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New ant species *Schismiscapus exstinctum* gen. et sp. nov. (Formicidae: Dolichoderinae) from Miocene Mexican amber

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ABSTRACT

A new species of ant (Formicidae: Dolichoderinae) in Miocene Mexican amber is diagnosed and described. *Schismiscapus exstinctum* gen. et sp. nov. is recognised by having the base of scape flattened and notched; mesosoma long, narrow, and sinuous; hypostomal bridge forming a U-shaped notch without any denticule; anteromedial mesosternum convex; compound eyes positioned anteriorly on head; long post peduncle that joints with the gaster and a long spur on the hind tibiae. A phylogenetic analysis was performed to identify the position of *S. exstinctum* among dolichoderine ant genera. A close relationship with the genus *Leptomymex* Mayr, 1862 was revealed with both ant genera sharing a hypostomal bridge forming a U-shaped notch without any denticule. Thus, the fossil record of *S. exstinctum* in Miocene tropics of southern Mexico provides new insights into the evolutionary history of the Leptomymecini clade that has a probable Neotropical origin.

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Ants; amber; Dolichoderinae; fossil; Mexico; new species

Introduction

Dolichoderinae is a cosmopolitan and diverse subfamily of ants comprising four monophyletic tribes: Bothriomyrmecini, Dolichoderini, Leptomymecini, and Tapinomini. Dolichoderinae is considered monophyletic with 28 genera and 713 species (Ward et al. 2010). It is distinguished by having a single-segmented petiole, with no constriction between the first and second segment of the gaster, and a slit-like opening at the end of the gaster (Shattuck 1992).

The Mexican territory has close to 1,191 extant species in 105 genera and 10 subfamilies (AntWeb). In contrast, the fossil record of ants from Mexico is limited to a few amber inclusions compared to other lagerstätten such as Dominican amber, which is about the same age as Mexican amber, but the number of genera and species are better known (Barden 2017). The fossil record of ants in Miocene Mexican amber comprises five subfamilies, with several genera and a few described species (LaPolla et al. 2013), including the subfamily Dolichoderinae, with the genera: *Azteca* Forel, 1878 and *Tapinoma* Foerster, 1850 (Solórzano-Kraemer, 2007), as well as the genus *Forelius* Emery, 1888 (Durán-Ruiz et al., 2013). Other fossil records include the subfamily Formicinae, with the genus *Camponotus* Mayr, 1861 (Solórzano-Kraemer 2007); the subfamily Myrmicinae, with the described species *Aphaenogaster praerelicta* De Andrade, 1995 (De Andrade, 1995), *Cephalotes maya* De Andrade, 1999, *Cephalotes olmecus* De Andrade, 1999; *Cephalotes poinari* De Andrade, 1999, and *Cephalotes ventriosus* De Andrade, 1999 (De Andrade and Baroni-Urbani, 1999); as well as *Cyphomyrmex maya* De Andrade, 2003 (De Andrade, 2003), and *Pheidole pauchil* Varela-Hernández & Riquelme, 2021 (Varela-Hernández and Riquelme, 2021); the subfamily Ponerinae, with the genus *Pachycondyla* Smith, 1858 (Solórzano-Kraemer 2007); and the subfamily Proceratiinae, with the species *Discothyrea maya* De Andrade, 1998 (De Andrade, 1998).

In the present work, we describe and illustrate a new genus and species of the subfamily Dolichoderinae in Miocene Mexican amber. A phylogenetic analysis based on morphological characteristics was also performed to address its relationship among other extant and fossil dolichoderine ant genera, such as *Leptomymex* Mayr, 1862 or *Technomyrmex* Mayr, 1872 with which it shares some morphological similarities.

Materials and methods

The type material, 137 amber inclusions, come from La Pimienta site, located in the town of Simojovel, Chiapas, Southwestern Mexico. Amber-bearing beds of Simojovel belong to Mazantic shale and Balumtum sandstone strata, Early Miocene (Durán-Ruiz et al. 2013; Riquelme et al. 2014). The sedimentary record and associated paleobiota suggest a lowland-fluvial environment close to a coastal plain (Graham 1999; Langenheim 2003; Durán-Ruiz et al. 2013). The amber botanical source is attributed to an extinct legume tree of the genus *Hymenaea* Linné (sensu Langenheim 1966), which shares chemical signatures with current plant resins of *Hymenaea courbaril* Linné and *Hymenaea verrucosa* Gaertner widely distributed in modern tropics (Langenheim 2003; Riquelme et al. 2014). Holotype and paratypes are deposited in the Colección de Paleontología maintained at the Universidad Autónoma del Estado de Morelos, Mexico (CPAL-UAEM).

Anatomical 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 and multiple images stacking for three-dimensional focus expansion as presented in Riquelme et al. (2014). The following measurements and indices were used (all measurements expressed in millimetres):

Head length (HL): in full-face view, the length between the midpoint of the anterior margin of the clypeus to the midpoint of a line tangent to the posterior margin of the head.

Head width (HW): in full-face view, the maximum width between the lateral margins of the head including the eyes that are within the cephalic capsule.

Scape length (SL): the maximum length of the scape excluding the basal constriction.

Weber's length (WL): in lateral view of the mesosoma, greatest distance from the approximate inflection point, where the pronotum curves into the cervical shield, to the posterior basal angle of the metapleuron.

Cephalic index (CI): $HW/HL \times 100$.

Scape index (SI): $SL/HL \times 100$.

Schematic drawings were hand traced by an electronic pen using a stereomicroscope and photomicrographs and Corel Draw X7® was used for graphic editing. The following Identification keys were used to identify and determine the specimens: Shattuck (1992) and Bolton (1994) for subfamily; Guerrero (2019) for genera and species level.

For the phylogenetic analysis, the morphological data of extant specimens were obtained from the material deposited at the Colección de Hymenoptera, maintained at the Laboratorio de Sistemática Molecular, Universidad Autónoma del Estado de Morelos, Mexico (COHYM-UAEM). For *Leptomyrme* Mayr, 1862 data provided by Barden et al. (2017) were used, whilst for *Technomyrmex hispaniolae* Wilson, 1985 and *Technomyrmex caritatis* Brandão et al., 1999 data from original descriptions and illustrations were used as presented in Brandão et al. (1999). Phylogenetic analysis was performed using NONA v.2.0 (Goloboff 1997) and displayed on the interface WinClada v.1.00.08 (Nixon 2002). Tree search implemented a heuristic search method, and the options were set to hold 1000 trees, 100 replications, 10 starting tree replications, and a multiple TBR+TBR search strategy. All characteristics were treated as unordered and weighted equally.

Results

Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Family Formicidae Latreille, 1809

Subfamily Dolichoderinae Forel, 1878

Schismiscapus gen. nov. Varela-Hernández, Riquelme & Guerrero 2022, monotypic.

ZooBank LSID: [urn:lsid:zoobank.org:act:D778078E-322F-43D6-AA20-BD24BA5B212B](https://zoobank.org/act:D778078E-322F-43D6-AA20-BD24BA5B212B)

Type species

Schismiscapus extinctum sp. nov. Varela-Hernández, Riquelme & Guerrero 2022.

Genus diagnosis based on workers

Ants belong to the Leptomyrmeini tribe sensu Ward et al. (2010), but with the following combination of diagnostic traits: (i) base of scape flattened and notched; (ii) mesosoma long, narrow and sinuous; (iii) hypostomal bridge forming a U-shaped notch without any denticule; (iv) propodeum with distinct anterior, dorsal and declivitous faces, dorsal face with a shallow mesal depression, dorsal and declivitous faces of propodeum forming a 90-degree angle, legs long and slender; (v) anteromedial mesosternum convex; (vi) compound eyes positioned anteriorly on head; and (vii) long petiolar peduncle that joints with the gaster.

Etymology

Schismiscapus derives from the Greek word *schismi-*, which means cleft, plus the term *-scapus*, the first long segment of the antenna. The name of the genus alludes to a distinctive deep cleft at the base of the scape.

Distribution

It is only known from the Miocene strata of southern Mexico.

Schismiscapus extinctum sp. nov. Varela-Hernández, Riquelme & Guerrero 2022, by original designation.

ZooBank LSID: [urn:lsid:zoobank.org:pub:B6A727D4-7665-4A6B-98FB-669848C2CA58](https://zoobank.org/pub:B6A727D4-7665-4A6B-98FB-669848C2CA58)

Etymology

The specific epithet *extinctum* is a Latin noun that refers to the fossil condition of the species.

Types

Holotype CPAL.447, amber inclusion (Figure 1B). Paratypes from CPAL.448/n.1 to CPAL.448/n.137, amber inclusions. The type material is housed in the Colección de Paleontología mantened at the Laboratorio de Sistemática Molecular, Universidad Autónoma del Estado de Morelos (CPAL-UAEM), Mexico.

Locality and Horizon

La Pimienta site: 17°09'11" N, 92°46'08" W, Simojovel, Chiapas, Mexico. Mazantic shale and Balumtum sandstone strata, Miocene (Riquelme et al. 2014).

Taphonomic notes

One hundred thirty-seven worker specimens are embedded in a single piece of amber, golden in colour, with a translucent glossiness (Figure 1A). The head of one worker specimen is more prominent than the others, suggesting polymorphism. It seems that all of these workers were trapped in the resin while foraging. Two other ant specimens identified as *Camponotus* sp. and *Pheidole* sp. were trapped in the same amber piece. Also, two specimens of Diptera, leaf litter, flower stamens, soil and bubble impressions, partially hiding some ants.

Species diagnosis

Scapes long, surpassing vertex of head by about twice the length of the scape, base of scape flattened and notched; compound eyes positioned anteriorly on head; mandibles with 15 teeth and denticles; hypostomal bridge forming a U-shaped notch without any denticule; mesosoma long, narrow and sinuous, mesonotum with two longitudinal dorsolateral carinae forming two angled process at the junction of the anterior and posterior faces of the mesonotum,

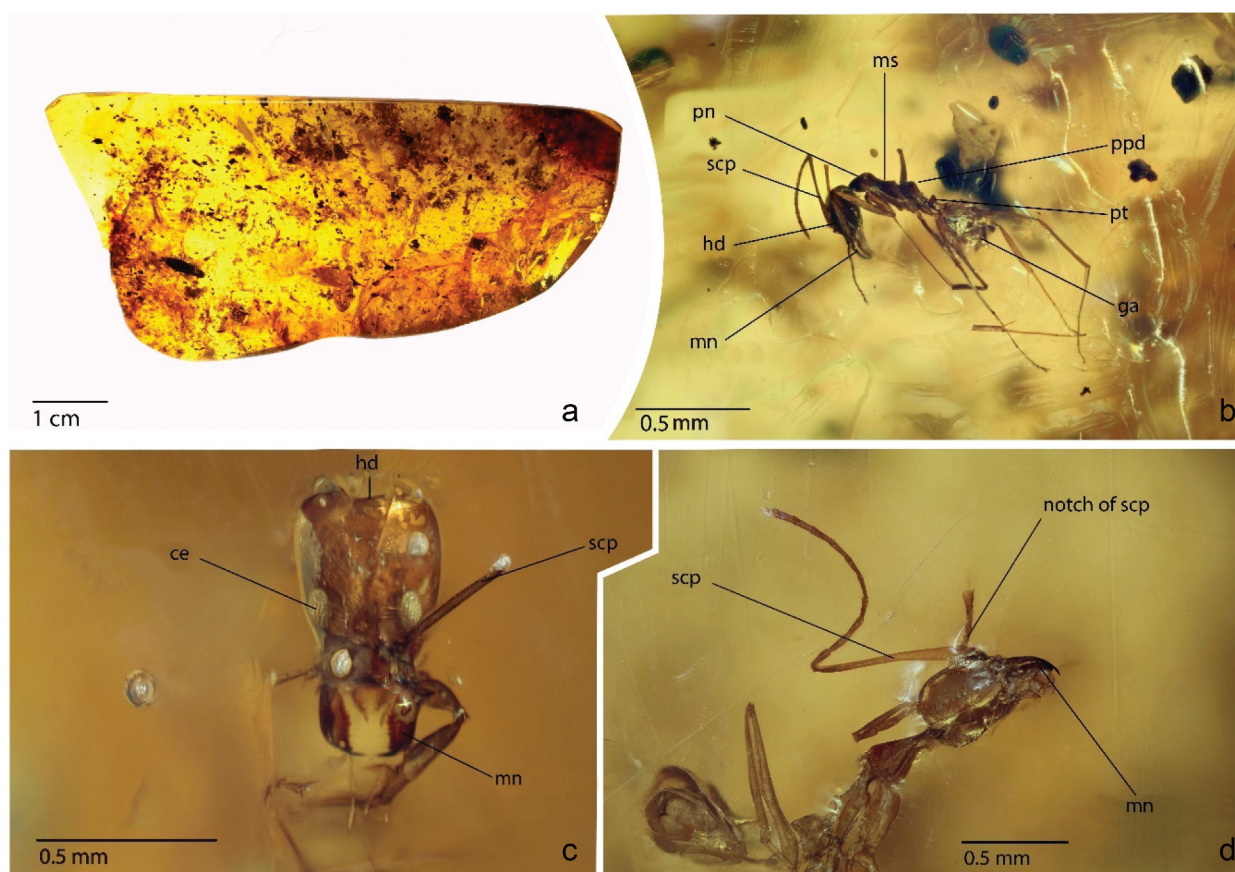


Figure 1. (A) Complete piece of amber; (B) Holotype *Deberia* ser CPAL.447 (C) Paratype CPAL.448/n.1 Head in frontal view; (D) Paratype CPAL.448/n.2 Oblique view. Abbreviations: (ce) compound eye, (hd) head, (ga) gaster, (mn) mandible, (ms) mesonotum, (ppd) propodeum, (pt) petiole, (scp) scape.

metathoracic spiracle protruding dorsolaterally but not surpassing the mesosoma profile in lateral view (more evident in dorsolateral view), metanotal groove wide and deep; propodeum with distinct anterior, dorsal and declivitous faces, dorsal face with a shallow mesal depression, dorsal and declivitous faces of propodeum forming a 90-degree angle, legs long and slender; long post peduncle that joints with the gaster; all body cuticle devoid of any ornamentation.

Worker description

Head

Longer than wide; sides subparallel, occipital border concave (Figure 1C); scape flattened at its base abruptly notched also at its base, long, surpassing the occipital border of the head by about twice the length of the scape, scape devoid of any kind of pilosity (Figure 1C; Figure 2D); antennal segments about the same size with sparse tiny decumbent hairs; eyes large, located below the midline of the head, close to the mandibles; antennal socket partially covered by an oval frontal lobe; frontal carinae extends to the posterior margin of the eyes, antennal fossa evident, depressing and connected with the posterior margin of the frontal carinae; clypeus with two long erect setae and anterolateral border angulate; mandibles with masticator and inner border evenly rounded, pattern dentition from apical to basal teeth as follows: apical and preapical teeth longer than all other teeth, apical tooth longer than preapical, two denticles after the preapical tooth, a longer tooth followed by a diastema with five denticles, a longer tooth after the last fifth tooth, two denticles followed by two longer teeth that coincide in

the curvature between the masticatory and the basal margin of the mandible, the latter with teeth that decrease in size to a crenulate surface (Figure 1C; Figure 2A); hypostomal bridge forming a U-shaped notch without any denticle; palp formula 6, 4, maxillary palp relatively long. **Mesosoma.** Greatly elongate and narrow, sinuous, promesonotal suture slightly impressed, dorsal face of pronotum flattened in lateral view, dorsal face of mesonotum forming two convexities in lateral view, promesonotal suture slightly impressed, mesonotum abruptly concave, metanotal groove concave, evident and wide (Figure 2(A,C, D)); in lateral view, propodeum unarmed, dorsal face of propodeum with transverse impression (Figure 2C), propodeal spiracle rounded, forming a posterodorsal projection, declivitous propodeal face slightly concave; anterior face and posterior face of the petiolar node form a triangle in lateral view, anterior face of petiolar node perpendicular to ventral face, posterior face inclined forward at approximately 45-degrees (Figure 2A; Figure 2C), node blunt in lateral view, rounded in anterior view, ventral face flat, without any type of process. **Legs.** Middle and hind tibiae with a single long simple spur, posterior femur with tiny decumbent hairs. **Gaster.** Gaster with short, fine, scatter, erect setae, dorsum of first gastral tergite finely aciculate; rest of the tergites smooth. Colour concolorous light yellow.

Remarks

Schismiscapus exstinctum gen et sp. nov. is closely related to members of the macro and micro *Leptomyrmex*. Lucky and Ward (2010) describe morphological characteristics observed in *Leptomyrmex* that

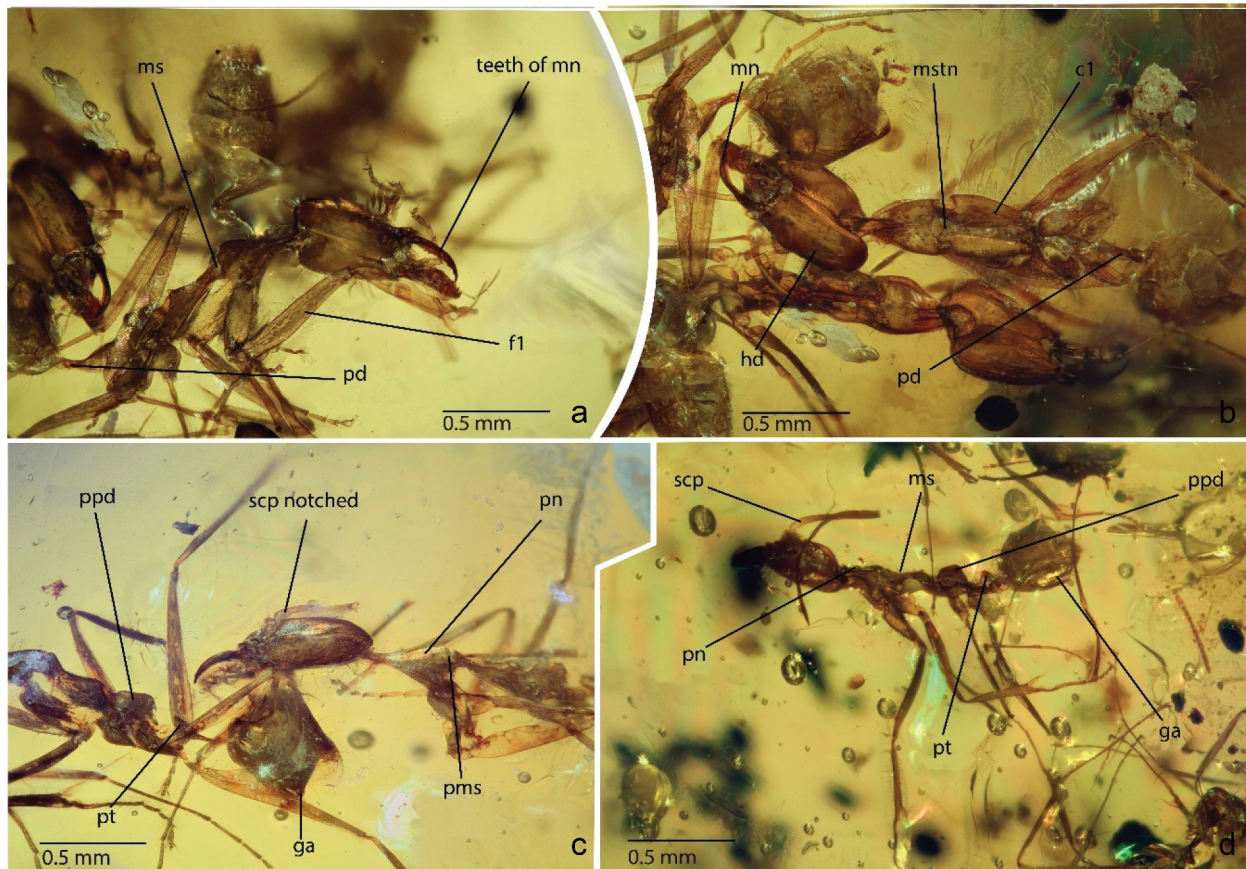


Figure 2. (A) Paratype CPAL.448/no.3 Mesosoma in profile and head in ventral view; (B) Paratypes CPAL.448/no.4 and CPAL.448/no.5 in ventral view; (C) Paratypes CPAL.448/no.6 and CPAL.448/no.7 in profile; (D) Paratype CPAL.448/no.8 in profile. Abbreviations: (c1) fore coxa, (f1) fore femur, (hd) head, (ga) gaster, (mn) mandible, (ms), mesonotum, (mstn) mesosternum, (pms) promesonotal suture, (ppd) propodeum, (pd) peduncle of petiole, (pn) pronotum, (pt) petiole, (scp) scape.

it shares with *S. exstinctum*: worker caste probable polymorphic, antenna 12 segmented, scape long, surpassing postocular margin by about one-half the distance of the scape, masticatory margin with apical tooth longer than the subapical one, basal margin denticulate distally, smooth proximally, declivitous face of propodeum flat, dorsal

face weakly convex, mesosomal spines absent, metanotal groove forming a distinct angle between the mesonotum and the propodeum, integument weakly sculptured. However, *S. exstinctum* differs by having distinct morphological features that include (i) anteromedial mesosternum even with the lateral regions in the *Leptomyrmex* ants

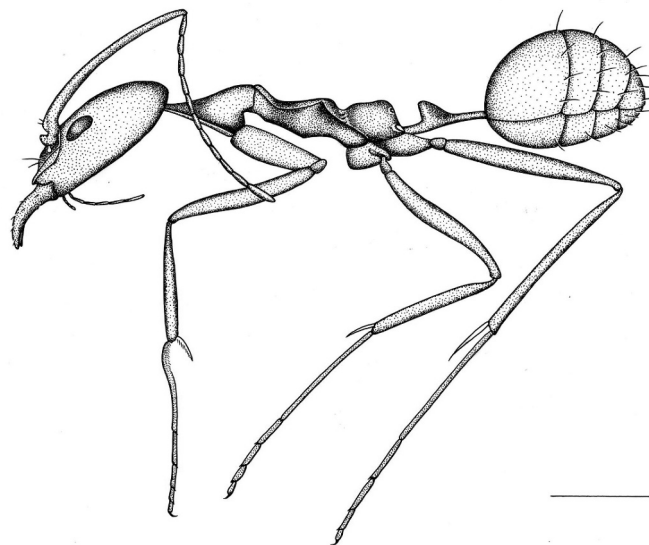


Figure 3. Schematic drawing of *Schismiscapus exstinctum* gen. et sp. nov. based on the reconstruction of different specimens. Bar = 0.5 mm.

Table 1. Comparative chart of morphological characteristics between *Leptomyrmex* and *Schismiscapus exstinctum* sp. nov.

Characteristics/Taxa	<i>Leptomyrmex</i>	<i>Schismiscapus exstinctum</i>
Form of anteromedial mesosternum	Even with the lateral regions	Convex (Figure 2B)
Position of eyes in frontal view	Posterior	Anterior (Figure 1C)
Size of anterolateral hypostomal	Reduced	Absent (Figures (2A, 2B))
Position of metanotal spiracle	On dorsal surface of propodeum	On posterior face of propodeum
Form of hind tibial spur	Pectinate	Smooth
Form of base of scape	Continuous	Notched (Figure 2C)
Presence of posterior peduncle	Absent	Present

(synapomorphy that separates tribe clades) but convex in *S. exstinctum* (Figure 2B); (ii) compound eyes posterior on head in *Leptomyrmex* but anterior on head in *S. exstinctum* (Figure 1C); (iii) anterolateral hypostomal reduced in *Leptomyrmex*, absent in *S. exstinctum* (Figure 2A, Figure 2B); (iv) metanotal spiracle laying on dorsal surface of propodeum in *Leptomyrmex* and laying in posterior face in *S. exstinctum*; (v) hind tibial spur pectinate basally in *Leptomyrmex* and smooth in *S. exstinctum*; (vi) scape continuous in *Leptomyrmex* and notched in *S. exstinctum* (Figure 2C); (vii) posterior peduncle of petiole absent in *Leptomyrmex* and present in *S. exstinctum*. A schematic reconstruction of *S. exstinctum* is shown in the drawing of Figure 3. Table 1 summarises the traits that separate *S. exstinctum* from other members of the *Leptomyrmex* group (Table 1).

Phylogenetic analysis

Twenty-nine morphological characteristics were used for phylogenetic tree reconstruction (Suppl. material), recovering one most parsimonious tree (Figure 4). *S. exstinctum* is a sister group of the *Leptomyrmex* clade supported by synapomorphy 7 (mandible

dentition), and synapomorphy 10 (hypostomal notch). The phylogenetic relationships of the other Dolichoderinae genera included in our analysis contrast substantially with previous proposals based on morphological and molecular data, and it is not part of our study to describe them here.

Discussion

S. exstinctum has all the morphological synapomorphies of the tribe Leptomyrmecini, except the straight anteromedial margin of the mesosternum. Among all the characteristics used to describe the tribes of the subfamily Dolichoderinae, according to Shattuck (1992), the anterior border of the mesosternum is used as a synapomorphy to determine and separate Dolichoderini from all other tribes; for example, convex in Dolichoderini and straight in all other tribes. However, *S. exstinctum* has a concave anterior edge of the mesosternum, which is recovered as an automorphy. Ward et al. (2010) define Leptomyrmecini as having a 'mesosternum with a straight anteromedial margin'. Consequently, we suggest including the diagnostic trait of this new genus fossil in the current concept of the tribe, as Leptomyrmecini may present a 'mesosternum with variable anteromedial margin, straight to concave'.

On the other hand, the hypostomal notch is diagnostic for living species of the genus *Leptomyrmex* (Lucky and Ward, 2010), a trait shared with the fossil species *S. exstinctum* (character 10), as well as mandible dentition (character 7) (Suppl. Information), both synapomorphies support the close phylogenetic relationship between *S. exstinctum* and *Leptomyrmex* (Figure 4). The hypostomal notch probably is associated with a shared ancestry between both lineages, according to the phylogenetic analysis (Figure 4). Other characteristics shared by both lineages is a body slender, the long legs, and long antennal scape. However, several characteristics consistently found in *Leptomyrmex* are absent in *S. exstinctum*, such as: sides of head parallel, compound eyes posterior on head, continuous mesosoma in profile, external sides of scapes continuous; node of petiole in profile, rounded, short post-peduncle of petiole that joints the gaster, and hind spur pectinate at its base. Phylogenetic analysis also shows that the

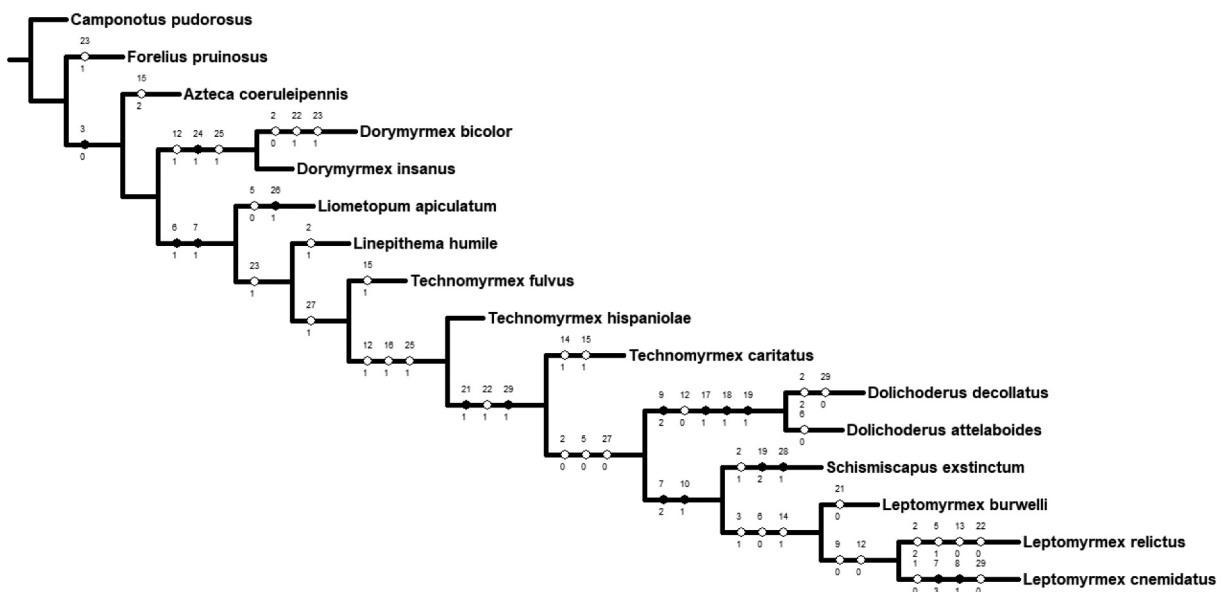


Figure 4. Phylogeny of some species of Dolichoderinae including *Schismiscapus exstinctum* gen. et sp. nov. based on 29 morphological characteristics (numbers above black and white dots); numbers below dots represent the characteristic codification. Consistency index = 0.48; retention index = 0.59. Black dots represent synapomorphies, white dots represent homoplasious characteristics.

presence of a fifth tergite in the gaster, which is diagnostic for the genus *Technomyrmex* (character 27), is recovered in *Technomyrmex* spp. and lost in the clade (*Dolichoderus* + (*S. exstinctum* + *Leptomyrmex*)) (Figure 4). Although the fossil workers of *S. exstinctum* and *Technomyrmex caritatis* are morphologically very similar to each other, this similarity is convergent.

In addition, the sinuous mesonotum (character 29) is recovered as a synapomorphy of the clade (*T. caritatis* + (*Dolichoderus* + (*S. exstinctum* + *Leptomyrmex*))), with a subsequent loss in *Dolichoderus decollatus* and *Leptomyrmex cnemidatus*. Thus, the sinuous mesonotum potentially relates *T. caritatis* to other species of *Leptomyrmex* and *Dolichoderus*, and the fossil species *S. exstinctum*. Barden (2017) defines a stem group as ‘non-crown taxa that are more closely related to the crown group than they are to the nearest extant sister group’. Accordingly, the new monospecific genus *Schismischapus* and its only known species *S. exstinctum* might be considered a stem group more closely related to *Leptomyrmex* (the crown group), than to any other extant group in the tribe Leptomyrmecini.

Conclusion

Previously, a molecular phylogenetic analysis has estimated that the subfamily Dolichoderinae probably emerged around 67 Ma, at the end of the Mesozoic (Ward et al. 2010). Later discoveries in the fossil record indicate that representatives of Dolichoderinae have been found since the Late Cretaceous (McKellar et al. 2013). i. e., Dolichoderinae appeared some 22 Ma after the first ant-like ancestor. The genera *Azteca* Forel, 1878, *Dolichoderus* Lund, 1831, *Gracilidris* Wild & Cuzzo, 2006, *Leptomyrmex* Mayr, 1862, *Tapinoma* Foerster, 1850, and *Technomyrmex* Mayr, 1872 are found in Dominican amber, Early-Middle Miocene (Baroni-Urbani, 1980; Wilson 1985); whereas *Azteca* Forel, 1878 and *Forelius* Emery, 1888 are recorded in Chiapas amber, Early Miocene (Solórzano-Kraemer 2007; Durán-Ruiz et al. 2013). Thus, the occurrence of *Azteca*, *Gracilidris*, and *Leptomyrmex* from Dominican amber (Baroni-Urbani 1980; Wilson 1985), as well as *Azteca* and *Forelius* from Mexican amber (Solórzano-Kraemer 2007; Durán-Ruiz et al., 2013), indicates that ants of Leptomyrmecini clades were well-distributed in the Miocene tropics of southern Mexico and Central America. Ward et al. (2010) proposed a probable Neotropical origin of Leptomyrmecini, which could have emerged between 33 and 23 Ma, in the Late Oligocene to Early Miocene, with a later diversification in North America and Australia. The hypothesis of the Neotropical origin of Leptomyrmecini has also been discussed elsewhere (Baroni-Urbani 1980; Baroni-Urbani and Wilson 1987; Boudinot et al. 2016). The occurrence of extant and fossil species of *Technomyrmex* in the New World has led to the hypothesis of a taxon that was once widely distributed but currently has a limited distribution in the Neotropics (Fernández and Guerrero 2008). *Leptomyrmex* may also have had a broader distribution in the Cenozoic, but with a more limited recent distribution (Baroni-Urbani and Wilson 1987). The occurrence of the fossil species *Leptomyrmex neotropicus* Baroni-Urbani, 1980 challenged the hypothesis about the origin of *Leptomyrmex*, which added to the subsequent discovery of *Leptomyrmex relictus* Boudinot, Probst et al., 2016 (Boudinot et al., 2016), have strengthened the hypothesis of a Neotropical origin of the genus with a later diversification in Australia. Accordingly, *S. exstinctum*, a fossil species exclusively distributed in the Miocene tropics of southern Mexico, also supports the Neotropical origin of Leptomyrmecini.

Disclosure statement

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

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