de nidification de Pachycondyla (= Neoponera) villosa (Fabr.)(Formicidae, Ponerinae). Behav. Processes. 21: 107–125.

Dejean, A. 2011. Prey capture behavior in an arboreal african ponerine ant. PLoS One. 6.

Delabie, J. H. C., C. D. S. F. Mariano, L. F. Mendes, S. das Graças Pompolo, and D. Fresnau.

2008. Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no gênero Pachycondyla na região neotropical: o caso do complexo apicalis.

Delabie, J. H. C., C. S. F. Mariano, L. F. Mendes, S. G. Pompolo, and D. Fresneau. **2008**. Problemas apontados por estudos morfológicos, ecológicos e citogenéticos no gênero Pachycondyla na região neotropical: o caso do complexo apicalis, pp. 196–222. *In* Vilela, E.F., Santos, I.A., Schoereder, J.H., Lino Neto, J., Campos, L.A.O., Serrão, J.E. (eds.), Insetos Sociais Da Biol. à Apl. Editora da Univ. Federal de Viçosa, 442 p., Viçosa, MG.

Delsinne, T., F. J. Serna, M. Leponce, and B. E. Boudinot. **2019**. Capítulo 13. Glosario de morfología, pp. 387–457. *In* Fernández, F., Guerrero, R., Delsinne, T. (eds.), Hormigas Colomb. Universidad Nacional de Colombia, Bogotá.

Djiéto-Lordon, C., J. Orivel, and A. Dejean. **2001**. Consuming large prey on the spot: The case of the arboreal foraging ponerine ant Platythyrea modesta (Hymenoptera, Formicidae). Insectes Soc. 48: 324–326.

Emery, C. 1890. Voyage de M. E. Simon au Venezuela (Décembre 1887 - Avril 1888). Formicides. Ann. la Société Entomol. Fr. 55–76.

Emery, C. 1901. Notes sur les sous-familles des dorylines et ponérines (famille des Formicides). Ann. la Société Entomol. Belgique. 45: 32–54.

Emery, C. 1904. Zur Kenntniss des Polymorphismus der Ameisen. Zool. Jahrbücher. Suppl. 587–610.

Emery, C. 1911. Hymenoptera. Fam. Formicidae. Subfam. Ponerinae, p. 124. *In* Wytsman, P. (ed.), Genera Insectorum. Bologne.

Eo, S. H., and J. A. DeWoody. **2010**. Evolutionary rates of mitochondrial genomes correspond to diversification rates and to contemporary species richness in birds and reptiles. Proc. R. Soc. B Biol. Sci. 277: 3587–3592.

Erwin, T., and C. Geraci. **2009**. Amazonian rainforests and their richness of Coleoptera, a dominant life form in the critical zone of the neotropicsitle, pp. 49–67. *In* Insect Biodivers. Sci. Soc. Blackwell Publishing Ltd.

Erwin, T. L. 2001. Forest canopies, animal diversity. *In* Encicl. Biodiversityciclopedia Biodivers.

3.

Fabricius, J. C. 1804. Systema Piezatorum secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus. Brunswick: C. Reichard.

Faircloth, B. C. 2016. PHYLUCE is a software package for the analysis of conserved genomic loci. Bioinformatics. 32: 786–788.

Faircloth, B. C., J. E. McCormack, N. G. Crawford, M. G. Harvey, R. T. Brumfield, and T. C. Glenn. **2012**. Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. Syst. Biol. 61: 717–726.

Faircloth, B. C., L. Sorenson, F. Santini, and M. E. Alfaro. **2013**. A Phylogenomic Perspective on the Radiation of Ray-Finned Fishes Based upon Targeted Sequencing of Ultraconserved Elements (UCEs). PLoS One. 8.

Federle, W., M. Riehle, A. S. G. Curtis, and R. J. Full. **2002**. An integrative study of insect adhesion: Mechanics and wet adhesion of pretarsal pads in ants. Integr. Comp. Biol. 42: 1100–1106.

Feng, S., M. Bai, I. Rivas-González, C. Li, S. Liu, Y. Tong, H. Yang, G. Chen, D. Xie, K. E. Sears, L. M. Franco, J. D. Gaitan-Espitia, R. F. Nespolo, W. E. Johnson, H. Yang, P. A. Brandies, C. J. Hogg, K. Belov, M. B. Renfree, K. M. Helgen, J. J. Boomsma, M. H. Schierup, and G. Zhang. **2022**. Incomplete lineage sorting and phenotypic evolution in marsupials. Cell. 185: 1646-1660.e18.

Fernandes, I. O., M. L. De Oliveira, and J. H. C. Delabie. **2014**. Description of two new species in the Neotropical Pachycondyla foetida complex (Hymenoptera: Formicidae: Ponerinae) and taxonomic notes on the genus. Myrmecological News. 19: 133–163.

Fernández, F., and R. J. Guerrero. **2019**. Capítulo 17. Subfamilia Ponerinae, pp. 509–553. *In* Fernández, F., Guerrero, R.J., Delsinne, T. (eds.), Hormigas Colomb. Universidad Nacional de Colombia, Bogotá.

Fernandez, F., and E. E. Palacio. **1995**. Hormigas de Colombia IV: nuevos registros de géneros y especies. Caldasia. 17: 587–596.

Fernández, F., E. E. Palacio, W. P. MacKay, and E. S. MacKay. **1996**. Introducción al estudio

de las hormigas (Hymenoptera: Formicidae) de Colombia, pp. 349–412. *In* Andrade, M.G., Amat García, G., Fernández, F. (eds.), Insectos Colomb. Estud. Escogidos. Academia Colombiana de Ciencias Exactas, Físicas y Naturales, 541 pp., Bogotá.

Ferreira, C. S., A. V. Figueira, R. Gribel, F. Wittmann, and M. T. Piedade. **2010**. Genetic variability, divergence and speciation in trees of periodically flooded forests of the Amazon: a case study of Himatanthus sucuuba (SPRUCE) WOODSON. In Amazonian Floodplain Forests, pp. 301–312. *In* Amaz. Floodpalin For.

Field, D. L., D. J. Ayre, R. J. Whelan, and A. M. Young. **2011**. Patterns of hybridization and asymmetrical gene flow in hybrid zones of the rare Eucalyptus aggregata and common E. rubida. Heredity (Edinb). 106: 841–853.

Fiorentino, G., J. Lattke, A. Troya, C. Sosiak, M. Dong, and P. Barden. **2022**. Deep time extinction of largest insular ant predators and the first fossil Neoponera (Formicidae: Ponerinae) from Miocene age Dominican amber. BMC Biol. 1–12.

Forel, A. 1899. Biologia Centrali-Americana; or, contributions to the knowledge of the fauna and flora of Mexico and Central America. In- secta. Hymenoptera. Vol. III. (Formicidae.), Biol. Cent. Hym. London.

Forel, A. 1901. Nouvelles espèces de Ponerinae. (Avec un nouveau sous-genre et une espèce nouvelle d'Eciton). Rev. Suisse Zool. 325–353.

Forel, A. 1912. Formicides néotropiques. Part I. Ann. la Société Entomol. Belgique.

ForestWatch.org. **2021**. Tree cover change Brazil. (www.globalforestwatch.org.).

Freeland, J., R. H. Crozier, and J. Marc. **1982**. on the Occurrence of Arolia in Ant Feet. Aust. J. Entomol. 21: 257–262.

Fresneau, D. 1985. Individual foraging and path fidelity in a ponerine ant. Insectes Soc. 32: 109–116.

Gallardo, A. 1918. Las hormigas de la República Argentina. Subfamilia Ponerinas. An. del Mus. Nac. Hist. Nat. Buenos Aires. 1–112.

De Geer, C. 1773. Mémoires pour servir à l'histoire des insectes. Tome troisième. Pierre Hesselberg, 696 pp., Stockholm.

Glenn, T. C., R. A. Nilsen, T. J. Kieran, J. G. Sanders, N. J. Bayona-Vásquez, J. W. Finger, T. W. Pierson, K. E. Bentley, S. L. Hoffberg, S. Louha, F. J. Garcia-De Leon, M. A. Del Rio Portilla, K. D. Reed, J. L. Anderson, J. K. Meece, S. E. Aggrey, R. Rekaya, M. Alabady, M. Belanger, K. Winker, and B. C. Faircloth. **2019**. Adapterama I: Universal stubs and primers for 384 unique dual-indexed or 147,456 combinatorially-indexed Illumina libraries (iTru & iNext). PeerJ. 2019: 1–31.

Gomes, J. P., L. Iannuzzi, and I. R. Leal. **2010**. Response of the ant community to attributes of fragments and vegetation in a northeastern Atlantic rain forest area, Brazil. Neotrop. Entomol. 39: 898–905.

Gómez, P. A., and L. A. Garcés. **2013**. Cultivos celulares de Choibá Dipteryx oleifera Benth. Rev. Colomb. Biotecnol. 15: 124–131.

Google. **2022**. Google Earth. (https://earth.google.com.).

Govaerts, R., J. Dransfield, S. Zona, D. Hodel, and A. Henderson. **2022**. World Checklist of Selected Plant Families. Facil. by R. Bot. Gard. Kew. (http://wcsp.science.kew.org/).

Guénard, B., M. D. Weiser, K. Gómez, N. Narula, and E. P. Economo. **2017**. The Global Ant Biodiversity Informatics (GABI) database: Synthesizing data on the geographic distribution of ant species (Hymenoptera: Formicidae). Myrmecological News. 24: 83–89.

Guindon, S., J. F. Dufayard, V. Lefort, M. Anisimova, W. Hordijk, and O. Gascuel. **2010**. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. Syst. Biol. 59: 307–321.

Gutiérrez-Valencia, J., G. Chomicki, and S. S. Renner. **2017**. Recurrent breakdowns of mutualisms with ants in the neotropical ant-plant genus Cecropia (Urticaceae). Mol. Phylogenet. Evol. 111: 196–205.

Harada, A. Y. 2016. State of Art of Ants (Hymenoptera: Formicidae) at Caxiuanã, Melgaco, Pará, Brazil. Adv. Entomol. 04: 115–132.

Harris, R. A. 1979. Glossary of surface sculpturing. Occas. Pap. Entomol. 32.

Haugaasen, T., and C. A. Peres. **2005**. Mammal assemblage structure in Amazonian flooded and unflooded forests. J. Trop. Ecol. 21: 133–145.

Hoang, D. T., O. Chernomor, A. Von Haeseler, B. Q. Minh, and L. S. Vinh. **2018**. UFBoot2: Improving the ultrafast bootstrap approximation. Mol. Biol. Evol. 35: 518–522.

Hughes, C., and R. Eastwood. **2006**. Island radiation on a continental scale : Exceptional rates of plant diversification after uplift of the Andes. 2006.

Hurvich, C. M., and C. - L Tsai. **1993**. A Corrected Akaike Information Criterion for vector autoregressive model selection. J. Time Ser. Anal. 14: 271–279.

ICZN. **1999**. International Code of Zoological Nomenclature. Int. Trust Zool. Nomencl.

Janicki, J., N. Narula, M. Ziegler, B. Guénard, and E. P. Economo. **2016**. Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. Ecol. Inform. 32: 185–193.

Kalyaanamoorthy, S., B. Q. Minh, T. K. F. Wong, A. Von Haeseler, and L. S. Jermiin. **2017**. ModelFinder: Fast model selection for accurate phylogenetic estimates. Nat. Methods. 14: 587–589.

Katoh, K., G. Asimenos, and H. Toh. **2009**. Multiple Alignment of DNA Sequences with MAFFT. Springer.

Keller, R. A. 2011. A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. Bull. Am. Museum Nat. Hist. 2011: 1–90.

Kempf, W. W. 1961. As formigas do gênero Pachycondyla Fr. Smith no Brasil (Hymenoptera: Formicidae). Rev. Bras. Entomol. 189–204.

Kempf, W. W. 1972. Catálogo Abreviado das formigas da Região Neotropical (Hymenoptera: Formicidae). Stud. Entomol.

Kolmer, H. 2002. Co-operation and conflict in societies of the ponerine ant genus Pachycondyla Kooperation und Konflikt in Staaten der Ameisengattung Pachycondyla. 109.

Leal, I. R., and P. S. Oliveira. **1995**. Behavioral ecology of the neotropical termite-hunting ant Pachycondyla (= Termitopone) marginata: colony founding, group-raiding and migratory patterns. Behav. Ecol. Sociobiol. 37: 373–383.

Lecocq de Pletincx, N., S. Dellicour, and S. Aron. **2021**. The evolution of ant worker polymorphism correlates with multiple social traits. Behav. Ecol. Sociobiol. 75.

Lemmon, A. R., J. M. Brown, K. Stanger-Hall, and E. M. Lemmon. **2009**. The effect of ambiguous data on phylogenetic estimates obtained by maximum likelihood and bayesian inference. Syst. Biol. 58: 130–145.

Lepeletier de Saint-Fargeau, A. 1835. Histoire naturelle des insectes. Hyménoptères. Tome I. Paris: Roret, Paris.

Leroy, C., F. Petitclerc, J. Orivel, B. Corbara, J. F. Carrias, A. Dejean, and R. Céréghino. **2017**. The influence of light, substrate and seed origin on the germination and establishment of an ant-garden bromeliad. Plant Biol. 19: 70–78.

Longino, J. 2010. Ants of Costa Rica. (https://ants.biology.utah.edu/AntsofCostaRica.html).

Longino, J. T., and M. G. Branstetter. **2020**. Phylogenomic Species Delimitation, Taxonomy, and 'Bird Guide' Identification for the Neotropical Ant Genus Rasopone (Hymenoptera: Formicidae), Insect Syst. Divers.

Löytynoja, A., and N. Goldman. **2008**. Phylogeny-aware gap placement prevents errors in sequence alignment and evolutionary analysis. Science (80-.). 320: 1632–1635.

Lucas, C., D. Fresneau, K. Kolmer, J. Heinze, J. H. C. Delabie, and D. B. Pho. **2002**. A multidisciplinary approach to discriminating different taxa in the species complex Pachycondyla villosa (Formicidae). Biol. J. Linn. Soc. 75: 249–259.

Lucky, A., M. Trautwein, G. Benoit, M. Weiser, and R. Dunn. **2013**. Tracing the Rise of Ants - Out of the Ground. PLoS One. 8: e84012.

Luebert, F. 2021. The two South American dry diagonals. Front. Biogeogr. 13: 0–14.

Luederwaldt, H. 1918. Notas myrmecologicas. Rev. do Mus. Paul. 29–64.

Macedo-Reis, L. E., A. C. Leite, T. J. Guerra, R. Antoniazzi, and F. D. S. Neves. **2019**. Suspended leaf litter in an understorey treelet as habitat extension for ground-dwelling ants in the Atlantic Forest, south-eastern Brazil. J. Trop. Ecol. 35: 247–250.

MacKay, W., and E. Mackay. **2010**. The systematics and biology of the New World ants of the genus Pachycondyla (Hymenoptera: Formicidae). Edwin Mellen Press.

Mackay, W. P. 2008. Género Pachycondyla, pp. 170–200. *In* Jiménez, E., Fernández, F., Arias, T.M., Lozano-Zambrano, F.H. (eds.), Sist. Biogeogr. y Conserv. Las Hormigas Cazadoras

Colomb. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, XIV + 609 pp., Bogotá.

Mayr, E. 1942. Systematics and the Origin of Species, 14th Editi. ed. Columbia University Press, New York.

Mayr, G. 1862. Myrmecologische Studien. Verhandlungen der Kais. Zool. Gesellschaft Wien. 649–776.

Mayr, G. 1863. Formicidarum index synonymicus. Verhandlungen der Kais. Zool. Gesellschaft Wien. 385–460.

Mayr, G. 1866. Myrmecologische Beiträge. Sitzungsberichte der Kais. Akad. der Wissenschaften Wien. Math. Classe. Abteilung I. 484–517.

Mayr, G. 1886. Notizen über die Formiciden-Sammlung des British Museum in London. Verhandlungen der Kais. Zool. Gesellschaft Wien. 353–368.

Mendoza-Ramírez, M., J. Gutiérrez-Rodríguez, C. Poteaux, P. Ornelas-García, and A. Zaldívar-Riverón. **2019**. Late Pleistocene genetic diversification and demographic expansion in the widely distributed neotropical ant Neoponera villosa (Ponerinae). Mitochondrial DNA Part A DNA Mapping, Seq. Anal. 30: 296–306.

Mill, A. E. 1982. Faunal studies on termites (Isoptera) and observations on their ant predators (Hymenoptera: Formicidae) in the Amazon Basin. Rev. Bras. Entomol. 26: 253–260.

Mill, A. E. 1984. Predation by the ponerine ant Pachycondyla commutata on termites of the genus Syntermes in Amazonian rain forest. J. Nat. Hist. 18: 405–410.

Minh, B. Q., M. A. T. Nguyen, and A. Von Haeseler. **2013**. Ultrafast approximation for phylogenetic bootstrap. Mol. Biol. Evol. 30: 1188–1195.

Narendra, A., and W. A. Ribi. **2017**. Ocellar structure is driven by the mode of locomotion and activity time in Myrmecia ants. J. Exp. Biol. 220: 4383–4390.

Nemésio, A., D. P. Silva, J. C. Nabout, and S. Varela. **2016**. Effects of climate change and habitat loss on a forest-dependent bee species in a tropical fragmented landscape. Insect Conserv. Divers. 9: 149–160.

Neves, D. M., K. G. Dexter, R. T. Pennington, M. L. Bueno, and A. T. Oliveira Filho. **2015**.

Environmental and historical controls of floristic composition across the South American Dry Diagonal. J. Biogeogr. 42: 1566–1576.

Neves, F. M., G. Alvarez, F. F. Corrêa, and J. B. L. Silva. **2021**. Drivers of vulnerability to climate change in the southernmost region of Bahia (Brazil). Soc. Nat. 34.

Nguyen, L. T., H. A. Schmidt, A. Von Haeseler, and B. Q. Minh. **2015**. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol. Biol. Evol. 32: 268–274.

Ogata, K. 1991. A generic synopsis of the poneroid complex of the family Formicidae (Hymenoptera). Part II. Subfamily Myrmicinae. Bull. Inst. trop. Agric. Kyushu Univ. 14: 61–149.

Orivel, J., A. Souchal, P. Cerdan, and A. Dejean. **2000**. Prey capture behavior of the arboreal ponerine ant Pachycondyla goeldii.pdf. Sociobiology. 35: 131–140.

Oster, G. F., and E. O. Wilson. **1978**. Caste and ecology in the social insects. Princeton University Press, Princeton.

Paez, A. 2017. Gray literature: An important resource in systematic reviews. J. Evid. Based. Med. 10: 233–240.

Pazmiño-Palomino, A., and A. Troya. **2022**. Ants of Ecuador : new species records for a megadiverse country in South America. Rev. Bras. Entomol. 66: 1–15.

Pérez-Lachaud, G., F. H. Rocha, C. Pozo, L. A. Kaminski, N. Seraphim, and J. P. Lachaud. **2021**. A new ant-butterfly symbiosis in the forest canopy fills an evolutionary gap. Sci. Rep. 11: 1–11.

Perez, B., J. P. Lachaud, and D. Fresnau. **1985**. La division del trabajo en la hormiga primitiva Neoponera villosa. Folia Entomol. Mex. 65: 119–130.

Pivello, V. R., I. Vieira, A. V. Christianini, D. B. Ribeiro, L. da Silva Menezes, C. N. Berlinck, F. P. L. Melo, J. A. Marengo, C. G. Tornquist, W. M. Tomas, and G. E. Overbeck. **2021**. Understanding Brazil's catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. Perspect. Ecol. Conserv. 19: 233–255.

Pollard, D. A., V. N. Iyer, A. M. Moses, and M. B. Eisen. **2006**. Widespread Discordance of

Gene Trees with Species Tree in Drosophila: Evidence for Incomplete Lineage Sorting. PLOS Genet. 2: e173.

Price, S. L., S. Powell, D. J. C. Kronauer, L. A. P. Tran, N. E. Pierce, and R. K. Wayne. **2014**. Renewed diversification is associated with new ecological opportunity in the Neotropical turtle ants. J. Evol. Biol. 27: 242–258.

Rakotonirina, J. C., and B. L. Fisher. **2013**. Revision of the Pachycondyla sikorae species-group (Hymenoptera: Formicidae) in Madagascar. Zootaxa. 3683: 447–485.

Ratnasingham, S., and P. D. N. Hebert. **2007**. BOLD: The Barcode of Life Data System: (www.barcodinglife.org). Mol. Ecol. Notes. 7: 355–364.

Rebolledo Monsalve, E., P. Jiménez Prado, J. Molinero Ortiz, and T. Toulkeridis. **2022**. Differences in Fish Abundance in Rivers under the Influence of Open-Pit Gold Mining in the Santiago-Cayapas Watershed, Esmeraldas, Ecuador. Water. 1–21.

Retzius, A. J. 1783. Caroli de Geer. Genera et species insectorum e generosissimi auctoris scriptis extraxit, digessit, Latine quoad partem reddidit, et terminologiam insectorum Linneanam addidit. Leipzig.

Roger, J. 1860. Die Ponera artigen ameisen. Berliner Entomol. Zeitschrift. 4: 278–312.

Roger, J. 1861. Die Ponera-artigen Ameisen (Schluss). Berliner Entomol. Zeitschrift. 1–54.

Roger, J. 1863. Verzeichniss der Formiciden-Gattungen und Arten. Berliner Entomol. Zeitschrift. 1–65.

Rohland, N., and D. Reich. **2012**. Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. Genome Res. 22: 939–946.

Santos-Filho, F. S., E. B. de Almeida, P. B. Lima, and C. J. dos R. S. Soares. **2015**. Checklist of the flora of the restingas of Piauí state, Northeast Brazil. Check List. 11.

Santos, R. P., C. S. F. Mariano, J. H. C. Delabie, M. A. Costa, K. M. Lima, S. G. Pompolo, I. O. Fernandes, E. A. Miranda, A. F. Carvalho, and J. G. Silva. **2018**. Genetic characterization of some Neoponera (Hymenoptera: Formicidae) Populations within the foetida Species Complex. J. Insect Sci. 18: 1–7.

Santschi, F. 1919. Nouveaux formicides de la République Argentine. An. la Soc. Cient. Argentina.

87: 37–57.

Santschi, F. 1921. Ponerinae, Dorylinae et quelques autres formicides néotropiques. Bull. Soc. Vaudoise Sci. Nat.

Santschi, F. 1923. Solenopsis et autres fourmis néotropicales. Rev. Suisse Zool. 30: 245–273.

Santschi, F. 1939. Études et descriptions de fourmis néotropiques. Rev. Entomol. 10: 312–330.

Schmidt, C. 2013. Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). 3647: 201–250.

Schmidt, C. A., and S. O. Shattuck. **2014**. The Higher Classification of the Ant Subfamily Ponerinae (Hymenoptera: Formicidae), with a Review of Ponerine Ecology and Behavior.

Schonberg, L. A., J. T. Longino, N. M. Nadkarni, S. P. Yanoviak, and J. C. Gering. **2004**. Arboreal ant species richness in primary forest, secondary forest, and pasture habitats of a tropical montane landscape. Biotropica. 36: 402–409.

Schwartz, R. S., and R. L. Mueller. **2010**. Branch length estimation and divergence dating: Estimates of error in Bayesian and maximum likelihood frameworks. BMC Evol. Biol. 10.

Schwarz, G. 1978. Estimating the Dimension of a Model. Ann. Stat. 6: 461–464.

Serna, F., and W. MacKay. **2010**. A descriptive morphology of the ant genus Procryptocerus (Hymenoptera: Formicidae). J. Insect Sci. 10.

Seyfullah, L. J., C. Beimforde, J. Dal Corso, V. Perrichot, J. Rikkinen, and A. R. Schmidt. **2018**. Production and preservation of resins – past and present. Biol. Rev. 93: 1684–1714.

da Silva, J. M. C. 2018. Bahia Interior Forest. (https://www.worldwildlife.org/ecoregions/nt0104).

Smith, F. 1858. Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. London: British Museum, London.

Swofford, D. L., P. J. Waddell, J. P. Huelsenbeck, P. G. Foster, P. O. Lewis, and J. S. Rogers. **2001**. Bias in phylogenetic estimation and its relevance to the choice between parsimony and likelihood methods. Syst. Biol. 50: 525–539.

Talavera, G., and J. Castresana. **2007**. Improvement of phylogenies after removing divergent

and ambiguously aligned blocks from protein sequence alignments. Syst. Biol. 56: 564–577.

Tamura, K., F. U. Battistuzzi, P. Billing-Ross, O. Murillo, A. Filipski, and S. Kumar. **2012**. Estimating divergence times in large molecular phylogenies. Proc. Natl. Acad. Sci. U. S. A. 109: 19333–19338.

Tamura, K., G. Stecher, and S. Kumar. **2021**. MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Mol. Biol. Evol. 38: 3022–3027.

Thompson, D. B. 1999. Genotype-environment interaction and the ontogeny of diet-induced phenotypic plasticity in size and shape of Melanoplus femurrubrum (Orthoptera: Acrididae). J. Evol. Biol. 12: 38–48.

To, T. H., M. Jung, S. Lycett, and O. Gascuel. **2016**. Fast Dating Using Least-Squares Criteria and Algorithms. Syst. Biol. 65: 82–97.

Tozetto, L., and J. E. Lattke. **2020**. Revealing male genital morphology in the giant ant genus Dinoponera with geometric morphometrics. Arthropod Struct. Dev. 57: 100943.

Troya, A., and J. Lattke. **2022**. Neoponera Emery, 1901 (Hymenoptera: Formicidae) revisited: 1. The N. laevigata species-group. Insect Syst. Evol. 1901: 1–76.

Troya, A., F. Marcineiro, J. E. Lattke, and J. Longino. **2022**. Igaponera curiosa, a new ponerine genus (Hymenoptera: Formicidae) from the Amazon. Eur. J. Taxon. 823: 82–101.

Tschinkel, W. R. 1988. Colony growth and the ontogeny of worker polymorphism in the fire ant, Solenopsis invicta. Behav. Ecol. Sociobiol. 22: 103–115.

Vale, P., H. Gibbs, R. Vale, J. Munger, A. Brandão, M. Christie, and E. Florence. **2019**. Mapping the cattle industry in Brazil's most dynamic cattle-ranching state: Slaughterhouses in Mato grosso, 1967-2016. PLoS One. 14: 1–25.

Ward, P. S., B. B. Blaimer, and B. L. Fisher. **2016**. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera Colobopsis and Dinomyrmex. Zootaxa. 4072: 343–357.

Ward, P. S., and B. E. Boudinot. **2021**. Grappling with homoplasy: taxonomic refinements and reassignments in the ant genera Camponotus and Colobopsis (Hymenoptera: Formicidae). Arthropod Syst. Phylogeny. 79: 37–56.

Ward, P. S., S. G. Brady, B. L. Fisher, and T. R. Schultz. **2015**. The evolution of myrmicine ants: Phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Syst. Entomol. 40: 61–81.

West-Eberhard, M. J. 2005. Phenotypic accommodation: Adaptive innovation due to developmental plasticity. J. Exp. Zool. 304: 610–618.

Weyna, A., L. Bourouina, N. Galtier, and J. Romiguier. **2022**. Detection of F1 Hybrids from Single-genome Data Reveals Frequent Hybridization in Hymenoptera and Particularly Ants. Mol. Biol. Evol. 39: 1–13.

Wheeler, D. E. 1991. The developmental basis of worker caste polymor- phism in ants. Am. Nat. 138: 1218–1238.

Wheeler, W. 1936. Ecological relations of ponerine and other ants to termites. Proc. Am. Acad. Arts Sci. 71: 158–243.

Wheeler, W. M. 1908. The ants of Texas, New Mexico and Arizona. (Part I.). Bull. Am. Museum Nat. Hist. 399–485.

Wheeler, W. M., and J. C. Bequaert. **1929**. Amazonian myrmecophytes and their ants. Zool. Anz. 82: 10–39.

Wild, A. L. 2005. Taxonomic revision of the Pachycondyla apicalis species complex (Hymenoptera: Formicidae). 25: 1–25.

Wiley, E. O., and B. S. Lieberman. **2011**. Phylogenetics: Theory and practice of phylogenetic systematics, Second edi. ed. Wiley-Blackwell.

Wills, B. D., S. Powell, M. D. Rivera, and A. V. Suarez. **2018**. Correlates and Consequences of Worker Polymorphism in Ants. Annu. Rev. Entomol. 63: 575–598.

Wilson, E. O. 1955. A Monographic Revision of the Ant Genus Lasius. Bull. Mus. Comp. Zool.

Yagound, B., R. Gouttefarde, C. Leroy, R. Belibel, C. Barbaud, D. Fresneau, S. Chameron, C. Poteaux, and N. Châline. **2015**. Fertility Signaling and Partitioning of Reproduction in the Ant Neoponera apicalis. J. Chem. Ecol. 41: 557–566.

Yoder, M. J., I. Mikó, K. C. Seltmann, M. A. Bertone, and A. R. Deans. **2010**. A gross anatomy ontology for hymenoptera. PLoS One. 5: e15991.

Yu, D. W., and N. E. Pierce. **1998**. A castration parasite of an ant ± plant mutualism.

Zalles, V., M. C. Hansen, P. V. Potapov, D. Parker, S. V. Stehman, A. H. Pickens, L. L. Parente, L. G. Ferreira, X. P. Song, A. Hernandez-Serna, and I. Kommareddy. **2021**. Rapid expansion of human impact on natural land in South America since 1985. Sci. Adv. 7: 1–12.