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A Miocene ant species of the genus *Forelius* Emery, 1888 (Hymenoptera: Formicidae: Dolichoderinae) from Mexico

Fernando Varela-Hernández, Francisco Riquelme, and Roberto J. Guerrero

ABSTRACT

The first fossil ant species of the New World genus *Forelius* (Formicidae: Dolichoderinae) is described. The type material is a Miocene amber inclusion from the Montecristo mine near Simojovel, Chiapas, southwestern Mexico. The new species is named *Forelius chenpauch* sp. nov. It differs from its congeners by having a unique combination of characters: antennal scapes reaching the posterior margin of the head; pronotum with six erect hairs; mesonotum with four erect hairs; propodeum with four erect hairs; front and dorsum of head, dorsum of pronotum, dorsum of mesonotum and propodeum covered with a fine striation. *Forelius chenpauch* sp. nov. has a rounded spiracle, which could be considered a plesiomorphic character closely related to the *Forelius* group from the north of the Amazon basin. Accordingly, the current divergence estimates of *Forelius* as a single genus from the *Leptomyrmex* + *Forelius* + *Dorymyrmex* clade (ca. 27 Ma) and the occurrence of *Forelius chenpauch* sp. nov. in the fossil record (ca. 23 Ma), may suggest that the rounded spiracle is a plesiomorphic state probably widespread since the Miocene from southern Mexico to northern South America.

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INTRODUCTION

The ant genus *Forelius* Emery, 1888 (Leptomyrmecini, Dolichoderinae) is endemic to the New World. It is distributed in arid and semi-arid ecosystems from the USA to Argentina (Guerrero, 2019). At the beginning of the twentieth century, the genus was considered monotypic, with *Forelius mccooki* (McCook, 1880) being the only recognizable species. Since then, new species were subsequently described or recently transferred to the genus (Emery, 1905; Cuezzo, 2000; Guerrero and Fernández, 2008; Guerrero, 2021). Cuezzo (2000) has extensively reviewed the nomenclature and taxonomy of the genus *Forelius*, describing new species and expanding their distribution range, particularly those in the southern hemisphere. *Forelius* comprises 19 extant species (Bolton, 2023) with no fossil species described to date. Ten years ago, a fossil ant specimen assigned to *Forelius* was recorded for the first time in Miocene Mexican amber, but no formally described species (Durán-Díaz et al., 2013).

In the present paper, we describe the first species that match the genus *Forelius* (sensu Shattuck, 1992 and Cuezzo, 2000), based on a Miocene amber inclusion recently recovered from the Montecristo mine in Simojovel, Chiapas, Mexico. Due to the preservation quality of its fossil inclusions, the Simojovel amber mines are part of a fossil preservation site known as Amber-Lagerstätte (Riquelme et al., 2014a, b); which also includes the mines and pits from Totolapa and Estrella de Belén near Palenque in the Chiapas Highlands (Riquelme et al., 2015). The Simojovel amber deposits belong to the Miocene-assigned Balumtum and Mazantic strata (Perrilliat et al., 2010; Durán-Díaz et al., 2013; Riquelme et al., 2014a, b). Another amber outcrop near Simojovel assigned to the La Quinta strata, predominantly marine and of Late Oligocene age has also been reported (Allison, 1967; Frost and Langenheim, 1974). The sedimentary environment of the amber deposits suggests a lowland fluvial environment close to the coastal plain (Allison, 1967; Frost and Langenheim, 1974; Graham, 1999; Langenheim, 2003). An extinct leguminous tree of the genus *Hymenaea* Linné is the botanical source of Chiapas amber from Miocene (Langenheim, 2003; Riquelme et al., 2014a)

MATERIALS AND METHODS

The fossil specimen studied here is an amber inclusion from the Montecristo mine near Simojovel, Chiapas, Southwestern Mexico. The fossil is embedded in a piece of translucent golden amber that has been cut and polished to obtain a flat surface, which allows observation by attenuating the optical distortions caused by the amber. Morphological data were collected using an Olympus® AZ binocular dissecting microscope (Laboratorio de Sistemática Molecular, Universidad Autónoma del Estado de Morelos), a Carl Zeiss® AXIO ZOOM.V16 microscope coupled to an Axiocam MRc5 camera, and the ZEN 2012 (Blue edition) program to stack the photomicrographs (Laboratorio de Microscopía y Fotografía de la Biodiversidad II, Instituto de Biología, Universidad Nacional Autónoma de México). Schematic drawings were hand traced using a stereomicroscope and photomicrographs in an electronic tablet. The Corel Draw X7® program was used for graphic editing. Taxonomy and terminology follow Shattuck (1992) for the genus and for the species Cuezzo (2000). Measurements and indices follow Cuezzo (2000) using an ocular micrometer at 80x. All the following measurements are expressed in millimeters:

TL = Total length. In lateral view, taken from anterior clypeal margin (excluding mandibles) to apex of last segment of metasoma.

HL = Head length. Maximum length, in full face view, from apex of clypeal plate to middle of posterior vertex margin.

HW = Head width. Maximum width in full face view excluding eyes.

EL = Eye length. Maximum length of eye in full face view

EW = Eye width. Width of eye perpendicular to maximum length.

IOD = Distance between inner-most edges of eyes. Measured in full face view, distance between edges of eyes.

COD = Clypeus-ocular distance. Shortest distance between posterior margin of clypeus and anterior margin of eye.

SL = Scape length. Maximum length of first antennal segment, excluding neck and basal condyle.

PSL = Propodeal spiracle length. Maximum length of propodeal spiracle.

PSW = Maximum width of propodeal spiracle. Measured perpendicularly to maximum length.

MsL = Mesosoma length. Straight-line distance measured in lateral view from anterior margin of pronotum (excluding collar) to posterior extremity of metapleural lobe.

CI = Cephalic index: (HW/HL)*100.

OI = Ocular index: (EL/EW)*100.

SI = Scape index: (SL/HW)*100.

The fossil inclusion was assigned as a holotype CPAL.464, which belongs to the Colección de Paleontología maintained at the Universidad Autonoma del Estado de Morelos, Mexico.

SYSTEMATIC PALEONTOLOGY

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Formicidae Latreille, 1809
Subfamily Dolichoderinae Forel, 1878
Tribe Leptomyrmecini Emery, 1913
Genus *Forelius* Emery, 1888

Type species. *Iridomyrmex mccooki* McCook, 1880

Forelius chenpauch sp. nov. Varela-Hernández, Guerrero and Riquelme
(Figures 1-2)

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Etymology. The specific epithet *chenpauch* means “from the amber cave” in the Tzotzil language, a name given by the local people of the Simojovel to the amber mines or pits.

Type material. Holotype CPAL.464 Worker, amber inclusion, complete specimen. It is deposited in the Colección de Paleontología, UAEM, Morelos, Mexico (Figure 1A)

Locality. Mexico, Chiapas, Simojovel, Montecristo mine: 17° 7' 45.99" N, 92°41'43" W.

Distribution. It is only known from the Miocene strata of Simojovel, Chiapas, southern Mexico.

Horizon. The Mazantic and Balumtum strata, Early Miocene (ca. 23 Ma).

Diagnosis. Antennal scape reaching the posterior margin of the head; pronotum with six erect hairs; mesonotum with four erect hairs; propodeum with four erect thin hairs; front and dorsum of head, dorsum of pronotum, dorsum of mesonotum, and propodeum covered with fine longitudinal striae.

Worker description

Measurements (mm). TL: 2.0; HL: 0.6; HW: 0.6; EL: 0.1; EW: 0.1; IOD: 0.4; SL: 0.5; PSL: 0.05; PSW: 0.05; MsL: 0.8; CI: 100; OI: 100; SI: 83.33.

Head. As long as broad; vertex of head weakly concave; antennal scapes reaching the posterior margin of the head; mandible with a basal and masticator margin differentiated, with six observable teeth in the latter (Figure 2B); clypeus with two slender, erect setae projecting onto the mandibles at the middle part, about the level of the antennal insertions; two other shorter setae on each side of the erect setae described previously: one at the lateral edge of the mandible and another between the latter and the one at the middle of the mandible; the dorsal face of mandibles covered with decumbent pilosity; dorsum of head finely striated (Figures 1B, 2A, 2B).

Mesosoma. Dorsal profile discontinuous. In dorsal view, well-impressed promesonotal suture; weak mesonotal groove in lateral view; pronotum with six thin, erect hairs, four located anteriorly, longer than the other two located posteriorly, two at the anteriormost humeral and the other two at the middle; dorsal surface of pronotum and mesonotum with weak transversal striae; dorsal and posterior face of propodeum rounded, with no apparent angle that differentiates the two faces; one pair of thin, erect hairs located dorsolaterally on the propodeum dorsal face and another pair posterolaterally on the propodeum posterior face; propodeal spiracle small and rounded (Figure 2A, 2B). Legs without pilosity.

Petiole. Scale present, inclined anteriorly, with a pair of erect setae, barely visible.

Gaster. First and second tergite with a row of short, thin, erect setae running along the apical fringe of tergites, sternites lost; gaster concolorous yellow with mesosoma.

Remarks. The worker (Holotype CPAL.464) studied here is classified in the genus *Forelius* since it presents the diagnostic characters of the genus, that is, the anterior clypeal margin with two long curved setae is observed in the specimen, which, although in the specimen the mandible is open, these clypeal hairs project reaching the external margin of the mandible. The configuration of the mandible and the dentition pattern on the masticatory margin agree with that of *Forelius* according to Shattuck (1992), that is, mandible with a smooth basal and masticatory margin differentiated, the latter armed with 6-7 teeth. The petiolar scale is reduced and strongly inclined anteriorly as well, however, in the specimen it appears relatively straight (Figures 1-2), but it is due to the position within the amber piece. The latter also makes it difficult to observe the first gastral segment projecting anteriorly and concealing petiole in dorsal view; however, an inclined view of the piece allowed us to observe a shallow depression on the anterior face of the first gastral tergite. *Forelius chenpauch* sp. nov. is a species with a rounded spiracle but differs from other *Forelius* species with this same condition by the characters listed below (Table 1).

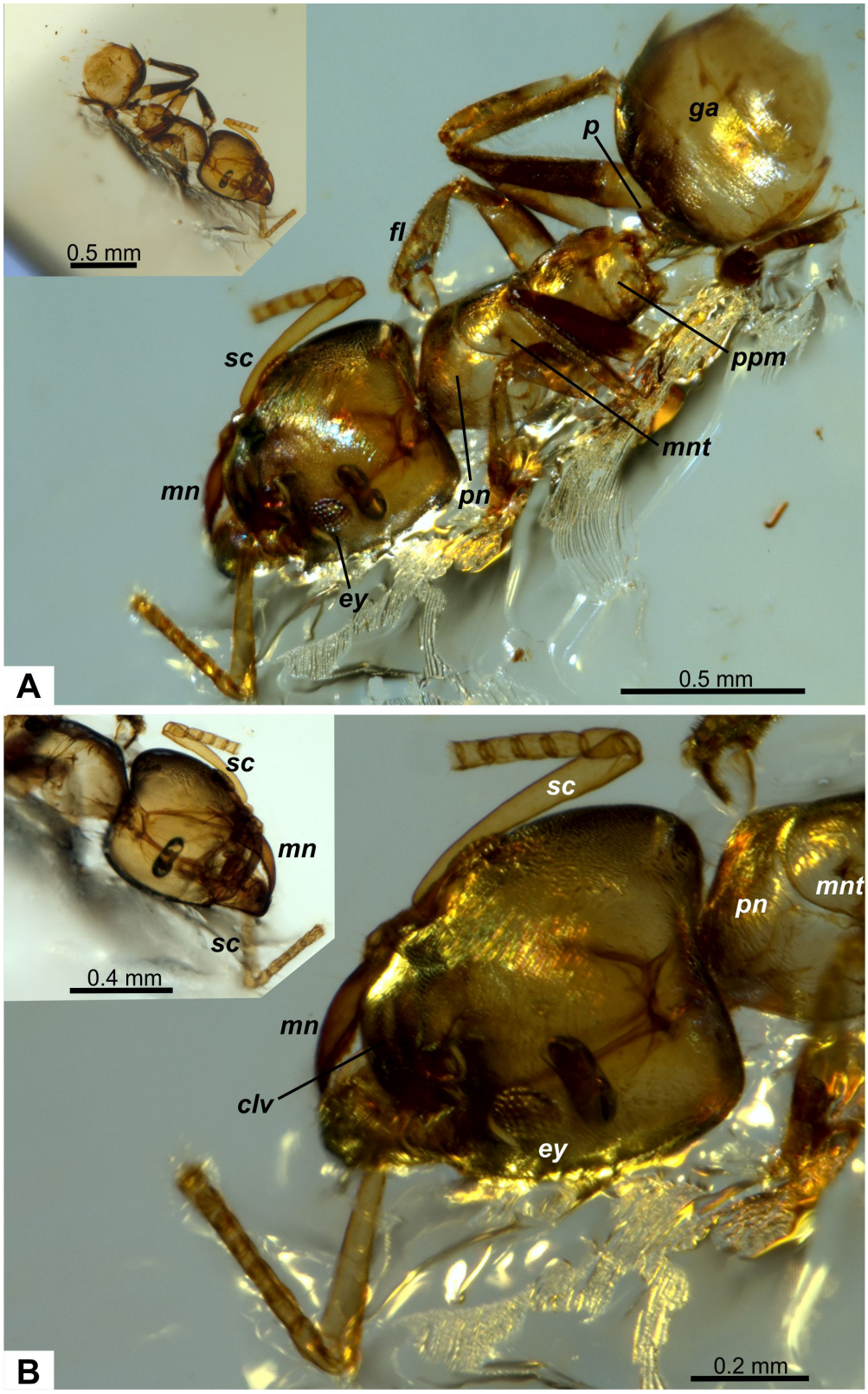

FIGURE 1. A *Forelius chenpauch* sp. nov. Holotype CPAL.464. Dorsolateral view of complete specimen showing: compound eye (ey); foreleg (fl); gaster (ga); mandible (mn), mesonotum (mnt); petiole (p); pronotum (pn); propodeum (ppm); scape (sc). **B** *Forelius chenpauch* sp. nov. Holotype CPAL.464. Microphotograph augmentation showing: clypeus (clv); compound eye (ey); mandible (mn); mesonotum (mnt); pronotum (pn); scape (sc).

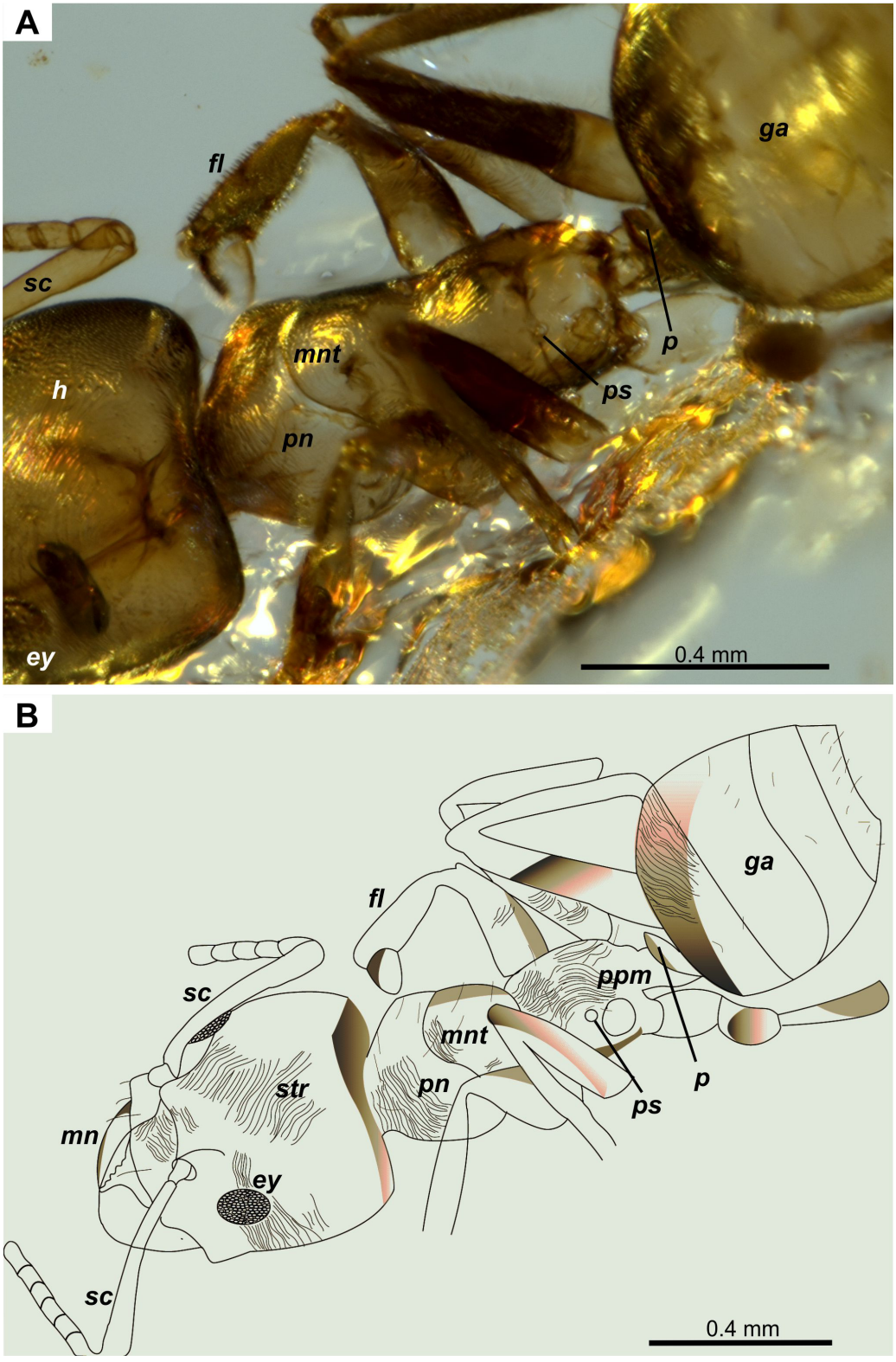

FIGURE 2. A *Forelius chenpauch* sp. nov. Holotype CPAL.464. Microphotograph augmentation of dorsolateral showing: head (h); foreleg (fl); gaster (ga); mesonotum (mnt); petiole (p); pronotum (pn); propodeal spiracle (ps); scape (sc). **B** *Forelius chenpauch* sp. nov. Drawing of Holotype CPAL.464 showing: clypeus (clv); compound eye (ey); foreleg (fl); gaster (ga); mandible (mn); mesonotum (mnt); petiole (p); pronotum (pn); propodeum (ppm); propodeal spiracle (ps); scape (sc); striae (str).

TABLE 1. Morphological comparison between *Forelius chenpauch* sp. nov. and the other *Forelius* species with a rounded spiracle present in the New World.

Taxon/Character	Scape length	Mandibular dentition	Hairs on the mesosoma	Mesosoma profile
Forelius chenpauch sp. nov.	Reaching the posterior margin of the head (SI= 0.83)	Six teeth and no denticles	Six on the pronotum, mesonotum with four erect hairs, and propodeum with four erect ones.	Discontinuous, promesonotum convex, differentiated from the anterior face of the propodeum
Forelius antarcticus (Forel, 1904)	Exceeding the posterior margin of the head capsule (SI = 0.98-1.04)	Five teeth and no denticles	Two on the pronotum, no erect hairs elsewhere on mesosoma	Discontinuous, promesonotum almost continuous, slightly differentiated from the anterior face of the propodeum
Forelius damiani Guerrero and Fernández, 2008	Short, reaching posterior margin of head (SI= 0.95 – 1.32)	Four teeth and two denticles	Two on the pronotum, no erect hairs elsewhere on mesosoma	Straight, pronotum in profile relatively low and flat
Forelius heyeri (Forel, 1902)	Short, well below or barely reaching the posterior cephalic margin by a length less than the width of the pedicel (SI= 0.8 – 0.91).	Five teeth and no denticles	Two on the pronotum, no erect hairs elsewhere on mesosoma	Continuous, slightly flat; promesonotum continuous and slightly differentiated from the propodeum
Forelius keiferi Wheeler, 1934	Exceeding the posterior cephalic margin by 1/5 of its length (SI= 0.98 – 1.05)	Five teeth and one denticle	Two to three on the pronotum	Discontinuous, strongly convex promesonotum differentiated from anterior face of propodeum
Forelius mccooki (McCook, 1880)	Exceeding the posterior cephalic margin by 1/5 of its length (SI= 0.98 – 1.05)	Four teeth and three to four denticles	Pronotum usually with six erect setae, rest of mesosomal dorsum with bearing more than 10 erect setae	Continuous, promesonotum continuous and slightly differentiated from anterior face of propodeum
Forelius pruinosus (Roger, 1863)	Exceeding the posterior cephalic margin by 1/5 of its length (SI= 1.07 – 1.14)	Five teeth and one or two denticles	Pronotum usually with four erect setae, rest of mesosomal dorsum with bearing 2 to 6 erect setae	Discontinuous, strongly convex promesonotum differentiated from strongly convex propodeum

Forelius chenpauch sp. nov. could be confused with extant dolichoderine ants of the genus *Liometopum* Mayr, 1861 and the genus *Tapinoma* Foerster, 1850, which can currently be found in Mexico. However, *Forelius chenpauch* sp. nov. is distinguished by having a mandible with a basal margin distinct from the masticatory margin (Figures 1A, 1B, 2B), whereas *Liometopum* and *Tapinoma* have an undifferentiated basal margin. In addition, *Forelius chenpauch* sp. nov. has a petiole scale anteriorly inclined (Figures 1A, 2A, 2B). In contrast, *Liometopum* has a vertical petiolar scale, that is, never anteriorly inclined; and in the currently known Neotropical species of *Tapinoma* the petiolar scale is strongly reduced, in most hidden by the first gastral segment (Guerrero unpublished data).

On the other hand, the genus *Forelius* and the genus *Azteca* Forel, 1878 have been recorded in Mexican and Dominican amber (Duran-Ruiz et al., 2013; Barden, 2017). However, the fossil record of *Forelius* is uncommon in both deposits, whereas *Azteca* is more frequent. *Forelius* is composed of hyperactive thermophilic ground-nesting ants (Ward, 2005) that are adapted to living in arid to semi-arid areas (Shattuck, 1992; Cuezzo, 2000) whilst *Azteca* encompasses ants that nest mainly in trees (Longino, 2007). Notably, the species *Azteca alpha* Wilson, 1985 constitutes 30 to 50% of the total number of ants found in Dominican amber (Barden, 2017). The highest frequency of *Azteca* records is consistent with an arboreal environment. The sedimentary data in Mexican amber deposits suggests a lowland fluvial environment close to the coastal plain (Allison, 1967; Frost and Langenheim, 1974; Graham, 1999; Langenheim, 2003; Riquelme et al., 2014a, 2015). Accordingly, the leguminous trees of *Hymenaea* (the botanical source of Mexican amber) were part of a tropical forest resembling modern mangroves (Langenheim, 2003) where a warmer (+1.99 °C) and drier (−337.7 mm) tropical climate have been estimated than the current average records (Hernández-Hernández et al., 2020). Although forested areas may have predominated, the Miocene tropical forest in southern Mexico possibly presented minor

arid to semi-arid zones that the *Forelius* could exploit to locate the colonies.

DISCUSSION

Taxonomy in the genus *Forelius* has received attention in the last decades. Initially, Shattuck (1992) offered clear morphological boundaries for the genus, allowing it to be differentiated from other relatively similar dolichoderine ants (e.g., *Dorymyrmex* Mayr, 1866; *Linepithema* Mayr, 1866 or *Tapinoma*). Cuezzo (2000) reviewed the *Forelius* species in the New World recognizing 18 species, some of which present uncertainties in their taxonomic limits and need to be revised—i.e., evidence of intergradation between *F. pruinosus* (Roger, 1863) and *F. mccooki* (McCook, 1860) (Ward 2005). Later works have increased the number of species within the genus (Guerrero and Fernandez 2008) and resolved some nomenclatural problems (Guerrero 2021) within the genus. In this work, we describe the first fossil *Forelius* species preserved in amber; a species with possible evolutionary affinity with those of northern South America and Central America due to the presence of the rounded spiracle.

The shape of the spiracle in *Forelius* was used as a taxonomic argument by Kusnezov (1963) to propose different genus names. This author proposed that the species with an elongated propodeal spiracle (slit-shaped), exclusive to South America, should be named *Neoforelius* Kusnezov, 1953 (a junior synonym of *Forelius* Shattuck, 1992) while those with a rounded propodeal spiracle should be classified as *Forelius.* Recent studies suggest that species with rounded propodeal spiracle occur north of the Amazon basin (Guerrero and Fernández, 2008), except for *F. antarticus* and *F. heyerii* (Guerrero, 2021). The other species with slit-shaped propodeal spiracles occur south of the Amazon basin. This distributional pattern separates two groups with a polymorphism associated to that trait (Guerrero and Fernández, 2008).

The occurrence of rounded spiracles on the new species *Forelius chenpauch* sp. nov. reinforces a biogepographic pattern previously described by Guerrero and Fernández (2008), in which the few species found north of the Amazon basin all have round spiracles, while south of the Amazon many species have elongate, slit-like spiracles, and only two species have round spiracles. Based on the distribution pattern, round spiracles could be plesiomorphic, apomorphic, or homoplasious in the genus *Forelius*. The fossil species *Forelius chenpauch* sp. nov. has a rounded propodeal spiracle, which could be considered a closely related plesiomorphic trait to those species distributed north of the Amazon basin (e.g., *Forelius pruinosus*). Thus, *Forelius chenpauch* sp. nov. is an essential clue to understanding the evolution of the *Forelius* genus. Whitin Leptomyrmecini, *Forelius* and *Dorymyrmex* probably diverged more than 35 Ma ago (Ward et al., 2010). If we consider the estimated upper limit for the occurrence of *Forelius* crown group (ca. 27 Ma), then *Forelius chenpauch* sp. nov., which lived in the Miocene (ca. 23 Ma) of southern Mexico, may be closely related to extant species distributed in northern of South America and Central America (i.e., north of the Amazon basin).

If the *Forelius* divergence times are true (Ward et al., 2010) and *Forelius chenpauch* sp. nov. shares common ancestry with the rest of the species distributed north of the Amazon basin, then it could be suggested that the rounded spiracle is a plesiomorphic state probably widespread since the Miocene from Southern Mexico to northern South America. Although the previously exposed hypothesis could receive support from the fossil record and estimation of divergence times, the presence of this morphological trait in *F. antarcticus* and *F. heyeri* is not supported; a possible explanation would be the independent evolution north and south of the Amazon (Guerrero and Fernández, 2008). Another subsequent diversification of species with slit-shaped spiracle should occur south of the Amazon basin (Guerrero and Fernández, 2008). Further phylogenetic work on the genus is needed to differentiate among these hypotheses. Phylogenetic information integrating a broad taxon sampling within *Forelius*, genomic data and detailed morphological analysis of fossil species such as *Forelius chenpauch* sp. nov. can provide more robust hypotheses about the evolution of the genus *Forelius* and fill in the gaps regarding the evolution of propodeal spiracle shape.

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