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# A Review of the Current State of Knowledge on *Liometopum apiculatum* Mayr, 1870 (Hymenoptera: Formicidae)

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**Abstract**

The velvety tree ant, or *Liometopum apiculatum*, is one of the seven species within its genus and among the three with the widest distribution across North and Central America. In 1870, Mayr described it based on worker ants; later, all castes were characterized. This species is distinguished by a pointed petiole and dense pubescence on the gaster. It inhabits diverse vegetation types, including oak and pinyon pine forests, as well as desert scrub, at altitudes ranging from 30 to 2,900 meters above sea level. *L. apiculatum* forms colonies in various substrates, such as rocks, dead tree trunks, and the base of the stem (lower part of the stem, near the roots), exhibiting both monodomous and polydomous nesting structures. Colony sizes range from a few hundred to hundreds of thousands of workers. The species is omnivorous, playing an ecological role in seed dispersal and nutrient cycling. In central Mexico, the larvae of the reproductive caste (escamoles) are considered a delicacy. Due to their high market value, excessive harvesting has led to overexploitation and population declines in some areas. Additional pressures, such as habitat conversion, overgrazing, extraction of host plants, and climate change, have also been reported to affect its populations, underscoring the urgency of conservation measures. Consequently, recent studies have primarily focused on its nutritional properties, use, and consumption. However, knowledge gaps persist regarding their distribution, ecology, interspecific interactions, intraspecific variation (morphological and genetic), nesting methods, colony establishment, and foraging strategies. This study updates and integrates available information to advance current understanding of *L. apiculatum* biology, given that the most recent compilation of its biology, ecology, and behavior is eleven years old. Likewise, this research provides valuable information to support and guide future conservation efforts for this species.

## Introduction

Ants are the most diverse group of social insects, with more than 17,428 described species (AntWeb, 2024) and an estimated 12,500 yet to be described (Ward, 2014). They are distributed across all continents except Antarctica and are recognized as the most abundant terrestrial arthropods in terms of both number and biomass (Hölldobler & Wilson, 1990; Lach et al., 2010; Ward, 2014; Parr & Bishop, 2022; Schultheiss et al., 2022). In addition, ants play crucial roles in ecosystem processes, acting as seed dispersers, natural pest control agents, soil bioturbators, and pollinators. They also

engage in diverse interactions with plants, including mutualisms with extrafloral nectary-bearing species and seed dispersal (myrmecochory), as well as interactions that can result in wood degradation. In addition, ants interact with other animals, for example as mutualists with trophobiont insects, as modifiers of invertebrate communities via predation and competition, as hosts for diverse myrmecophiles, and as participants in food webs as both predators and prey (Hölldobler & Wilson, 1990; Lach et al., 2010; Del Toro et al., 2012; Schultheiss et al., 2022).

However, ants can also negatively affect ecosystems and human well-being. Their bites may impact human health, they can become household and agricultural pests, and they may cause structural damage to buildings (Klotz et al., 1995; Del Toro et al., 2009; Wetterer, 2010). Invasive species further affect livestock and native fauna, altering biodiversity and disrupting ecosystem services such as plant productivity and nutrient cycling, leading to significant economic losses worldwide (Chapman & Bourke, 2001; Del Toro et al., 2009). Certain pest species infest wood, including moisture ants (*Lasius* spp.) and carpenter ants (*Camponotus* spp.). The subfamily Dolichoderinae also includes wood-destroying species such as the omnivorous velvety tree ants (*Liometopum* spp.) (Hoey-Chamberlain et al., 2013).

Velvety tree ants are polymorphic, possess a single node, and form colonies with multiple queens (Del Toro et al., 2009). They typically nest in trees and shrubs and are often observed tending hemipterans. There are three North American species: *Liometopum apiculatum* Mayr (Figure 1), *Liometopum luctuosum* Wheeler, and *Liometopum occidentale* Emery (Del Toro et al., 2009; Hoey-Chamberlain et al., 2013). All three species have been observed to exhibit aggressive behaviors when disturbed, including the release of strong alarm odors (Hoey-Chamberlain et al., 2013). Of these, *L. apiculatum* maintains the closest relationship with humans. This species, distributed in the southwestern United States, Mexico, and Guatemala (Del Toro et al., 2009; Hoey-Chamberlain et al., 2013; Guenard et al., 2017; Berumen Jiménez et al., 2021), is not typically considered a pest. On the contrary, its immature reproductive castes have traditionally been harvested in Mexico as a delicacy known as "escamoles," a highly valued food rich in proteins, carbohydrates, and lipids (Hoey-Chamberlain et al., 2013; Ramírez-García et al., 2022). This study presents the current state of knowledge on *Liometopum apiculatum*.

### *Systematic and Taxonomy*

The family Formicidae has been recognized as monophyletic, comprising all species within the family, which has been subdivided into 10–20 subfamilies, depending on the taxonomic classification scheme adopted by different authors (Astruc et al., 2004). The cosmopolitan subfamily Dolichoderinae is the fourth largest, with 22 genera (Ward et al., 2010).

The genus *Liometopum* is classified within the Tapinomini tribe of the Dolichoderinae subfamily. Ants of this tribe possess a reduced petiole and exhibit either a mediodorsally positioned propodeal spiracle or a weakly developed metanotal groove, resulting in a continuous convex surface formed by the mesonotum and propodeum, as seen in *Liometopum.* The phylogenetic position of *Liometopum* based on morphological and molecular characters, including three mitochondrial genes and ten nuclear genes, has revealed that *Liometopum* is a close sister taxon to *Tapinoma* and is also related to *Technomyrmex*, *Axinidris*, and *Aptinoma* (Shattuck, 1995; Chiotis et al., 2000; Ward et al., 2010; Parker & Kronauer, 2021). Consistent with these findings, *L. apiculatum* has appeared as the sister group of *L. occidentale* (Brady et al., 2006; Ward et al., 2010).

### *Morphological Characteristics*

*Liometopum apiculatum* was initially described as *Formica masonium* by Buckley (1866). Mayr (1870) subsequently reclassified, redescribed, and renamed it *Liometopum apiculatum* based on worker specimens collected by Prof. Bilimek (Del Toro et al., 2009; Wheeler, 1905). Later, Wheeler (1905) and Wheeler and Wheeler (1951) provided descriptions of the males and larvae. Although the type specimens of *F. masonium* and *L. apiculatum* remain unlocated, the descriptions have indicated that both taxa are identical. Wheeler (1905) provided a detailed description of the worker, female, and male of *L. apiculatum*, using multiple specimens from several localities, thereby refining the diagnostic morphology used to identify the species. While Buckley's original description (1866) contained inaccuracies regarding cuticular pigmentation, mandibular tooth count, and head shape, these features nonetheless have

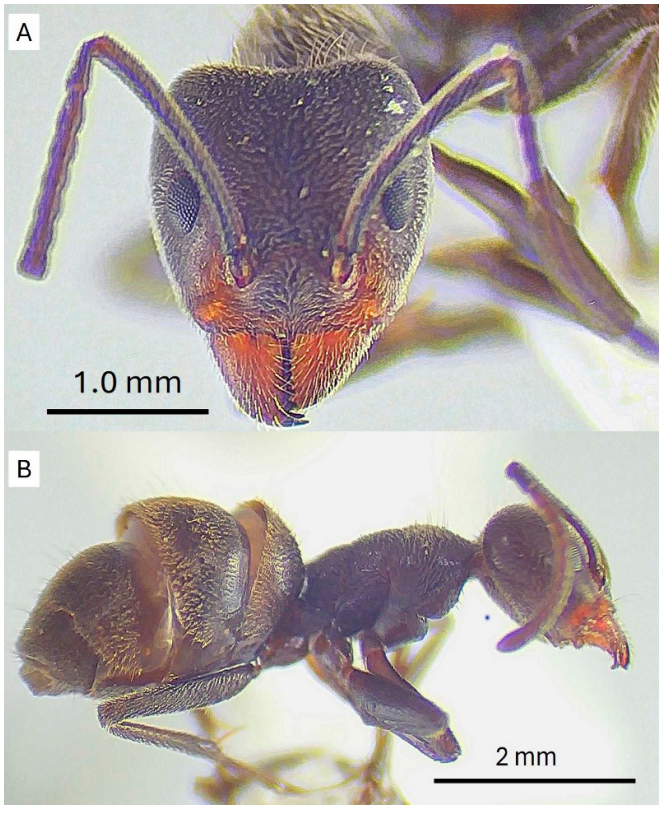


**Fig 1.** *Liometopum apiculatum* Worker. A: Head in frontal view. B: Body lateral view.

aligned with the general characteristics of *L. apiculatum* (Del Toro et al., 2009).

Morphologically, *L. apiculatum* is characterized by a pointed petiole and dense pubescence on the gaster (Wheeler, 1905). Workers of this species can be distinguished from *L. occidentale* and *L. microcephalum* based on coloration: *L. apiculatum* workers are concolorous dark brown to black, whereas *L. occidentale* and *L. microcephalum* are bicolored (dark brown or black with lighter regions) (Del Toro et al., 2009; Petráková & Schlaghamerský, 2017). Workers can also be separated from *L. luctuosum* by their denser pilosity and the morphology of the scape: in *L. luctuosum*, the scape is broader (0.22 mm) and does not extend beyond the posterior margin of the head by at least twice its maximum thickness (Del Toro et al., 2009).

Also, *L. luctuosum* workers are smaller (3.6 mm), exhibit a depressed mesosoma at the metanotal suture, and have very sparse or absent erect hairs on the gaster dorsum. Hairs on the thorax are mostly confined to the pronotum (Del Toro et al., 2009). *Liometopum lindgreeni* can be separated from *L. apiculatum* based on cephalic characters (having a narrower head), mesosomal characters (rounded dorsal face of propodeum), and petiolar characters (flat at petiolar apex) (Del Toro et al., 2009; Dubovikoff & Terekhova, 2015). In the case of *L. orientale*, it is distinguished by the lack of decumbent pilosity along the posterior margin of the head and by the presence of two long, erect hairs on each scape, located at the articulation between the scape and the funiculus. The species *L. sinense* is distinguished from other *Liometopum* species by its restricted geographic distribution in central China. *L. sinense* gynes are larger (>12 mm) than those of other *Liometopum* species (<12 mm). Males of *L. apiculatum* are larger and possess more than 20 hamuli on the hind wing, differentiating them from other *Liometopum* males (Del Toro et al., 2009) (Table 1).

According to Boudinot et al. (2022), *Lasius escamole* Reza 1925 must be regarded as a junior synonym of *Liometopum apiculatum*. They stated, "*Although Reza's description and illustrations are extremely vague, it is possible to see details that point to a dolichoderine identity*" (Boudinot et al., 2022). Descriptions of *L. apiculatum* workers consistently note a black to dark brown body color, long and thin antennae and legs, small ocelli, and a round head with a posterior depression (Del Toro et al., 2009). The anterior clypeal margin is straight, the eyes are large, and they are located in front of the middle of the head; the pronotum is convex, from the dorsal view, widest point is narrower than the maximum head width, with a very distinct promesonotal and metanotal suture weakly defined; the petiole is produced upward into a sharp point which in some specimens may be prolonged into a soft spine, and the first gastral tergite is partially overlapping the petiole (Del Toro et al., 2009; Wheeler, 1905).

Del Toro et al. (2009) described *L. apiculatum* workers, adding the following features: eyes large and oval-shaped, comprising 110-125 ommatidia; scapes extending beyond the posterior margin of the head by a distance at least twice the maximum thickness of the scape; an 11-segmented funiculus, with the first and terminal segments being the largest; punctate mandibles, bearing 8 teeth along the masticatory margin and 4-5 smaller teeth on the basal margin. Antennae exhibiting short, appressed pubescence, more than 20 long, erect hairs along the anterior margin of the clypeus. Mesosoma entirely covered in pubescence, and 12 or more long, erect hairs on the dorsum of the pronotum.

Females have been reported to measure 12–15 mm in length (Wheeler, 1905; Del Toro et al., 2009). Concolorous, dark brown to black, with short, dense, and abundant body hairs. Petiole scale-like, from lateral view with a sharp, angular node, from dorsal view apex bidentate, leaning anteriorly. Del Toro et al. (2009) add that the head is wider than long, with a strong posterior medial concavity apparent. Ocelli present. Eyes located more laterally than in workers, large oval-shaped, with over 150 ommatidia. Scapes do not surpass the posterior margin of the head. Mandibles punctate, 8-10 teeth on masticatory margin, 3-5 teeth on basal margin. Mesosoma is convex, smooth, lacking sculpturing, and the pronotum dorsal face is straight. Mesonotum is strongly arched; from a dorsal view, the mesonotum is globular, and the metanotal suture is distinct. Hind wing medial cells close with more than 20 hamuli. Gastral tergites 1-3 have equal width in lateral view, 4 and 5 decrease in total size. Antennae with dense, appressed pubescence. More than 25 long, erect hairs surpassing the anterior clypeal margin. Dense pubescence covering the entire gastral surface. Pubescence is light yellow to dark brown.

While Wheeler (1905) provided the first description of the males, Del Toro et al. (2009) redescribed them, highlighting several additional features. A notable discrepancy arises in the description of the funicular segments. Del Toro et al. (2009) reported equal-length segments, while Wheeler (1905) described the first joint as more than half the length of the second, with the third-to-last joints subequal and slightly shorter. A key attribute emphasized by Del Toro et al. (2009) for *L. apiculatum* males is the presence of 20 hamuli on the wings.

### *Distribution and habitat*

A comprehensive retrospective search of multiple databases (Guénard et al., 2017; Antsweb, GBIF, UNIBIO) has yielded more than 2,500 records of *Liometopum apiculatum* presence in North America and Central America. This ant species has been recorded in the southern United States, including Arkansas, Arizona, California, Colorado, New Mexico, and Texas. In Mexico, it has been reported from 25 of 32 states: Aguascalientes, Baja California, Chihuahua, Coahuila, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Mexico City, Michoacán, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Sinaloa, Sonora, State of Mexico, Tamaulipas, Tlaxcala, Veracruz and Zacatecas. The southernmost known distribution of this species encompasses the Petén department in Guatemala (Del Toro et al., 2009;

**Table 1**. Morphological characteristics of castes in *Liometopum* species.

| Species | Worker | Gyne | Male | Larvae |
|---|---|---|---|---|
| *Liometopum apiculatum* | Workers are light brown to dark brown. The antennal scape is long and thin, with short and erect hairs, and surpasses the posterior margin of the head by at least twice the maximum thickness of the scape. The dorsum of the mesosoma is convex with hairs on all surfaces; the longest hairs are on the dorsal surface of the pronotum (Del Toro et al., 2012). | Gynes are dark brown to black. They are large at over 15.0 mm in total length. The mesosomal dorsum is covered with many long, erect hairs and with dense appressed pubescence. The metanotal suture is distinct but does not break the smooth dorsal mesosomal margin (Del Toro et al., 2012). | Males are black and smaller in total length (11.3 mm) than gynes. The mesosoma is convex and smooth. The hind wings of males have 20 or more hamuli. The volsella has dense erect pilosity along the ventral margin and is finely denticulate along the posterior margin. The aedeagus has more than 20 denticles along the ventral margin (Del Toro et al., 2012). | Anterior end formed by the enlarged dorsal portion of the prothorax; head ventral near the anterior end. Anus ventral. Leg and gonopod vestiges present. Spiracles small but not uniform in size; first abdominal the largest, eighth abdominal the smallest. Body practically naked; hairs exceedingly few, widely scattered, stout, slightly curved, short. Few head hairs and exceedingly minute. The large antennae. Labrum short and broad; anterior surface with four scattered sensilla and two-minute hairs. Mandibles small and feebly sclerotized. Maxillae with a lateral patch of isolated spinules between palp and galea. Labium with spinules and a few sensilla on the anterior surface. Hypopharynx spiculose, the spinules arranged in sub transverse rows grouped in two narrow sub triangles which have their bases near the middle (Wheeler & Wheeler, 1951). |
| | **Worker** | **Gyne** | **Male** | |
| *Liometopum luctuosum* | Workers are small to medium-sized *Liometopum luctuosum* is a concolorous dark brown, feebly shining species with a cuticle covered in dense, appressed pubescence. The scapes do not surpass the posterior margin of the head by two times the maximum thickness of the scape. The metanotal suture is slightly depressed and breaks the continuity of the posterior mesosomal margin. Erect hairs on dorsum of gaster very sparse or absent, those on thorax mostly confined to pronotum (Wheeler and Wheeler, 1986; Del Toro et al., 2012). | Gynes are four times larger than the workers, slightly larger than the males and are light to dark brown. The dorsum of the mesosoma is covered with short erect hairs of equal length. The metanotal suture is clearly defined and depressed (Del Toro et al., 2012). | Males are black and smaller than the gynes. The hind wing has 14-18 hamuli. The volsella lacks pilosity along the ventral margin. The posterior ventral margin of the aedeagus has more than 20 defined triangular denticles with the posterior vertex of the aedeagus coming to a triangular apex (Del Toro et al., 2012). | |
| *Liometopum microcephalum* | Workers are bicolored, with a dark brown head, gaster, and legs, the mesosoma is lighter colored. The cuticle is covered in dense pubescence, interspersed with erect and suberect hairs. The longest erect hairs are on the pronotum. The scapes do not surpass the posterior margin of the head (Del Toro et al., 2012). | Gynes are slightly larger than males. The mandibular apical tooth is distinctly larger than the remaining masticatory teeth. The medial cephalic concavity is clearly defined (Del Toro et al., 2012). | Males are dark brown to black. The anterior clypeal margin is concave medially; it is straight in males of other species that were seen. The dorsal mesosomal margin is convex and notably depressed at the metanotal suture. The posterior lobe of the volsella has a straight posterior margin. The aedeagus has 15-18 small triangular denticles along the ventral margin (Del Toro et al., 2012). | |
| *Liometopum occidentale* | Workers are a bicolored species, having a dark brown head and gaster with a lighter colored mesosoma, usually golden yellow, but some may be light brown. The antennal scapes are short and surpass the posterior margin of the head by less than twice the maximum thickness of the scape. The scape has few short hairs. The longest erect hairs are on the dorsal surface of the pronotum. The mesosoma is convex with the highest point at the mesonotum (Del Toro et al., 2012). | Gynes of this species are dark brown to dull yellow. Queens are slightly larger (11 mm). The metanotal suture is distinct, but weakly depressed and does not break the continuity of the mesosomal margin (Del Toro et al., 2012). | Males of this species are dark brown to black. The first discoidal cell of the forewing is rectangular, the hind wings have 15-17 hamuli. The posterior lobe of the volsella has a strong concavity along the dorsal margin. The aedeagal ventral margin has 15-18 small triangular denticles covering the half of the ventral aedeagal margin, with an even concavity posterior to the denticles (Del Toro et al., 2012). | |
| | **Worker** | | **Male** | |
| *Liometopum orientale* | This species lacks pilosity along the posterior margin of the head, and the scapes present two long, erect hairs at the junction of the scape and the funiculus. The first funicular segment is three times longer than wide. The petiole is spade-like and it is rounded at the apex (Kupyanskaya, 1988; Del Toro et al., 2012). | | In the males of this species, the parameters are triangular shaped, the ventral margin of the paramere is straight, and lacking the concavity (Kupyanskaya, 1988; Del Toro et al., 2012). | |
| | **Worker** | | | |
| *Liometopum lindgreeni* | The workers are light brown with a dull sheen on their cuticle, which is covered in short pubescence and has a low density of pilosity on the dorsal surface of the gaster. Their antennal scapes extend beyond the posterior margin of the head by at least twice the scape's maximum thickness. The mandibles are much less curved and longer than those of microcephalic individuals, featuring a long terminal edge with approximately 8–10 teeth, smooth and shiny. The head is heart-shaped with convex sides. The first funicular segment is three times longer than it is wide. The anterior clypeal margin is straight and bears 10–12 hairs that extend beyond the margin. The pronotum is slightly convex, while the metanotal suture is weakly concave. The petiole is scale-like and flattened at the apex (Forel, 1902; Del Toro et al., 2012). | | | |
| *Liometopum sinense* | The workers range in color from dark brown to copper and are densely covered in pubescence across their entire body, with finer pubescence on the mesosoma compared to the gaster. The antennal scapes reach but do not extend beyond the posterior margin of the head and are also covered in pubescence. The anterior clypeal margin is slightly concave, while the mandibles are punctate, with the apical tooth being the largest. Major workers possess a medial ocellus and have 8–10 teeth along the masticatory margin, with an additional 3–4 teeth on the basal margin of the mandible. The pronotum features 8–12 long, erect hairs on its dorsal surface. Fine, appressed pubescence covers the entire mesosoma, which is moderately convex, reaching its highest point at the mesonotum. The petiole is scale-like with a sharply pointed apex (Del Toro et al., 2012). | | | |

Hoey-Chamberlain et al., 2013; Guenard et al., 2017; Dáttilo et al., 2020; Berumen Jiménez et al., 2021) (Figure 2). The occurrence of *L. apiculatum* in British Columbia, Canada, as reported by Naumann et al. (1999), has remained a matter of debate and is considered likely a misidentification (Higgins & Lindgren, 2010).

The species has been recorded at elevations ranging from 30 to 2,900 m a.s.l. (Del 162 Toro et al., 2009; Hoey-Chamberlain et al., 2013; Lara-Juárez et al., 2015; Berumen Jiménez et al., 2021) and occurs across a wide range of vegetation types, including oak forests, pinyon pine, ponderosa pine, cedar, riparian vegetation, xeric scrub, and grasslands (Del Toro et al., 2009; Hoey-Chamberlain et al., 2013; Lara-Juárez et al., 2015; Miller, 2007; Ramos Elorduy et al., 1988; Rodríguez Elizalde & Castaño Meneses, 2024; Van Pelt, 1971). Dubovikoff et al. (2012) documented nesting association of *L. apiculatum* colonies with 11 distinct plant communities in Tamaulipas, Mexico: *Pinus cembroides* Forest, *Quercus* Forest, *Quercus-Juniperus* Forest, rosetophyllous *Yucca filifera*, Forest Subcadocylian Tropical, Forest Tropical Deciduous, Tamaulipan Thorny Scrub, Microphyllous Scrub, Rosetophilous Scrub of *Dasylirion miquihuanense*, Quercus Scrub in Pinus Forest, and Submontane Scrub.

Berumen-Jiménez (2018) overlaid occurrence records of *L. apiculatum* with a climatic (García, 1998) and edaphic map layers (INIFAP & CONABIO, 1995) to identify the range of environmental types encompassed within its distribution in Mexico. Although these do not represent direct records of nesting sites, they indicate that the species' distribution overlaps with twelve climatic categories according to the Köppen classification (1936): BS0k(x') (temperate arid), BS1kw (temperate semi-arid), BS0hw (warm arid), C (w1) (temperate sub-humid), Cb (w2 ) (cool sub-humid, with a long and cool summer), BS1 hw (warm semi-arid), BS0 (h') (x') (warm arid) BWhw (warm very arid), (A)C(w1) (warm sub-humid of group C), A(C)w2(w) (warm sub-humid), Aw1 (x') (warm sub-humid) and C(f) (temperate humid) reflecting a broad tolerance to contrasting temperature and moisture regimes. Within these regions, the species occurs across multiple soil subtypes inferred from that analysis, including: calcareous phaeozem, calcareous regosol, calcium xerosol, chromic luvisol, dystric regosol, eutric cambisol, eutric fluvisol, eutric histosol, eutric regosol, gypsic xerosol, haplic chestnut, haplic phaeozem, haplic xerosol, humic acrisol, humic andosol, lithosol, luvic phaeozem, luvic xerosol, mollic planosol, ortic luvisol, ortic solonchak, pelic vertisol, rendzina, and vertic luvisol (Berumen-Jiménez, 2018). These soil types, climates, together with the corresponding vegetation (from xerophytic scrub to oak-pine forest), suggest that *L. apiculatum* can occupy a wide range of environmental conditions within its distribution. Finally, the distribution of *L. apiculatum* has encompassed several lithological types, including rhyolite-tuff-volcanic, shale-sandstone, limestone, and alluvial deposits (Lara-Juárez et al., 2015).

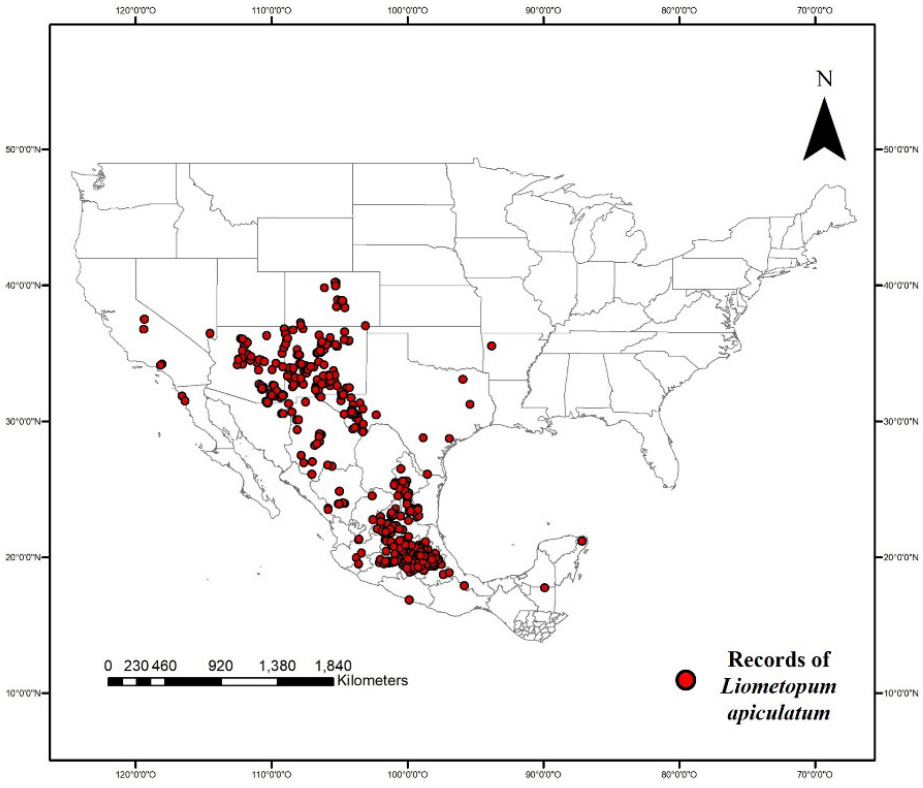


**Fig 2.** Geographical distribution of *Liometopum apiculatum*.

*Nest*

These ants have been reported to nest in a wide variety of sites, including under rocks, within dead tree trunks, and at the base of numerous plant species such as *Agave salmiana* subsp. *crassispina* (Trel.), *Agave lechuguilla* Torr., *Agave chisosensis* C.H. Mull., *Yucca filifera* Chabaud, *Cylindropuntia tunicata* (Lehm.) Link & Otto, *Cylindropuntia imbricata* (Haw.) DC., *Ferocactus pilosus* (Gal.) Werderm., *Myrtillocactus geometrizans* (Mart.) DC., *Quercus* spp., *Pinus ponderosa* Douglas ex Lawson, *Pinus cembroides* Zucc., *Juniperus monosperma* (Engelm.) Sarg., other *Juniperus* spp., *Prosopis juliflora* (Sw.) DC., *Senecio praecox* DC., and *Schinus molle* L. (Cuadriello, 1980; Miller, 2007; Hoey-Chamberlain et al., 2013; Cruz-Labana et al., 2014; Lara-Juárez et al., 2015; Rafael-Valdéz et al., 2017; Romero-Jiménez et al., 2024). Nests have also been reported in glass containers and rubber tires (Hoey-Chamberlain et al., 2013).

The trabecula, a porous structural mass that forms part of the nest, has been described as spherical, ovoid, cylindrical, or star-shaped, with large interconnected meshes resembling a sponge. It is composed primarily of mineral materials and, to a lesser extent, organic substances such as plant fibers (roots and branches) and finer mycelial threads of some fungi (Conconi et al., 1987; Hoey-Chamberlain et al., 2013; Lara-Juárez et al., 2015). Sand and clay particles are solidly cemented together, and crystals of various substances are incorporated, some of which look like mica flakes. All the materials would seem to be held together also by the salivary secretion produced by the ant workers (Cuadriello, 1980; Gulmahamad, 1995; Ramos Elorduy et al., 1988). The trabecula is attached to the walls of the soil, and it can be enlarged by workers as the colony grows, as evidenced by the different colors of the trabecula. This structure serves to hold and protect the immature stages of the species (Cuadriello, 1980). The queen is always well protected and is usually in a remote place about 6-8 m from the largest chamber, where the brood is stored, and the chambers are connected by various galleries (Hoey-Chamberlain et al., 2013). Nest entrances have been reported to range from 1.5 to 5.0 cm in diameter and are surrounded by debris, including the remains of dead workers, soil, and sand. From each entrance, three to five paths arise, and the width of each path has been related to nest age (Cuadriello, 1980; Ramos Elorduy et al., 1988; Miranda Román et al., 2011).

Seasonal variations in average temperature and relative humidity within nests have been observed. During summer (June to September), which includes the dry/warm and rainy seasons, temperatures of 22 °C and 21 °C were recorded, accompanied by relative humidity of 93.1% and 91.5%, respectively. Towards the end of summer, values have been reported as 19.5 °C and 80.6%, whereas the dry/cold season (winter) has exhibited 16.1 °C and 81.3 % (Cruz-Labana et al., 2024).

Nest density has been linked to vegetation cover, which protects from sunlight. In overgrazed grasslands, densities have been reported as low (1.19 $ha^{-1}$). In sites with more appropriate plant cover or with moderate disturbance, densities increase to 11.9–14 $ha^{-1}$; however, many of these nests have been abandoned, and *L. apiculatum* colonies were no longer present (Lara-Juárez et al., 2015). Likewise, in some places, a positive relationship has been observed between *L. apiculatum*, the density of *Agave salmiana* and *A. crassispina*, and the presence of hemipterans (Cruz-Labana et al., 2014).

*Colonies*

Colonies have exhibited significant variability, ranging from a few hundred workers to as many as 250,000 individuals, and can include multiple queens (Gregg, 1963; Ramos-Elorduy & Levieux, 1992). Colonies exploited for humans have contained between 65,000 and 85,000 individuals (Lara-Juárez et al., 2015). *L. apiculatum* colony foundation occurs by haplometrosis (non-cooperative), in which a solitary fertile queen establishes each colony; however, foundation behavior has not been uniform among queens. Behaviors such as exploring, excavating, and removing excavated materials and waste are usually higher throughout the day, while oviposition, brood care, and inactivity increase at night (Conconi et al., 1987). Founding queens prefer sites close to bodies of water; however, sites slightly further from water are better for the establishment of a prosperous colony, as high humidity will result in the early death of a colony due to fungal invasion (Conconi et al., 1983a).

*Liometopum apiculatum* colonies can be monodomic (one nest) (Wheeler, 1905; Cruz-Labana et al., 2014; Lara-Juárez et al., 2015; ) or polydomic (multiple nests) (Del Toro et al., 2009; Hoey-Chamberlain et al., 2013). Despite the importance of understanding the nesting strategy of *L. apiculatum* to determine population limits in ecosystems, studies on their nests and colonies have remained scarce. Colony boundaries play a crucial role in shaping the evolution and ecology of ants, as well as their interactions with other organisms and the environment. This aspect is especially relevant for species conservation and assessing the impacts of invasive species. Therefore, the effort level and the optimal strategy conservation will depend on the population size of the species in question (Shaffer, 1981; Ellis et al., 2017), and the determination of the colony boundaries is vital to ensure the generation of scienti-fically sound conclusions (Ellis et al., 2017); this topic remains unexplored in *L. apiculatum* and could guiding commercial management strategies.

According to a literature review of the physical and chemical characteristics of *L. apiculatum* nests, Cruz-Labana et al. (2024) reported that soil moisture levels within nests reach 10.7%, compared to 8.8% in random soil samples. This difference is likely due to the presence and activities of the ants. Other notable variations include: the bulk density of the nests is 1.2 $g/cm^3$, while soil samples from nearby random sites (taken outside the nests as controls) had a density of 1.3 $g/cm^3$. The nests exhibit a mechanical penetration resistance of 2.05 ± 0.98 MPa, whereas random sites have a resistance

of 2.87 ± 0.75 MPa at a depth of 10 cm. In terms of chemical properties, the pH of the nests is slightly higher (7.2) compared to random sites (7.0). Electrical conductivity is also greater in nests (*L. apiculatum*: 321.9 µS/cm) than in random soil samples (203.5 µS/cm). Additionally, the organic matter content in the nests (6.9%) is nearly double that at random sites (3.8%). The authors attributed these differences to bioturbation processes and nest architecture, which influence the soil's physical and chemical properties.

*Chemistry*

Cruz Labana et al. (2023) have evaluated foraging trails and gaster composition using electronic nose (e-nose) analysis and chromatographic techniques. The semiochemicals of *L. apiculatum* have been identified during pre-season, season, and post-season larval collection. Thirty-two semiochemicals were identified: nine (28%) in pre-season, nine (28%) in season, and 14 in post-season (44%). Semiochemicals identified in *L. apiculatum* nests can induce behavioral or physiological responses; for example, 5-methylundecane (PRE), 7- methyltridecane and tridecane (post-season) are volatiles that have been identified in virgin females and queens of *Formica polyctena* with some intraspecific function (Löfqvist & Bergström, 1980; Bos & d'Ettorre, 2012). It has been proposed that eicosane may stimulate recognition among conspecific colonies (Santos-Junior et al., 2022) and mark trunk routes leading to food sources (Hölldobler et al., 2004).

In other social arthropods, the hydrocarbon 1-tetradecene ($CH_2$=CH-($CH_2$)$_{11}$-$CH_3$) has been reported to function as an antimicrobial agent (Lammers et al., 2021). It is possible that *L. apiculatum* produces this compound as a cuticular hydrocarbon (CHC), which acts as a defense against pathogens. Undecane ($C_{11}H_{24}$), an alkane observed in season and post-season nests, possibly affected intra and interspecific communication in *L. apiculatum* (Cruz-Labana et al., 2023). The abundant presence of dodecane ($C_{12}H_{26}$) has been shown to stimulate aggression in *Pogonomyrmex* spp. It may also play a role in colony return guidance, as well as defense and alarm signaling in interspecific interactions (Welzel et al., 2018).

*Feeding*

*Liometopum apiculatum* has been described as an omnivorous ant that consumes a variety of foods, including secretions, excretions, and the buds of various plants. It also consumes living or dead animals, wasps, crustaceans, annelids, mollusks, butterfly larvae, beetle larvae, and adult insects, as well as animal and human excrement (Cuadriello, 1980; Velasco Corona et al., 2007). Likewise, a group of individuals has recently been found feeding on *Centruroides infamatus* C. L. Koch, 1944, a scorpion belonging to the family Buthidae (Chávez-Samayoa et al., 2021). *Liometopum apiculatum* has exhibited a dietary behavior of consuming waste products from other ant species, such as *Pogonomyrmex barbatus*, *Camponotus sayi*, and *Solenopsis xyloni*. However, their main energy source is the honeydew exuded by hemipterans (Lara-Juárez et al., 2015; Velasco Corona et al., 2007): coccids, aphids, pseudococcid scales, or dactylopiid scales (Cuadriello, 1980; Hoey-Chamberlain et al., 2013; Lara-Juárez et al., 2015; Velasco Corona et al., 2007) (Table 2).

*Foraging*

*Liometopum apiculatum* forages from March to September; during winter, it does not hibernate but maintains reduced patrolling activity, which can increase temporarily after warm days (Mackay & Mackay, 2002; Hoey-Chamberlain et al., 2013). Workers forage along 2-3 cm-wide trails on the soil surface; when the temperature rises at midday, they stop foraging and shelter under stones (Conconi et al., 1983a; Ramos-Elorduy & Levieux, 1992). Shapley (1920) described that *L. apiculatum* maintains foraging trails for several years; ants walk toward or away from the nest, allegedly patrolling. These ants exhibit both diurnal and nocturnal activity, and the differences in size of the workers allow the possible correlation of activity with their hardiness and size (Shapley, 1920; Ramos-Elorduy & Levieux, 1992). Foraging activity occurs across a wide range of environmental factors, including temperature, humidity, light, and wind (Shapley, 1920; Mackay & Mackay, 2002). Ants have maintained trails across a range of relative humidity, from near 100% to as low as 5%. Patrol activity occurs at temperatures up to 38°C and down to below 8°C, even near snow banks (Shapley, 1920). Large nest populations of *Liometopum* result in high trail densities. During warmer months and under favorable weather conditions, colony populations can number in the tens of thousands, with up to 140,000 ants observed moving in and out of nests (Ramos-Elorduy & Levieux, 1992; Hoey-Chamberlain et al., 2013). The kinetic response of these ants is primarily a function of temperature, with other meteorological factors having little to no impact on foraging speed, including light and time of day. The maximum activity has been recorded between noon and midnight, at 14–38 °C (Shapley, 1920).

According to Cruz-Labana et al. (2014), in semi-arid habitats where agaves are abundant, foraging trails are commonly distributed throughout agave plants, which provide both thermal regulation and foraging opportunities; in fact, 61% of the agaves near nests have exhibited scale insect infestations. Ants have established trails near agave plants that harbor scale insects, from which they feed on secretions year-round (Velasco-Corona et al., 2007). In these environments, mesquite, yucca, and juniper also provide suitable vegetation for foraging activities. Nevertheless, vegetation structure can also influence the distribution of insect food sources and the selection of nesting sites (Cruz-Labana et al., 2014).

Colonies commonly maintain one to six foraging trails, whose length varies according to habitat conditions, and none of which intersect (Lara-Juárez et al., 2015; Rafael-Valdez et al., 2017). The foraging area of *L. apiculatum* has been reported to range from 468 to 2,467.2 m² (Ramos-Elorduy & Levieux,

**Table 2.** Species of Hemipterans associated with *Liometopum apiculatum*: potential food sources and host plants.

| Familia | Especie | Hospedero | Reference |
|---|---|---|---|
| **Membracidae** | *Vanduzea segmentata* Fowlwe | *Nolina erumpens* | (Van Pelt, 1971; Velasco et al, 2007) |
| **Aphididae** | *Cinara* sp.1 | *Pinus rudis* y *Junip erus deppeana* | (Velasco et al, 2007) |
| | *Cinara* sp.2 | *Pinus rudis* y *Juniperus deppeana* | (Velasco et al, 2007) |
| | *Anoecia cornicola* | *Schizachyrium sanguineum* | (Velasco et al, 2007) |
| | *Aphis lugentis* | *Senecio salignus* | (Velasco et al, 2007) |
| | *Aphis solitaria* | *Stevia subpubescens* | (Velasco et al, 2007) |
| | *Aphis helianthi* | *Agave* sp. | (Velasco et al, 2007) |
| | *Aphis* sp. | *Castilleja tenuiflora* | (Velasco et al, 2007) |
| | *Aphis* sp. 1 | *Gnaphalium* sp. | (Cuadriello, 1980) |
| | *Aphis* sp. 2 | *Myrtillocactus geometrizans* | (Cuadriello, 1980) |
| | *Aphis* sp. 3 | *Myrtillocactus geometrizans* | (Cuadriello, 1980) |
| | *Aphis* sp. 4 | *Senecio praecox* | (Cuadriello, 1980) |
| **Pseudococcidae** | *Dysmicoccus brevipes* | *Agave* sp. | (Velasco et al, 2007) |
| | No identified | *Loeselia mexicana* | (Velasco et al, 2007) |
| | *Pseudococcus agavis* | *Agave* sp. | (Cuadriello, 1980) |
| | *Anisococcus* sp. | *Viguiera dentata* | (Cuadriello, 1980) |
| | *Crisicoccus* sp. | *quercus* sp. | (Cuadriello, 1980) |
| | *Puto yuccae* | *Opunita* sp. *Agave* sp. | (Cuadriello, 1980) |
| | *Cataenococcus olivaceus* | - | (Cuadriello, 1980) |
| **Coccidae** | *Saissetia oleae* | *Baccharis conferta* | (Velasco et al, 2007) |
| | *Saissetia* sp.1 | *Stevia salicifolia* | (Velasco et al, 2007) |
| | *Saissetia* sp.2 | *Phoradendron minutifolium* | (Velasco et al, 2007) |
| | *Neolecanium herrerae.* | *Agave* sp. | (Cuadriello, 1980) |
| | *Coccus pseudomagnoliarum* | *Physalis* sp. | (Cuadriello, 1980) |
| | *Ceroplastes sinensis* | *Baccharis conferta* | (Cuadriello, 1980) |
| | *Saissetia oleae* | *Schinus molle* | (Cuadriello, 1980) |
| | *Saissetia nigra* | *Schinus molle* | (Cuadriello, 1980) |
| **Dactylopiidae** | *Eriococcu* sp. | Baccharis conferta | (Velasco et al, 2007) |
| **Ortheziidae** | No identified | *Stipa ichu* | (Velasco et al, 2007) |
| | *Orthezia* sp. | *Zaluzania* sp. | (Cuadriello, 1980) |
| **Eriococcidae** | *Eurycoccus copallinae* | *Agave lechuguilla* | (Cuadriello, 1980) |
| | *Alpinococcus* sp. 1 | *Eupatorium capilifolium* | (Cuadriello, 1980) |
| | *Alpinococcus* sp. 2 | *Brickellia veronicifolia* | (Cuadriello, 1980) |
| | *Ovaticoccus agavium* | *Parthenium hysterophorus* | (Cuadriello, 1980) |
| | *Eriococcus* sp. | *Zaluzania* sp. | (Cuadriello, 1980) |
| **Diaspididae** | *Acutaspis agavis* | *Agave* sp. | (Cuadriello, 1980) |
| | *Odanaspis* sp. | *Zaluzania* sp. | (Cuadriello, 1980) |
| | *Hemiberlesia lataniae* | *Opunita* sp. | (Cuadriello, 1980) |

1992; Rafael-Valdez et al., 2017). Earlier, Ramos-Elorduy and Levieux (1992) reported smaller foraging territories, ranging from 708 m² to xxx m² (mean 612 m²), and noted that colonies exploited only 16–30% of their territory at any given time. The average distance from nest to substrate is 24.3 m (Rafael-Valdez et al., 2017), although personal observations indicate maximum foraging distances of 40 m and up to 100 m (Cuadriello, 1980). These values should be interpreted with caution, as comparisons under different scenarios show large differences in coverage (2,467.2, 5,026.55, and 31,415.93 m², respectively).

Foraging distances may be influenced by both biotic and abiotic factors, including interspecific competition, resource availability, and ground complexity (Hoey-Chamberlain et al., 2013; Lara-Juárez et al., 2015; Berumen-Jiménez et al., 2021). Key variables determining foraging area size include the presence of plants such as *Agave salmiana, Yucca* spp., *Prosopis* spp., and *Acacia farnesiana*, as well as soil cover (Rafael-Valdez et al., 2017).

*Life cycle*

The life cycle of *L. apiculatum* includes four stages: egg, larva, pupa, and adult. Immature stages of the reproductive caste have been found in nests from May to August, whereas the rest of the year, the brood is the worker caste (Conconi et al., 1983b; Del Toro et al., 2009). Feeding has been shown to release hormones in Formicidae, including juvenile hormone and ecdysteroids, as well as neurohormones such as octopamine and dopamine, which together regulate development, reproduction, metabolism, and social behavior (Hölldobler & Wilson, 1990; Eelen et al., 2006).

Seasonal food availability directly influences the life cycle of the colonies, since carbohydrate-rich resources sustain worker activity, while protein-rich resources are required for larval development and the production of new individuals (Ramos-Elorduy & Levieux, 1992; Miller, 2007). Periods of higher food availability, mainly in spring and summer, coincide with increased brood rearing and reproductive activity within the colonies (Ramos-Elorduy et al., 1988). Volatile organic compounds (VOCs) have been detected in the habitat of *L. apiculatum* both before and during the production of the ant's reproductive caste. These compounds include saturated hydrocarbons, aldehydes, alcohols, and esters, with variations observed between the preseason and the escamol production season (Hernández-Roldán et al., 2024). Some of these VOCs play key roles in the life cycle of ants, such as trail marking, danger signaling, and mating (Gordon, 2021; Paterson & Adams, 2022). Reproductive events have been synchronized with seasonal food availability, which ensures sufficient resources for the establishment and initial development of new colonies. Nuptial flights of this species have usually occurred the day after heavy rains in April or May (Lara-Juárez et al., 2015). Males and gynes have been collected outside nests from June to August, while queens (likely founding queens) have been reported in July and August under stones and other landscape features (Del Toro et al., 2009).

Rainwater must enter the site where the nest will be established; it has been proposed that humidity facilitates the excavation of fertilized gynes during nest founding. Nuptial flights have usually occurred on warm, sunny days (26 °C) between 10:00 and 12:00 a.m. (Conconi et al., 1983b). They begin with workers leaving the nest in an agitated manner, followed by the emergence of gynes and males. Once outside, workers bite the legs and wings of the reproductives until they take flight (Conconi et al., 1983b; Cuadriello, 1980). The flight lasts 10–12 minutes, during which reproductive individuals travel an average of 150 m from the original nest. Gynes are the first to take flight, followed by males, which ascend in vertical zigzagging movements. Both sexes rise to 12–15 m, where copulation occurs, after which they begin their descent. Upon landing, they separate, and the males die shortly afterward. Gynes may mate with several males (polyandrous fertilization) and store between seven and 300 million spermatozoa in their spermatheca (Fernández, 2003). Once on the ground, queen detach their wings themselves and eat them, then walk to find a site for nest foundation, usually under a stone or near the base of a shrub, where they begin digging (Conconi et al., 1983b).

A single queen per nest establishes the colony through haplometrosis (Conconi et al., 1987b). Oviposition begins two days following the nuptial flight, and by the fifth day, the queen have deposited 400-600 eggs. Maternal care is exhibited: the first eggs are carried in her mandible and placed beneath her, as if she were incubating them, and the queen uses her jaw to relocate the eggs and position them beneath her, simulating incubation (Conconi et al., 1983b).

Only a small percentage of eggs reach the adult stage; most of the smaller eggs, known as trophic eggs, are ingested. Once the queen has laid her first batch of eggs, she delays further oviposition until these eggs have developed into pupae. When the first workers emerge, the queen ceases laying trophic eggs, reducing the total number of eggs but increasing the proportion of viable ones. Eggs have been laid throughout the year (Conconi et al., 1983b). As a survival strategy, some unfertilized queens emerge from the nest, remove their wings, and dig without mating. Queens exhibit maternal care only toward recently oviposited eggs that have not undergone discoloration or desiccation (Conconi et al., 1983b). If the queen dies within a colony, workers may continue brood care and nest development; in some cases, they will lay unfertilized eggs that are eaten or develop only into males (Hoey-Chamberlain et al., 2013). Nest growth begins after the second worker generation, when the queen focuses on oviposition, and workers build nest structures, feed the queen, and transport eggs to the trabecula (Ramos-Elorduy et al., 1988). In this stage, the worker population has been observed to grow exponentially in response to food availability (Hölldobler & Wilson, 1990).

Conconi et al. (1983a) studied the *L. apiculatum* life cycle under laboratory conditions. Queens were collected post-nuptial flight and maintained in glass tubes with water and cotton in jars with soil. This research was performed across a range of temperature, humidity, and substrate conditions: 28.23 ± 4 days at 30 °C and 70-80% relative humidity in glass tubes, and 70.83 ± 11.3 days at 26 °C and 40-50% relative humidity in soil-filled containers with stones. Nonetheless, the life cycle duration showed a three-fold increase when queens were maintained under natural environmental conditions. The artificial environment of glass tubes significantly impacts worker production, reducing it to 12.5% of the average. Optimal worker production and growth have been shown to depend on temperature and feeding conditions, with a preference for temperatures around 26 °C and for soil substrates, specifically soil-filled containers with stones (Table 3).

*Biotic Interactions*

Various organisms have been documented within the nests of *L. apiculatum*, with variations observed among different colonies. Beetles of the Staphylinidae family, including *Sceptobius schmitti* Wasmann 1901, *Dinaridella liometopi* Wasmann 1901, *Dinaridella mexicana* Mann. 1914, and *Sceptobius dispar* Sharp 1883, have been found within nests (Danoff-Burg, 2002). The weevil *Liometophilus manni* Fall, 1912 has also been discovered in *L. apiculatum* galleries (Mann, 1914). The behavior of *Sceptobius* beetles has been characterized by their long legs and swift movements, allowing them to rapidly approach ant colonies, engage in brief grooming interactions, and then retreat to the nest periphery. The interactions between *Dinaridella mexicana* and *D. liometopi*, and their host ants, have been described as active and sometimes aggressive. A beetle approaches a stationary ant laterally, grooms its legs with its mouthparts, and then mounts the ant to groom its dorsum. This interaction lasts 3 to 20 minutes and has been suggested as a mechanism for transferring cuticular hydrocarbons that specify colony odor from the ant to the beetle (Danoff-Burg, 1994).

Other interactions include predation: the snake *Conopsis lineata* feeding on larvae of *L. apiculatum* and the red mite *Trombidium holosericeum* near the foraging paths inside and outside the nest (Ramos Elorduy et al., 1988), feeding on eggs and pupae (Cuadriello, 1980). The ants do not attack the mite because of its intense red color, which can alert the ants to the presence of toxic substances (Cuadriello, 1980). Within some *L. apiculatum* nests, crickets of the genus *Myrmecophila* have been observed; these adopt the color and odor of the ants and feed on ant regurgitations (Desutter-Grandcolas, 1997).

**Table 3**. Developmental timeline of *Liometopum apiculatum* colonies under different environmental conditions (modified from Ramos-Elorduy et al., 1983).

| Developmental Stage | Glass Tubes (32 °C, 70-80% RH) | Jar with Soil (26 °C, 40-50% RH) |
|---|---|---|
| **First egg laid** | 11.00 ± 2.3 days | 27.80 ± 6.9 days |
| **First larva observed** | 9.84 ± 2.4 days | 25.16 ± 7.8 days |
| **First pupa formed** | 9.61 ± 2.1 days | 24.20 ± 6.2 days |
| **First adult emerged** | 28.23 ± 4.0 days | 70.83 ± 11.3 days |
| **Total development time** | 28.23 ± 5.0 days | 70.83 ± 11.4 days |

Hemipterans and *Liometopum apiculatum* workers exhibit a trophobiotic interaction, characterized by the provision of honeydew by hemipterans (Way, 1963) and the facilitation of plant space occupation for insect feeding by ants (Delabie, 2001). In some instances, hemipterans have been impregnated with the colony odor (Fernández, 2003). Currently, *L. apiculatum* has been reported to interact with eight hemipteran families: Membracidae, Aphididae, Pseudococcidae, Coccidae, Dactylopiidae, Ortheziidae, Eriococcidae, and Diaspididae (Table 2).

*Liometopum apiculatum* is also associated with hemipteran host plants, such as *Agave salmiana* Otto ex Salm (Aphididae and Pseudococcidae), *Baccharis conferta* Kunth (Aphididae and Coccidae), *Castilleja tenuiflora* Benth. (Aphididae), *Juniperus deppeana* Steud. (Diaspididae and Pseudococcidae), *Loeselia mexicana* (Lam.) Brand. (Aphididae and Membracidae), *Phoradendron minutifolium* Trel. (Aphididae and Coccidae), *Pinus rudis* Endl. (Pseudococcidae), *Schizachyrium sanguineum* (Resyz.) Alston (Aphididae), *Senecio salignus* DC. (Aphididae and Coccidae), *Stevia salicifolia* Cav. (Aphididae and Pseudococcidae), *Stevia subpubescens* Lag. (Aphididae and Membracidae), and *Stipa ichu* (Ruiz & Pav.) Kunth (Aphididae) (Velasco Corona et al., 2007).

The bacterial community in larvae and guts, as analyzed by González-Escobar (2020), has a complex composition, including Proteobacteria, Firmicutes, and Actinobacteria. Species have included *Exiguobacterium* sp., *Acinetobacter johnsonii, Pantoea agglomerans, Serratia marcescens, Serratia rubidaea, Enterobacter asburiae, Serratia ficaria, Bacillus simplex, Bacillus pumillus, Dietzia natronolimnaea, Staphylococcus warneri,* and *Bacillus pumillus*, associated with the production of cellulases, amylases, xylanases, and ligninases.

Likewise, other microorganisms have been detected, including *Serratia ficaria, Enterobacter asburiae, Pantoea agglomerans, Acinetobacter johnsonii, Serratia rubidaea,*

*Serratia marcescens, Staphylococcus warneri, Microbacterium hydrocarbonoxydans, Pseudomonas graminis, Rhodococcus,* and *Bacillus simp*lex, which have been associated with the degradation of aromatic compounds such as phthalate esters, phenol, polychlorinated biphenyls, and bisphenol-A. Furthermore, the *L. apiculatum* microbial community has been shown to degrade polysaccharides, including starch, cellulose, and xylan. These findings suggest a correlation with feeding behavior, since ants have specialized in collecting diverse food sources in arid and semi-arid ecosystems, requiring enzymatic digestion. Symbionts of *L. apiculatum* not only contribute to feeding but also represent a potential source of enzymes for biotechnological applications, including lignocellulosic biomass hydrolysis and bioremediation (González-Escobar et al., 2020).

*Liometopum apiculatum* inhabits arid and semi-arid zones, characterized by extreme temperature variation and limited flora and fauna. The abundance of symbiotic microorganisms has been suggested to relate to nutrient acquisition and protective mechanisms aiding survival (Soen, 2014). Specialist bacterial genera, including *Weissella, Lactococcus, Bacillus,* and *Macrococcus*, have been identified. Their functional roles may involve carbohydrate utilization for energy during larval development. Furthermore, these bacteria are known for antimicrobial activity via organic acid and bacteriocin production, which serve as protective agents since larvae are highly susceptible to infections (Audisio et al., 2011; Engel et al., 2012). González-Escobar et al. (2018) described the microbial composition in adult ants as dominated by the orders Pseudomonadales, Flavobacteriales, Sphingobacteriales, and Sphingomonadales; notably, these orders have also been reported within the core microbiome of agave species (Coleman-Derr et al., 2016).

*Nutritional value*

The larvae of *L. apiculatum*, known in Mexico as "escamoles", have been consumed in Central Mexico since the pre-Hispanic era due to their exquisite flavor and nutritional value (Ladrón de Guevara et al., 1995; Ramos Rostrol et al., 2012; Melo-Ruiz et al., 2013). The nutritional composition of "escamoles" has been characterized by a high protein content (42%) with a favorable essential amino acid profile. They have also been reported as rich in essential lipids, including oleic (67.66%), linoleic (2.61%), and arachidonic (0.16%) acids, and they contain vitamins A and E, thiamin, riboflavin, and niacin (Melo-Ruiz et al., 2016). The protein content in 100 grams of larvae surpasses that of beef, chicken, eggs, and fish. Lipids are present in significant amounts and include true fats, essential fatty acids, compound lipids, and fat-soluble vitamins or provitamins such as carotenoids. The mineral content has been reported at approximately 7.19 ± 0.1%. Dietary fiber, representing non-digestible carbohydrates, is present in low amounts, while soluble carbohydrates, an energy source, are relatively deficient compared with dietary requirements. The amino acid profile includes essential amino acids such as methionine and tryptophan, the latter being a precursor of niacin (vitamin B3) (Ladrón de Guevara et al., 1995; Ramos Rostrol et al., 2012; Melo-Ruiz et al., 2013, 2016).

The butter-frying of escamoles has been shown to accelerate the degradation of triacylglycerides, yielding free fatty acids, with oleic acid accounting for 17.48%. This process also leads to an increase in lipids with double linkages (133.79 cg I2 $g^{-1}$) and the formation of oxidation products (3.60 meq O2 $kg^{-1}$ of oil). Escamol oil extracted from dehydrated and butter-fried escamoles has been characterized by the presence of fatty acids, including lauric acid [C12:0 (41.00-56.00%)], monounsaturated palmitoleic acid [C16:1 (12.00%)], oleic acid [C18:1 (3.50-11.00%)], and polyunsaturated linoleic acid [C18:2 (1.00-2.5%)]. Frying escamoles has resulted in only minimal alterations in the chemical composition of the oil and its fatty acids (Ariza & Rosales, 2021).

*Threats and Conservation Considerations*

Although *Liometopum apiculatum* shows a wide distribution and low biological vulnerability, this means a low risk of population decline or extinction due to its broad ecological tolerance and geographic range (Berumen-Jiménez et al., 2021). However, it has been increasingly threatened by human impacts on its habitats. Among these, the overexploitation of "escamoles" stands out, driven by growing gastronomic demand and high market prices. This exploitation has been reported to include harvesting at inappropriate times, excessive opening of nests, and clandestine commercialization. Such practices have been shown to damage colonies and reduce the recruitment of new generations (Lara-Juárez et al., 2015; Tarango-Arámbula & Méndez-Gallegos, 2018).

Habitat transformation through agriculture, livestock grazing, and urban expansion has also been identified as a risk factor, as it alters vegetation cover and soil where nests are established. In several localities of north-central Mexico, the negative effects of overgrazing have been documented, for example, on colony density and "escamoles" production, since it reduces the vegetation cover that protects foraging workers from high temperatures (Cruz-Labana et al., 2014; Lara-Juárez et al., 2015). Furthermore, the intensive extraction of associated resources, such as maguey (*Agave* spp.), yucca (*Yucca* spp.), and cactus (*Opuntia* spp.), which have been reported as nesting and foraging substrates, has contributed to habitat degradation (Tarango-Arámbula & Méndez-Gallegos, 2018; Rafael-Valdez et al., 2019).

Climate change represents an additional risk for *L. apiculatum*. Variations in precipitation and temperature have been reported to affect reproductive phenology and nuptial flights, processes that are essential for the establishment of new colonies (Lara-Juárez et al., 2015). Moreover, it has been noted that ants, like other social insects, have relatively narrow thermal tolerance ranges, so increases in extreme temperatures may disrupt foraging activity, reduce the availability of shelters, and generate physiological stress (Parr & Bishop, 2022).

In this context, it becomes a priority to design sustainable management and conservation strategies, including the regulation of harvesting, the strengthening of responsible traditional practices and systematic monitoring of populations. These actions will help ensure the persistence of the species while also preserving a cultural, economic, and ecological resource of great importance in Mexico (Berumen-Jiménez et al., 2021).

**Discussion**

Since Gustav Ludwig Mayr described *L. apiculatum* in 1870, various biological aspects of this ant species have been documented. A review titled "Biology, Ecology and Behavior of Velvety Tree Ants of North America" was published eleven years ago (Hoey-Chamberlain, 2013); since then, more than 30 publications related to *L. apiculatum* have been published, and over 30% of the references have been compiled in this study. Over the past 30 years (1993-2024), most research on *L. apiculatum* has focused on food resources, nest density, trophic relationships, habitat variables, microbiota, ethnobiology, and the chemical composition of larvae. A substantial proportion of these studies has addressed the exploitation of the species. However, knowledge gaps remain. Aspects such as fully understanding its interactions with plants, mapping worker foraging strategies, and studying intraspecific diversity among colonies from different environments (morphologically and genetically) have remained underexplored.

Del Toro et al. (2009) documented the distribution of the ant across fifteen states in Mexico and four in the United States. Subsequently, Berumen Jiménez et al. (2021) used updated databases to expand the distribution to 24 Mexican states. Guénard et al. (2017) added three U.S. states, and database records have also revealed the southernmost occurrence in Guatemala, thus extending the species' range into Central America.

Establishing the comprehensive distribution of *L. apiculatum* is of paramount importance for elucidating its biological characteristics. Furthermore, integrating Geographic Information Systems (GIS), ecological data, and software enables ecological niche modeling and the generation of predictive maps under climate change scenarios. Alterations in distribution patterns can exert substantial effects on habitat ecology (Fareen et al., 2022).

The compilation of plant species lists is an important consideration, since trophobiotic interactions with other insects may be modulated by vegetation diversity (Blüthgen et al., 2006). Research has investigated vegetation types and associations that ant species establish with different plants (Van Pelt, 1971; Ramos Elorduy et al., 1988; Ramos-Elorduy & Levieux, 1992; Miller, 2007; Del Toro et al., 2009; Hoey-Chamberlain et al., 2013; Cruz-Labana et al., 2014). However, many of the biological interactions of *L. apiculatum* with plants, associated arthropods, and other co-distributed species remain poorly understood. Comprehensive inventories of vegetation in *L. apiculatum* habitats are essential for clarifying its preferences and habits. Notably, predators and competing species have been largely absent from the literature, particularly regarding their distributions and ecological roles.

Del Toro et al. (2009) claimed that this velvety tree ant is polydomous, a nesting strategy where a colony occupies two or more spatially separated nests. However, the mechanism by which this was determined was not described, and colony boundaries remain unclear. Various methods have been proposed for identifying boundaries of polydomous colonies, including worker/food marking, trail observation, ecological inference, inter-nest aggression assays, spatial clustering analysis, genetic differentiation (Fst), relatedness, G-distance, rate genotype sisterhoods, Bayesian clustering, and mtDNA sequencing (Ellis et al., 2017). Applying such techniques could help delimit *L. apiculatum* colonies, thereby allowing a clearer understanding of its ecology and evolution.

The foraging area of *L. apiculatum* has been reported in some studies. For example, Rafael-Valdez et al. (2017) estimated that colonies maintain an average of 3.7 foraging paths, with straight foraging distances of 38.6 ± 17.18 m. Reported foraging areas have ranged from 361.5–580 m² (Ramos-Elorduy & Levieux, 1992) to 607.25–2,467.2 m², with average straight distances of 24.3 ± 11.36 m (Rafael-Valdez et al., 2019). Different foraging strategies have been proposed (Lanan, 2014), considering that the spatial and temporal distribution of food resources may strongly influence strategy choice. In the case of the escamolera ant, describing its foraging strategies could represent an important element in local conservation planning.

The intraspecific genetic diversity of *L. apiculatum* has remained poorly understood, with only a single study (Hipolito-Cruz et al., 2020) analyzing partial mitochondrial COI sequences from Central Mexican populations. Likewise, the intraspecific morphological variation has not yet been characterized. Both genetic and morphological investigations could yield valuable knowledge about adaptation and morphological plasticity in relation to ecological community composition (Gaudard et al., 2019; Ibarra-Isassi et al., 2023).

The traditional use of *Liometopum* larvae ("escamoles") as food in rural Mexico has been threatened by increased demand and trade, leading to colony decline (Ramos-Elorduy et al., 2006; Zavala-Sánchez et al., 2024). In addition to overharvesting, other pressures such as habitat conversion for agriculture and livestock grazing, overgrazing, and the intensive extraction of host plants like *Agave* and *Yucca* further contribute to habitat degradation (Cruz-Labana et al., 2014; Tarango-Arámbula & Méndez-Gallegos, 2018). Moreover, climate change has been reported to affect reproductive phenology and foraging activity, potentially increasing the species' vulnerability (Parr & Bishop, 2022). Therefore, studying the biology and ecology of *L. apiculatum* is crucial for developing preservation, conservation, and management strategies.

## Conclusions

This review provides an update on current knowledge of *Liometopum apiculatum*. The topics addressed encompass a description and comparative analysis with other extant species within the genus *Liometopum*; an updated distribution record; habitat characteristics; nest structures; colony dynamics; feeding ecology; foraging activity patterns; life cycle stages; biotic interactions; nutritional value; and the chemical factors that modulate its behavior. Despite the current knowledge on this ant, there are important gaps. These gaps include evaluating intraspecific variation in morphology and genetics between colonies; understanding its specific foraging strategies; understanding specific patterns of founding, establishment, and maintenance of a nest; and expanding knowledge of its biotic interactions, both animal and vegetative. As an edible insect with cultural and economic importance in Mexico, this species requires a comprehensive study for its conservation and sustainable use. A deeper understanding of its biology, ecology, and genetics is crucial for identifying vulnerable periods, restoring habitats with essential resources, safeguarding the species and its ecological network, and genetically monitoring colony adaptation to environmental changes.

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## Authors' Contribution

M.B-J.: Conceptualization, investigation, data curation, formal analysis, visualization, writing-original draft, writing-review & Editing.
E.A.M.-S.: Writing-review & editing.
M.R.M: Writing-review & editing.
L.A.T-A: Writing-review & editing.
R.R-V.: Conceptualization, visualization, supervision, project administration, writing-original draft, writing-review & editing.

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