

Ants from the Miocene Totolapa amber (Chiapas, Mexico), with the first record of the genus *Forelius* (Hymenoptera, Formicidae)

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Abstract: Totolapa is one of the amber Lagerstätten from Chiapas, southwestern Mexico, which include the Simojovel and Huitiupán deposits. Despite the remarkable paleobiological heritage of Chiapas amber biota, the fossil record of ants from Totolapa has so far not been well studied. Based on exceptionally preserved specimens, four ant genera from the Totolapa amber deposits are reported in this paper, including *Forelius*, *Azteca*, *Tapinoma*, and *Camponotus* (Hymenoptera, Formicidae). Whereas the genera *Azteca*, *Tapinoma*, and *Camponotus* are previously known from amber quarries of Simojovel, this paper represents the first record of the presence of *Forelius* in Chiapas amber.

Résumé : Totolapa constitue un des Lagerstätten de l'ambre du Chiapas, au sud-ouest du Mexique, où se trouvent aussi les dépôts de Simojovel et Huitiupán. En dépit de l'étonnant patrimoine paléobiologique des biotes contenus dans l'ambre chiapanèque, les fossiles de fourmis de Totolapa ont été peu étudiés jusqu'à présent. A partir de l'étude de spécimens exceptionnellement préservés des dépôts d'ambre du Totolapa, cet article présente quatre genres de fourmis: *Forelius*, *Azteca*, *Tapinoma*, et *Camponotus* (Hymenoptera, Formicidae). Alors que les genres *Azteca*, *Tapinoma* et *Camponotus* ont déjà été inventoriés dans les carrières d'ambre de Simojovel, la présence de *Forelius* est inédite concernant l'ambre du Chiapas.

Introduction

Totolapa is an outstanding Chiapas amber deposit that may be considered a Konservat-Lagerstätte on the basis of its exceptional fossil preservation. Plants and animals trapped within fossil resin show an almost intact morphology preserved. The Totolapa amber outcrops are strongly associated with the Simojovel and Huitiupán amber-bearing beds, which have been assigned to a section of the Mazantic Shale and Balumtum Sandstone strata, dated as Early to Middle Miocene in age (Langenheim 1966; Poinar 1992; Graham 1999; Langenheim 2003). The authors of these earlier studies also mention an amber record from the La Quinta unit, which is thought to be late Oligocene in age. Other recently published studies suggest that Chiapas amber from Simojovel has been deposited within the boundaries of the Early Miocene period (Vega et al. 2009; Perrilliat et al. 2010), and Solórzano-Kraemer (2007, 2010) proposes a Lower Middle Miocene age associated with Dominican and Puerto Rican ambers, based on their coeval insect faunas.

Chiapas amber is closely related to the resinous exudates of the extant tree *Hymenaea courbaril*, as indicated by its similar chemotaxonomic characters (*sensu* Langenheim 1966). The paleobotanical affinities of Chiapas amber have been published elsewhere (Poinar 1992; Graham 1999; Poinar and Brown 2002; Langenheim 2003; Castañeda-Posadas and Cevallos-Ferriz 2007; Calvillo-Canadell et al. 2010; Solórzano-Kraemer 2010). It seems that both Totolapa and Simojovel amber come from an ancient *Hymenaea* tree. This suggestion is based primarily on their chemical similarities (Lambert et al. 1989; Langenheim 1995, 2003).

The previously published fossil record of Formicidae in Chiapas amber has been geographically assigned to outcrops from the Simojovel area; thus, the ant genera include *Camponotus*,

Tapinoma, *Azteca*, *Pheidole*, *Cephalotes*, *Solenopsis*, *Crematogaster*, *Pachycondyla*, *Dorymyrmex*, *Lasius*?, *Mycetosoritis*, *Stenamma*, and *Proceratium*, as well as species *Cyphomyrmex maya* and *Aphaenogaster praerelicta* (De Andrade 1995; Poinar 1992; De Andrade 2003; Baroni-Urbani and De Andrade 2003; Solórzano-Kraemer 2007). The aim of the present paper is to report the first record of fossil ants found in Totolapa amber outcrops.

Geological setting

The amber inclusions are from the quarries at the Río Salado locality, located at the west end of the town of Totolapa, Chiapas, Mexico, at 16°32'28.86"N, 92°41'4.74"W and at an altitude of 532 m above mean sea level (Fig. 1).

The amber-bearing beds are exposed in unconnected sections, separate for fault zones, from the Río Salado and Río Yalbantuc. Both rivers are located in the vicinity of the town of Totolapa, approximately 20 km south of the town of San Cristobal de Las Casas and 66 km south of the town of Simojovel (Fig. 1).

The section of Totolapa amber consists of sandstones, lignite interbeds, friable coal, non-consolidate conglomerates, and displaced clay lenses (Fig. 2). This sequence may be primarily related to the Balumtum and Mazantic Shale strata (Miocene), as mentioned in Frost and Langenheim (1974), Poinar (1992), Graham (1999), and Perrilliat et al. (2010). The section overlies a limestone succession with interbedded sandstones from the uppermost part of the Eocene Lomut Formation, as described by Meneses-Rocha (2001). Such limestones change upsection into carbonates with coral, ichnofossil galleries, and bivalve packstones and grainstones probably linked to sea-rimmed margins. The section is also top-constrained by a terrigenous rock bed of fine mudstones, with

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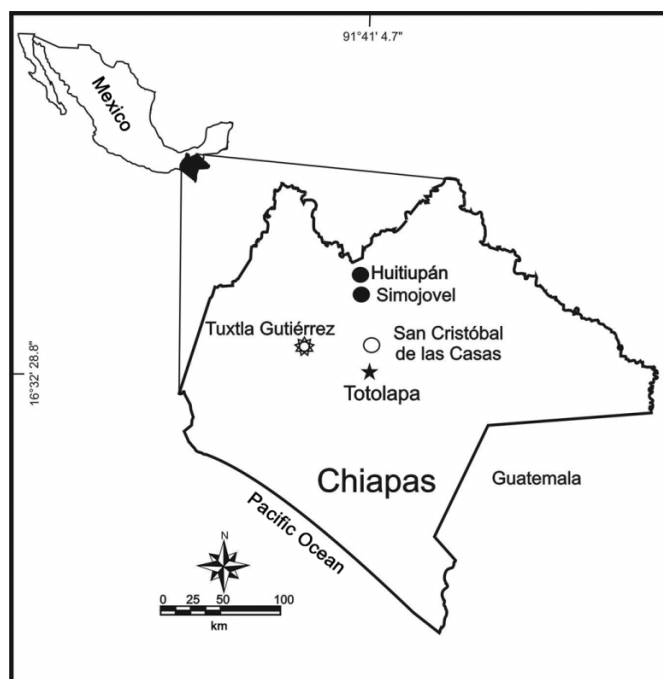
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Fig. 1. Location of Totolapa amber-bearing beds, Chiapas, southwestern Mexico.



volcanic–volcaniclastic deposits assigned to the upper Paleogene (see Meneses-Rocha 1985).

The sedimentary rock source of this sandstone–lignite sequence is predominantly interpreted as being part of the Cenozoic terrigenous clastic rocks from the geologic province referred to as the Chiapas thrust-fold belt in the context of the Maya block (Sedlock et al. 1993) (Fig. 2).

Materials and methods

The specimens are housed in the Museo de Paleontología Eliseo Palacios Aguilera in Tuxtla Gutiérrez, Chiapas, Mexico. Institutional abbreviation: IHNFG, Instituto de Historia Natural Fósiles Geográficos.

A relatively simple technique for sample preparation was used for microscopic analysis: the amber was cut and polished to get closer to the specimens. Photomicrographs were acquired with a Leica DFC90 stereomicroscope and a digital charge-coupled device (CCD) camera, and Leica Application Suite software was used for image processing.

Measurements are expressed in millimetres. In accordance with Cuzzo (2000) and Wild and Cuzzo (2006), the abbreviations are as follows: RL, relative length; HW, head width; HL, head length; CI, cephalic index; EL, eye length; EW, eye width; OI, ocular index; SL, antennal scape length; SI, scape index; MML, maximum mesosomal length.

Systematic paleontology

Family	Formicidae Latreille, 1809
Subfamily	Dolichoderinae Forel, 1878
Tribe	Dolichoderini Forel, 1878
Genus	<i>Forelius</i> Emery, 1888

TYPE SPECIES: *Iridomyrmex mccooki* Emery, 1888

DIAGNOSIS: Anterior clypeal margin with long and curved setae in the ventral region that extend to or beyond the anterior margin of closed mandibles. Mandible with 4–6 teeth and 0–4 denticles. Pronotum with two long, erect setae and 0–4 short setae. Petiolar

scale strongly projected to the mesosoma. In dorsal view, the first gastral tergite is interiorly projected over the petiole. Propodeal spiracle long or rounded with a long and erect seta in dorsal and ventrally located respect to the spiracle (Cuzzo 2000).

MATERIAL: IHNFG-4646. Worker ant. Complete fossil specimen.

LOCALITY: Totolapa amber, State of Chiapas, southwestern Mexico.

AGE: Miocene.

MEASUREMENTS: (mm) RL: 2.1; HW: 0.75; HL: 0.5; CI: 150; EL: 0.11; EW: 0.1; OI: 110; SL: 0.55; SI: 73.33; MML: 0.35.

DESCRIPTION:

Head: Concave posterior cephalic margin. Surface with three oval clefts. Ocelli absent. Antenna with 12 segments.

Mouthparts: Anterior clypeal margin with long and curved setae to ventral region that extend towards the mandibles (Figs. 3a, 3b).

Mesosoma: Profile discontinuous, interrupted by metatotal and promesonotal suture. Pronotum with erects and shorts setae (Figs. 3c, 3d). Propodeal spiracle rounded (Figs. 3b, 3d).

Petiole: Projected to the mesosoma (Fig. 3b).

Gaster: Five segments.

REMARKS: Based on the combination of diagnostic characters mentioned in the preceding text, this fossil ant can be assigned to the genus *Forelius*. Differs from *Linepithema* in the mesosomal dorsum and the anterior clypeal margin, mostly because the erect hairs are absent in *Linepithema* and the anterior clypeal margin show short and erect setae as well (Mackay and Mackay 1989; Creighton 1950; Wild 2007). Also differs from *Liometopum* in the mesosomal profile with its continuous shape, because the metatotal suture is reduced in *Liometopum*. Finally, differs from *Tapinoma* in the mesosoma, petiolar scale, and gastric tergites. Basically, *Tapinoma* lacks hairs in the mesosoma, the petiolar scale is absent, and only four gastric tergites are present (Fisher and Cover 2007). This fossil represents the first record of *Forelius* in the Neotropical Chiapas amber. Fossil specimens of the genus *Forelius* have also been reported from the mid-Eocene Green River deposits in western North America (Dlussky and Rasnitsyn 2002).

Genus *Azteca* Forel, 1878

TYPE SPECIES: *Liometopum xanthochroum* Forel, 1878

DIAGNOSIS: Head with concave margin of vertex, mandible with 5–10 teeth and 0–4 denticles, mandibular apical tooth at least slightly longer than preapical (Bolton 1994).

MATERIAL: IHNFG-4647 (a–i). Nine worker ants. Complete fossil specimens.

LOCALITY: Totolapa amber, State of Chiapas, southwestern Mexico.

AGE: Miocene.

MEASUREMENTS: (mm) RL: 7.12; HW: 1.12; HL: 1.37; CI: 81.75; EL: 0.15; EI: 77.67; EW: 0.12; OI: 125; SL: 0.87; MML: 1.37.

DESCRIPTION:

Head: Cordate head shape, cephalic margin concave and longer than wide (Figs. 4c, 4d). Antenna with 12 segments. Ocelli absent.

Mouthparts: Anterior clypeal margin straight. Mandible with nine teeth, with apical tooth slightly longer than preapical (Figs. 3c, 3d).

Mesosoma: Mesonotum higher than pronotum in lateral view (Fig. 4f).

Petiole: Projected to the mesosoma.

REMARKS: On the basis of combined diagnostic characters as described in the preceding text, this fossil specimen can be affiliated to the genus *Azteca*. According to Cuzzo (2003), similarities between *Azteca* and *Bothriomyrmex* can be ambiguous; however, *Azteca* has a longer propodeum dorsum than *Bothriomyrmex*, as seen in this fossil. Also differs from *Iridomyrmex* in the propodeum dorsum and cephalic margin. *Iridomyrmex* has a thoracic spiracle with protuberance and a medium anterior clypeus margin with a

Fig. 2. Stratigraphic column chart of the Totolapa amber-bearing beds, showing the geological section at the Río Salado locality. (a) Synthesis of correlative stratigraphy for central and eastern Chiapas from the Cretaceous to Quaternary. (b) Partial column of Totolapa amber showing the sedimentary input from transitional to continental. Cenoman., Cenomanian; CSD, conglomerate sandstone; Fm, Formation; LS, limestone; S, sand; SD, sandstone; SH, shale.

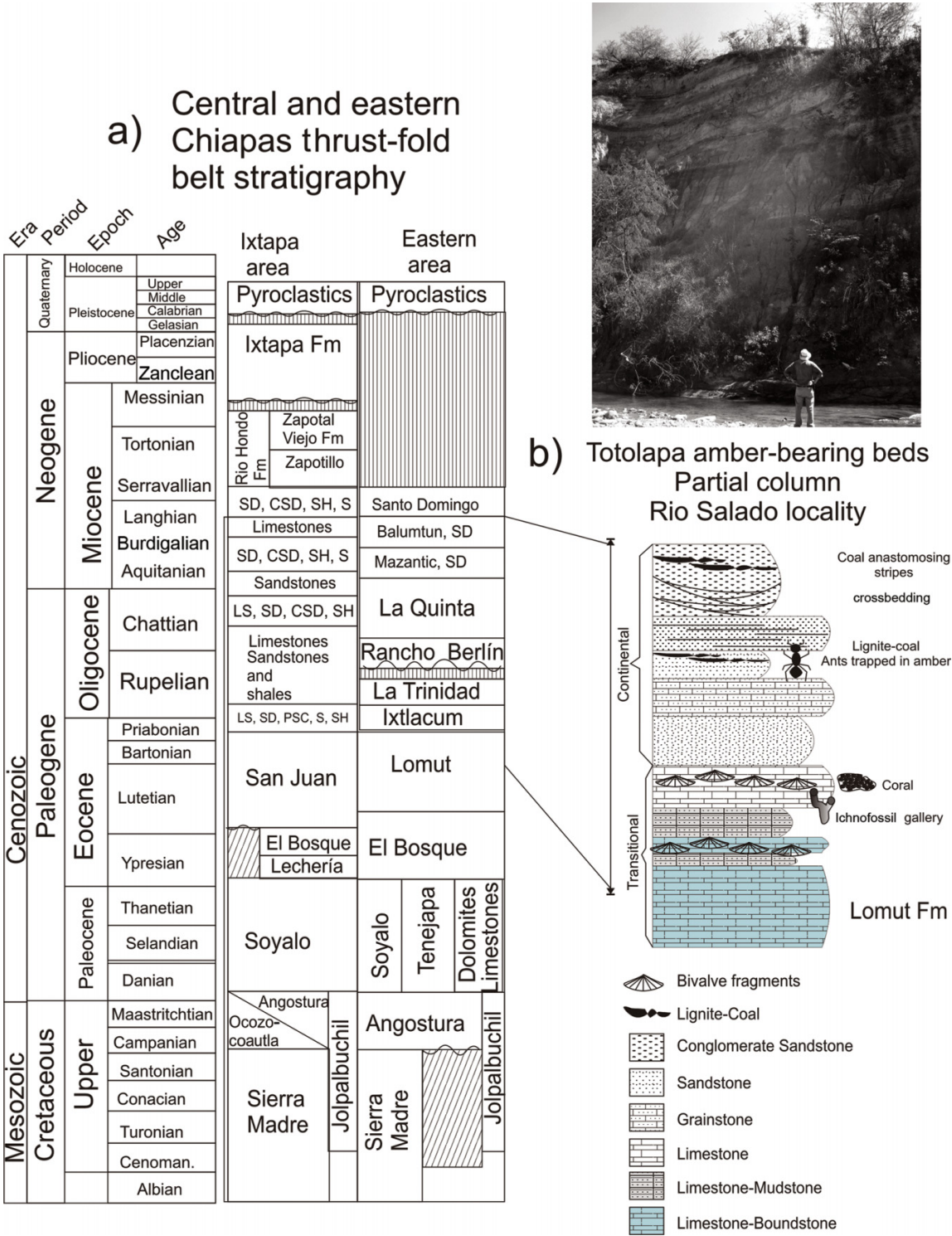
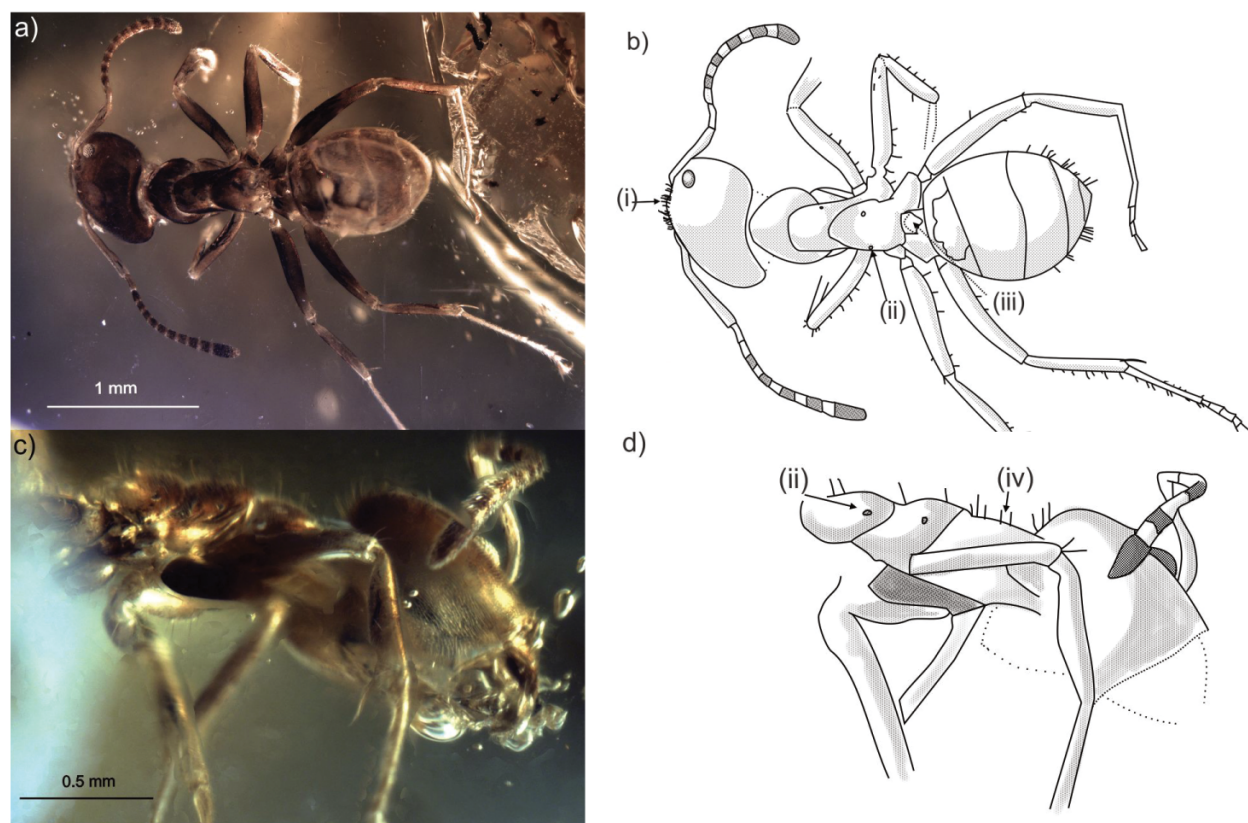


Fig. 3. *Forelius* Emery, 1888, specimen IHNFG-4646 in (a, b) dorsal view and (c, d) antero-lateral view. (a) and (c) are photomicrographs and (b) and (d) are corresponding illustrations, respectively. In (b), the dorsal imprint shows the anterior clypeal margin with long and curved setae (i), the propodeal spiracles (ii), and petiole (iii). In (d), the antero-lateral imprint shows the mesosoma with setae (iv).



protuberance; both protuberances are absent in the present specimen, which is more clearly in accordance with *Azteca* (Heterick and Shattuck 2011). This genus *Azteca* has previously been found in Simojovel amber (Chiapas) (Brown 1973; Solórzano-Kraemer 2007), as well as in Dominican amber (Wilson 1985a, 1985c; Johnson et al. 2001).

Genus *Tapinoma* Foerster, 1850

TYPE SPECIES: *Tapinoma collina* Foerster, 1850 (junior synonym of *Formica erratica* Latreille, 1798)

DIAGNOSIS: Absence of the petiolar scale; there are only four gastric tergites (Fisher and Cover 2007).

MATERIAL: IHNFG-4648. Worker ant. Fossil specimen partially preserved.

LOCALITY: Totolapa amber, State of Chiapas, southwestern Mexico.

AGE: Miocene.

MEASUREMENTS: (mm) RL: 1.7; HW: 0.62; HL: 0.4; CI: 155; EL: 0.1; EW: 0.05; OI: 2; SL: 0.45; SI: 72.58.

DESCRIPTION:

Head: Cordate head shape. Eyes present. Ocelli absent. Antenna with 12 segments.

Mouthparts: Small closed mandibles.

Mesosoma: Discontinuous; pilosity absent (Fig. 5b).

Gaster: Four tergites (Fig. 5d); sternites unknown.

REMARKS: This specimen is similar to the genus *Tapinoma*; however, it is not possible to observe the gastric sternites, which is a meaningful character for genus description, because the body position of the specimen trapped in amber obscures the details. Accordingly, the placement of this fossil in the genus *Tapinoma* should be considered preliminary. Despite the partial preserva-

tion of the body, it differs from extant specimens of *Bothriomyrmex*, *Doleromyrma*, and *Plagiolepis* in its well-developed petiolar scale (Shattuck 1999; Cuzzo 2000). Also differs from *Bothriomyrmex* in the size of the eyes. Differs from *Plagiolepis* (Formicinae) in the acidopore and the antenna with 11 segments. Differs from *Liometopum* and *Forelius* in the mesosoma, with erect hairs and developed petiole scale (Fisher and Cover 2007). Finally, also differs from *Technomyrmex* in the five gaster tergites (dorsal view), whereas this fossil has only four, which more readily agrees with *Tapinoma*. The genus *Tapinoma* has previously been found in Simojovel (Chiapas) (Solórzano-Kraemer 2007) and Dominican amber (Late Oligocene) (Wilson 1985a, 1985c), as well as in Baltic amber (Late Eocene) (Dlussky and Rasnitsyn 2009) and Ukrainian amber (Rovno, Late Eocene) (Perkovsky et al. 2003; Dlussky and Rasnitsyn 2009).

Subfamily Formicinae Latreille, 1809

Tribe Camponotini Forel, 1878

Genus *Camponotus* Mayr, 1861

TYPE SPECIES: *Formica ligniperda*, Mayr, 1861; by the subsequent designation of Bingham, 1903: 347.

DIAGNOSIS: Anterior clypeal margin are separated from the antennal sockets by a distance equal to or greater than the socket diameter. Metapleural gland absent (Fernández 2003).

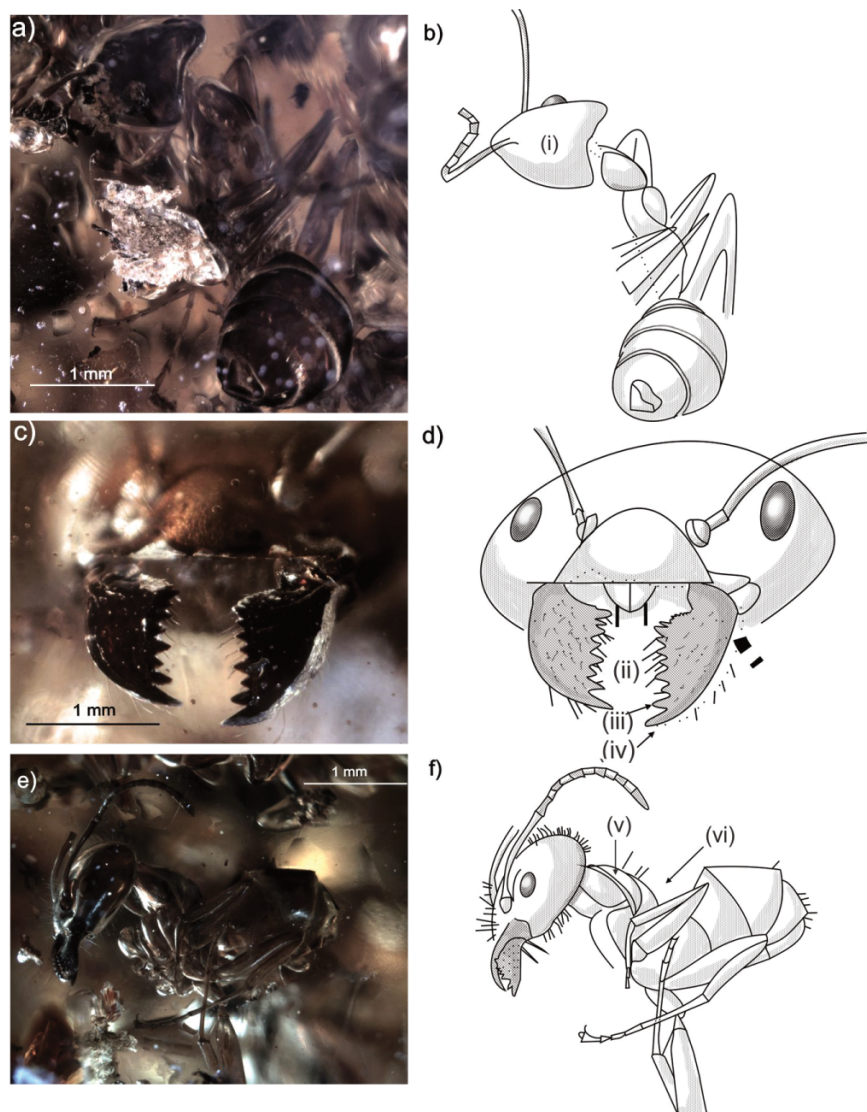
MATERIAL: IHNFG-4649. Worker ant. Complete fossil specimen.

LOCALITY: Totolapa amber, State of Chiapas, southwestern Mexico.

AGE: Miocene.

MEASUREMENTS: (mm) RL: 10.5; HL: 1.87; EL: 0.9; OI: 100; SL: 2.62.

Fig. 4. *Azteca* Forel, 1878, (a, b) specimen IHNFG-4647a in dorsal view, (c, d) specimen IHNFG-4647b in frontal view, and (e, f) specimen IHNFG-4647c in lateral view. In (b), dorsal imprint shows the cordate head shape (i). In (d), the frontal imprint shows mandibles with nine teeth (ii) and the apical tooth (iv) slightly longer than the preapical (iii). In (f), the lateral imprint shows mesonotum higher (vi) than pronotum (v).



DESCRIPTION:

Head: Ovoid in lateral view. Eyes located sideways. Ocelli absent. Filiform antenna with 12 segments; antennal sockets are away from clypeus.

Mesosoma: Profile convex; metapleural gland is absent (Fig. 6b).

Petiole: Sub-square.

Gaster: Five segments.

REMARKS: The specimen is placed into genus *Camponotus* on the basis of the diagnosis. Differs from *Formica* in the mesosomal shape and the position of the antennal sockets. In *Formica* the mesosoma is discontinuous for the transverse groove crossing the mesosomal dorsum; in contrast, it is continuous in *Camponotus*. The antennal sockets in *Formica* are located at or adjacent to the posterior clypeal margin, whereas in *Camponotus* they are clearly far from it, as they are in the present specimen (Fernández 2003; Fisher and Cover 2007). The genus *Camponotus* has been previously found in Simojovel amber (Chiapas, Mexico) (Brown 1973; Solórzano-Kraemer 2007) and Dominican amber (Late Oligocene) (Wilson 1985a), as well as in North American (Flossissant, Early Oligocene) (Carpenter 1930; Dlussky and Rasnitsyn 2002), Ukrainian

(Rovno, Late Eocene) (Perkovsky 2009), and Baltic amber (Late Eocene) (Mayr 1868; Wheeler 1915; Dlussky and Rasnitsyn 2009).

Discussion

An important aspect of the present research concerns the unprecedented record of the ant genus *Forelius* Emery, 1888, in Chiapas amber paleobiota, which includes amber inclusions from Simojovel, Huitiupán, and Totolapa deposits. Based on *Forelius* materials newly found in Totolapa, the authors of the present paper are in the process of compiling a report that shows clear diagnostic characters at the species level. To our knowledge, *Forelius* has not been previously recorded for Dominican amber either, which apparently also shares paleobiological relationships with Chiapas amber (Poinar 1992; Langenheim 2003; Solórzano-Kraemer 2007, 2010; others). Fossil ants of Dominican amber include the genera *Technomyrmex*, *Acropyga*, *Solenopsis*, *Crematogaster*, *Oligomyrmex*, *Pheidole*, *Gnamptogenys*, *Neivamyrmex*, *Dolichoderus*, *Monacis*, *Hypoclinea*, *Azteca*, *Iridomyrmex*, *Tapinoma*, *Camponotus*, *Leptomyrmex*, *Ilemomyrmex*, *Oxydris*, *Pseudomyrmex*, *Aphaenogaster*, and *Cyphomyrmex* (Wilson 1985a, 1985b, 1985c; Ward

Fig. 5. *Tapinoma* Foerster, 1850, specimen IHNFG-4648 in dorsal view. In (b), the dorsal imprint displays part of the mesosoma without hairs (i); (d) shows a gaster with four tergites (ii).

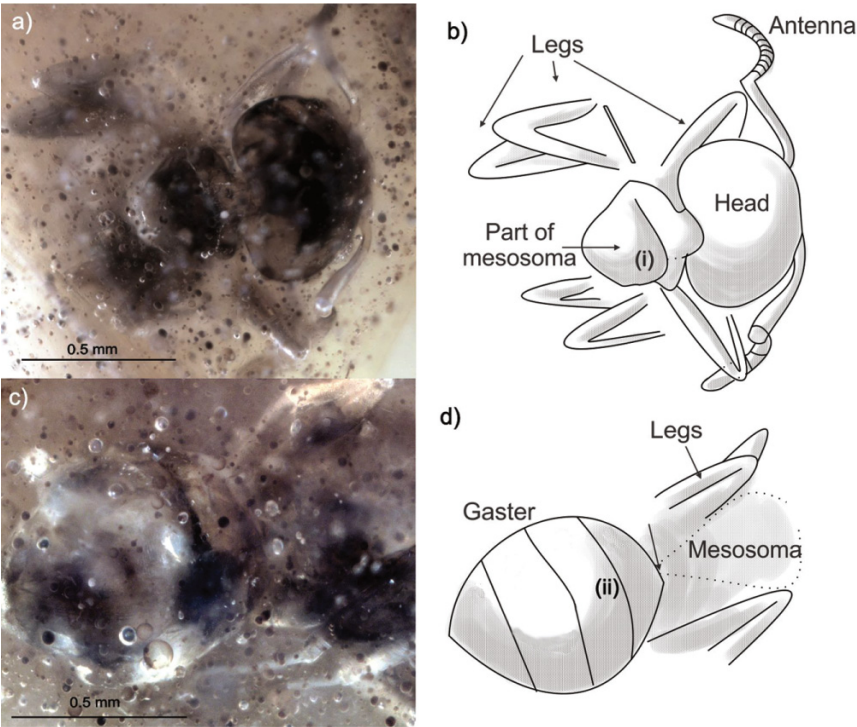
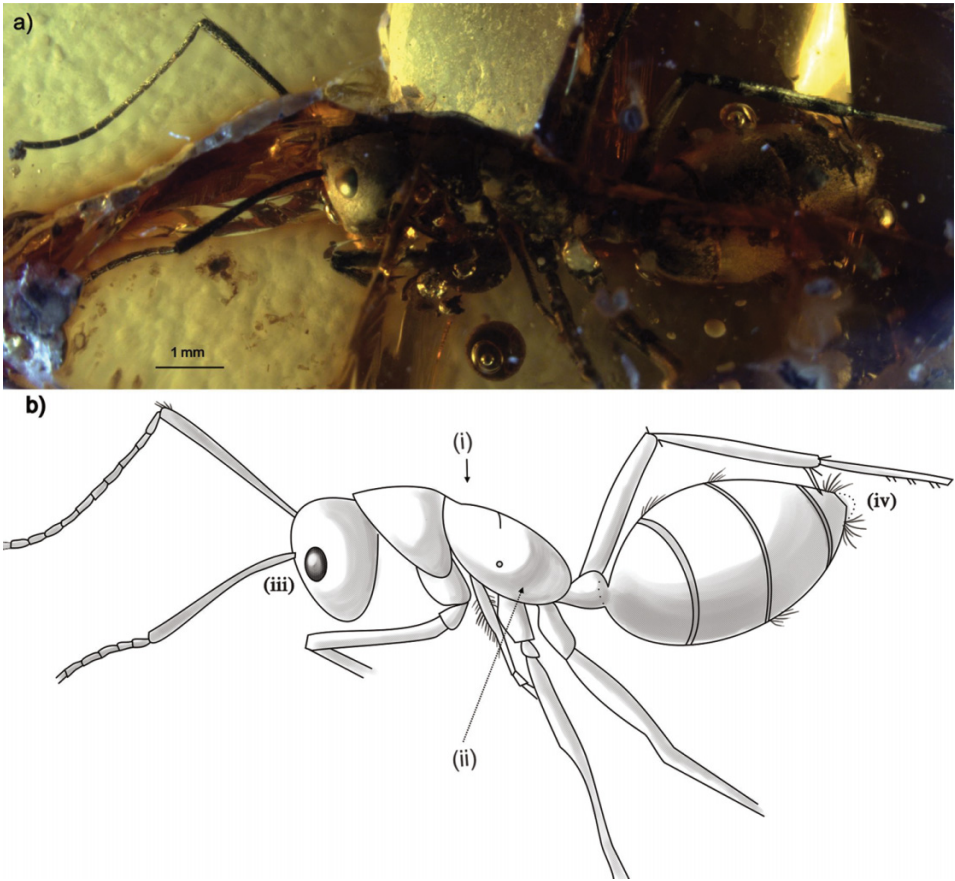


Fig. 6. *Camponotus* Mayr, 1861, specimen IHNFG-4649 in lateral view. (a) is a photomicrograph and (b) its corresponding illustration. In (b), the lateral imprint shows the convex mesosoma (i), an absent metapleural gland (ii), the anterior clypeal margin far from the antennal sockets (iii), and the presence of an acidopore (iv).



1992; De Andrade 1995, 2003; Devries and Poinar 1997; Brandão et al. 1999; Grimaldi and Agosti 2000; Johnson et al. 2001).

Accordingly, the occurrence of *Azteca*, *Tapinoma*, *Camponotus*, and *Forelius* in Totolapa amber represents a significant contribution to the understanding of the Neotropical distribution of ant genera in the Americas, as well as an increase in our knowledge about the Chiapas amber paleobiota.

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