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The *Pheidole* Westwood, 1839 ants (Formicidae: Myrmicinae) in Colombia: new records including two species with remarkable morphology

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ABSTRACT

Pheidole is one of the most diverse groups of ants in the World, with more than 630 species known from the Neotropical Region. As part of studies on the ant fauna of Colombia, a contribution to the taxonomy of these ants is presented here. The worker subcastes of Pheidole praeusta Roger are redescribed, this being the first record of a trimorphic species outside the Nearctic region. Pheidole amata Forel is proposed as a junior synonym of Pheidole praeusta. Pheidole rogeripolita Longino is identified as the first species in the New World with a 5-segmented antennal club, and the third species with such antennal club in the world. Pheidole distorta Forel, a species described 120 years ago, is redescribed, and notes on its reproductive caste are offered. The description and diagnosis of the Pheidole iceni Fernández soldier is amended. New species records for the country and South America are listed. Multifocus photographs of P. praeusta, and P. rogeripolita are offered.

Key words: Colombian dry forest, distribution expansion, hyperdiverse genus, new synonym, polymorphism, South America

Introduction

Pheidole is one of the largest ant genera, with 1,167 species and 129 subspecies described (Bolton 2022). More than 630 species occur in the Neotropical Region (AntWeb 2022). The neotropics undoubtedly harbor many species yet to be discovered and described, especially in South America. The diversity of these ants is not only represented by its species number, but also in morphology, nesting habits, food sources, association with plants, and forms within the worker caste (Pie & Traniello 2007; Moreau 2008; Mertl & Traniello 2009; Economo *et al.* 2015; Economo *et al.* 2019; Lillico-Ouachour & Abouheif 2016; Mertl *et al.* 2010; Waxman *et al.* 2017; Tschá & Pie 2018). In addition, several species are economically important pests (Sarnat *et al.* 2015). It is of great importance to discover and describe the diversity of these ants, given their ubiquity in various ecosystems and their rich biology.

Based on the now classic revision of the New World *Pheidole* by Wilson (2003), Longino (2009a; 2019) has made two contributions, emphasizing Costa Rica and the Mesoamerican region, where new synonyms are proposed, and new species are described. Comprehensive studies such as aforementioned have not been produced for South America, a region where more diversity is anticipated. However, there are ongoing research projects that have advanced in the knowledge of the distribution and composition of species of *Pheidole* in this continent (Camargo-Vanegas & Guerrero 2020; Casadei-Ferreira *et al.* 2020).

Colombia is one of the Neotropical countries with the highest number of ant genera (109) and species (~1200) of ants (Fernández *et al.* 2021). Much of that diversity is represented in genera such as *Camponotus* (~114 species (Mackay & Mackay 2019)) and *Pheidole* (~120 species (García *et al.* 2020)). The genus *Pheidole* is taxonomically challenging, as species delimitation is largely based soldiers. Despite the taxonomic difficulties, *Pheidole* is of great interest due to their enormous diversity and potential threat from invasive species. Accordingly, the taxonomy of

Pheidole in Colombia has received great attention in recent years through "The Pheidole ants of Colombia" project. This project aims to analyze the composition and distribution of the species of this genus at a regional scale. Advances in this project have made it possible to expand the distribution range of several species to Colombia and South America (Guerrero et al. 2018; García et al. 2020), as well as to detect exotic species such as Pheidole indica Mayr, 1879 in Colombia (Camargo-Vanegas & Guerrero 2020). As part of the analysis of the Pheidole ants in Colombia, this contribution highlights unusual species such as the first species in the New World with a 5-segmented antennal club (and the third in the world), and the discovery of a trimorphic species, the first with this condition outside the Nearctic region. The contribution includes new biological notes, a redescription of different species, and new records for the country and South America.

Materials and methods

Traditionally, the infertile worker caste in *Pheidole* is divided into major and minor worker subcastes and, in some species, there are super major workers (see Wilson 2003). We adopt the nomenclature proposed by Peeters (2019), namely: minor worker, soldier, and super soldier for those forms traditionally called minor, major and super major subcastes, respectively.

The diagnosis and description of the species were made based on Longino's (2009a; 2019) work scheme. For a general discussion about characters in *Pheidole* see Longino (2009a) and *Pheidole* Working Group (Longino 2009b). Measurements were recorded for all worker subcastes and, where possible, the reproductive caste following Longino (2009a). The specimens were examined using two stereomicroscopes (Nikon SMZ 745 and Carl Zeiss Stemmi 305) at magnifications of 60-80x. For comparison purposes, type specimens of different *Pheidole* species were studied from high-quality images downloaded from www.antweb.org (AntWeb 2022); unique specimen codes are offered in all cases.

Measurements

HL: head length; in full-face view, maximum length of head, from line tangent to anteriormost projection of head capsule or clypeus to line tangent to posteriormost projection of vertex margin (including occipital carina, if visible).

HW: head width; in full-face view, maximum width of head capsule, not including eyes.

SL: scape length; length of scape shaft from apex to basal flange, not including basal condyle and neck.

EL: eye length; maximum length of compound eye.

WL: Weber or mesosoma length; in lateral view, distance from base of anterior face of pronotum (at the inflection point between downward-sloping anterior face and flange-like anteriormost projection of pronotum) to posteriormost extension of metapleural or propodeal lobes.

PSL: propodeal spine length; viewed laterally such that side of spine is roughly perpendicular to viewing angle, distance from inflection point between dorsal face of propodeum and base of spine to tip of spine.

PTW: petiole width; maximum width of petiole in dorsal view.

PPW: postpetiole width; maximum width of postpetiole in dorsal view.

CI: cephalic index; 100*HW/HL. SI: scape index; 100*SL/HW.

PSLI: propodeal spine index; 100*PSL/HL. PPI: Postpetiole index; 100*PPW/PTW.

New material identified as *Pheidole praeusta* Roger, 1863 was composed of minor workers and the soldiers, the latter with several individuals with large heads and others with relatively smaller heads, showing apparent dimorphism. To explore that variability in the soldier subcaste, we constructed bivariate graphs contrasting HL vs HW; furthermore, we explored the possible relationship between mesosoma length (WL) and head length (HL) to support that possible dimorphism within the soldier subcaste. The bivariate plots were made with the ggplot2 library version 3.3.3 of RStudio 4.0.3 (R Core Team 2021).

High quality images

Multifocus images were generated using a Leica M250A automated stereoscope equipped with a Leica DFC540 camera. The automatic assembly of the different photographs was processed with the Leica® LAS module. Brightness and contrast were improved using the Edit Image option of the Leica® LAS module.

Specimen Depository

The material upon which this study is based is located and/or was examined at the following collections or institutions:

CBUM. Colecciones Biológicas, Centro de Colecciones Científicas, Universidad del Magdalena, Santa Marta, Colombia

ICN. Colección de Insectos, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia.

IAvH. Colección de Insectos, Instituto Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia.

MHNG. Muséum d'Histoire Naturelle, Geneva, Switzerland.

MPUJ. Colección Entomológica de la Pontificia Universidad Javeriana, Bogotá.

NHMUK. Natural History Museum, London, United Kingdom.

Results

Species accounts

Pheidole arachnion Wilson, 2003

Minor worker measurements (n= 1): HW 0.65, HL 0.65, SL 0.69, EL 0.10, WL 0.80, PSL 0.02, PTW 0.10, PPW 0.16, CI 100, SI 106, PSLI 303, PPI 160.

Soldier measurements (n= 1): HW 1.59, HL 1.65, SL 0.65, EL 0.14, WL 1.20, PSL 0.14, PTW 0.24, PPW 0.49, CI 96, SI 41, PSLI 8, PPI 208.

Material examined. Colombia: 1 minor worker, 2 soldiers, Caquetá, Belén de los Andaquíes, 1.6817, -75.9047, 25. Jan. 2017. Coll. D. Castro [ICN].

Comments. *Pheidole arachnion* is a new record for Colombia and South America. This species was known only from Nicaragua and Costa Rica (Wilson 2003). The only studied specimen of the subcaste soldier of *Pheidole arachnion* from Colombia differs from those from Costa Rica by the face having a strong rugoreticulation, areolate and opaque surface, with small patches smooth and shiny between the frontal carinae.

Pheidole bufo Wilson, 2003

Minor worker measurements (n= 2): HW 0.73–0.75, HL 0.69–0.71, SL 0.69, EL 0.14–0.16, WL 0.80–0.92, PSL 0.25–0.27, PTW 0.12–0.14, PPW 0.18–0.20, CI 106, SI 92–95, PSLI 39–37, PPI 129–167.

Material examined. Colombia: 2 minor workers, Amazonas, Araracuara, 1998. Coll. C. Gangi [MPUJ].

Comments. This is the first record of *Pheidole bufo* for Colombia. It was previously known for French Guiana, Ecuador, and Brazil (Wilson 2003). The image of a paratype minor worker on AntWeb (CASENT0624236) has the face largely smooth and shining between sparse longitudinal carinulae. In contrast, the only specimen from the Colombian Amazon has the face with dense shallow punctuation between the carinulae. In dorsal view of the gaster, that paratype (CASENT0624236) with the dorsum of the first tergite completely smooth, while the specimen from Colombia has the first tergite with short faint longitudinal costulae extending from the base to 1/4 of the length of the tergite.

Minor worker measurements (n= 1): HW 0.35, HL 0.37, SL 0.27, EL 0.08, WL 0.37, PSL 0.06, PTW 0.08, PPW 0.12, CI 95, SI 78, PSLI 16, PPI 150.

Soldier measurements (n= 1): HW 0.71, HL 0.73, SL 0.39, EL 0.10, WL 0.53, PSL 0.10, PTW 0.10, PPW 0.16, CI 97, SI 56, PSLI 11, PPI 160.

Material examined. Colombia: 1 minor worker, 1 soldier, Vaupés, Mitú, Trubon, floodplain forest, 1.2054, -70.0695, alt. 196m, 24. Mar. 2019. Coll. D. Castro, winkler [ICN].

Comments. This species is a new record for Colombia with previous records from Ecuador and Peru (Wilson 2003). The examined soldier is relatively like that described by Wilson (2003). The paratype soldier on AntWeb (JTLC000016340) has a marked antennal scrobe; in contrast the antennal scrobe of the Vaupés soldier is barely perceptible. Another contrasting feature is the dorsal surface of the pronotum, uniformly foveate in the paratype soldier while strongly transversely costulate in the Vaupés collection.

Pheidole distorta Forel, 1899

Minor worker measurements (n= 10): HW 0.61–0.65, HL 0.60–0.65, SL 0.52–0.56, EL 0.12–0.14, WL 0.70–0.75, PTW 0.12–0.14, PPW 0.16–0.18, CI 97–108, SI 81–93, PPI 129–133.

Soldier measurements (n= 10): HW 1.41–1.49, HL 1.22–1.26, SL 0.57–0.63, EL 0.18–0.20, WL 1.20–1.31, PSL 0.02, PTW 0.35–0.37, PPW 0.47–0.53, CI 84–89, SI 45–51, PSLI 1, PPI 133–142.

Queen measurements (n= 10): HW 1.10–1.16, HL 0.98–1.04, SL 0.53–0.63, EL 0.20–0.31, WL 1.71–1.78, PSL 0.02, PTW 0.45, PPW 0.55, CI 108–112, SI 47–58, PSLI 2, PPI 122.

Male measurements (n= 10): HW 0.51–0.53, HL 0.57–0.59, SL 0.12–0.16, EL 0.35, WL 1.49–1.57, PTW 0.20, PPW 0.24, CI 87–93, SI 22–27, PPI 120.

Diagnosis. *Pheidole distorta* is distinguished from the rest of the members of the *distorta* group by the short or absent propodeal spines. Other species have longer propodeal spines.

Description. Minor worker: head, pronotum, propodeum and gaster smooth and shiny; developed pronotal shoulders; promesonotal hump-shaped bulge, with a pair of tubercle-shaped protrusions; katepisternum foveatereticulated, most often with a smooth, shiny patch in the middle. Soldier: head strongly rugoreticulate, forming an areolate and shiny surface, with a shallow depression in the middle part; mesosome surface like that on the head; in profile, petiole with developed longitudinal ventral process; dorsum of first gastral tergite opaque, longitudinally costulate, the costulae fading towards an anterior quarter of the tergite; very fine granular microsculpture extending in the posterior region of the first tergite. Queen (previously undescribed): reddish-brown ants with shiny surface; punctuation and rugoreticulated sculpture on the head, forming an areolate surface; scape strongly angled towards the base; strongly curved hypostomal margin, with a reduced middle tooth, barely protruding by a blunt bulge, absent inner hypostomal teeth, short and pointed outer hypostomal teeth; mesomal sculpture as on the head, except for the anterior part of the anepisternum and katepisternum which lack rugoreticulae; propodeum with reduced propodeal spines, forming an obtuse angle; petiole with developed longitudinal ventral process. Male (previously undescribed): head covered with longitudinal carinae and conspicuous punctuation; compound eyes protruding from the cephalic margins; yellow mandible, with brown masticatory margin, a single developed apical tooth and blunt to semi-square basal tooth; short scape, with globose pedicel; in ventral view, head with transverse costulae extending from the postgenal suture towards the eyes, surface with conspicuous punctuation; in profile view, 1/3 of the posterior part of the anepisternum with punctuation and fine costulae; axilla covered with fovea; propodeum with a foveate surface and sparsely costulate, devoid of angles that resemble a propodeal spine; petiole with longitudinal process less developed than in the queen.

Material examined. Colombia, Magdalena: 18 soldiers, 48 minor workers, 2 queens, Santa Marta, campus Universidad del Magdalena, shade of trees, hard ground, 11.2246, -74.1853, 14. May. 2019. Coll. M. Escárraga, hand collecting, nest # 1[CBUM]; 8 soldiers, 16 workers, same data except by nest excavated in hard soil, 2. Jun. 2019. Coll. M. Escárraga & E. García, nest # 2 [CBUM]; 26 soldiers, 37 minor workers, 1 queen, 116 males, Santa Marta, Universidad del Magdalena, nest excavated in hard soil, 11.2246, -74.1853, alt. 25m, 6. Jul. 2019. Coll. M. Escárraga & J. Roncallo, nest # 3 [CBUM]; 8 soldiers, 55 minor workers, 93 alate queens, 1 queen, same data except by Coll. E. García & H. Sierra, nest # 4 [CBUM].

Comments. This species is known only from northern Colombia. The minor workers and soldiers of *Pheidole distorta* examined here are identical to the minor worker (CASENT0908310) and soldier (CASENT0908309) syntypes imaged on AntWeb. We observed an additional distinctive character of *P. distorta*: the soldier, queen, and male have a longitudinal ventral process on the petiole.

Pheidole distorta was known only from the type specimens used by Forel (1899), with no further specimens deposited in museums or other biological collections. During field work within the Universidad del Magdalena campus, we detected several nests of *P. distorta* in an area smaller than 100 m². These nests were excavated and contained minor workers, soldiers, males, and delate/alate queens.

The excavation of ant nests not only favors the possibility of associating castes to the same species (e.g., soldiers and minor workers in *Pheidole*) but also the possibility of understanding the colonial structure of species (Buhl *et al.* 2004; Forti *et al.* 2007). A finding from the excavation of *Pheidole distorta* nests documented in this study is related to the asymmetric sex ratio found in the colonies. We found colonies exclusively producing males or females (alate queens) in different nests during the same dry climatic season, with a single queen in each of these nests (i.e., monogynic colonies). The production of males or females in different nests has apparently not been documented in species of ants that inhabit the dry forest. This behavior has also been found in other *Pheidole* species in Santa Marta, such as *Pheidole fallax* Mayr, 1870 and *Pheidole urbana* Camargo-Vanegas & Guerrero, 2020 (Guerrero *et al.* unpublished data). The data provided here provide base line for analyzing the factors that can promote and determine the reproductive phenology of *Pheidole distorta* populations in this forest type. Identification of flight patterns in taxocenes, as well as mechanisms driving the reproductive phenology of populations of dry forest ant species, would allow us to continue understanding the evolution of the taxonomic diversity of this type of ant assemblage.

Pheidole fera Santschi, 1925

Soldier measurements (n=3): HW 1.53–1.73, HL 1.73–1.88, SL 0.78–0.82, EL 0.20, WL 1.27–1.37, PSL 0.08, PTW 0.22–0.27, PPW 0.35–0.43, CI 89–92, SI 48–51, PSLI 4–5, PPI 146–164.

Material examined. Colombia: 1 soldier, Meta, Puerto López, Remolino, Centro Cafam Llanos, alt. 210m, 19. Apr. 2012. Coll. E. Sesquilé, pitfall [MPUJ]; 1 soldier, Puerto López, Remolino, Cafam Llanos, Piedra Candela, forest, alt. 240m, 19. Apr. 2012. Coll. D. Villa, corner trap [MPUJ]; 1 soldier, Amazonas, Leticia, Monilla Amena, alt. 70m, 19. Mar. 2004. Coll. B. Rippe, pitfall [MPUJ].

Comments. This species is a new record for Colombia with previous records only from Brazil (Wilson 2003). The lectotype soldier (CASENT0913328) has longitudinal costulae that occupy the anterior half of the face. In contrast, these costulae occupy the anterior 2/3 of the face on the Colombian specimens.

Pheidole iceni Fernández, 2011.

Amended description of soldier. Mandible smooth and shiny, with abundant piligerous puncta, reclinated short hairs and longer erect hairs on masticatory border; frontal carinae slightly obliquely slanted posteriorly, central clypeus, area between frontal carinae and vertex with longitudinal striation, otherwise head densely striate reticulate, head with dense appressed short setae and two rows of central long setae; scape smooth and shining, terete at base, with abundant erect setae as longer as maximum width of scape; hypostomal margin sinuous (in both sides of the middle); median tooth absent; inner hypostomal teeth small, stout; outer hypostomal teeth large, pointed; promesonotal groove present; propodeal spines present and prominent; metanotal groove deep; pronotum with transverse striation, including sides; rest of mesosomal dorsum with oblique transverse striations; sides of mesosoma with irregular longitudinal rugulae; dorsal (outer) margin of hind tibia with abundant suberect setae shorter than maximum width of tibia; pilosity abundant on mesosomal dorsum; postpetiole in dorsal view diamond shaped, much broader than long, with transverse striations; first gastral tergite with very fine and dense longitudinal striations, with abundant long erect setae; color red brown, head darker, hairs lighter.

Comments. Due to an error at the time of publication, the description of the soldier was incorrect, and was text from a previously described species. The description of the worker, as well as the measurements of the worker and soldier, photographs and location are correct in Fernández (2011). We provide here a corrected description of the

soldier and comments on the separation of the species from *P. fiorii*. The rest of the information is as provided in Fernández (2011).

The smooth and shiny head, well developed occipital carinae, and long, downturned propodeal spines differentiate the minor worker of this species from any other in the genus, including those in the *fallax* group. *Pheidole fiorii* Emery is closely related to this species, but with clear differences (see diagnosis), including setae (shorter in *iceni*), color (light brown in *iceni*) the smooth and shining pronotum, and sides of the petiole (variably foveolated in *fiorii*).

The dense head sculpturing, the transverse striation of mesosomal dorsum and postpetiole, deep metanotal groove, and conspicuous propodeal spines differentiate the soldier of this species from any other in the genus, including the *fallax* group.

Pheidole indagatrix Wilson, 2003

Minor worker measurements (n=2): HW 0.59, HL 0.73–0.75, SL 1.08–1.10, EL 0.16, WL 0.94, PSL 0.06, PTW 0.12, PPW 0.16–0.18, CI 79–81, SI 183–187, PSLI 8, PPI 133–150.

Soldier measurements (n=2): HW 1.22–1.47, HL 1.33–1.41, SL 1.00–1.08, EL 0.18–0.20, WL 1.14, PSL 0.08–0.10, PTW 0.16–0.18, PPW 0.29–0.31, CI 91–104, SI 73–82, PSLI 6–7, PPI 178–188.

Material examined. Colombia: 1 minor worker, 1 soldier, Cauca, Mpio Santa Rosa, San Juan de Villalobos, 1.5018889, -76.3647778, alt. 1400m, 23. Nov. 2019. Coll. M. Escárraga, hand collecting [CBUM]; 1 minor worker, 1 soldier, Valle del Cauca, Calima, Coll. Aldana [ICN].

Comments. This is a new record for Colombia and South America, with previous records from Honduras, Nicaragua, Costa Rica, and Panama (Wilson 2003). The soldiers of *P. indagatrix* collected in Cauca and Valle del Cauca localities match the holotype described by Wilson (2003), except that the holotype has the frontal lobes mostly rugoreticulate while in Colombian soldiers there are semi-straight longitudinal costulae extending between the frontal carinae. The minor worker paratype has conspicuous punctuation on the area around the inner margin of the eyes; in contrast, Colombian material has a few inconspicuous punctuations and transverse costulae in that same head region.

Pheidole lineafrons Longino, 2019

Minor worker measurements (n=1): HW 0.71, HL 0.88, SL 1.25, EL 0.16, WL 1.10, PSL 0.02, PTW 0.16, PPW 0.24, CI 80, SI 178, PSLI 2, PPI 150.

Soldier measurements (n=1): HW 1.57, HL 1.65, SL 1.33, EL 0.22, WL 1.45, PSL 0.08, PTW 0.29, PPW 0.51, CI 95, SI 85, PSLI 5, PPI 173.

Material examined. Colombia: 2 minor workers, 1 soldier, Caldas, Aguadas, La Playa, alt. 1610m, 21. Jan. 1990. Coll. C. Cárdenas [IAvH].

Comments. This is a new record for Colombia and South America with previous record from Costa Rica (Longino 2019). The Colombian material is very similar to the holotype (soldier, CASENT0644875) and the minor worker paratype (CASENT0644874), except that the mesosome length of the soldier is shorter, as is the scape length of the minor worker.

Pheidole meinerti Forel, 1905

Minor worker measurements (n=1): HW 0.39, HL 0.55, SL 0.67, EL 0.12, WL 0.61, PSL 0.06, PTW 0.10, PPW 0.14, CI 71, SI 170, PSLI 11, PPI 140.

Soldier measurements (n=1): HW 0.84, HL 0.80, SL 0.55, EL 0.12, WL 0.71, PSL 0.06, PTW 0.10, PPW 0.18, CI 105, SI 65, PSLI 7, PPI 180.

Material examined. Colombia: 1 minor worker, 1 soldier, Guaviare, Calamar, Chiribiquete, Cerro Campana, 1.2805, -72.6314, alt. 253m, 3–6. Mar. 2018. Coll. D. Luna & A. Pinzón, winkler [ICN].

Comments. This is a new record for Colombia, but the species was previously known from Venezuela, Guyana, Ecuador, Peru, and Brazil (Wilson 2003). The soldier matches the original in Wilson (2003). The Colombian specimen has short, decumbent, clavate hairs like the holotype (CASENT0908289), but with fewer hairs on the first gastral tergite.

Pheidole obscurithorax Naves, 1985

Minor worker measurements (n=1): HW 0.71, HL 0.82, SL 1.10, EL 0.20, WL 1.12, PSL 0.02, PTW 0.14, PPW 0.20, CI 86, SI 156, PSLI 2, PPI 143.

Soldier measurements (n=3): HW 1.63–1.73, HL 1.69–1.78, SL 0.98–1.10, EL 0.24–0.27, WL 1.47–1.65, PSL 0.06–0.10, PTW 0.25–0.29, PPW 0.35–0.47, CI 95–98, SI 61–67, PSLI 3–6, PPI 138–160.

Material examined. Colombia: 1 soldier, Meta, San Martin, Reserva Natural el Caduceo, km 4.5 vía San Francisco, 3.6655, -73.6583, alt. 309m, 10-14. Mar. 2014. Coll. T. Velasco, pitfall [MPUJ]; 1 minor worker, same data except by Coll. L. Rodríguez [MPUJ]; 1 soldier, Puerto Gaitán, Altamira, Club los Llaneros, alt. 140m, 22. Oct. 2006. Coll. K. Avellaneda, D. Rincón & D. Rodríguez, pitfall [MPUJ]; 1 soldier, Puerto López, La Libertad, alt. 366m, Oct. 2006 Coll. J. Arce [MPUJ].

Comments. This is a new record for Colombia, although previously known in several other South American countries including French Guiana, Ecuador, Peru, Bolivia, Brazil, Paraguay, Uruguay, Argentina. The species is exotic in the USA (Wilson 2003). *Pheidole obscurithorax* soldiers from Colombia are identical to the holotype from Argentina.

Pheidole otisi Wilson, 2003

Minor worker measurements (n= 1): HW 0.33, HL 0.37, SL 0.33, EL 0.08, WL 0.41, PSL 0.06, PTW 0.08, PPW 0.10, CI 89, SI 100, PSLI 16, PPI 125.

Soldier measurements (n= 1): HW 0.57, HL 0.63, SL 0.33, EL 0.10, WL 0.53, PSL 0.06, PTW 0.12, PPW 0.16, CI 91, SI 59, PSLI 9, PPI 133.

Material examined. Colombia: 1 minor worker, 1 soldier, Nariño, Barbacoas, Reserva Natural El Pangán, 1.3636, -78.0791, alt. 640m, 27. Jul. 2006. Coll. A. Miranda & O. Reyes, hand collecting [ICN].

Comments. This is a new record for Colombia and South America with previous records known from Honduras, Nicaragua, and Costa Rica (Wilson 2003). In the soldier's illustration by Wilson (2003), this one has well-marked rugoreticulae towards the middle of the vertex and the anterior portion of the vertex lobes, while on the Colombian specimen the rugoreticulae are arranged in a horizontal patch that fades towards the middle of the vertex and the anterior portion of the vertexal lobes, without extending to the posterior portion.

Pheidole praeusta Roger, 1863 (Figures 1–8)

Pheidole praeusta Roger, 1863: 197. Holotype soldier, "Island", Colombia [MHNG, AntWeb image of holotype examined, CASENT0915435]. Forel (1901): 361: minor worker described, Barranquilla, Colombia [NHMUK, AntWeb image of minor worker examined, CASENT0281753].

Pheidole amata Forel (1901): 360. Lectotype soldier, Orihueca, Río Frio, Magdalena, Colombia [MHNG, AntWeb images examined, CASENT0908158]. **New synonym**.

Minor worker measurements (n=12): HW 0.47–0.61, HL 0.61–0.82, SL 0.80–1.00, EL 0.16–0.20, WL 0.80–1.04, PTW 0.10–0.12, PPW 0.16–0.20, CI 71–91, SI 163–175, PPI 150–200.

Soldier measurements (n= 7): HW 1.51–1.55, HL 1.86–1.90, SL 0.78–0.80, EL 0.27, WL 1.43–1.47, PSL 0.10, PTW 0.24–0.25, PPW 0.45–0.51, CI 81–82, SI 51–52, PSLI 5, PPI 192–200.

Super soldier measurements (n= 8): HW 2.17–2.46, HL 2.52–2.90, SL 0.87–1.10, EL 0.29–0.31, WL 1.22–1.88, PSL 0.12–0.17, PTW 0.29–0.35, PPW 0.46–0.65, CI 85–88, SI 40–47, PSLI 4–7, PPI 160–191.

Description. Minor worker: In full-face view, oval-shaped head, with a smooth and shiny surface, with a developed occiput and occipital cavity; antennal fossa covered with punctuation and longitudinal carinulae. Very long antennal escape. In lateral view, pronotum smooth and shiny, mesopleura and propodeum covered with punctuation fine and very indistinct, the latter with propodeal spines reduced to a pair of denticles. Petiole and postpetiole with inconspicuous punctuation. Dorsum of first gastral tergite smooth and shiny. Long yellowish hairs covering the entire surface of the body. Soldier: In full face view, anterior half of the head with parallel longitudinal costulae; posterior part of antennal fossa covered with rugoreticulae. Striae surrounding the eyes longer than those formed between the frontal carinae, forming a "w"-shaped pattern, the entire costulae covered by fine and indistinct punctuation. Smooth and shiny occipital lobes. hypostomal margin straight, with a large, blunt, gibbous middle tooth, prominent outer hypostomal teeth, broad towards the base and pointed towards the apex, separated from each other; inner hypostomal teeth pointed, protruding behind the outer ones. In lateral view, pronotum striated transversely, with indistinct punctuation, and a smooth, shiny patch in the middle; mesopleura with conspicuous punctuation; propodeum provided with developed propodeal spines, dorsal surface covered with conspicuous punctuation and some longitudinal striae. In dorsal view, pronotum covered with short transverse carinulae, with a smooth and shiny medium patch. Anterior portion of the first gastral tergite covered with very short carinulae that extend from the helcium, the rest of the tergum is smooth and shiny, covered with conspicuous foveae, and abundant yellowish, long and suberect hairs emerge. Super soldier. In dorsal view, clypeus as in the soldier. Dorsal surface of the head covered by costulae arranged in a "w" pattern, although unlike the soldier, those costulae originating between the frontal carinae are longer, reaching and sometimes exceeding the length of the costulae close to the eyes, occipital lobes smooth and shiny. Hypostomal margin concave, with prominent middle tooth, thick and gibbous, inner hypostomal teeth broad towards the base and pointed towards the apex, prominent and triangular outer hypostomal teeth. In lateral view, mesosome covered with conspicuous transverse striae; pronotum with small medium patch smooth and shiny; propodeum provided with slender propodeal spines. In dorsal view, mid-posterior portion of the pronotum smooth and shiny, the rest covered by transverse striae; Propodeum covered with transverse striae and conspicuous punctuation. Anterior portion of the first tergite of the gaster covered with short longitudinal carinulae extending from the helcium. Head and mesosome covered with erect and suberect yellowish hairs. Petiole, postpetiole and gaster with yellow and decumbent hairs.

Material examined. Colombia: 1 soldier, Magdalena, Aracataca, Vereda Macaraquilla, Finca San José Sur, Oil palm plantation, 10.5721, -74.1933, alt. 41m, 22. Oct. 2017. Coll. T. Franco & J M Ramírez, pitfall [CBUM]; 5 minor workers, 4 soldier, 5 super soldiers, Aracataca, Vereda Macaraquilla, Finca Macaraquilla, Oil palm plantation, 10.5759, -74.1764, alt. 51m, 22. Oct. 2017. Coll. T. Franco & J M Ramírez, pitfall [CBUM]; 2 minor workers, Aracataca, Vereda Macaraquilla, Finca San José Sur, Oil palm plantation, 10.5721, -74.1922, alt. 40m, 21. Oct. 2017. Coll. T. Franco & J M Ramírez, pitfall [CBUM]; 1 super soldier, Aracataca, Vereda Macaraquilla, Finca San José Sur, Oil palm plantation, 10.5725, -74.1864, alt. 41m, 17. Sep. 2017. Coll. T. Franco & J M Ramírez, pitfall [CBUM]. 10 minor workers, 3 soldiers, 3 super soldiers, Santa Marta, Parcela Bosque Seco Universidad del Magdalena, 11.2167, y -74.1833, alt. 21 m, 13. Oct. 2021. Coll. R.J. Guerrero, dug nest [CBUM].

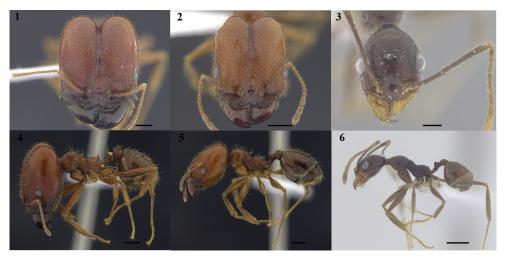
Comments. This species is known from Colombia, Ecuador, and Brazil. *Pheidole praeusta* is recorded here as the first currently known trimorphic worker subcaste species for South America, possessing an unusually large super soldier subcaste in addition to the typical minor worker and soldier subcastes.

Pheidole praeusta was described from a single soldier by Roger (1863), which prevented him from commenting on the remarkable morphology of this species. Later, Forel (1901) observed the nest structure of *P. praeusta* in different sites in the Colombian Caribbean region and commented on the exaggerated differences in head size between workers and "soldiers". Despite the excavation of nests of *P. praeusta*, Forel (1901) does not comment on the dimorphism among the soldier subcaste that we recorded here.

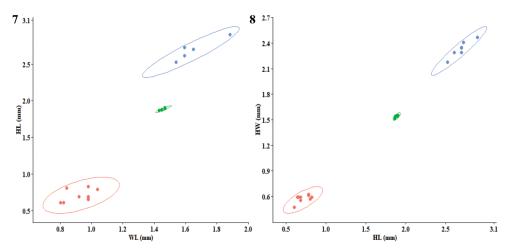
Specimens collected from pitfalls in Aracataca (Magdalena, Colombia) allowed us to identify within the series several ants with a soldier-like morphology different in the size of the head and mesosoma from those described in *P. preusta*. Since *P. praeusta* was previously recorded in the dry forest reserve of the Universidad del Magdalena in Santa Marta (Ramos *et al.* 2022), RJG installed protein baits at various points within the reserve, attracting workers and a soldier of *P. praeusta*. Those ants were followed to the nest, which was partially excavated, extracting 10 minor workers, three soldier-like workers, and three super soldier workers. The ants collected in Aracataca and Santa Marta show that *P. preusta* colonies are composed of minor workers, soldiers, and super soldiers morphometrically different from each other (i.e., the soldiers are dimorphic); soldiers have a shorter mesosoma than super soldiers

(Fig. 7), and there is a strong gap in head size between the two subcastes (Fig. 8). It is observed that the variance in the size of the head is lower for the soldiers than for the supersoldiers, but in this last subcaste with a growth of the head. The lower variance in the dimorphic soldiers of *P. praeusta* apparently contrasts with that shown in another trimorphic species, *Pheidole rhea* Wheeler, W.M., 1908, in which the soldiers show greater variability than the super soldiers (Huang & Wheeler 2011). The data on *Pheidole praeusta* are just an approximation to the contrasting pattern shown by other trimorphic species, however the exploration of more nests covering the distribution of this species would allow for more information to analyze possible allometric patterns.

The minor workers and soldiers of *P. praeusta* are very similar to these subcastes of *P. amata* Forel 1901, based on morphometrics (using Longino 2009b) and examining images. The morphometric traits HL, HW, SL, and WL of the *P. praeusta* minor worker and soldier completely matched those measurements recorded for *P. amata* Likewise, the morphological features shape of anteroclypeal margin, occipital cleft deep, carinule pattern on head, and erect pilosity on body match among the soldiers of both taxa. Wilson (2003) suggests several differences between minor workers of *P. praeusta* and *P. amata* (e.g., propodeal spine reduced to denticle vs propodeal spine absent, respectively) but we find no morphological evidence to separate them, as suggested by Forel (1901). Given the morphological similarity of the worker and soldier subcastes as well as the proximity of the type localities, they are almost certainly the same species, and we synonymize *P. amata* under *P. praeusta*.



FIGURES 1–6. *Pheidole praeusta* Roger. 1) Head in full-face view of the super soldier subcaste. 2) Head in full-face view of the soldier subcaste. 3) Head in full-face view of the worker subcaste. 4) Body in lateral view of the super soldier subcaste. 5) Body in lateral view of the soldier subcaste. 6) Body in lateral view of the worker subcaste. Scale bar= 0.5 mm. Super soldier (CBUMAG:ENT13467), soldier (CBUMAG:ENT13071), and minor worker (CBUMAG:ENT13463) photos by R.J. Guerrero.



FIGURES 7–8. Bivariate plots of measurements of *Pheidole praeusta* Roger. 7. Relationship between WL and HL. 8. Relationship between HL and HW. The red solid line green solid line, and blue solid line correspond to the minor worker, soldier, and super soldier subcastes measurements, respectively.

Pheidole rogeripolita **Longino, 2019** (Figures 7–10)

Material examined. Colombia: 4 minor workers, 1 soldier, Nariño, Altaquer, Barbacoas, El Barro, Reserva Natural Río Ñambí, grassy slope, 1.03, -78.083, alt. 1200m, Mar. 2006. Coll. S. Cabrera, at bait N°114 [ICN, CBUM, IAvH, MCZC, USNM].

Minor worker measurements (n= 4): HW 0.83–0.93, HL 1.12–1.17, SL 1.63–1.88, EL 0.17–0.20, WL 1.51–1.61, PSL 0.61–0.63, PTW 0.15, PPW 0.24–0.29, CI 73–79, SI 129–139, PSLI 10, PPI 167–171.

Soldier measurements (n= 1): HW 2.49, HL 2.24, SL 1.66, EL 0.27, WL 2.24, PSL 0.44, PTW 0.24, PPW 0.59, CI 98, SI 67, PSLI 17, PPI 240.

Distribution. Costa Rica, Colombia.

Comments. Longino (2019) described *Pheidole rogeripolita* as an ecological variant of the very similar *P. rogeri* Emery, 1896, and DNA sequence data identify them as sister species (Longino, pers. com.). Longino (2019) stated that the soldiers of both species are very similar and indistinguishable, and the species could only be separated by the subtle surface sculpture differences in the minor worker. Longino (2019), however, overlooked an extremely different character between the two species: the antennal club. We examined images of the type series of *P. rogero-polita* (CASENT0646359, CASENT0636564, CASENT0646364, and JTLC000006466) and our ants collected in Nariño (Colombia), and both minor workers and soldiers have a five-segment antennal club, whereas *P. rogeri* has a typical three-segmented antennal club.

Pheidole rogeripolita is the only known species with a five-segmented antennal club in the New World. Two other species, *Pheidole sabahna* Eguchi 2000 and *Pheidole quinata* Eguchi 2000, have a five-segmented club. These two species are from Borneo, Java, and Sumatra (Eguchi 2000). The five-segmented club is convergent, since *P. rogeripolita* is sister to *P. rogeri* within a New World group, while *P. sabahna* (and possibly *P. quinata* considering its morphological similarity and shared distribution with *P. sabahna*) is in a monophyletic subgroup within the Asia-Africa clade (Economo *et al.* 2019).

Pheidole simonsi Wilson, 2003

Minor worker measurements (n=2): HW 0.65, HL 0.65, SL 0.65, EL 0.14, WL 0.78, PSL 0.18–0.20, PTW 0.10–0.12, PPW 0.16–0.18, CI 100, SI 100, PSLI 27–30, PPI 150–160.

Material examined. Colombia: 2 minor workers, Cesar, Valledupar, Garupal, 10.2251, -73.7506, alt. 648m, 29. Mar. 2016. Coll. R. Achury, pitfall [IAvH].

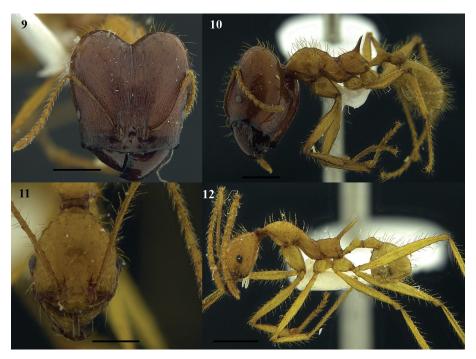
Comments. This is a new record for Colombia and South America with previous records known from Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama (Wilson 2003; Longino 2009a). The minor workers of *P. simonsi* from Colombia are identical to those of Panama with a weakly developed nuchal carinae but differing in the orientation of the propodeal spine, which is more ventrally arched in the Colombian specimens (like those of *P. simonsi*).

Pheidole walkeri Mann, 1922

Soldier measurements (n=1): HW 1.37, HL 1.51, SL 0.84, EL 0.18, WL 1.33, PSL 0.08, PTW 0.20, PPW 0.35, CI 91, SI 61, PSLI 5, PPI 180.

Material examined. Colombia: 1 soldier, Cundinamarca, Reserva Chicaque, Quebrada el Carmen, alt. 2229m, 24–28. Feb. 2014. Coll. D. Forero [MPUJ].

Comments. This is the first record for Colombia and South America, but previously known from Mexico, Guatemala, Belize, Honduras, Nicaragua, and Costa Rica (Wilson 2003, Longino 2009a). The *P. walkeri* soldier from Colombia has face sculpture like that of the Honduran type on AntWeb (CASENT0645893) except that in the latter, carinulae originating in frontal lobes abruptly diverge posteriorly to reach the sides of the head below its midheight, while in the Colombian specimen these carinulae reach the sides of the head slightly above mid-head.



FIGURES 9–12. *Pheidole rogeripolita* Longino. 9) Head in full-face view of the soldier. 10) Body in dorsal view of the soldier. 11) Head in full-face view of the worker. 12) Body in lateral view of the worker. Scale bar= 1 mm, except in Fig. 3 (Scale bar= 0.5 mm). Soldier (CBUMA:ENT20911) and minor worker (CBUMAG:ENT20912) photos by R.J. Guerrero.



FIGURE 13. *Pheidole* species richness in the Neotropical region. Note that Brazil and Colombia in South America and Costa Rica and Mexico in Central America present richness values above 150 species. Data downloaded from Guénard *et al.* (2017).

Discussion

We report here the first record for the Neotropical region of a species with a trimorphic worker caste. *Pheidole praeusta* is the ninth trimorphic species within the *Pheidole* ants in the New World, with the majority concentrated in the USA and some of them reaching as far as southern Mexico (e.g., *Pheidole obtusospinosa* Pergande, 1896). Although the polymorphism among the eight previously known trimorphic species evolved at least four times (Moreau 2008), including *P. praeusta* in robust phylogenetic analyses of *Pheidole* species would allow knowing the relative

position of this Neotropical species and evaluating if its particular morphology is related to some of the trimorphic species or if it follows a pattern of convergent evolution. In addition, more field work (e.g., nest excavation) is necessary to know if other Neotropical species with large soldiers could be trimorphic.

The genus *Pheidole* in Colombia is currently represented by 157 species, including the eight new records. 50% of these new species records expand their distribution to South America since they were previously known species from Central America. Colombia is the fourth richest country in *Pheidole* ant species within the Neotropical region (Fig. 13), while in South America it is the second one after Brazil (193 species). The species richness throughout the Neotropical region is concentrated in four countries (Brazil, Mexico, Costa Rica, and Colombia) and in general, more than 90% of the Neotropical countries register a richness of less than 90 species. Many of these countries have ecologically heterogeneous terrestrial ecosystems (Amazon Forest, montane forest, among others) and the richness differences are almost certainly due to undersampling. More research is needed to better understand true spatial variation in species richness.

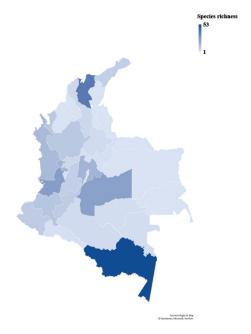


FIGURE 14. *Pheidole* species richness in the 32 departments of Colombia. Note that the highest species richness values are in the north (Magdalena) and south of the country (Amazonas).

The imbalance in the *Pheidole* species richness among the countries of the Neotropical region is a pattern that is reflected on a smaller geographic scale in Colombia. The highest number of *Pheidole* species are concentrated in the Amazon and Magdalena (Fig. 14), but departments such as Meta and Valle del Cauca can host more than 20 species. The panorama suggests that landscapes such as the savannas in the Caribbean, the eastern plains and a large part of the mountain forests need to be further explored, through both examination of material deposited in museums and in additional field sampling.

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References

- Antweb (2022) Antweb. Version 8.68.7. Available from: https://www.antweb.org (accessed 15 January 2022)
- Bolton, B. (2022) An online catalog of the ants of the world. Available from: https://antcat.org (accessed 10 January 2022)
- Buhl, J., Gantries, J., Deneubourg, J.L. & Theraulaz, G. (2004) Nest excavation in ants: group size effects on the size and structure of tunneling networks. *Naturwissenschaften*, 91 (12), 602–606. https://doi.org/10.1007/s00114-004-0577-x
- Camargo-Vanegas, J.J. & Guerrero, R.J. (2020) Las hormigas *Pheidole* (Formicidae: Myrmicinae) en el bosque seco tropical de Santa Marta, Colombia. *Revista Colombiana de Entomología*, 46 (2), e8433. https://doi.org/10.25100/socolen.v46i2.8433
- Casadei-Ferreira, A., Economo, E.P. & Feitosa, R.M. (2020) Additions to the taxonomy of *Pheidole* (Hymenoptera: Formicidae) from the southern grasslands of Brazil. *Revista Brasileira de Entomologia*, 64 (4), e20200068. https://doi.org/10.1590/1806-9665-RBENT-2020-0068
- Economo, E.P., Huang, J.-P., Fischer, G., Sarnat, E.M., Narula, N., Janda, M., Guénard, B., Longino, J.T. & Knowles, L.L. (2019) Evolution of the latitudinal diversity gradient in the hyperdiverse ant genus *Pheidole. Global Ecology and Biogeography*, 28, 456–470. https://doi.org/10.1111/geb.12867
- Economo, E.P., Klimov, P., Sarnat, E.M., Guénard, B., Weiser, M.D., Lecroq, B. & Knowles, L.L. (2015) Global phylogenetic structure of the hyperdiverse ant genus *Pheidole* reveals the repeated evolution of macroecological patterns. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20141416. https://doi.org/10.1098/rspb.2014.1416
- Eguchi, K. (2000) Two new *Pheidole* species with a 5-segmented antennal club (Hymenoptera: Formicidae). *Entomological Science*, 3 (4), 687–692.
- Fernández, F. (2011) *Pheidole iceni* n. sp. (Hymenoptera: Formicidae), a new ant for an old institution. *Caldasia*, 33 (2), 583–588.
- Forel, A. (1905) Miscellanea myrmécologiques II (1905). Annales de la Société Entomologique de Belgique, 49, 155-185.
- Forel, A. (1901) Variétés myrmécologiques. Annales de la Société Entomologique de Belgique, 45, 334–382.
- Forel, A. (1899) Formicidae. [part]. Biologia Centrali-Americana Hym, 3, 57-80.
- Forti, L.C., Camargo, R.S., Fujihara, R.T. & Lopes, J.F. (2007) The nest architecture of the ant, *Pheidole oxyops* Forel, 1908 (Hymenoptera: Formicidae). *Insect Science*, 14 (5), 437–442. https://doi.org/10.1111/j.1744-7917.2007.00171.x
- García, E., Tocora, M.C., Fiorentio, G., Escárraga, M.E., Fernández, F., Guerrero, R.J. (2020) New records of ants (Hymenoptera: Formicidae) for Colombia. *Biota Neotropica*, 20, e20201088. https://doi.org/10.1590/1676-0611-BN-2020-1088
- Guénard, B., Weiser, M., Gomez, K., Narula, N. & Economo, E.P. (2017) The Global Ant Biodiversity Informatics (GABI) database: a synthesis of ant species geographic distributions. *Myrmecological News*, 24, 83–89.
- Huang, M.H. & Wheeler, D.E. (2011) Colony demographics of rare soldier-polymorphic worker caste systems in *Pheidole* ants (Hymenoptera, Formicidae). *Insectes Sociaux*, 58, 539–549. https://doi.org/10.1007/s00040-011-0176-8
- Lillico-Ouachour, A. & Abouheif, E. (2016) Regulation, development, and evolution of caste ratios in the hyperdiverse ant genus *Pheidole. Current Opinion in Insect Science*, 19, 43–51. https://doi.org/10.1016/j.cois.2016.11.003
- Longino, J.T. (2009a) Additions to the taxonomy of New World *Pheidole* (Hymenoptera: Formicidae). *Zootaxa*, 2181 (1), 1–90.
 - https://doi.org/10.11646/zootaxa.2181.1.1
- Longino, J.T. (2009b) *Pheidole* Working Group. Available from: https://ants.biology.utah.edu/pheidoleworkinggroup/index.htm (accessed 15 December 2021)
- Longino, J.T. (2019) *Pheidole* (Hymenoptera, Formicidae) of Middle American wet forest. *Zootaxa*, 4599 (1), 1–126. https://doi.org/10.11646/zootaxa.4599.1.1
- Mackay, W. & Mackay, E. (2019) Género *Camponotus*. In: Fernández, F., Guerrero, R.J. & Delsinne, T. (Eds.), *Hormigas de Colombia*. Universidad Nacional Colombia, Bogotá, pp. 743–789.
- Mann, W.M. (1922) Ants from Honduras and Guatemala. *Proceedings of the United States National Museum*, 61 (2434), 1–54.
 - https://doi.org/10.5479/si.00963801.61-2434.1
- Mayr, G. (1870) Neue Formiciden. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, 20, 939–996.
- Mertl, A., Sorenson, M. & Traniello, J. (2010) Community-level interactions and functional ecology of major workers in the hyperdiverse ground-foraging *Pheidole* (Hymenoptera, Formicidae) of Amazonian Ecuador. *Insectes Sociaux*, 57, 441–452. https://doi.org/10.1007/s00040-010-0102-5
- Mertl, A.L. & Traniello, J.F.A. (2009) Behavioral evolution in the major worker subcaste of twig-nesting *Pheidole* (Hymenoptera: Formicidae): does morphological specialization influence task plasticity? *Behavioral Ecology and Sociobiology*, 63,

- 1411-1426.
- https://doi.org/10.1007/s00265-009-0797-3
- Moreau, C.S. (2008) Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution*, 48, 224–239.
 - https://doi.org/10.1016/j.ympev.2008.02.020
- Naves, M.A. (1985) A monograph of the genus *Pheidole* in Florida, USA (Hymenoptera: Formicidae). *Insecta Mundi*, 1 (2), 53–90.
- Peeters, C. (2019) Castas: homología y analogía en la forma y función. In: Fernández, F., Guerrero, R.J. & Delsinne, T. (Eds.), *Hormigas de Colombia*. Universidad Nacional Colombia, Bogotá, pp. 159–164.
- Pergande, T. (1896) Mexican Formicidae. Proceedings of the California Academy of Sciences, Series 2, 5, 858–896.
- Pie, M.R. & Traniello, J.F.A. (2007) Morphological evolution in a hyperdiverse clade: the ant genus *Pheidole. Journal of Zoology*, 271, 99–109.
 - https://doi.org/10.1111/j.1469-7998.2006.00239.x
- Ramos, L.M., Sierra, H.A., Roncallo, J.D. & Guerrero, R.J. (2022) Hormigas asociadas a fragmentos de bosque seco y ambientes urbanos de Santa Marta, Colombia. Hormigas asociadas a fragmentos de bosque seco y ambientes urbanos de Santa Marta, Colombia. *Biota Colombiana*, 23 (1), e978. https://doi.org/10.21068/2539200X.978
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org/ (accessed 25 Mar 2022)
- Roger, J. (1863) Die neu aufgeführten Gattungen und Arten meines Formiciden-Verzeichnisses nebst Ergänzung einiger früher gegebenen Beschreibungen. *Berliner Entomologische Zeitschrift*, 7, 131–214.
- Santschi, F. (1925) Nouveaux Formicides brésiliens et autres. *Bulletin et Annales de la Société Entomologique de Belgique*, 65, 221–247.
- Sarnat, E.M., Fischer, G., Guénard, B. & Economo, E.P. (2015) Introduced *Pheidole* of the world: taxonomy, biology, and distribution. *ZooKeys*, 543, 1–109. https://doi.org/10.3897/zookeys.543.6050
- Tschá, M.K. & Pie, M.R. (2018) Correlates of ecological dominance within *Pheidole* ants (Hymenoptera: Formicidae). *Ecological Entomology*, 44, 163–171. https://doi.org/10.1111/een.12685
- Waxman, H.K., Muscedere, M.L. & Traniello, J.F. (2017) Behavioral performance and neural systems are robust to sensory injury in workers of the ant *Pheidole dentata*. *Brain, behavior, and evolution*, 89, 195–208. https://doi.org/10.1159/000470899
- Westwood, J.O. (1839) An introduction to the modern classification of insects; founded on the natural habits and corresponding organisation of the different families. Vol. 2. Part XI. Longman, Orme, Brown, Green and Longmans, London, pp. 193–224.
- Wheeler, W.M. (1925) Neotropical ants in the collections of the Royal Museum of Stockholm. *Arkiv för Zoologi*, 17A (8), 1–55.
- Wilson, E.O. (2003) *Pheidole in the New World: A dominant, hyperdiverse ant genus*. Harvard University Press, Cambridge, Massachusetts, 794 pp.