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Pheidole praehistorica sp. nov., a new addition to spiny ants of the genus *Pheidole* Westwood, 1839 (Formicidae, Myrmicinae) from Oligo–Miocene Mexican amber

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Abstract. A fossil species of ant, *Pheidole praehistorica* sp. nov. (Hymenoptera, Formicidae, Myrmicinae), is described and illustrated from the late Oligocene and early Miocene amber-bearing beds of Mexico. The type material comprises five amber inclusions from the Simojovel site in Chiapas. *Pheidole praehistorica* is recognized by having compound eyes positioned mesad on the head and protruded laterally from the head's margins; pronotum long, forming a neck, with a pair of spines directed dorsolaterally; mesonotal groove deep forming a more or less U-shape concavity in lateral view; dorsal and declivitous faces of the propodeum well differentiated, comprising an approximately 90 degrees angle; propodeum with a pair of long spines; peduncle of the petiole long, as long as the spines of the propodeum. A phylogenetic analysis was also performed using *Formica integroides*, *Camponotus chartifex*, *Dolichoderus spurius*, *Cephalotes minutus* and *Atta mexicana* to assess the relationships of *P. praehistorica* with its fossil spiny congeners from Dominican amber and closely related extant species. The results show close morphological and phylogenetic affinities between the fossil ant *P. praehistorica* with *P. primigenia* and *P. tethepa* from Dominican amber, which may suggest that the shared spinescence character in *Pheidole* has a probable New World ancestry. The new record of *P. praehistorica* in the Oligo–Miocene strata of southernmost North America provides further evidence for the ancient distribution of spiny ants of the genus *Pheidole* in the New World.

Keywords. Formicidae, Myrmicinae, *Pheidole*, new species, phylogeny.

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Introduction

The genus *Pheidole* Westwood, 1839 (Hymenoptera, Formicidae, Myrmicinae) comprises 1160 extant species, 124 subspecies, and eight valid fossil species worldwide (Bolton 2023). There are 126 extant

species and two fossils on Mexican territory (Dáttilo *et al.* 2019; Varela-Hernández & Riquelme 2021). *Pheidole* representatives live in almost any terrestrial ecosystem, mainly soils, although they are also arboreal (Zara & Fowler 2005). They play significant ecological roles (Whitford *et al.* 1981) and exhibit a complex morphology at the species level (Camargo-Vanegas & Guerrero 2020). *Pheidole* is known to have the highest number of species among ants (Longino 2009). However, its fossil record is scarce (Varela-Hernández & Riquelme 2021). The oldest fossil species is *Pheidole tertiaria* Carpenter, 1930, from the uppermost Eocene Florissant Formation in Colorado, USA (Carpenter 1930). The Miocene fossil record includes three amber species from the Dominican Republic: *Pheidole tethepa* Wilson, 1985, *Pheidole primigenia* Baroni Urbani, 1995 and *Pheidole anticua* Casadei-Ferreira, Chaul & Feitosa, 2019, and two from Oligo–Miocene Mexican amber: *Pheidole pauchil* Varela-Hernández & Riquelme, 2021 and *Pheidole chaan* Varela-Hernández & Flores-Zapoteco, 2024.

The amber-bearing beds of Simojovel are located in the state of Chiapas, south Mexico, in the upper portion of the Simojovel Formation (Riquelme *et al*. 2024). According to Allison (1967) and Frost & Langenheim (1974), this formation is also known as the La Quinta Formation. Other authors assigned it to the Early Miocene Mazantic Shale, as stated by Perrilliat *et al.* (2010). The sedimentary environment matches a lowland fluvial environment close to a coastal plain (Frost & Langenheim 1974; Graham 1999; Langenheim 2003; Riquelme *et al.* 2024), most likely a tropical mangrove forest (Graham 1999; Langenheim 2003; Riquelme *et al.* 2024). The botanical source of amber is attributed to an extinct legume of the genus *Hymenaea* L. (sensu Langenheim 1966). Simojovel amber shares chemical signatures with extant plant resins of *Hymenaea courbaril* L. and *Hymenaea verrucosa* Gaertn., which are currently distributed in the tropics of Mexico, Central America, Antilles, and South America (Langenheim 2003; Riquelme *et al.* 2014b).

In this paper, we describe and illustrate a new species of spiny ant of the genus *Pheidole* from the Oligo-Miocene amber bearing beds at Simojovel. We also performed a phylogenetic analysis to address the phylogenetic position of the new species among the close fossil relatives of Dominican amber: *P. tethepa* and *P. primigenia.*

Material and methods

Fossil material

Five fossil specimens found embedded in a single piece of amber from the Montecristo mine near Simojovel, Chiapas, Mexico, were studied. The holotype and paratypes are currently deposited in the Colección de Paleontología maintained at the Laboratorio de Sistemática Molecular, Universidad Autónoma del Estado de Morelos, Mexico (Varela-Hernández & Riquelme 2021). The piece of amber that encompasses the holotype underwent cutting and polishing using various abrasive materials to produce a smooth and level surface that was as close to the inclusion as possible. This was done to minimize the distortions that the amber surface may cause.

Morphological analysis

Data and measurements were collected using an Olympus AZ binocular dissecting microscope and a U-OCM10/100 1 mm micrometer with 0.1 mm intervals. Photomicrographs were obtained using a Carl Zeiss Axio Zoom V16 microscope coupled to an Axio Cam MRC5 camera. Photomicrographs were acquired by applying multiple image stacking for three-dimensional focus expansion, as seen in Riquelme *et al.* (2014a, 2015). Identification on genus level followed MacKay & MacKay (1989) and Baccaro *et al.* (2015). For species-level identification, we used the free version of Lucid software ver. 3.3 for the New World *Pheidole* data. Abbreviations and indices follow Longino (2019).

Measurements

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 perpendicular 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 antennal bulb 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

Indices

CI = Cephalic index: HW/HL × 100
SI = Scape index: SL/HL × 100

Measurements are expressed in millimeters.

Phylogenetic analysis

The NONA ver. 2.0 program (Goloboff 1997) and the WinClada ver. 1.00.08 interface (Nixon 2002) were used. A heuristic search method for searching trees was implemented, and the options were set to contain 1000 trees, 100 replicates, ten initial tree replicates, and a TBR+TBR multiple search strategy. All characters were treated as unordered and weighted equally. A bootstrap analysis was also used to determine the support of the branches. Morphological data from the original descriptions and illustrations were used to construct the data matrix that includes *P. tethepa* and *P. primigenia* as described respectively in Wilson (1985) and Baroni-Urbani (1995).

For the phylogenetic analysis, the morphological data of extant specimens were obtained from the material deposited at the Colección Paleontológica maintained at the Laboratorio de Sistemática Molecular, Universidad Autónoma del Estado de Morelos, Mexico (CPAL-UAEM). The ingroup included the following extant species *Pheidole dwyeri* Gregg, 1969, *P. granulata* Pergande, 1896, *P. obtusospinosa* Pergande, 1896, *P. morelosana* Wilson, 2003, *P. tepicana* Pergande, 1896, *P. coracina* Wilson, 2003, *P. gouldi* Forel, 1886, *P. yucatana* Wilson, 2003, *P. optiva* Forel, 1901. The ingroup also included the fossil species *P. primigenia* Baroni-Urbani, 1995 and *P. tethepa* Wilson, 1985. To root the tree two formicine species, *Formica integroides* Wheeler, 1913 and *Camponotus chartifex* (Smith, 1860), one dolichoderine species, *Dolichoderus spurius* Forel, 1903 and two myrmicine ants *Cephalotes minutus* (Fabricius, 1804) and *Atta mexicana* (Smith, 1858) were included.

Results

Systematic palaeontology

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

Genus ***Pheidole*** Westwood, 1839

Type species

Pheidole providens (Sykes, 1835).

Pheidole praehistorica sp. nov.
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Figs 1–3

Diagnosis

Pheidole praehistorica sp. nov. differs significantly from the other two Dominican fossil spiny species as follows: *P. primigenia* has an average size of 2.88–3.56 mm, while *P. praehistorica* is smaller, with an average total length of 2.3 mm. It also differs by longer pronotal spines in *P. primigenia* and smaller ones in *P. praehistorica*. *Pheidole praehistorica* has a deeper mesonotal groove than *P. primigenia*; propodeal spines are curved downwards in *P. primigenia* but straight in *P. praehistorica*; *P. primigenia* differs markedly by the shape of the anterior edge of the clypeus, which is "slightly prominent in the middle and straight" (Baroni-Urbani 1995), while it is formed by a median projection with a minute denticle in the middle and a lateral denticle on each side of the median projection in *P. praehistorica* (Fig. 1A–E).

Pheidole tethepa is another fossil species from Dominican amber with pronotal spines similar to those of *P. primigenia* and *P. praehistorica* sp. nov. However, *P. tethepa* has a pair of gular spines not found in *P. primigenia* or *P. praehistorica*. In contrast, *P. primigenia* and *P. praehistorica* have a well-formed head collar not found in *P. tethepa.* In addition, *P. tethepa* differs markedly from *P. praehistorica* in the shape of the middle of the anterior edge of the clypeus which is convex in *P. tethepa*, but in *P. praehistorica* it is formed by a median projection with a tiny denticle at its middle.

Etymology

The specific Latin epithet refers to the fossil (prehistoric) condition of the new species.

Type material

Holotype

MEXICO • Chiapas, Simojovel, Montrecristo mine; 17°09′11″ N, 92°46′08″ W; CPAL-UAEM, CPAL.464 (Fig. 1A–C).

Paratypes

MEXICO • 4 specs; same data as for holotype; CPAL-UAEM, CPAL.465 to CPAL.468 (Fig. 1D–E).

Remarks

The paratypes are fossil inclusions, complete articulated specimens except CPAL.468, which is disarticulated medially (Fig. 1E). All specimens are embedded in a single piece of amber, surrounded by plant remains and soil. They are housed in the Colección de Paleontología (CPAL-UAEM), Morelos, Mexico.

Locality and horizon

Mexico, Chiapas, Simojovel, Montrecristo mine: 17°09′11″ N, 92°46′08″ W. Upper strata of the Simojovel Formation at the late Oligocene and early Miocene boundary (Riquelme *et al.* 2024).

Worker description

Measurements (n = 1). HL 0.65, HW 0.50, SL 0.85, WL 0.9, CI 76.92, SI 130, PNS 0.15, PPS 0.35 (Figs 1A, 2A).

Head. Slightly longer than wide; sides subparallel, occipital border straight, post occipital border forming a 'collar' (Fig. 1A–D). Gena reticule-striated, the occipital border with scattered small bulges, frontal carenas parallel, the area between frontal carenas smooth, posterior margin of clypeus convex, anterior

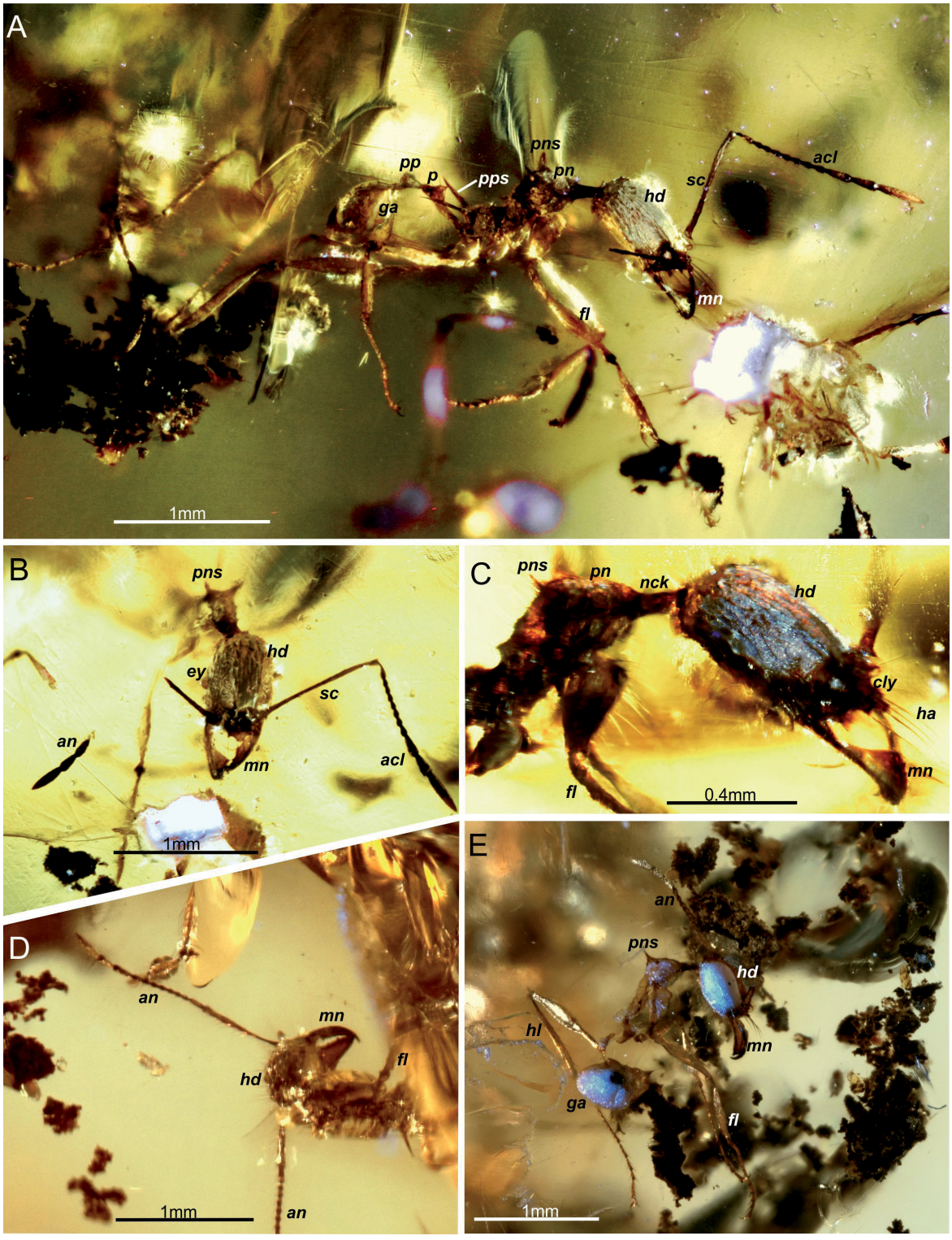

Fig. 1. *Pheidole praehistorica* sp. nov. **A–C**. Holotype (CPAL.464). **A**. Profile view. **B**. Frontal view. **C**. Closer lateral view of the head and mesosoma. **D**. Paratype (CPAL.465), latero-frontal view of the head. **E**. Paratype (CPAL.468), profile view. Abbreviations: acl = antennal club; an = antenna; cly = clypeus; ey = eyes; fl = foreleg; ga = gaster; ha = hairs on clypeus; hd = head; hl = hind leg; mn = mandible; nck = neck; p = petiole; pn = pronotum; pns = pronotal spine; pp = postpetiole; pps = propodeal spine; sc = scape.

margin discontinuous, formed by a median projection with a tiny denticle at the middle of it, then the margin of clypeus creating a curve to the lateral sides before projecting again as a denticle on each side (Figs 1A–E, 2B). Clypeus with four long hairs, two on each side of the median denticle and one on each of the lateral ones (Figs 1A–C, 2B). The antenna scape long, surpassing the occipital border of the head by about twice the length of the scape, scape with 12 segments, three-clubbed, club as long as the rest of the funicle (Figs 1A–B, 2A–B); antenna covered with long fine erect setae. Mandibles triangular, masticatory and inner border angled, straight, and smooth. Pattern dentition from apical to basal teeth

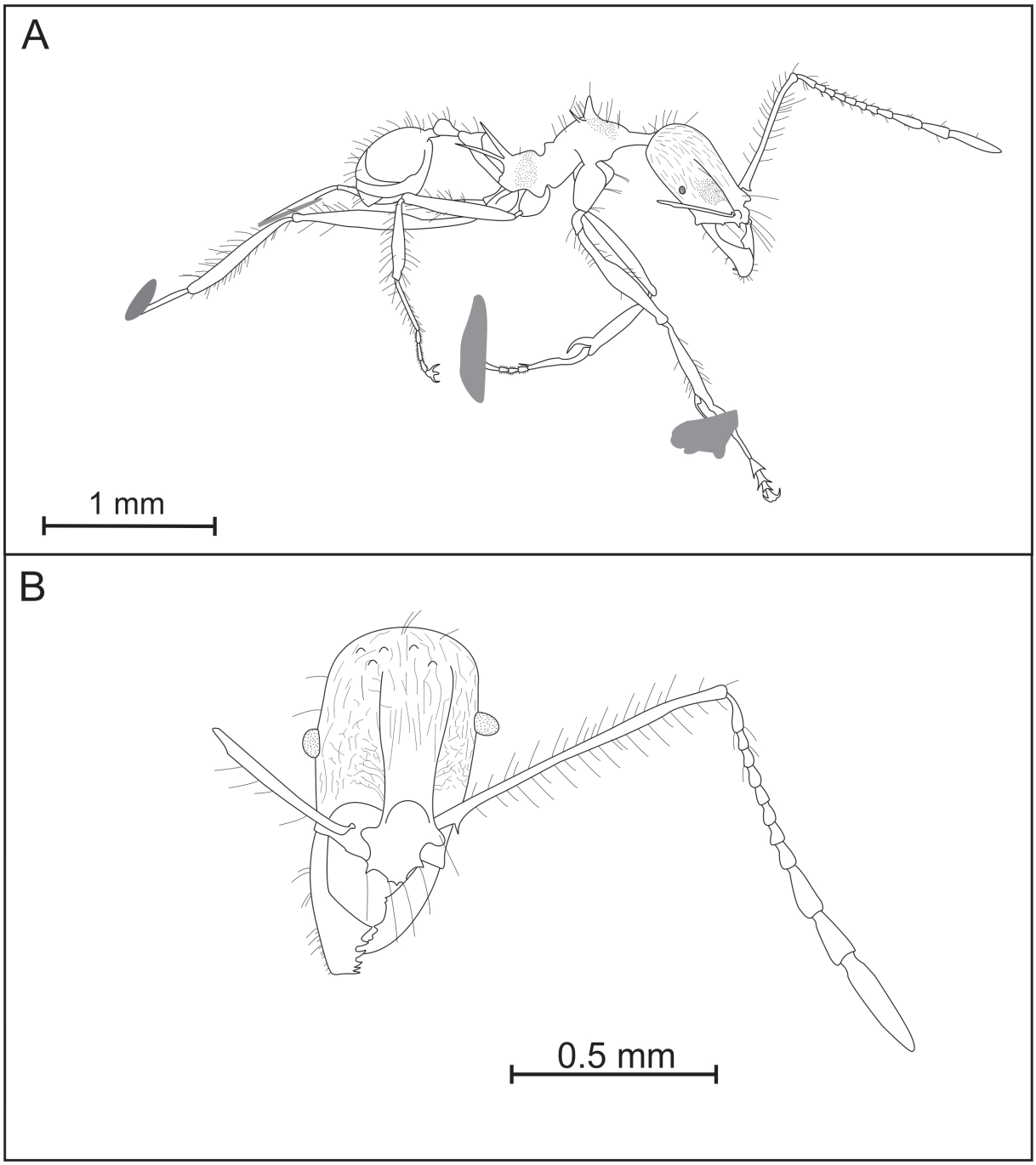

Fig. 2. *Pheidole praehistorica* sp. nov., holotype (CPAL.464), schematic drawing. **A**. Profile view. **B**. Frontal view.

as follows: apical and preapical teeth longer than all other teeth, apical tooth longer than preapical, one tiny denticle, one tooth, three denticles, and a tooth located at the junction of the masticatory and the inner border.

Mesosoma. Apparently hard, with intricate sculpture, striated and punctured. Pronotum long, forming a long neck in profile view, convex, with a pair of spines that project dorsolaterally. Promesonotal suture slightly marked (Fig. 1A, C, E). Mesonotum curved, U-shape margin in profile view so that the posterior extreme of the U connects with the promesonotal suture. The mesonotal groove deep and U-shaped. Propodeum with a pair of long straight spines projecting posteriorly (Figs 1A, C, E, 2A), dorsal and declivitous margins well differentiated, forming a 90 degrees angle. The petiole with a long slender stalk, the petiole node relatively short, anterior and posterior faces of the petiolar node form a triangle in lateral view (Figs 1A, C, E, 2A).

Legs. Mid and hind tibiae devoided of spurs, hind femur with minute decumbent hairs.

Gaster. With long, slender, erect setae, setae scattered, dorsum of first gastral tergite finely aciculate.

Color. Body with solid cuticle, covered with long erect setae, concolorous light yellow in amber preservation (Fig. 1A–D).

Phylogenetic analysis

Results show three most parsimonious cladograms. Here, we present the strict consensus one (Fig. 3). In the cladogram, *C. chartifex* and *F. integroides* and *D. spurius* form independent clades out of the Myrmicinae clade. The Myrmicinae clade is well supported by synapomorphies 8, 22, 23, 24 and 26. There is a polytomy formed by *A. mexicana*, *C. minutus*, ((*P. primigenia* + *P. praehistorica*) + *Pheidole tethepa*) and all the species of *Pheidole* (Fig. 3). However, two internal clades are recognized, one of them consists of all species of *Pheidole* included in this analysis and the other consisting of *Pheidole* fossil ants, which is well supported by synapomorphies 1, 5, 7, 10, and 21 (Fig. 3). Accordingly, *P. praehistorica* sp. nov. provides new insights into a spinescence character found in New World species from the late Oligocene and early Miocene boundary.

Discussion

Close morphological and phylogenetical affinities between *P. praehistorica* sp. nov. with *P. primigenia* and *P. tethepa* from Dominican amber may suggest a shared New World ancestry of the spinescence character in *Pheidole*. *Pheidole primigenia* and *P. tethepa* from Dominican amber belong more likely to spiny ants with different ancestry to *Pheidole* spiny ants that are currently restricted to Indomalaya, Australasia, and Oceania (Baroni-Urbani 1995). Wilson (2003) suggested a broader biogeographical interpretation of the *Pheidole* spiny ants that may be obtained when new records and species are found. Molecular phylogenetic analysis at the global level is consistent with a broad relationship pattern for *Pheidole*. Accordingly, the Old World clade is nested within the New World clade (Economo *et al.* 2015). Wilson (2003) initially suggested that *Pheidole* originated in the New World, and subsequent phylogenetic analyses support this hypothesis (Moreau 2008; Economo *et al.* 2015). Ward *et al.* (2015) also noted that *Pheidole* is one of the most successful groups that diversified in a narrow time window (compressed diversification) since the Eocene. So, if *Pheidole* has a New World origin, the spinescence character found in *Pheidole* fossils from Oligo-Miocene Mexican amber and Miocene Dominican amber may also have radiated from an ancestral New World form.

According to Sarnat & Moreau (2011) and Sarnat *et al.* (2017), spinescence evolved de novo in Hymenoptera as a defensive mechanism to compensate for the loss of wing escape. These same authors conclude that spinescence evolved at least seven times in the genus *Pheidole*; however, it is still unclear

whether spinescence evolved because of new genetic traits or as a latent developmental potential retained from a New World ancestor. Although the fossil record is incomplete, with no fossils found in the Indomalaya Australasia-Oceania region, the new fossil species *P. praehistorica* sp. nov. found in the Oligo-Miocene strata of southernmost North America provides further evidence for an ancient distribution of spiny *Pheidole* ants in the New World.

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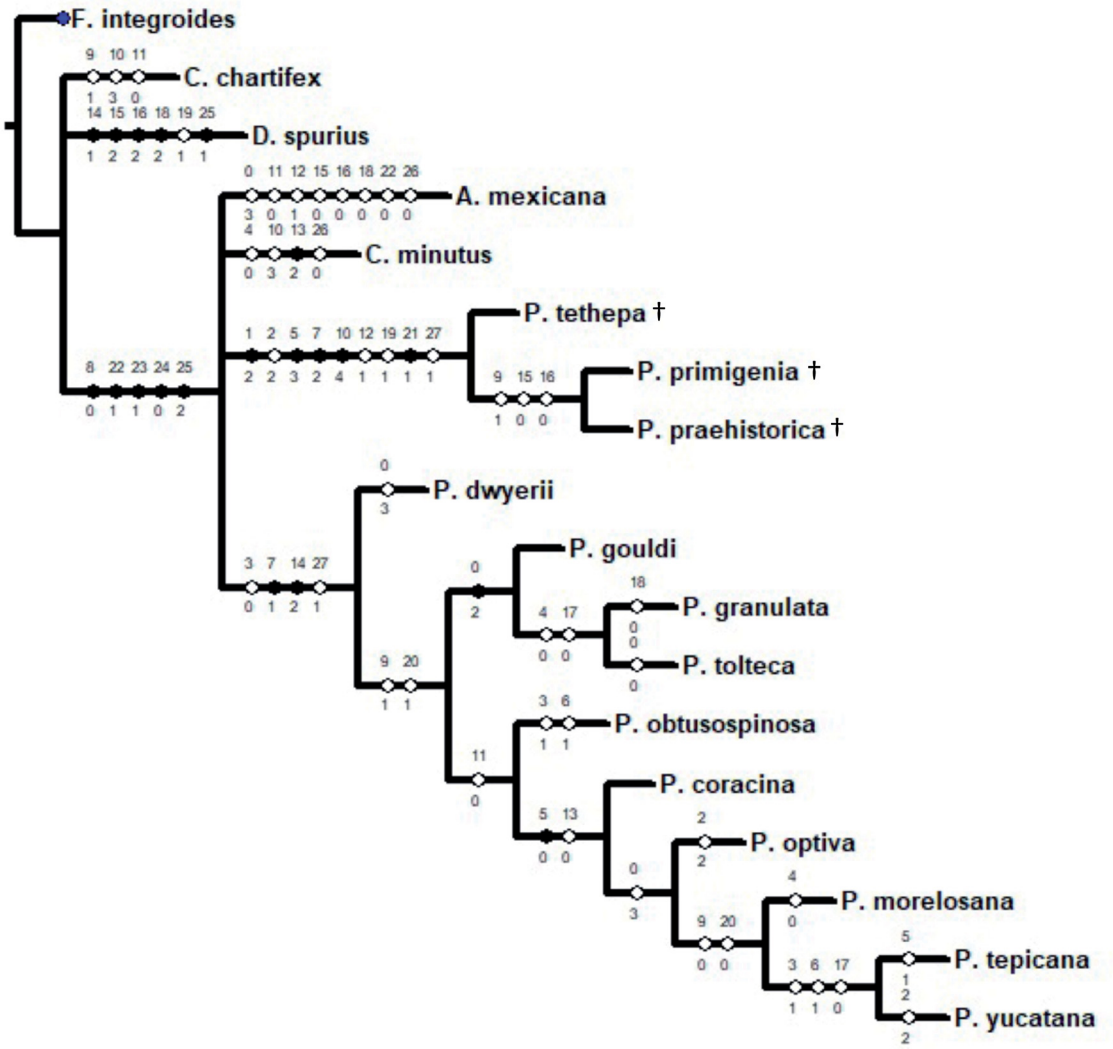

Fig. 3. The phylogenetic status of *Pheidole praehistorica* sp. nov. among fossil and extant congeners inferred from the list of characters (Supp. file 1: Table S1) and the data matrix (Supp. file 1: Table S2), shows the twenty-eight morphological characters to construct the most parsimonious tree. The numbers above the white and black dots represent morphological characters, and the numbers below represent the character encoding. Black dots represent synapomorphies, and white dots represent homoplasies. † represents fossil species from Dominican and Mexican amber. Consistency index = 0.52; retention index = 0.65.

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Table S1. List of characters.

Table S2. Data matrix