



# New Miocene Mexican amber ant (Formicidae, Myrmicinae) of the genus *Pheidole* Westwood, 1839

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## ABSTRACT

The genus *Pheidole* Westwood, 1839 is considered the most species-diverse group of extant ants in the World. A new fossil species of ant *Pheidole chaan* sp. nov. (Formicidae, Myrmicinae) based on one worker and one soldier is described and illustrated from the Miocene of México. The type material comprises a syninclusion from Simojovel, Chiapas, México, providing the elements to recognise the new species through morphological characters of soldier and worker castes. *Pheidole chaan* sp. nov. is characterised by the following combination of characters: Soldier. Head longitudinally striated; median impression area between vertex of head and posterior margin of clypeus, close to the frontal carenas; dorsal surface of mandibles smooth, lateral surface of mandibles longitudinally striated; internal margin of scapes sinuous; propodeal spines well-developed with basal area as width as tall. Worker: vertex of head concave; entire head with coarse punctures; compound eyes protruding laterally from margin of head; mesonotal groove deep, forming a U-shape concavity; petiole forming a thin triangular-shaped node. *Pheidole chaan* sp. nov. from Miocene increases the knowledge of myrmecological biodiversity of the genus *Pheidole* and helps elucidate the origins and history of recent past of the clade in the New World.

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## Introduction

The genus *Pheidole* Westwood 1839 (Formicidae: Myrmicinae) is a worldwide diversified clade with 1160 extant species, 124 subspecies and seven valid fossil species (Bolton 2023). It is considered the most species-diverse group of extant ants in the World. After Wilson (2003) monograph, the number of species described within the genus has increased significantly with many of these new described species coming from local or regional myrmecological inventory studies (Longino 2009, 2019; Casadei-Ferreira et al. 2020). Some molecular phylogenetic works support a Neotropical origin of the genus around 29 Mya (Moreau 2008; Economo et al. 2015). The ecological and taxonomic dominance of the genus was achieved through subsequent localised adaptive radiations (Economo et al. 2019).

The 126 extant species of *Pheidole* recognised for México so far, accomplish ~ 11% of the total number of species worldwide (Dáttilo et al. 2019). However, the number of fossil species described for the genus remains relatively scarce in general and for México in particular, for example, the genus *Cephalotes* Latreille 1802 has more species described for the Dominican and Mexican amber than the species of *Pheidole* (De Andrade and Baroni Urbani 1999). Another example is the genus *Cyphomyrmex* Mayr, 1862 with species that have already been described in the Dominican and Mexican amber (De Andrade 2003), although their colonies are very small, probably no more than 500 workers (compared to the more abundant species of *Pheidole*) and predominantly live in rotten wood, leaf litter, dead decaying tree limbs or hollow dead twigs (Snelling and Longino 1992).

*Pheidole tertiaria* Carpenter 1930 is the oldest fossil known of this genus, dated from Eocene of the Florissant formation in strata of Colorado (Carpenter 1930). However, in spite of being 'the

largest ant genus and among the largest genera of life in general' (Longino 2009), the fossil record in this genus is represented by few species (Varela-Hernández and Riquelme 2021). *Pheidole* fossils from Miocene are representatives of the Dominican Republic amber which include *Pheidole tethepa* Wilson 1985a; *Pheidole primigenia* Baroni-Urbani 1995; and *Pheidole anticua* Casadei-Ferreira et al. 2019. Recently, Varela-Hernández and Riquelme (2021) described *Pheidole pauchil* Varela-Hernández and Riquelme 2021 subscribed to the Amber-bearing beds of Simojovel, Chiapas, dated as early as middle Miocene, ca. 23–13 Mya (Poinar 1992; Perrilliat et al. 2010).

In this work, we describe and illustrate a new species of the genus *Pheidole* from Miocene Mexican amber. The new species is based on a worker and a soldier.

## Materials and methods

The type material comprises a syninclusion. The amber comes from the Amber-bearing beds of Simojovel which belong to Mazantic shale and Balumtum sandstone strata estimated as early Miocene (Perrilliat et al. 2010; Riquelme et al. 2014a). The botanical source that produced the resins is attributed to an extinct legume of the genus *Hymenaea* Linné (sensu Langenheim 1966). Extant species of *Hymenaea*, for example, *Hymenaea courbaril* Linné and *Hymenaea verrucosa* Gaertner are currently distributed in the tropics of México, Central America, Antilles, and South America and share chemical signatures with the amber of the extinct *Hymenaea* (Langenheim 2003; Riquelme et al. 2014b).

The syninclusion is immersed in a translucent golden piece of amber that was faceted and polished to optimise morphological

analysis. Morphological data and measurements were collected using an Olympus AZ binocular dissecting microscope and a U-OCM10/100 1 mm micrometre with 0.1 mm intervals. To document morphological characters, photograph series in different planes were taken with a digital camera (Canon EOS Rebel T5), with an 18–55 mm f/3.5–5.6 IS II objective adapted to a macro-extension tube to amplify the insect inclusion. An automated Wemacro rail was used to calculate intervals for images. Images were stacked, processed, and edited with Zerene Stacker and Photoshop CC 2019 software. Schematic drawings were performed using Corel Draw Graphic Suite X7.

Identification for genus level followed Mackay and Mackay (1989) and Baccaro et al. (2015). For identification to species level, we followed two approaches: first, we followed Wilson (2003) for *Pheidole* of the New World. Then, we used the free version of Lucid software v.3.3 for the New World *Pheidole* data. Abbreviations and indices follow Longino (2019). The specimen is deposited in the Colección de Paleontología maintained at the Laboratorio de Sistemática Molecular, Universidad Autónoma del Estado de Morelos, México.

Measurements and indices: HL – Head length: In full-face view, the length between the mid-point of the anterior margin of the clypeus to the mid-point of a line tangent to the posterior margin of the head. HW – Head width: In full-face view, the maximum width between the lateral margins of the head, including the eyes, which are within the cephalic capsule. SL – Scape length: the maximum length of the scape excluding the basal constriction. WL – Weber's length: In lateral view of the mesosoma, the greatest distance from the approximate inflection point, where the pronotum curves into the cervical shield, to the posterior basal angle of the metapleuron. CI – Cephalic index:  $HW/HL \times 100$ . SI – Scape index:  $SL/HL \times 100$ . Measurements are expressed in millimetres.

## Results

### Systematic Palaeontology

Class **Insecta** Linnaeus 1758

Order **Hymenoptera** Linnaeus 1758

Family **Formicidae** Latreille 1802

Subfamily **Myrmicinae** Lepeletier de Saint Fargeau 1835

Genus ***Pheidole*** Westwood 1839

Type species ***Pheidole providens*** (Sykes 1835)

***Pheidole chaan* sp. nov.** Varela-Hernández & Flores-Zapoteco

ZooBank LSID: urn:lsid:zoobank.org:pub:E72BAB32-9F40-40C0-BDFB-AA0010CF38C9

### Type material

The complete piece of amber (Figure 1A) includes a syninclusion with the Holotype CPAL.469 and paratype CPAL.470 (Figures 1A, 1B). The complete piece of amber is housed in the Colección de Paleontología (CPAL-UAEM), Morelos, México.

### Locality

Simojovel, Los Pocitos mine, Simojovel, Chiapas, México.

### Horizon

Mazantic shale and Balumtum sandstone strata, Early Miocene (Riquelme et al. 2014b, 2015).

### Etymology

The specific epithet 'chaan' derives from Mayan language which means 'tiny, small', alluding to the tiny size of this species.



**Figure 1.** (A) complete piece of amber showing Holotype CPAL.469 (soldier) and Paratype CPAL.470 (worker) of *Pheidole chaan* sp. nov. (B) Micrograph of soldier (in lateral view) and worker (oblique view) of *Pheidole chaan* sp. nov. (C) Head, in frontal view, of soldier of *Pheidole chaan* sp. nov.

## Diagnosis

### Soldier

The holotype can be recognised by the following combination of characters: (1) Head longitudinally striated, except vertexes that are punctured in frontal view; (2) area between vertex of head and posterior margin of clypeus and close to the frontal carenas, scooped-off; (3) dorsal surface of mandibles smooth, lateral surface of mandibles longitudinally striated; (4) promesonotum continuously arched in lateral view; (5) internal margin of scapes sinuous; (6) propodeal spines well-developed with basal area as wide as tall; (7) node of petiole angled (acute) in lateral view, bifurcated in oblique view; (8) postpetiole angled posteriorly.

### Worker

With the following combination of characters: (1) Vertex of head concave; (2) entire head with coarse punctures; (3) compound eyes protruding laterally from margin of head; (4) mesonotal groove deep, forming a U-shape concavity; (5) propodeal spines long and slender; (6) petiole forming a thin triangular-shaped node.

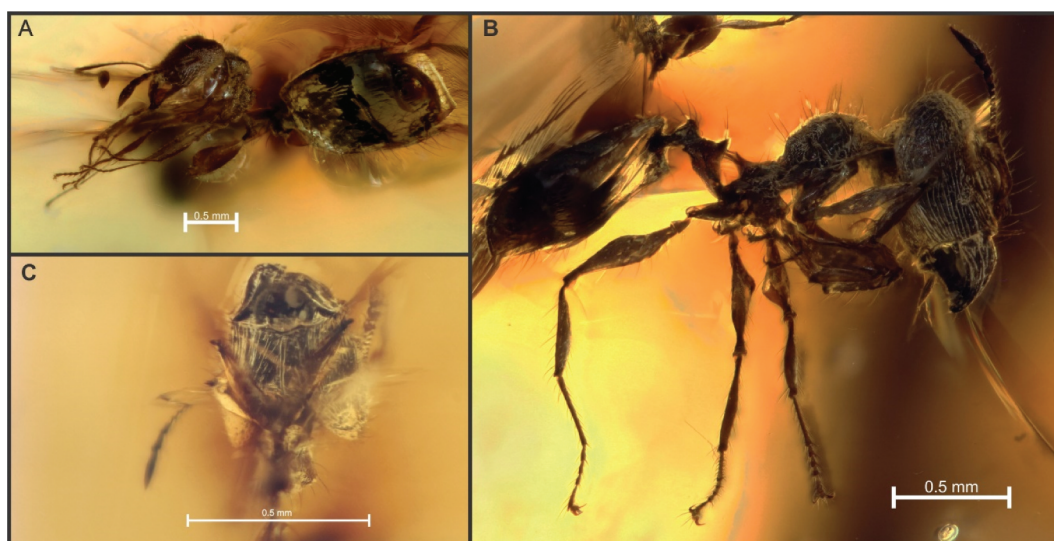
### Soldier description

Measurements ( $n = 1$ ): one soldier, small ant, body length 2.4 mm. General measurements: HL 0.7, HW 0.65, SL 0.3, WL 0.8, CI 88.57, SI 42.85.

### Head

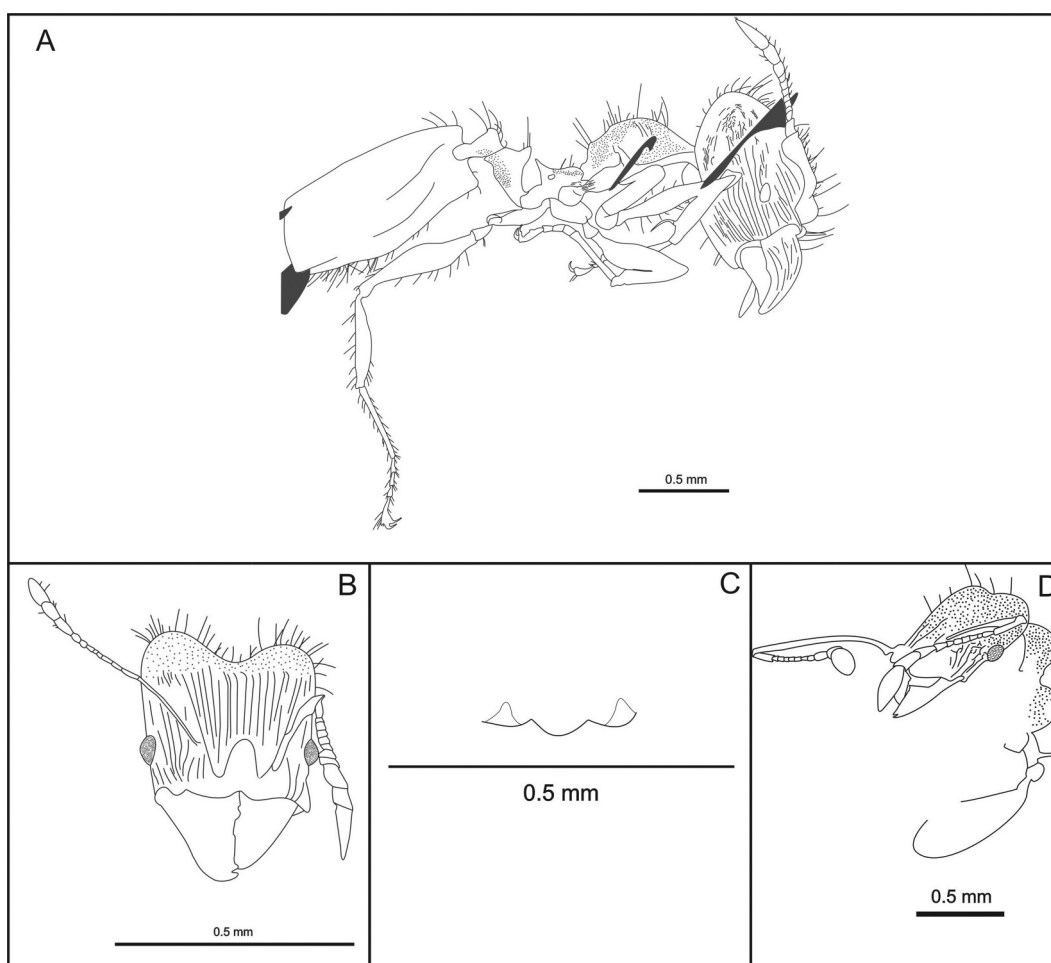
Longer than wide, sides subparallel, vertex of head deeply concave (Figures 1B, 1C, 2B, 3A, 3B), vertex and dorsum of head with moderate long erect hairs, entire head with thick longitudinal striae, except vertexes that are punctured in frontal view and a small area between occipital corner and compound eyes in lateral view, frontal carenas divergent posteriorly, reaching about 2/3 the length of head, posterior border of clypeus wide and deeply inserted between the frontal carenas forming a well-marked inverted U, anterior margin of clypeus sinuous, this sinuosity is formed by a clear notch at the middle, then a small teeth directed anteriorly on each side of the notch and then another continuous notch that runs from each teeth to the base of mandibles (Figures 1C, 3B); compound eyes small, in frontal view, eyes protruding laterally from margin of head, eyes

positioned anteroventrally; mandibles triangular, masticatory margin with no teeth except for an apical and a subapical tooth, apical tooth longer than subapical, dorsal surface of mandibles smooth and shiny, sides of mandibles longitudinally striated (Figures 1B, 2B, 3A); antenna twelve-segmented, antennal club three-segmented, club slightly longer than the other segments of funiculus together, scapes reaching  $\frac{3}{4}$  the length of head, without pilosity, as seen in lateral view, external margin straight, internal margin sinuous, narrowest area at base of scape reaching its maximum width at about  $\frac{3}{4}$  the length of scape (Figures 1B, 1C, 3B); two blunt inner hypostomal teeth present, closer to the midline of the hypostomal margin (Figures 2C, 3C). **Mesosoma.** Promesonotum continuously arched in lateral view, pronotum, in dorsal view rhomboidal, maximum width taken from the transverse line that connects both extremes of humerus; mesonotum, in lateral view, convex, continuous to the line of pronotum, but with a posterior margin formed by a straight angle between dorsal margin and posterior margin (Figures 1B, 2B, 3A); in dorsal view, mesonotum stretching posteriorly with its thinnest area just before the junction with propodeum, mesonotal groove deep, forming a U-shape concavity (Figures 1B, 2B, 3A), bottom half of mesopleuron longitudinally striated, top half smooth; dorsal margin of propodeum, in lateral view flat; propodeal spines long and robust at base in lateral view, anterior margin of spines with a continuous convex curve to the tip of spines, posterior face of spines straight, meeting posterior margin of propodeum in a 90 degrees angle; posterior face of propodeum flat, relatively long; petiole peduncle wide, a little bit longer than tall, gradually widening from base to apex, node of petiole angled (acute) in lateral view, node of petiole in oblique view bifurcated, notched at the middle of it, each bifurcation with a long erect hair, posterior margin of petiole, in lateral view, forming a 45 degrees angle; postpetiole with node well-differentiated, discontinuous, anterior and posterior margins joining at an angle (Figures 1B, 2B, 3A). **Legs.** Dorsal margin of middle and hind femora with suberect pilosity; dorsal margin of middle and hind tibiae with suberect pilosity, longer hairs as long as maximum width of tibiae, basitarsus as long as the other tarsus together, fifth tarsus as long as third and fourth tarsus together. **Gaster.** Smooth and shining with long erect hairs ventrally in the last two sternites (Figure 2A).



**Figure 2.** (A) Three quarter view of worker and posterior view of soldier (showing gaster) of *Pheidole chaan* sp. nov. (B) Lateral view of soldier of *Pheidole chaan* sp. nov. (C) ventral view of head of soldier of *Pheidole chaan* sp. nov. showing hypostomal teeth.





**Figure 3.** Schematic drawings of *Pheidole chaan* sp. nov. showing: A) Profile of soldier. B) Head of soldier in frontal view. C) Hypostomal teeth of soldier. D) Three quarter view of worker.

### Worker description

One worker, small ant, body length 1.3 mm. General measurements: ( $n = 1$ ) HL 0.3, HW 0.3, SL 0.4, WL 0.8, IC 100, SI 133.33.

### Head

Slightly longer than wide (Figures 2A, 3D), sides concave, vertex of head concave, dorsum of head with sparse long erect hairs, entire head with coarse punctures, except area between antennal fossa and anterior border of eyes that is longitudinally striated, frontal carinas parallel, reaching at most the baseline of eyes, anterior border of clypeus concave, forming a well-marked and narrowed inverted U; eyes prominent, compound eyes protruding laterally from margin of head (Figures 1B, 2C, 3D), eyes positioned slightly antero-ventrally; mandibles triangular, basal margin and masticatory margin forming a 90 degrees angle, masticatory margin with the following pattern of teeth: two apical teeth, subequal in length, then a three-fold repeated pattern of a denticle and a tooth; scapes twelve-segmented, antennal club three-segmented, club 1/5 longer than the other segments of funiculus together (Figures 1B, 2C, 3D).

**Mesosoma.** In oblique-dorsal view pronotum with a well-marked humerus that connects the posterior edge of pronotum forming a slight concavity, pronotum with two pairs of long, fine erect hairs, one humeral and one at the posterior end of pronotum; mesonotum composed of anterior and posterior faces joining at a 45 degrees angle, mesonotal groove deep, forming a U-shape concavity

(Figure 1B); mesopleuron completely punctured; in lateral view, dorsal face of propodeum more or less flattened with a well-marked angle at the junction with the mesonotal groove; propodeal spines relatively long and slender, thin and curving posterodorsally; petiole with a well-developed node, in lateral view, anterior and posterior faces forming a thin triangular-shaped node, tip of node acute, posterior face flat and vertical, in oblique view, node bifurcated; postpetiole very poorly developed with one anterior and two posterior erect hairs on its dorsum. **Legs.** Dorsal margin of middle and hind femora with scattered suberect pilosity, dorsal margin of fore, middle and hind tibiae with suberect pilosity, longer hairs as long as maximum width of tibiae, basitarsus longer than the other tarsus together, second, third and fifth tarsus equal in length, fourth a little bit shorter. **Gaster.** Smooth and shining with long erect hairs ventrally in the last two sternites.

### Remarks

*Pheidole chaan* sp. nov. differs notably from the other fossil *Pheidole* species as follows: it can easily be separated from both *Pheidole tethepa* Wilson 1985a and *Pheidole primigenia* Baroni Urbani, 1995 because these last species are spiny ants, that is, they have pronotal spines, while *P. chaan* sp. nov. has not pronotal spines. *Pheidole tertiaria* Carpenter 1930 is a female 7.0 mm long, with head coarsely and reticulately rugose, in contrast, *P. chaan* sp.

nov. has a maximum body length 1.3 mm long, almost entire head with thick longitudinal striae. *Pheidole chaan* sp. nov. differs from *Pheidole anticua* in that *P. anticua* has pronotum, in lateral view, flat, katapisternum areolate, node of petiole smoothie rounded, while *P. chaan* sp. nov. has pronotum, in lateral view convex, katapisternum with bottom half longitudinally striated, top half smooth and node of petiole angled posteriorly. *Pheidole chaan* sp. nov. also differs from *P. pauchil* because *P. pauchil* has a pronotum with a well-developed neck, anterior and posterior margins of node of petiole meeting apically forming a more or less triangle, extensor surface of hind femur flattened forming an acute angle while *P. chaan* sp. nov. does not form any pronotal neck, the node of petiole is angled posteriorly and hind femur is cylindrical, not forming any angle.

*Pheidole chaan* sp. nov. has some affinities with the *punctatissima* group (sensu Wilson 2003) because it shares the following combination of characters. Small species, head width of major 0.7–1.0 mm; major with medium to long antennal scapes, such that when the tip of the scape is touched to the lateral border of the head in full-face view, it reaches halfway between the eye and occipital border, or farther; antennal scape of the minor moderately long, so that when laid across the occipital corner the scape in full face view exceeds the corner by at least 4X the maximum scape width; its posterior dorsal half completely foveolate with no other sculpturing except, at most short carinulate on the antennal fossa.

However, *Pheidole chaan* sp. nov. can be separated from all species of the *punctatissima* group because of the presence of a deep median impression on head of the soldier in *Pheidole chaan* sp. nov. and absent in all species of the *punctatissima* group. The species of the *punctatissima* group have propodeal spines short and relatively slender in comparison to *P. chaan* sp. nov. which has well developed and thick propodeal spines. Most species of the *punctatissima* group have a promesonotal concavity well-defined, instead *P. chaan* sp. nov. has no promesonotal concavity. The exception to this character in the *punctatissima* group are *Pheidole onyx* Wilson 2003 and *P. citrina* Wilson 2003. In both species, major's bottom half of head is devoid of any sculpturing, in short, this area is smooth and shiny, in contrast this area is densely striated in *P. chaan* sp. nov.

When using Lucid software v.3.3 for the New World *Pheidole* data, from the 726 species recorded, the number of species are reduced dramatically to three when submitting the HW (Head width), HL (Head Length) and SL (Scape Length): *Pheidole janzeni* Longino 2009; *P. protensa* (Wilson 2003), *Pheidole* JTL264, but when CI (Cephalic Index) and SI (Scape index) are submitted the key leads to *Pheidole* JTL264. All these three species are tiny ants whose morphometric profiles are similar, but *P. chaan* sp. nov. is still smaller. The soldier of *Pheidole janzeni* has a median impression on head but differs from the soldier of *P. chaan* sp. nov. in head and body sculpturing, *P. janzeni* has face smooth and shining, katapisternum with medial shiny area surrounded by foveolae, and has propodeal spines barely developed, whereas *P. chaan* sp. nov. has head striated and body foveolate, bottom half of katapisternum striated and top half smooth and has well-developed propodeal spines. *Pheidole protensa* can be separated from *P. chaan* sp. nov. by the following traits: 'Soldier has a small but distinct mesonotal convexity; propodeal spines reduced to denticles' (Wilson 2003), while *P. chaan* sp. nov. has no distinct mesonotal convexity and has well-developed propodeal spines. *Pheidole* JTL264 is known only by apparent ergatoid queens which differ notoriously by having smooth head and propodeal spines not developed, while the worker of *P. chaan* sp. nov. has coarse punctures in all head and well-developed propodeal spines.

## Discussion

In this work, we report a Miocene amber fossil which contains the first syninclusion composed of two *Pheidole* ant individuals of different castes, one soldier and one worker (Carpenter 1930; Wilson 1985a; Baroni-Urbani 1995; Casadei-Ferreira et al. 2020; Varela-Hernández and Riquelme 2021). Castes are morphologically discrete entities within ants, where soldiers are defined as 'wingless sterile individuals with body size intermediate between ordinary workers and queens, and having traits that are absent in workers' (Peeters 2019).

The rarity of finding species of *Pheidole* in amber could be the fact that although *Pheidole* is the extant most species rich ant genus, there is evidence that they are more adapted to nest in soils than on trees or arboreal canopies (Serna et al. 2019). For example, in a fogging experiment to determine the number of genera and species of ants nesting and living on trees of primary and disturbed forests, only two out of 143 and zero out of 21 species belonged to *Pheidole*, respectively (Floren et al. 2002). Wilson (1985b) also mentions that there are arboreal genera other than *Pheidole* that are dominant in canopies of the Peruvian Amazon forests in terms of frequency and number of species.

The rarity of founding both castes in the same piece of amber might be explained because of different tasks of castes. For example, it is assumed that the soldiers of *Pheidole* are more related to food processing, food transportation and defending ant colony. In contrast, workers are more related to foraging and doing most of the tasks in a colony (Serna et al. 2019), so that it would be more likely to find workers than soldiers.

Another explanation is related to the investment of species to soldier production. McGlynn et al. (2012) showed that the proportion of soldiers was significantly related to variation in body size, that is, greater investment in soldiers was associated to smaller size of both workers and soldiers of different species of *Pheidole*. Thus, reducing the threshold of body size could increase the possibility to produce more soldiers in a colony.

Global molecular phylogenetic analyses have proved to be consistent in recovering broad relationship patterns for *Pheidole*, for example, the Old World clade nests within the New World clade (Economo et al. 2015). Wilson (2003) initially suggested that *Pheidole* originated in the New World and subsequent phylogenies support this hypothesis (Moreau 2008; Economo et al. 2015). Ward et al. (2015) mention that *Pheidole* is one of the most successful genera that diversified recently in a short period of time (compressed diversification) since Eocene, about 35.2 Ma (24.9–46.5 Ma). Considering that Dominican and Mexican fossils are about the same age (20.5 and 19.5 Ma, respectively; Barden 2017), and that *Pheidole* originated in the New World (Moreau 2008), it follows that, according to the fossil record, the genus, including *P. chaan* sp. nov. was well-diversified by Miocene.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

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