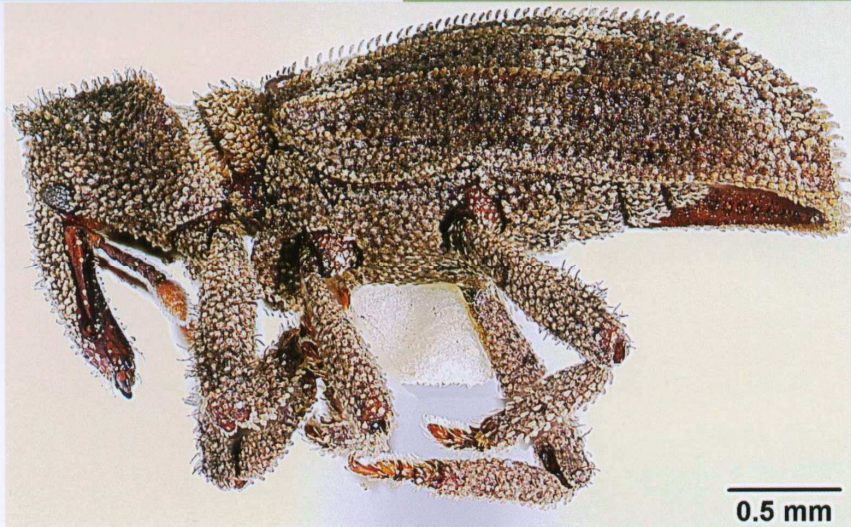
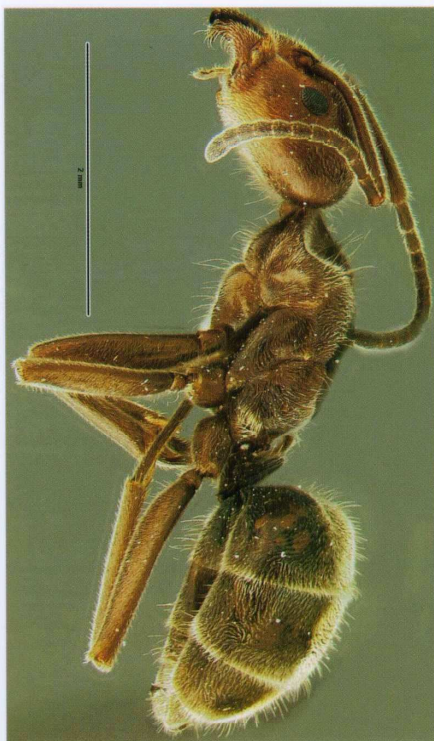


# Sociobiology, Vol. 53, No. 2A, 2009



**SOCIOBIOLOGY**  
**Vol. 53, No. 2A, 2009**

**Revision of the Ant Genus *Liometopum***  
**(Hymenoptera: Formicidae)**

by

**Israel Del Toro, José A. Pacheco &**  
**William P. Mackay**

**CONTENTS**

Abstract..... 299

Introduction..... 299

Methods and Materials.....300

    Specimens Examined.....300

    Morphological/Morphometric Assessment.....301

    Species Delineation .....303

    Statistical Analysis .....303

    Digital Imaging and Distributional Mapping.....304

Results/Taxonomy .....304

    Generic Level Diagnosis.....304

    Synopsis of *Liometopum* Species.....306

Key to the Species of *Liometopum* Based on Workers, Males and Gynes.....

    .....306

*Liometopum apiculatum* Mayr .....309

*Liometopum lindgreeni* Forel .....317

*Liometopum luctuosum* Wheeler.....319

<i>Liometopum microcephalum</i> Panzer .....	325
<i>Liometopum occidentale</i> Emery .....	330
<i>Liometopum orientale</i> Karamajeo .....	337
<i>Liometopum sinense</i> Wheeler .....	338
<i>Liometopum minimum</i> Zhou = <i>Chronoxenus myops</i> (Forel) .....	340
Statistical Analysis .....	340
Discussion.....	341
Figures and Tables.....	345
Line Drawings .....	345
Maps.....	354
Digital Figures .....	357
Canonical Scores Plots.....	362
Tables.....	364
Acknowledgments .....	364
References.....	365
Index compiled by Brian G. Taylor.....	371

#### ABOUT THE COVER

The cover shows *Liometopum apiculatum* (right) and *L. luctuosum* (left), two of the more frequent ants of the springtime in California. The lower figure is of *Liometophilus manni*. Weevils are not found with ants very often but this one has been captured several times. For more details see the monograph.

## Home page:

[www.csuchico.edu/biol/Sociobiology/sociobiologyindex.html](http://www.csuchico.edu/biol/Sociobiology/sociobiologyindex.html)

Editor: David H. Kistner, Dept. of Biological Sciences, California State University, Chico, CA 95929-0515, U.S.A.

## Resident Associate Editor:

Michael J. Erpino, Dept. of Biological Sciences, California State University, Chico, CA 95929-0515, U.S.A.

## Associate Editor:

Murray S. Blum, Dept. of Entomology, University of Georgia, Athens, GA 30601, U.S.A.

## Assistant Editor/Graphic Designer:

Brian G. Taylor, Dept. of Biological Sciences, California State University, Chico, CA 95929-0515, U.S.A.

## Web Page Editor:

Kelly Wood-Hohenstein, Dept. of Biology, Butte College, 3536 Butte Campus Drive, Oroville, CA 95965-8399, U.S.A.

## Revision of the Ant Genus *Liometopum* Mayr (Hymenoptera: Formicidae)

by

Israel Del Toro<sup>1</sup>, José A. Pacheco<sup>2</sup>, and William P. Mackay<sup>1</sup>

### ABSTRACT

*Liometopum* Mayr is a Holarctic ant genus with representatives in North America, Europe, Asia Minor, India and Asia. This genus has never been completely revised. The most comprehensive taxonomic study was completed in 1905, and only included the North American representatives. In this work we address the taxonomy of the eleven extant taxa and provide descriptions, illustrations, maps and identification keys. Additionally, Discriminant and Canonical Correlation Analyses were used to assess morphometric variation. We recognize the validity of seven species, three are found in North America and the remaining four are found Europe, Asia Minor, India and Asia. The valid species are: *Liometopum apiculatum* Mayr (= *Formica masonia* Buckley **New Synonym**), *L. lindgreeni* Forel, *L. luctuosum* Wheeler, *L. microcephalum* Panzer, *L. occidentale* Emery, *Liometopum orientale* Karavaiev, and *Liometopum sinense* Wheeler (= *L. sinense* var. *sericatum* Wheeler **New Synonym**, = *L. dentimandibulum* Chang He **New Synonym**). *Liometopum minimum* Zhou is shown to be a synonym of *Chronoxenus myops* (Forel) (**New Combination**).

### INTRODUCTION

Ants in the genus *Liometopum* Mayr, known by the common name of “velvety tree ants”, are widely distributed in the Holarctic region. Bolton *et al.* (2006) list nineteen valid species-group names in the genus: nine fossil species, ten extant species, and one extant subspecies. Three extant species are currently recognized in the New World, *Liometopum apiculatum*, *L. luctuosum*, and *L. occidentale*, with a fourth name, *L. masonium*, treated as *incertae sedis* (Bolton, 1995). Two species, *L. microcephalum* and *L. orientale*, are found in the Palearctic region. In

Asia this genus is represented by *L. dentimandibulum*, *L. lindgreeni*, *L. minimum*, *L. sinense* and *L. sinense sericatum*.

This group is in major need of revision, as it has not had a taxonomic treatment in over 100 years (i.e., since Wheeler 1905). Shattuck (1992) addressed the taxonomy of the three New World species in his generic revision of the Dolichoderinae but did not review the Old World species. Here we present a taxonomic revision that includes all eleven extant representatives of the genus.

The nine fossil *Liometopum* species are *L. antiquum* Mayr, 1867, *L. eremicum* Zhang, 1989, *L. goepperti* Mayr, 1868, *L. imhoffi* Heer, 1850, *L. lubricum* Zhang *et al.* 1994, *L. miocenicum* Carpenter, 1930, *L. oligocenicum* Wheeler, W.M. 1915, *L. potamophilum* Zhang, 1989, and *L. scudderi* Carpenter, 1930. Of these species *L. miocenicum* and *L. scudderi* are reported in the New World, while the remaining species are found in the Palearctic region and one (*L. oligocenicum*) is found in Baltic Amber. We do not address the taxonomy of these species in this work.

Our primary objective is to organize the taxonomy of the extant members of this group and provide keys to the workers, males and gynes. Additionally, illustrations are presented with complete morphometric data. *Liometopum* is an extremely polymorphic genus; therefore, ranges as well as averages of morphometric characters are included.

## METHODS AND MATERIALS

### Specimens Examined

A total of 1697 specimens were analyzed and identified to species. Of the specimens analyzed 852 were dried and mounted, 845 were in alcohol, 58 specimens were males, and 63 were gynes. In addition to examining older museum material, new field collection of the three North American species was conducted from October 2004 to May 2007. The majority of the material collected consisted of foraging workers. Field sites were distributed throughout the southwestern United States (Texas, New Mexico, Arizona, and California) and northern and central Mexico (Chihuahua, Michoacán, Tamaulipas, and Nuevo Leon).

Type specimens of *L. luctuosum*, *L. sinense*, *L. sinense* var. *sericatum*, *L. lindgreeni*, and *L. minimum* were examined. Males and

gynes of *L. apiculatum*, *L. luctuosum*, *L. occidentale*, and *L. microcephalum* were also studied. The following collections were used:

California Academy of Sciences Entomology Collection (CASC)  
Museum of Natural History in Geneva, Switzerland (MHNG)  
Shan-Yi Zhou Collection at Guangxi Normal University (GNUC)  
Los Angeles County Museum of Natural History (LACM)  
Museum of Comparative Zoology at Cambridge (MCZC)  
The Smithsonian National Museum of Natural History (USNM)  
Universidad Autónoma de Guadalajara (UAGC)  
Universidad Autónoma de Querétaro (UAQC)  
William and Emma Mackay Collection at the University of Texas  
at El Paso (CWEM)

### **Morphological/Morphometric Assessment**

Specimens were measured and described using a Wild stereoscope equipped with a micrometer at magnifications of 6X, 12X or 24X. Measurements were recorded with an accuracy of  $\pm 0.01$  mm. Cephalic characters were taken in full face view; mesosomal characters were measured in lateral view. An ocular grid was also used to produce drawings. The following measurements and indices were used:

**Total Length (TL)**- Measured in lateral view from the most anterior portion of the face to the most posterior point of the pygidium, when the head is anteriorly directed, and the mesosoma and gaster are on the same horizontal axis. This measurement can be inconsistent due to specimen shrinkage and is influenced by how the head and gaster are flexed. This character is included for general comparison of overall size, especially in the reproductive castes. Head length and width are more accurate measurements.

**Head Length (HL)**- In full face view, the midline length of the head proper, from the anterior clypeal margin to the midpoint of a line drawn across the posterior margin.

**Head Width (HW)**- In full face view, the maximum width of the head, including the eyes.

**Eye Length (EL)**- The maximum length of the compound eye.

**Eye Width (EW)**- The maximum width of the compound eye perpendicular to EL.

**Scape Length (SL)**- The maximum length of the scape exclusive of the basal condyle.

**Petiole Height (PH)**- In side view, the maximum distance from the base of the petiolar sternite to the petiolar node apex.

**Petiole Length (PL)**- In side view, maximum length of the petiole from the most anterior region of the peduncle to the most posterior region of the petiole.

**Wing Length (WL)**- In lateral view, maximum length from the base to the apex of the forewing.

**Cephalic Index (CI)**-  $HW/HL \times 100$ .

**Scape Index (SI)**-  $SL/HW \times 100$ .

**Petiolar Index (PI)**-  $PL/PH \times 100$ .

Measurement ranges followed by means (in parentheses) are reported for each species. Additional morphological characters that were analyzed include:

**Number of ommatidia**- Numbers of ommatidia are reported in the species description but not accurately illustrated, due to their small size.

**Antennal structure**- The degree to which the scape surpasses the posterior cephalic margin is included. Length and width of individual funicular segments (especially the first funicular segment) are of taxonomic importance.

**Clypeal margin**- The form of the anterior clypeal margin was considered. Species vary in whether the anterior clypeal margin is straight or weakly concave.

**Mandibular Structure**- The mandible is finely punctate. Mandibular teeth along the basal and masticatory margin as well as relative sizes of the apical, subapical and basal teeth were considered.

**Mesosoma Shape and Structure**- The degree of convexity along the dorsal mesosomal margin is of taxonomic importance, varying from straight to extremely convex. Additional mesosomal characters considered are propodeal shape along the dorsal and posterior margins, the definition (angulate, or round) of the metapleural angle and the degree of indentation of the metanotal suture.

**Petiolar shape**- Observed in lateral view, the shape of the petiolar apex varies among species (angulate or round). The petiole may be inclined anteriorly or completely vertical.



**Coloration-** This is an extremely variable character, of little taxonomic importance. However coloration ranges are noted in the corresponding species descriptions.

**Pilosity-** The degree of pilosity is variable among species, particularly between *L. luctuosum* and *L. apiculatum*. All species are covered in appressed pubescence but pilosity in certain areas (posterior cephalic margin, dorsal surface of the pronotum and the dorsal petiolar surface) is of taxonomic importance.

**Wings-** Wing characters were considered for the males and the gyness of *L. apiculatum*, *L. luctuosum*, and *L. occidentale*. There is much variation that occurs in venation patterns among species. Forewing cells of taxonomic importance are the radial, submarginal and discoidal cells, and the hind wing medial cell. Hind wing hamuli varied between *L. apiculatum* and *L. luctuosum* (Figures 62-68).

**Male Genitalia-** In treating males, genitalia were dissected. The genital capsule was extracted and placed in 10% KOH solution for a period of 24 hours. When the capsule was soft and easily disarticulated, components were dissected, and illustrated (Figs. 36-54). Dissected components were placed in genital capsule vials and preserved in glycerin. The vial was pinned with the corresponding specimen and returned to the source collection. Characters of taxonomic importance include the shape of the posterior ventral paramere margin, posterior volsella margin, posterior subgenital plate margin, and the number of aedeagal denticles along the aedeagus ventral margin.

### **Species delineation**

We employ the Biological Species Concept as defined by Mayr (1942, modified in 1995), which states that species are groups of interbreeding natural populations that are reproductively isolated from other such groups. Our primary criteria for assessing the Biological Species Concept are similarities and differences in morphology, discrete variation in zones of sympatry, and ecological differences.

### **Statistical Analysis**

Discriminant analysis was conducted on the data matrix to identify statistically significant characters ( $p < 0.05$ ), using SYSTAT 12 (Table 1 and Table 2). For taxonomic and determination processes, Discriminant

Analysis is used to determine which characters best explain an individual's species membership (Moder et al., 2007). The data matrix was organized with species as columns and morphometric variables as rows. Canonical Correlation Analysis can be seen as the problem of finding vectors for two sets of variables such that the correlation between the projections of the variables onto these basis vectors are mutually maximized (Hotelling 1936). Following a forward stepwise variable selection using discriminant analysis ( $F$  to enter  $>4.0$ ,  $F$  to exclude  $<3.9$ ), characters were plotted using canonical correlation plots (Fig. 106, 107).

### **Digital imaging and Distributional Mapping**

Representative specimens of each of the species were photographed using a Leica MZ16 microscope equipped with Auto-Montage software at the MCZC.

Distribution data were mapped using ArcView 9.1. Only material examined was plotted on distribution maps.

## RESULTS/ TAXONOMY

### **Generic Level Diagnosis:**

Workers: Polymorphic, 3.3-5.5 mm in total length. Mandibles with 7-10 teeth along masticatory margin, 3-5 teeth along basal margin, apical tooth larger. Moderate concavity along anterior clypeal border, lacking teeth. Strong concavity along posterior margin of head. Antenna 12 segmented, scape may or may not surpass posterior margin of head. Majors usually possess ocelli. Compound eyes with 90-140 ommatidia. 6 segmented maxillary palp, 4 segmented labial palp. All surfaces covered in dense, pubescence, largest hairs on dorsal surface of pronotum. Cuticle smooth. Mesosoma broadly convex (similar to *Camponotus* spp.); metanotal groove reduced to suture. Petiole scale-like, usually leaning anteriorly, subpetiolar process not developed. Legs long, slender, 1 tibial spur present on each tibia. First gastral tergite largest, usually not concealing petiole. Coloration variable, usually reddish to dark brown.

Gynes: Large, reaching up to 16.5 mm in total length. Mandibles punctate, 7-10 masticatory teeth, 2-3 teeth on basal margin. Clypeus with broad, shallow concavity, lacking teeth. Posterior margin of head moderately concave. 12 segmented antenna, scape reaching posterior

margin of head. Compound eyes with 100-145 ommatidia. Three ocelli present and equal in size. 6 segmented maxillary palp, 4 segmented labial palp. Cuticle smooth. Long erect hairs on dorsal surface of head. Highest hair density on dorsal surface of propodeum. Petiolar scale-like, bidentate, ventral margin keel-shaped. Subpetiolar process not developed. Gaster extremely large, up to half total length. First gastral tergite may conceal petiole, tergites 1-3 of approximately equal width when seen in lateral view, tergites 4-5 smaller. Legs, long and slender, single tibial spur present on each tibia. Forewing, radial, submarginal and discoidal cells closed. Hind wing with two closed cells, 15-24 hamuli. Concolorous, light brown to black.

Males: Variable in size, 8.8-13.5 mm in total length. Head small, quadrate, posterior margin weakly concave, ocelli present, covered in long, decumbent hairs. Mandibles punctate, masticatory margin with 8-12 teeth, basal margin with 0-4 small teeth. Clypeus straight, lacking teeth. Antenna 13 segmented, scape never surpassing posterior margin of head. Eyes large, about 1/3 of total head length. Palpal formula 6,4. Mesosoma smooth, metanotal suture weakly indented. Petiole scale-like, bidentate at apex. Genitalia large, genital capsule 2/3 exposed. Parameres large, covered in long, decumbent hairs, sometimes concave along ventral margin. Volsella with posterior margin straight or weakly concave. Aedeagus with 15 to 25 denticles on ventral margin, posterior margin rounded or triangular. Subgenital plate notched along posterior margin. Forewing with submarginal and discoidal cells closed. Hind wing with medial cells closed, all other cells open, 13-22 hamuli. Concolorous dark brown to black.

Larvae: (From Wheeler & Wheeler 1951) "Body and head practically naked, body hairs exceedingly few; short and widely scattered. Head hairs very few, exceeding minute, widely scattered. Antennae rather large. Posterior surface of labrum with two subventral rows of sensilla near the middle and near the ventral border, short transverse rows of minute spinules. Mandible small. Maxillae with a lateral patch of isolated spinules between palp and galea; spinules with stout base and needle-like apex; palp a low convexity bearing one large and three small sensilla. Labium with spinules and a few sensilla on the anterior surface, palp a low convexity bearing one large and three small sensilla."

### Synopsis of *Liometopum* species

- L. antiquum* Mayr, 1867: 60 \*
- L. apiculatum* Mayr, 1870: 961 **Nomen Protectum**  
= *L. masonium* Buckley, 1866: 165 **Nomen Oblitum**
- L. eremicum* Zhang, 1989: 281 \*
- L. goepperti* Mayr, 1868: 56 \*
- L. imhoffii* Heer, 1850: 138 \*  
= *Formica schmidtii* Heer, 1850: 138
- L. lindgreeni* Forel, 1902: 293
- L. lubricum* Zhang, Sun & Zhang, 1994: 165 \*
- L. luctuosum* Wheeler, 1905: 325
- L. microcephalum* Panzer, 1798: 2  
= *Formica austriaca* Mayr, 1853:144
- L. miocenicum* Carpenter, 1930:46 \*
- L. occidentale* Emery, 1895: 330
- L. oligocenicum* Wheeler, 1915: 95 \*
- L. orientale* Karavaiev, 1927: 339
- L. potamophilum* Zhang, 1989: 280 \*
- L. scudderi* Carpenter, 1930: 47 \*
- L. sinense* Wheeler, 1921: 541  
= *L. sinense sericatum* Wheeler, 1921: 541 **New Synonymy**  
= *L. dentimandibulum* Chang & He, 2002: 110 **New Synonymy**

### Name excluded from *Liometopum*

- Chronoxenus myops* (Forel, 1895:471)  
= *L. minimum* (Zhou, 2001:557) **New Combination, New Synonymy**

\* indicates species known only from fossils

## KEYS TO THE SPECIES OF *LIOMETOPUM* BASED ON WORKERS, MALES, AND GYNES

### Key to *Liometopum* Workers

1. Long erect hairs (0.30 mm) present on dorsum of gaster (Fig. 2) mixed with shorter erect hairs (0.12 mm), some hairs nearly as long as those on

- pronotum, pilosity may or may not cover entire gastral surface; mesosoma evenly convex, not depressed at metanotal suture (Fig. 2).....2
- Erect hairs on dorsum of gaster (Fig. 12) short (0.10 mm), or absent and of approximately equal length or usually shorter than erect hairs on pronotum; mesosoma convex but strongly depressed at metanotal suture (Fig. 12); Washington State to West Texas and Central Mexico..... *luctuosum*
- 2(1). Antennal scape surpassing posterior margin of head by at least twice maximum thickness of scape (Fig. 1, Fig. 7).....3
- Antennal scape of largest workers surpassing posterior margin of head by amount that does not exceed maximum thickness of scape (Fig. 11).....4
- 3(2). When seen from dorsal view, petiole coming to sharp angular apex; in lateral view metapleural angle straight, posterior propodeal face vertical (Fig. 2); entire gastral surface covered in pilosity; common from Southwestern United States, west to West Texas, south to Southeastern Mexico (Quintana Roo)..... *apiculatum*
- When seen from dorsal view, petiole flat and straight at node; in lateral view metapleural angle rounded, dorsal propodeal face rounded (Fig. 8); gaster shiny with long appressed pilosity, not covering entire gastral surface; known only from type locality, India, Assam Province.....*lindgreeni*
- 4(2). Bicolored, head and gaster darker than mesosoma; from dorsal view petiolar apex sharply angular or rounded; USA Pacific Coast south to northern Mexican Pacific Coast or throughout European continent.....5
- Concolorous dark brown to light brown; from dorsal view petiolar apex always sharply angular; common throughout central China.....*sinense*
- 5(4). Suberect pilosity present along posterior cephalic margin (Fig. 17, Fig. 23); scapes with short erect hairs at junction of scape and funiculus; first funicular segment equally long as wide; in posterior view, petiolar node sharply angular (Fig. 31); in New World common along Pacific coast from northwestern USA to northwestern Mexico, in Old World common throughout southern Europe, east to Asia Minor, and south to Israel.....6
- Without decumbent pilosity along posterior margin of head (Fig. 29); scapes with two notable long erect hairs at junction of scape and funiculus; first funicular segment two times longer than wide; petiolar node rounded when seen from posterior view (Fig. 30); Russia and northeastern Europe.....*orientale*

6(5). Larger, Eye Length (EL) 0.27-0.31 mm on average ~0.28 mm; Scape Length (SL) 1.10-1.25 mm on average ~1.16 mm; southern European continent, west to Asia Minor, south to Israel.....*microcephalum*  
 -Smaller, EL 0.20-0.25 mm on average ~0.24 mm; SL 0.75-1.15 mm on average 1.03 mm; Pacific West Coast from Washington (USA) south to Baja California (Mexico).....*occidentale*

**Key to *Liometopum* Gynes (*L. orientale*, *L. lindgreeni*, and *L. sinense* not included)**

1. Head length (HL) greater than 2.20 mm; with multiple long (0.20 mm), erect, suberect, subdecumbent or decumbent hairs along the posterior cephalic margin (Fig. 3).....*apiculatum*  
 -HL less than 2.00 mm; hairs on posterior cephalic margin short (0.08 mm), erect and suberect (Fig. 13)..... 2  
 2(1). Glossy dark brown appearance; medial posterior cephalic concavity well defined, HL usually less than 1.65 mm; well defined metanotal suture (Fig. 14); 7-8 masticatory teeth; California to West Texas, south to central Mexico..... *luctuosum*  
 -Dull, dark yellow to light brown appearance; HL 1.63-1.85 mm; metanotal suture not clearly depressed (Fig. 20, Fig. 26); 8-10 masticatory teeth; in New World commonly collected along Pacific coast from northeastern USA to northeastern Mexico, in Old World commonly collected throughout southern Europe, east to Asia Minor, and south to Israel.....3  
 3(2). Medial cephalic margin straight, not concave (Fig. 25); collected only in New World from Washington State (USA), south to Baja California (Mexico)..... *occidentale*  
 -Medial cephalic margin clearly concave (Fig. 19); collected only in the Old World, throughout southern Europe west to Asia Minor, south to Israel..... *microcephalum*

**Key to *Liometopum* Males (*L. lindgreeni* and *L. sinense* not included)**

1. 20 or more hamuli on anterior edge of posterior wing (Fig 62 B), anterior wing length greater than 12.25 mm (Fig 61); dark brown to black;

- TL greater than 11.3 mm (consistently larger than all other species); Arizona to West Texas to Southeastern Mexico.....*apiculatum*  
 - 14-18 hamuli (Fig. 66), anterior wing length less than 12.25 mm (Fig. 65); light brown to dark brown; TL does not exceed 11.1 mm; in New World, California, to West Texas to Central Mexico, in Old World throughout European Continent west to Asia Minor, south to Israel.....2  
 2(1). Ventral margin of paramere straight (Fig. 34), not concave; collected in Russia and northeastern Europe.....*orientale*  
 -Ventral margin of paramere concave (Fig. 46); in New world collected from Northwestern United States west to West Texas south to Central Mexico, in Old World collected throughout southern Europe, east to Asia Minor, and south to Israel.....3  
 3. Aedeagus ventral margin emarginate posteriorly to aedeagal denticles (Fig. 48); volsella dorsal margin straight (Fig. 49); collected throughout southern Europe, east to Asia Minor, and south to Israel.....*microcephalum*  
 -Aedeagus ventral margin rounded posteriorly to aedeagal denticles (Fig. 53), volsella dorsal margin concave or straight (Fig. 54), collected in New World only (Northwestern United States southeast to West Texas, south to Central Mexico).....4  
 4. Volsella dorsal margin concave (Fig. 54), 15-18 aedeagal denticles covering 1/2 of ventral aedeagal margin, posterior aedeagal margin rounded (Fig. 53)..... *occidentale*  
 - Volsella dorsal margin straight, more than 20 aedeagal denticles covering 2/3 of ventral aedeagal margin, posterior aedeagal margin triangular (Fig. 43)..... *luctuosum*

#### SPECIES SYNOPSES

*Liometopum apiculatum* Mayr  
 Figs. 1-6, 35-39, 61-64, 69, 75-80

*Formica masonium* Buckley 1866: 165, worker, USA: Texas, Fort Mason, **New Synonymy, *Nomen Oblitum***

*Liometopum apiculatum* Mayr 1870: 961, worker, MEXICO; Emery 1895: 331, queen, USA: Texas; Wheeler 1905: 324, male, USA: Arizona; Wheeler & Wheeler 1951: 181, larva, USA: California, ***Nomen Protectum***

## Diagnosis

**Worker:** This species is concolorous light brown to dark brown. The antennal scape is long (1.2 mm) and slender, with short, erect and appressed 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 appressed hairs on all surfaces; the longest hairs are on the dorsal surface of the pronotum.

**Gyne:** Gynes are concolorous dark brown to black. They are extremely large at over 15.0 mm in total length. The mesosomal dorsum is covered with many long (0.24 mm), erect hairs and with dense appressed pubescence. The metanotal suture is distinct but does not break the smooth dorsal mesosomal margin.

**Male:** Males of this species are concolorous black and smaller in total length (11.3 mm) than gynes, but are larger than males of other *Liometopum* species. The mesosoma is convex and smooth. The hind wings of males have 20 or more hamuli; the anterior wing length is greater than 12.25 mm. The volsella has dense erect pilosity along the ventral margin and is finely denticulate along the posterior margin (Fig. 39). The aedeagus has more than 20 denticles along the ventral margin (Fig. 38).

**Comments:** The worker of this species can be separated from that of *L. luctuosum* based on greater hair density and scape morphology. In *L. luctuosum*, the scape is wider (0.22 mm) and does not extend past the posterior margin of the head by at least twice the maximum thickness of the scape. The *L. luctuosum* worker is smaller in total length (3.6 mm), with the mesosoma depressed at the metanotal suture. *Liometopum apiculatum* workers can be separated from those of *L. occidentale* based on color, being concolorous dark brown to black (*L. occidentale* is bicolored). *Liometopum occidentale* is found along the Pacific coast of United States and Northern Mexico. Gynes of this species are easily separated from those of *L. luctuosum* and *L. occidentale* based on their larger size, (greater than 14 mm in total length); the other species' queens do not exceed 12 mm in total length. Males of *L. apiculatum* are also consistently larger than those of the other two species. Additionally males can be separated by having more than 20 hamuli on the hind wing (fewer than 15 on the other two species) and an anterior



wing length that is greater than 12.25 mm (less than 11.10 mm in the other two species).

## Caste Descriptions

### *Workers (n=10)*

TL 4.15-5.25 (4.64), HL 0.93-1.23 (1.19), HW 1.20-1.56 (1.42), EL 0.21-0.25 (0.23), EW 0.14-0.20 (0.15), SL 1.06-1.37 (1.21), PH 0.31-0.55 (0.45), PL 0.22-0.32 (0.26), CI 103-135 (119), SI 93-106 (102), PI 46-72 (58)

**HEAD:** Wider than long, posterior medial concavity well defined; largest workers with ocelli. Eyes large, medial rather than lateral, 110 to 125 ommatidia. Scapes long and thin, surpassing posterior margin of head by at least two times maximum thickness of scape. Funiculus 11 segmented, first and last segments largest. Anterior clypeal margin straight. Mandibles punctate, 8 teeth along masticatory margin, 4 to 5 smaller teeth on basal margin. **MESOSOMA:** Slightly convex. Pronotum convex, from dorsal view widest point narrower than maximum head width. Metanotal suture weakly defined, not breaking dorsal margin of mesosoma. Propodeal spiracle small, round. Petiole scale-like, sharp angular apex. Legs long, slender. **GASTER:** First gastral tergite partially overlapping petiole. **COLORATION AND PILOSITY:** Concolorous light brown to dark brown. Coloration similar in members of same series. Cuticle covered in dense appressed pubescence to erect pilosity. Subdecumbent to erect pilosity along posterior margin of head. Antennae with short, appressed pubescence. More than 20 long erect hairs along anterior clypeal margin. Mesosoma completely covered in pubescence. Longest erect hairs on pronotal dorsum (12 or more hairs). Suberect pubescence covering petiolar anterior surface. Pilosity coloration light grey to golden brown.

### *Gynes (n=5)*

TL 14.50-16.25 (15.23), HL 2.30-2.43 (2.37), HW 2.63-3.00 (2.76), EL 0.45-0.50 (0.49), EW 0.38-0.50 (0.43), SL 1.63-1.80 (1.73), PH 1.15-1.65 (1.37), PL 0.80-1.00 (0.90), CI 111-130 (117), SI 70-77 (73), PI 49-70 (67), WL 13.25-17.25 (15.30)

**HEAD:** Wider than long, strong posterior medial concavity apparent. Ocelli present, medial ocellus circular, lateral ocelli oval-shaped. Eyes located more laterally than in workers, large oval-shaped with over 150 ommatidia. Scapes not surpassing posterior margin of head. Anterior clypeal margin weakly concave. Mandibles punctate, 8-10 teeth on masticatory margin, 3-5 teeth on basal margin. **MESOSOMA:** Strongly convex, smooth, lacking sculpturing, pronotum dorsal face straight. Mesonotum strongly arched, from dorsal view mesonotum globular, metanotal suture distinct. Legs long, slender. Forewing, radial, submarginal and discoidal cells closed. Hind wing medial cells closed with more than 20 hamuli. Propodeal dorsal margin round, spiracle large, circular. Petiole scale-like, from lateral view with sharp angular node, from dorsal view apex bidentate, leaning anteriorly. **GASTER:** Gaster large,  $\frac{1}{2}$  of total length, overhanging petiole. Gastral tergites 1-3 equal width in lateral view, 4 and 5 decreasing in total size. **COLORATION AND PILOSITY:** Concolorous, dark brown to black. Dense pilosity covering entire cuticular surface. Cephalic margins covered in subdecumbent pubescence. Antennae with dense, appressed pubescence. More than 25 long, erect hairs surpassing anterior clypeal margin. Mesosoma covered in erect pilosity. Dorsal mesonotal surface with lower hair density. Dense pilosity covering propodeal spiracle. Lacking pubescence on posterior petiolar surface. Dense pubescence covering entire gastral surface. Pubescence light yellow to dark brown.

*Males (n=5)*

TL 10.13-13.50 (11.56), HL 1.28-1.50 (1.38), HW 1.58-1.67 (1.67), EL 0.45-0.50 (0.48), EW 0.35-0.43 (0.39), SL 0.60-0.75 (0.69), PH 1.00-1.25 (1.08), PL 0.50-0.65 (0.54), CI 105-132 (122), SI 43-55 (50), PI 44-55 (50), WL 12.25-13.75 (13.13)

**HEAD:** Wider than long, lacking concavity along posterior cephalic margin. Ocelli present, equal in size, oval-shaped. Eyes lateral with more than 140 ommatidia. Scape never surpassing posterior margin of head. Funicular segments equal in length. Anterior clypeal margin straight. Mandibles punctate, 9-11 teeth on masticatory margin, 1-2 teeth on basal margin. **MESOSOMA:** Strongly convex, mesonotum arched. Legs long and slender, femur  $\frac{3}{4}$  length of tibia and tarsus combined. Submarginal and discoidal forewing cells closed. Discoidal cell quadrate. Hind wing with more than 20

hamuli. Dorsal surface of propodeum forming angle. Petiole scale-like with sharp, angular node, straight, not leaning anteriorly. GASTER: First gastral tergite larger than 2-5. Genital capsule large, parameres large, ventral margin of paramere weakly concave. Volsella finely denticulate along posterior margin. Aedeagus with more than 20 triangular denticles along ventral margin, rounded at ventral margin apex. Posterior margin of subgenital plate medially emarginate. COLORATION AND PILOSITY: Concolorous dark brown to black. Dense appressed to erect pilosity covering all surfaces. Lateral surfaces of head with dense suberect and decumbent pilosity. Dorsal surface of mesonotum with most dense pubescence. Appressed and suberect pubescence covering gastral surface. Genital capsule lacking pubescence, except on posterior margin. Parameres with long, suberect hairs. Volsella with erect pilosity along ventral margin. Subgenital plate covered with decumbent to erect pilosity.

### Distribution

Southwestern United States & Northwestern to Southeastern Mexico, Quintana Roo.

*Type Material:* No type material was examined

### Material Examined

**MEXICO- Chihuahua:** 100 m above Rio Urique, 84 S of Creel, 28.ii.66, J. Reddell, W. Bell. **Coahuila:** Arteaga, Cañon San Lorenzo, 25°23'28.0"N 100°42'49.8"W, WY 57 nr. Lirios, 10.vii.1973, R. Snelling. **Colima:** Volcan de Colima. **Durango:** Durango, Revolcaderos, 21.vii.1965, E.M. Fisher. **Guanajuato:** Camino 57, Km. 306, Rancho Jardin, 10.viii.1965, Cornell University Mexico Field Party. **Hidalgo:** Grutas de Xoxa, 19.vii.1965, J. Reddell; Guerrero Mill, W.M. Mann. **Mexico:** Piñón del Marquis, near Mexico City, 27.iii.1933; Teozulcan, 9.vi.1929, W.M. Wheeler. **Michoacán:** South of Zitacuaro, 9.vii.1965, R. Snelling; 18.2 km. South Nupecuato; 12.3 miles E. Morelia, R. Snelling; Zacapu, vi.45, A.J. Sharp. **Nuevo Leon:** Near Monterrey, Mesa de Chipinque, 16-18.vii.1965, Cornell University Mexico Field Party; Galeana, Cerro El Potosí, 24°53'19.9"N 100°11'58.0"W; 30.5 km east of Arroyo San Pedro Garza Garcia, W.P. Mackay; Parque Chipinque, Camino al Pinar, 25°36'05.5"N 100°19'57.4"W; 5 mi W Iturbide, 9.xi.46,

Ross Collection. **Querétaro:** Municipio Queretaro, La Barreta, 20°49.35'N 100°30.939'W, M. Rocha. **Quintana Roo:** Lazaro Cardenas, El Eden Ecological Reserve, 25 km NNE Leona Vicario Det. W.P. Mackay 2002. **San Luis Potosí:** 10 miles N.E San Luis Potosí, vii-22-1954, J. Bequaert; Rio Verde, Valle de los Fantasma, 22°03'76.9"N 100°36'83.6"W. **Sinaloa:** 6.5 mi E. Potrillos, 21.viii.1964, Hwy. 40, R. Schlinger. **Tamaulipas:** Miquihuana, Camino a San Jose del Llano, 23°32'27.7"N 99°48'02.8"W, M. Bolaños. **Zacatecas:** Pinos Los Alpes, Nopalera, M. Bolaños. **USA-Arizona:** Oracle, 16.iii.1919, W.M.Wheeler; Ash Spring, 6 miles SW Portal, 31.iii.1966, B. Vogel; Hilltop, Portal, 20-27.vii.1967, G. Alpert; Mt. Lemmon, 36 miles N. of Tucson, 30.vii.1965, Freitag & Gibson; Montezuma Pass, Coronado Nat. Mem., 9.ix.1965; Coronado Nat. Memorial, 31.viii.1972; Madera Canyon, Santa Rita Mts., L. Martin; Ramsey Canyon, Huachuca Mts., Mann; Huachuca Mts. 21.vii.1937, Knull; Cooper Canyon, 8.1 Miles SE Sunnyside, 26.viii.1972, R. Snelling; Chiricahua Mts., Sycamore Spring; 1 mi. N. Paradise; 12 miles NW Portal, Carr Canyon, Huachuca Mts., 23.viii.1972, R. Snelling; 5 miles W Portal, 30.vi.1970; Stewart Camp, 2 miles W Portal, Chiricahua Mts., 28.viii.1965; Dragoon Mtns., Cochise Stronghold, 21.vii.1993, S.P. Cover; Black Hills, 16.9 mi. ENE RT. 89 on Rt. 89 A 34, 41.47"N, 112, 10.13"W, 20.viii.1998, S.P. Cover. **Colorado:** Manitou, 17.vii.1903; Garden of the Gods, 1.viii.1941; Canon City, 2.vi.1900, W.M. Wheeler; Boulder, 7.vii.1927, W.S. Creighton; Boulder, Gregory Canyon, 27.iii.1932, L.F. Bayns; Colorado Springs and vicinity, W.M. Wheeler. **New Mexico:** Alamogordo, G. Krockow; Cimarron Canyon, 26.vii.1962, A.C. Cole; Silver City, 15.viii.1952; Bernardo, 10.ix.1951, A.C. Cole; Bandelier 45 km NE Las Cruces, W.P. Mackay; Bandelier Natl. Mon, 30.vii.1952, A.C. Cole; Silver City, on state 61, 14.viii.1952; Cherry Creek Recreation Area, near Silver City, 9.vii.1963, P.J. Spangler; Stratton, 27.vii.1917, W.M. Wheeler; Hwy. 78 at Arizona State Line, Gila National Forest, 7.ix.1972, R. Snelling; Catwalk, W.P Mackay; 15 k NW Datil, W.&E. Mackay; Ox Spring Canyon, W.&E. Mackay; Snow Lake, W.&E. Mackay; Gila Mts., W.&E. Mackay; Iron Creek, W.&E. Mackay; Wright's Cabin, W.&E. Mackay, 77 k E Silver City, W.&E. Mackay; 88 k E. Silver City, W.&E. Mackay; 9 k NW White Signal, W.&E. Mackay; Los Alamos, W.&E. Mackay; Rio Grande, W.&E. Mackay; Abiquiu Dam, W.&E. Mackay; 26 k S Cuba, W.&E. Mackay; Magdalena Mts., Water Canyon, W.&E. Mackay; Sacramento Mts., Ruthven, W.&E. Mackay; Highrolls, 12.vi.1902. **Texas:** Franklin Mts., R. Worthington; Ft. Davis Mts., 19.vii.1933, Creighton; Ft.

Davis, 10.vi.1902; McKittrick Canyon, 3.iv.69; 30 mi S. Ft. Stockton, J.M. Tenorio; Big Bend Nat. Park, Juniper Cyn., 3.vi.1970; Green Gulch, Big Bend Nat. Park., 5.vii.1970, O'Brien; Davis Mts., 3.vi.1970, C.W. O'Brien; Chisos Basin, Big Bend Nat. Park, 18.vii.1966, A.E. Lewis; Chisos Mts., 13.vii.1933, W.S. Creighton; Paisano Pass, 11.xii.1901.

### **Habitat**

This species nests in a wide variety of substrates in oak forests, at elevation ranges of 1000 m to 2500 m. The prime habitat is oak forests around an elevation of 2000 m, but can be found in higher elevations in areas of pinyon pine, up to ponderosa pine and riparian sites. It also nests in creosote bush scrub and grasslands. At higher elevations, this species abundance decreases and is replaced by *L. luctuosum*.

### **Biology**

This species is commonly found nesting in dead logs, under stones, and in decaying stalks of *Yucca* spp. (Miller, 2007). Nests have even been collected in glass containers and rubber tires. It is polydomous with segments of nests scattered over the landscape. Nests from Colorado Springs, Colorado, are carton nests, but are usually difficult to reach, as they are usually deep under heavy boulders or large trees (Wheeler 1905; Gregg 1963). It is the dominant ant in most of the oak forests in the southwestern United States and can be easily found foraging on the sides of oak trees. Colonies are variable in size ranging from a few hundred workers to 85,000 workers per colony (Ramoselorduy & Levieux, 1992). Behavioral dominance has also been observed in this group (Andersen, 1997). This species is opportunistic, but larger colonies are predaceous, while other colonies have been observed foraging for dead insects and tending Homoptera (Shapley, 1920).

The primary mode of defense is to emit a strong odor and attack aggressively in large numbers. *Liometopum apiculatum* has a mutualistic relationship with the cholla cactus, *Opuntia imbricata*, and uses its aggressive behavior to protect the cactus from herbivores and seed predators and collects the extrafloral nectars produced by the plant (Miller, 2007). Workers actively forage from March to September, and cover a range up to 580 m<sup>2</sup> (Mackay & Mackay, 2002; Ramoselorduy & Levieux, 1992). Sexuials occur in nests from May to August. Males and gynes were collected on the ground in June to August; queens were commonly collected in July and August under stones, cow manure or logs.

Inquilines appear to be especially common in the nests of this species. The small cricket, *Myrmecophila* spp. occurs in the nests throughout its range. Staphylinids including *Sceptobius dispar* Sharp (Fig. 103) and *Dinardilla liometopi* Wasmann (Fig. 104) are also found in nests, often taking food from the ants. Navarette et al., (2006) provide the most comprehensive analysis of these inquiline guests. Other known myrmecophiles include *Liometophilus manni* (Fig. 105). *Dinardilla* species often directly interact with *L. apiculatum* while *Sceptobius* beetles tend to avoid direct contact with their host (Danoffburg, 1994).

### Species Summary

We consider *Liometopum masonium* (Buckley, 1866) to be a synonym of *L. apiculatum*. Although *L. masonium* is the senior name, *L. apiculatum* has been in wide usage for the past 141 years. For *L. apiculatum* to qualify for *nomen protectum* status, *L. masonium* must not have been used as a valid name after 1899 (ICZN 23.9.1.1) and *L. apiculatum* must be mentioned in at least 25 works, published by at least 10 authors since 1957 encompassing a span of not less than 10 years (ICZN 23.9.1.2). *Liometopum masonium* has only been mentioned as *insertis sedis* since 1899 (Shattuck, 1994). More than 25 works, by more than 10 authors in the preceding 50 years refer to this species as *L. apiculatum* not *L. masonium*. Examples of such works include: (Gregg, 1963; Gulmahamad, 1995; Mackay et al. 1988, Mackay & Mackay, 2002; Merickel & Clark, 1994; Moreno-Garcia et. al 2003; Shattuck, 1992, 1994; Kupyanskaya, 1988; Wheeler & Wheeler 1973, 1986; Bolton 1995, Bolton et al., 2006; Miller, 2007; Navarette et al., 2007; and Dannoffburg, 1994). Therefore, *L. masonium* is considered as *nomen oblitum* and *L. apiculatum* as *nomen protectum* as ICZN criteria proposed by Article 23.9.1.1 and 23.9.1.2 are both met.

Even though the types for *L. masonium* and *L. apiculatum* could not be located, we are confident (based on the original descriptions) that these two taxa are identical. The type description of *L. apiculatum* is somewhat short and vague. However, Wheeler, (1905) provides extremely accurate descriptions of the worker, gyne and male. These descriptions consider multiple specimens from different localities and provide an accurate definition of the morphology used to distinguish *L. apiculatum*. Based on this description we were able to easily identify *L. apiculatum*.

The vague description presented by Buckley is indicative of *L. apiculatum*, which we have collected several times in the same region of

Texas (Fort Mason) where the *L. masonium* holotype specimen was collected. Many of the characters mentioned by Buckley are characteristic of *L. apiculatum* (cuticular coloration, number of mandibular teeth, cephalic shape). Additionally, most of these characters provide a generalized description of all species within the genus.

We recognize the uniqueness of the specimen from Southeastern Mexico (Quintana Roo), which represents a disjunction in distribution. We have extensively collected throughout the region of the Isthmus of Tehuantepec and the Yucatan Peninsula and have not found any other *Liometopum* specimens. *Dolichoderus bispinosus* is the dominant Dolichoderine species in this geographic region. The specimen from Quintana Roo may represent an isolated or relic population.

***Liometopum lindgreeni* Forel**

Figs. 7-8, 70, 99-100

*Liometopum lindgreeni* Forel 1902: 293, worker, INDIA: Assam, Debrugharh.  
[holotype examined]

**Diagnosis**

Worker: This species is only known from the holotype collected in Assam, India. It is a concolorous light brown specimen with a dull luster on the cuticle. The cuticle is covered in short pubescence with a low pilosity density on the dorsal surface of the gaster. The antennal scapes surpass the posterior margin of the head by at least two times the maximum thickness of the scape. The first funicular segment is three times longer than wide. The anterior clypeal margin is straight with 10-12 hairs surpassing the margin. The pronotum is weakly convex, the metanotal suture is weakly concave. The petiole is scale-like, and flat at the apex when seen from posterior view. The longest decumbent hairs are found on the anterior petiolar surface.

Comments: This species can be separated from other Old World species by having a narrow head (1.20 mm wide). *Liometopum lindgreeni* is unique in that dense pilosity does not cover the entire cuticular surface. The petiole is also unique when seen from posterior view, in that it is flat and emarginate at the apex, in the other species the petiolar node forms a sharp angle.

Gyne and Male: Unknown

### **Caste Description**

*Worker (n=1)*

TL 5.35, HL 1.06, HW 1.20, EL 0.24, EW 0.15, SL 1.03, PH 0.35, PL 0.23, CI 129, SI 96, PI 64

**HEAD:** Posterior medial concavity well defined. Lacking ocelli. Eyes oval-shaped, medial rather than lateral, with 115 ommatidia. Antennal scapes slender (0.10 mm) surpassing posterior cephalic margin by more than two times maximum scape width. First and last funicular segments longest (0.18 mm), segments 1-5 and 11 longer than wide, segments 6-10 equally wide as long or wider than long. Anterior clypeal margin straight. Mandibles finely punctate, 10 teeth on masticatory margin, 2 reduced denticles on basal margin. **MESOSOMA:** Anteriorly convex, posteriorly straight, in dorsal view widest at posterior edge of pronotum. Pronotum, arched. Promesonotum strongly convex. Metanotum straight, weakly depressed at metanotal suture. Legs long, slender, tibia 2/3 length of maximum femur length. Propodeal dorsal margin weakly convex. Posterior metapleural angle absent, dorsal posterior face of propodeum rounded, spiracle small, oval-shaped on posterior dorsal lateral surface. Petiole scale-like from posterior view, flat at apex, leaning anteriorly. **GASTER:** Smooth, lacking sculpturing, tergites 1-3 equal in size, 4-5 decreasing in size. **COLORATION AND PILOSITY:** Concolorous light brown species. Dorsal lateral cephalic margins with short, appressed pubescence. Antennal scapes with short, suberect hairs, funiculus with suberect to decumbent hairs. Up to 20 erect to suberect hairs surpassing anterior clypeal margin. Dorsal mesosomal surface covered in appressed pubescence, longest hairs on anterior dorsal mesonotum. Lateral mesosomal surface with sparse pubescence. Posterior petiolar surface lacking hair. Gaster entirely covered in appressed to suberect pubescence. Pubescence light brown to yellow.

### **Distribution**

Known only from type locality in the Assam Province of India.

*Type Material:* Holotype worker: India (MHNG).



## Material Examined

**INDIA:** Assam: Debrugarh, O. Lindgreeni, Holotype.

**Habitat and Biology:** Unknown

## Species Summary

This is the least collected species of the genus. A suite of morphological differences in cephalic characters (having a narrower head), mesosomal characters (rounded dorsal face of propodeum), and petiolar characters (flat at petiolar apex), indicate that this is a valid species and should retain its current status. To support our hypothesis more material needs to be analyzed, however no reports or additional collections of this species were encountered. We believe that the sample size constraints are not a major issue in retaining a valid species status for this taxon.

### *Liometopum luctuosum* Wheeler

Figs. 11-16, 40-44, 65-68, 71, 81-86

*Liometopum apiculatum* subsp. *luctuosum* Wheeler 1905: 325, worker, USA: Colorado Springs, Colorado; Forel 1914: 619, male; USA: California, Lake Tahoe; *Liometopum occidentale* subsp. *luctuosum* [2 Examined]: Creighton 1950: 339; *Liometopum luctuosum*: Wheeler & Wheeler 1986: 55, larva, USA: Nevada.

## Diagnosis

Worker: *Liometopum luctuosum* is a concolorous dark brown species with a glossy 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. *Liometopum luctuosum* is less commonly encountered than *L. apiculatum* or *L. occidentale*. This species is usually collected at elevations higher than 1600 m.

Gyne: Queens are four times larger than the workers, slightly larger than the males and are concolorous light to dark brown. The dorsum of the

mesosoma is covered with short erect hairs of equal length (0.18 mm). The metanotal suture is clearly defined and strongly depressed, breaking the even dorsal mesosomal margin.

**Male:** Males are concolorous black and smaller than the gynes. The hind wing has 14-18 hamuli. The volsella lacks pilosity along the ventral margin and has a straight posterior margin. The posterior ventral margin of the aedeagus has more than 20 clearly defined triangular denticles with the posterior vertex of the aedeagus coming to a triangular apex. Males of this species are usually collected at elevations higher than 1900 m and range from Pacific West Coast east to West Texas and south to Central Mexico.

**Comments:** Workers of this small concolorous dark brown species are easily separated from *L. occidentale* workers, which are bicolored. *Liometopum luctuosum* workers can be separated from those of *L. apiculatum* by having a smaller total length, a metanotal suture that breaks the straight dorsal outline, and a shorter antennal scape (~0.88 mm). Gynes of *Liometopum luctuosum* can be separated from those of *L. apiculatum* and *L. occidentale* by having a smaller total size and by having a lower pilosity density than those of the other Nearctic species. *Liometopum luctuosum* males separate from those of *L. occidentale* and *L. microcephalum* by having more than 20 clearly defined triangular denticles along the posterior ventral margin of the aedeagus and having a triangular posterior aedeagal apex.

## Caste Descriptions

### *Workers (n=10)*

TL 3.31-4.31 (3.68), HL 0.75-1.05 (0.95), HW 0.78-1.14 (1.06), EL 0.19-0.23 (0.20), EW 0.11-0.15 (0.13), SL 0.88-0.93 (0.89), PH 0.25-0.37 (0.29), PL 0.13-0.25 (0.16), CI 105-121 (111), SI 90-107 (87), PI 50-75 (54)

**HEAD:** Wider than long, posterior medial concavity well defined. Majors without ocelli. Eyes medial rather than lateral, 90 to 100 ommatidia. Scape surpasses posterior margin of head by less than two times maximum width of scape. Anterior clypeal margin straight. Mandibles finely punctate, 8 teeth along masticatory margin, 3-4 teeth along basal margin. Apical teeth largest, teeth decreasing in size along masticatory margin. **MESOSOMA:** Mesosoma convex, metanotal suture breaking dorsal outline. In dorsal view widest at middle of pronotum, as wide as head. Metanotal suture well defined,

depressed. Legs long, slender, femur as long as tibia. Propodeal dorsal margin rounded into posterior face, propodeal spiracle small and round. Petiole small, scale-like with sharp apex, leaning anteriorly, higher than long (0.29 mm high, 0.16 mm long). GASTER: First gastral tergite largest, tergites decreasing in size posteriorly. In dorsal view gaster rounded at pygidium. COLORATION AND PILOSITY: Concolorous light golden brown to dark brown. Cuticle covered in short, appressed pubescence. Head covered in appressed pubescence, with short, erect hairs on antennal scapes and posterior cephalic margin. Fewer than 10 short, erect hairs surpassing anterior clypeal margin. Longest erect pilosity on pronotal dorsum (fewer than 15 erect hairs). Pilosity on petiolar lateral surfaces, few hairs on anterior petiolar surface. Pilosity dull gray to silver.

*Gynes (n=10)*

TL 9.50-10.63 (10.16), HL 1.48-1.65 (1.57), HW 1.75-2.06 (1.93), EL 0.35- 0.40 (0.38), EW 0.25-0.35 (0.29), SL 1.13-1.38 (1.22), PH 0.63-0.79 (0.73), PL 0.29-0.44 (0.34), WL 11.00-12.25 (11.61), CI 112-131 (120), SI 76- 86 (79), PI 38-58 (50)

HEAD: Wider than long, posterior cephalic margin weakly concave. Lateral ocelli longer than wide, medial ocellus circular. Eyes medial rather than lateral, oval-shaped with 140-150 ommatidia. Scapes never surpassing posterior margin of head. Anterior clypeal margin concave. Mandibles coarsely punctate, with suberect hairs originating at punctures, 7-8 teeth along masticatory margin, 3 smaller teeth along basal margin, apical and subapical teeth largest. MESOSOMA: Dorsum convex. From dorsal view widest at pronotum, lateral dorsal corner of pronotum touching axillary sclerite. Metanotal suture clearly defined. Legs long and slender, femur and tibia subequal in length. Propodeum arched, ventrally emarginate, spiracle round. Petiole scale-like, bidentate at apex, petiolar apex rounded rather than sharp, when seen in posterior view, large lateral spiracle on lower lateral half. GASTER: Gaster large, first gastral tergite wider than second through fifth, continuously decreasing in size. COLORATION AND PILOSITY: Concolorous light brown. Short, appressed pubescence on all cuticular surfaces. Dorsal and lateral cephalic margins with decumbent hairs, 15 to 20 suberect hairs surpassing anterior clypeal margin. Antennae covered with short suberect hairs. Mesosoma covered in short appressed hairs, short erect hairs of equal length along dorsal surface. Suberect hairs on anterior and

lateral petiolar surfaces. Gaster mostly with appressed pubescence, short erect hairs along ventral and dorsal surfaces. Pilosity golden yellow.

*Males (n=8)*

TL 7.13-10.50 (8.86), HL 1.00-1.10 (1.03), HW 1.10-1.25 (1.22), EL 0.38-0.44 (0.41), EW 0.31-0.38 (0.34), SL 0.48- 0.56 (0.51), PH 0.80- 0.85 (0.83), PL 0.29-0.38 (0.33), WL 9.21-11.25 (10.05), CI 125-127 (126), SI 51-53 (52), PI 50-51 (50)

**HEAD:** Wider than long. Ocelli present, lateral ocelli longer than wide, medial ocellus round. Eyes lateral, extending past lateral cephalic margin, with more than 140 ommatidia. Scapes never surpassing posterior cephalic margin. All funicular segments longer than wide. Anterior clypeal margin straight (sometimes weakly convex). Mandibles finely punctate, 10 teeth along masticatory margin, 3-4 teeth along basal margin. **MESOSOMA:** Strongly convex. Anterior pronotal margin straight, vertical. Mesonotum convex. Widest at anterior edge of scutellum. Legs long and slender, femur 1/4 longer than tibia. Dorsal posterior surface of propodeum rounded. Propodeal spiracle round and very small. Petiole scale-like, bidentate and upright, apex sharp. **GASTER:** First gastral tergite largest, others continuously decreasing in size. Genital capsule smooth and glossy. Parameres large, strongly concave dorsally, ventrally weakly concave. Volsella large and lobose, posterior margin straight. Aedeagus large, with 20-25 triangular denticles along posterior ventral margin. Posterior aedeagal apex triangular. Subgenital plate with rounded notch along posterior margin. **COLORATION AND PILOSITY:** Concolorous light to dark brown. Appressed pubescence on most cuticular surfaces. Head with long, suberect pubescence. Mandibles with decumbent pubescence. Lateral surfaces of mesosoma lacking appressed pubescence, resulting in glossy appearance, dorsal surface covered in dense, appressed pubescence. Gaster covered with appressed pubescence. Genital capsule without pilosity. Parameres with long, suberect hairs on ventral surface. Pilosity golden yellow.

**Distribution**

Northwestern United States (Washington State), south and west to Western Texas, south to Central Mexico.

*Type Material:* 2 cotype workers examined: USA (MCZC); 2 syntype males examined: USA (MHNG).

## Material Examined

**MEXICO- Coahuila:** Arteaga, El Paraíso, 30.x.2005, 25°23'28.0" N 100°42'49.8" W, J.L. Navarrete; 53 km E. Arteaga, 24.ix.1987, W.P. Mackay. **Guanajuato:** Parque Nacional Jose Morelos, 22.v.1988, W.P. Mackay. **Michoacán:** Aguililla, Paracho, 19°36'05.4" N 102°05'06.1" W, F. Núñez, L.A. Navarrete, J. Cortes, M. Vásquez. **Nuevo Leon:** San Pedro Garza Garcia, Parque Chipinque, Camino al Piñar, 11.x.2005, M. Vásquez. **Zacatecas:** Teul de González, Ortega camino a Millipillas, 1-6.ii.2004, 21°19' 43.8" N, 103°35'21.0" W, M. Vásquez. **USA- Arizona:** Chiricahua Mts., 11.7 Km. W Portal, 31'56' N 109'15.8"W, 5-14.viii.1976; Stoneman Lake, 28.viii.1933, R. Lingenberry; San Francisco Mts., 0.6 miles SW Jct. Rt. 89 on FSR 420, 8.vii.1992, S.P. Cover; 48 miles NW Nixon Spring, 5.viii.1969, R. Snelling; Chiricahua Mts., Herb Martyr Dam, 6.viii.1963; 5.xii.1998, N. Cobb; Grand Canyon, 20.vii.1931, A.C. Cole; Nixon Spring, 5.vii.1969, R. Snelling; Overguard, 30.vii.1950, R.G. Robinson; Granite Dells, 4 mi W. Prescott, 15.vii.1971, L. Martin; Sunny Flat Campground, 31°88' N 109° 17' W, 22-24.viii.1993, B.V. Brown. **California:** San Gabriel Mts., Charlton Flat, 19.vii.1963; Blue Ridge, San Gabriel Mts.; Figueroa Mt. Campground; Mirror Lake, Yosemite Park 23.v.1930; Carrol Cr., 6 mi N Bishop, 20.viii.1960, E. Schlinger; San Gabriel Mts., 13.vii.1966, R. Snelling; 3 mi W Cachuma Lake, 06.vii.1959; Mill Portero, Arroyo Seco, Santa Lucia Mts., 16.v.1978, J.P. Donahue; Eagle Lake, 11.vii.1970, H. Jacobson; Sierra N.F., 4.4 mi. SW Big Creek, 16.v.1976, A. Newton; Caruthers Canyon, 35°15'N 115°18'W, 22.iii.1996, P.S. Ward; Cold Canyon, 15.iii.1983, J. Longino; Sta. Rosa Mountains, 4.ii.1984, J. Longino. **Colorado:** Decker, 29.vii.1941, Buren; Cheyenne Canyon, Near Colorado Springs, 20.vii.1903, MCZ Cotype, W.M. Wheeler; Colorado Springs, 18.vii.1903. **New Mexico:** Jemez Springs, 25.v.1988, R. S. Peigler. **Nevada:** Sparks, 20.x.1979; Geiger Grande, 6 mi. SW Reno, C&J Wheeler; Elk Point, La Rivers, Hiko, 7.viii.1974; White Canyon on Mt. Rose, 19.vi.1977; Verde Wash, 9.vi.1951, W.M. Wheeler; Reno, 12.vii.1949, R.C. Bretcher; Sparks, 7.viii.1974, R.C. Bechtel; Elk Point, 9.v.1970, G.&J. Wheeler; Charleston Park, Lake Tahoe, 29.vi.1954, A.C. Cole; 12.3 Km. SSE Miden; Reno, 12.vii.1978; Charleston Park, 9.v.1970. **Texas:** McCutchens Ranch, 7.v.1912, J.D. Mitchel. **Utah:** Zion National Park, 22.vii.1932, W.S. Creighton; Hach Canyon, 21.vi.1935. **Washington:** Chelan, 14.v.1983, J. Longino; Eightmile Campground, near Leavenworth, 23.v.2007, J. Longino, 3 km NE Lyle; Klickitat 18.iv.2003, J. Longino.

## Habitat

This species has a strong association with pine trees. However, it has also been reported in sagebrush, oak forests, ponderosa pine-riparian, Douglas fir, and riparian habitats at high elevations. *Liometopum luctuosum* has recently been reported from Idaho nesting in rock crevices in juniper woodlands (Clark & Bloom, 2007). It usually occurs at elevations higher than 2000 m., however in coastal environments, this species may be collected at lower elevations.

## Biology

This species is less common and a morphologically smaller species than *L. apiculatum*. Nests are commonly located under rocks, under decaying logs or at the base of large trees. This species also constructs carton nests much like *L. apiculatum*, which are often located in very inaccessible places. *Liometopum luctuosum* has been reported as being a competitor with *Camponotus* species in Idaho, since both of these genera compete for similar nesting sites (Merickel & Clark, 1994). The staphylinid genus *Liometoxenus* was first described from specimens found foraging next to colonies of *L. luctuosum* and *L. occidentale* (Kistner et al., 2002). Reproductive castes are usually observed during the months of June and July and can easily be collected the day after the flight by looking in large bodies of water or using a backlight trap.

This species has been collected in or around rural housing areas and can be considered a minor pest. No severe damages to housing or property have been reported, but the uncomfortable bite and smell of this ant makes it a nuisance to affected residents. Additionally, *L. luctuosum* is of particular interest in the Idaho National Laboratories, where it can potentially uncover buried waste materials (Clark & Blom, 2007).

This species tends to be very easily disturbed and aggravated. When this occurs a strong odor is released from the anal glands and the ants begin to attack and bite any intruder, making this species just as aggressive as *L. apiculatum*.

## Species Summary

We recognize this species as valid. Syntypes of the males to this species were examined, illustrated, described and photographed. Multiple works (Mackay and Mackay, 2002; Shattuck, 1992; Cook, 1953) make

reference to this species and provide additional morphological characters, which were helpful in identifying *L. luctuosum*. Gynes of this species were not described in detail prior to the work presented here. There are multiple morphological differences identified in the gyne caste (pilosity, total size, suture definition, wing venation), which aid in the identification of *L. luctuosum* gynes. This species has been considered to be a subspecies of both *L. apiculatum* and *L. occidentale*. However, the lack of intermediates and species clines suggests that this species is reproductively isolated. Even though, the ranges of *L. luctuosum* apparently do overlap with those of *L. apiculatum* and *L. occidentale*, collecting experience suggests that this species typically occurs at elevations above 1600 m while *L. apiculatum* and *L. occidentale* are normally lower elevation species typically inhabiting regions with a maximum elevation of 1500 m. There is no evidence of hybridization in zones of sympatry.

***Liometopum microcephalum* Panzer**

Figs. 17-22, 31, 45-49, 72, 93-98

*Formica microcephala* Panzer 1798: 1652, male, GERMANY; *Liometopum microcephalum*: Mayr 1861: 39, worker and queen, AUSTRIA.

*Formica austriaca* Mayr 1853: 144, worker, AUSTRIA (Junior Synonym of *microcephalum* Mayr 1861: 39)

**Diagnosis**

Worker: *Liometopum microcephalum* is 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 (0.40 mm long). The scapes do not surpass the posterior margin of the head.

Gyne: Queens are slightly larger than males and similar in morphology to queens of *L. occidentale*. The mandibular apical tooth is distinctly larger than the remaining masticatory teeth. The medial cephalic concavity is clearly defined and not as straight as in *L. occidentale*.

Male: Males are concolorous 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 parameres are large with the ventral margin concave and dorsal margin convex. The posterior lobe of the volsella has a straight posterior margin. The aedeagus has 15-18 small triangular denticles along the ventral margin with a triangular notch posterior to the denticles.

Comments: *Liometopum microcephalum* can be separated from other Old World species based on the consistency of the bicoloration, not seen in *L. lindgreeni* or *L. sinense*. Having a moderate concavity on the anterior clypeal margin can also be used to separate this species from *L. lindgreeni*, which has a straight anterior clypeal margin. *Liometopum sinense* only occurs in China, and *L. microcephalum* has a more western distribution. This species is morphologically similar to *L. occidentale*, but geographic isolation and morphometric statistical analysis of the two taxa suggest that the two species are different (Fig. 107). Males of *L. microcephalum* can be separated from those of *L. orientale* by having a paramere with a concave ventral margin, which is straight in *L. orientale*. Males of this species also separate from males found in the New World by having fewer denticles along the posterior ventral aedeagal margin than *L. apiculatum* and *L. luctuosum*. Additionally the aedeagal ventral margin is notched whereas in *L. orientale* the aedeagal ventral margin is concave but not notched.

### Caste Descriptions

#### *Workers (n=10)*

TL 4.19-6.00 (5.13), HL 1.28-1.41 (1.35), HW 1.54-1.63 (1.55), EL 0.27-0.31 (0.28), EW 0.18-0.21 (0.19), SL 1.10-1.25 (1.16), PH 0.46-0.58 (0.53), PL 0.20-0.31 (0.26), CI 110-120 (115), SI 78-92 (86), PI 42-54 (48)  
 HEAD: Wider than long, posterior medial concavity well defined. Majors with ocelli. Eyes large, medial rather than lateral, with 115-120 ommatidia. Scape slender (diameter = 0.22 mm), does not surpass posterior cephalic margin by more than two times maximum thickness. Funiculus 11 segmented, segments longer than wide, first and last segment longest. Clypeal anterior margin medially concave. Mandibles punctate, 8-10 teeth along masticatory margin, 2-3 smaller teeth along basal margin. Apicalmost teeth largest. MESOSOMA: Strongly convex (similar to *Camponotus* spp.). Pronotum convex, widest at dorsal medial point of



pronotum, as wide as maximum head width. Mesonotum arched, metanotal suture distinct, but not depressed. Legs long and slender, femur and tibia of equal length. Propodeal dorsal margin round, vertical at posterior face, spiracle, round. Petiole scale-like, with sharp angular apex in dorsal view, rounded at apex, inclined anteriorly. GASTER: First gastral tergite largest, others decreasing continuously in size. Rounded at pygidium. COLORATION AND PILOSITY: Bicolored, head, gaster and legs darker brown than golden yellow mesosoma. Dense appressed pubescence covering entire cuticular surface. Lateral and posterior cephalic margins with appressed pilosity, few short decumbent hairs along posterior cephalic margin. No more than 20 short erect hairs surpassing anterior clypeal margin. Dorsal mesosomal surface covered in dense appressed pubescence. Longest hairs on posterior dorsal edge of pronotum (0.25 mm). Lateral surfaces of mesosoma with fewer erect and suberect hairs. Short erect to appressed pilosity on anterior surface of petiole. Dense appressed pubescence covering entire gastral surface. Pilosity golden yellow.

*Gynes* ( $n=2$ )

TL 11.5-12.0, HL 1.81-1.88, HW 2.23-2.37, EL 0.44, EW 0.38-0.40, SL 1.35-1.50, PH 0.79-1.00, PL 0.25-0.35, CI 124-126, SI 75-80, PI 32-35, WL 13.00

HEAD: Wider than long, posterior cephalic margin concave. Ocelli present, lateral ocelli longer than wide, medial ocellus circular. Eyes medial rather than lateral, large, oval-shaped, with more than 150 ommatidia. Scapes not surpassing posterior cephalic margin, funicular segments longer than wide, first and second segments, longest. Anterior clypeal margin medially concave. Mandibles punctate, 8-9 teeth along masticatory margin, 2-3 reduced teeth along basal margin. MESOSOMA: Strongly convex, weakly depressed at metanotal suture. Dorsal pronotal surface vertical, finely punctate. Anterior mesonotum convex, rounded posteriorly. Metanotal suture weakly depressed, touching axillary sclerite. Wing discoidal and submarginal cells closed. Second submarginal cell triangular, first discoidal cell rectangular-shaped. Legs long, and slender, tibia 2/3 length of femur. Dorsal propodeal margin rounded, posterior surface vertical. Propodeal spiracle lateral, medially located, small and round. Petiolar scale with sharp apex, from posterior view, bidentate at apex. GASTER: Gaster large half of total length, first tergum widest, tergites 2-5 decreasing in width. COLORATION

AND PILOSITY: Concolorous brown. Dense pilosity covering most cuticular surfaces. Erect to sub-decumbent pilosity along posterior and lateral cephalic margins. Antennae covered with short, appressed pubescence. 15-20 hairs surpassing anterior clypeal margin. Mesosomal dorsal surface covered in appressed to erect hairs, longest hairs on propodeum 0.20 mm. Dorsal face of propodeum with 30-40 short erect hairs of equal length. Suberect pilosity on anterior petiolar surface. Appressed pubescence covering entire gastral surface, erect and suberect hairs on dorsal and ventral surfaces. Pubescence golden yellow to silver.

Males (n=1)

TL 9.13, HL 1.10, HW 1.65, EL 0.40, EW 0.31, SL 0.50, PH 0.69, PL 0.31, CI 150.0, SI 45.4, PI 45.4, WL 11.00

HEAD: Wider than long, posterior cephalic margin straight, lacking concavity. Ocelli present, medial ocellus wider than long, lateral ocelli longer than wide. Eyes lateral rather than medial, extending past lateral cephalic margins, large, with more than 145 ommatidia. Antennal scapes reduced, never surpassing posterior cephalic margin. Funiculus 12 segmented, segments longer than wide. Anterior clypeal margin convex medially. Mandibles with 8-9 teeth on masticatory margin, no teeth on basal margin, two apical teeth largest. MESOSOMA: Strongly convex. Dorsal margin of mesonotum anteriorly vertical, medially convex. Widest at posterior mesonotum from dorsal view. Metanotal suture well defined, depressed. Discoidal and submarginal wing cells closed. Second submarginal cell triangular, first discoidal cell rectangular. Posterior wing with 14 hamuli. Legs long, slender, tibia 3/4 length of femur. Propodeum arched, dorsal margin rounded. Propodeal spiracle, round. Petiole scale-like, bidentate at petiolar apex, vertical. GASTER: First gastral segment largest, overhanging petiole. Genital capsule large, parameres large, ventral margin concave, dorsal margins convex. Volsella large, posterior margin straight. Aedeagus with 15-18 denticles covering 1/2 of ventral margin, posterior apex rounded and overhanging. Subgenital plate medially notched in U-shape along posterior margin. COLORATION AND PILOSITY: Concolorous dark brown. Dense appressed pubescence covering all body surfaces. Erect to decumbent hairs along posterior and lateral cephalic margins. 22 hairs surpassing anterior clypeal margin. Dorsal and ventral mesosomal surfaces

with appressed pilosity, lateral surfaces with short, appressed pubescence. Gaster covered in appressed pubescence, genital capsule lacking pilosity. Suberect to decumbent pilosity on parameres. Pilosity golden yellow.

### Distribution

Southern Europe, Italy east to Asia Minor, south to Israel.

*Type Material:* No type material was examined.

### Material Examined

**ALBANIA- Corovade:** Karkrake, 40°32'17"N 20°10'32"E. **AUSTRIA- Neiderosterrrieich:** 30 km W. Vienna. **Laxenburg:** Scholsspark, 16.35° E, 48.07° N, 13. ix. 2002, B.C. Schlicksteiner. **BOSNIA-** 25km. W. Banja Luka, 44°42'08" N 16°52'30"; 32 km. S. Mostar 43°03'06" N 17°51'44" E. **BULGARIA- Oblast Lovech:** Lukowit, 01.33 43°11' N 24°15" E. **Rila:** Pilo Selo, Forel Collection. **CROATIA- Brgat:** 42°39'15"N 18°08'37" E. **CZECHOSLOVAKIA- Moravia:** mer. Lednice, 30.v.1982, P. Bezdeck, 1gt. P. Werner. **GREECE- Lefkada:** Karva, 38°45' N 20°40' E. **HUNGARY- Szekesfeharvar:** 47°09'N 18°20' E, 25 km, 1981, A. Hefetz. **ITALY- Portici:** A. Forel. **LEBANON- Christilansen:** Hasbani River Source, 27.ii.1953. **ROMANIA- Juderul:** Siba. **SERBIA-** Frusva Gora Mt., 14.v.1989, leg. I. Petrov; **Kosovo,** Doljani 42°27'42"N 19°18'30"E. **Vojvodina:** Vrdnik, Lediniko Jezero. **UKRAINE- Piatyhatky.**

### Habitat

This is a wide ranging species, collected throughout southern and Eastern Europe (Atanassov & Duluski, 1992; Baroni Urbani, 1971; Brako, 2003; Kutter, 1977; Weist, 1967). This species builds carton nests in the crevices of trees, particularly oaks. Habitats may range from coastal environments, to floodplain and oak forests.

### Biology

A great deal is known concerning the biology of this species. In recent years the potential for this species to be used as a method of biological control of *Cameraria ohridella* has been investigated (Grabenerger *et al.*, 2005). It is believed that populations of this species may be endangered due to habitat loss (Schlick-Steiner *et al.*, 2003). Colonies are extremely large and

may be composed of several thousand individuals (Zettel et al., 2004). Foraging trails are large and cover up to 80 m in length. This species has been observed tending homopterous insects; however predaceous behavior has been documented in larger colonies (Brako, 2003). This species is extremely aggressive and will defend the colony by standing on its hind legs and biting the intruder (Martinez & Tinaut, 2001). Natural predators that specialize in preying on *L. microcephalum* include *Tracheliodes curvitarisus* and *T. varus* (Hymenoptera: Crabronidae) (Zettel et al., 2004).

### Species Summary

*Liometopum microcephalum* is extremely similar to *L. occidentale* morphologically. However, we retain its current status as a valid species due to its separation based on morphological differences in the reproductive castes, unique morphometric characteristics (Fig. 107) and geographic isolation. Workers of this species were analyzed using the descriptions provided by Mayr 1861. For a more detailed account of the morphology of *L. microcephalum* we used the descriptions and drawings provided by Kupyanskaya (1988). *Liometopum orientale* was considered a subspecies of *L. microcephalum* (Karavaiev, 1927). Kupyanskaya (1988) later raised *L. orientale* to valid species status based on a suite of morphological characters, most importantly significant differences on exterior male genitalia morphology. No new synonymies are presented for this species.

### *Liometopum occidentale* Emery

Figs. 23-28, 50-54, 73, 87-92

*Liometopum microcephalum* var. *occidentale* Emery 1895: 330, worker and male, USA:

California, San Jacinto; *Liometopum apiculatum* var. *occidentale*:

Wheeler 1905:

324, USA: California, San Jacinto; *Liometopum occidentale* Wheeler 1917: 521, queen, USA: California, San Jacinto

### Diagnosis

Worker: This is a common 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 (1.02 mm) and surpass the posterior margin of the head by less than twice the maximum

thickness of the scape. The scape has few short, decumbent hairs (no more than 20). The longest erect hairs are on the dorsal surface of the pronotum (0.26 mm in length). The mesosoma is convex with the highest point at the mesonotum.

**Gyne:** Queens of this species are concolorous dark brown to dull yellow. *Liometopum occidentale* queens are slightly larger (TL ~11 mm) than queens of *L. luctuosum* but not as large as the queens of *L. apiculatum*. The metanotal suture is distinct, but weakly depressed and does not break the continuity of the mesosomal margin.

**Male:** Males of this species are concolorous dark brown to black. The first discoidal cell of the forewing is rectangular, the hind wings have only 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 1/2 of the ventral aedeagal margin, with an even concavity posterior to the denticles.

**Comments:** The worker of *Liometopum occidentale* can be separated from other species by cuticle coloration, which is bicolored in this species and concolorous in *L. apiculatum* and *L. luctuosum*. Additionally, it differs from *L. apiculatum* by having antennal scapes that do not surpass the posterior margin of head by twice the maximum thickness of the scape. Also it differs from *L. luctuosum* by having a continuous mesosomal outline whereas in *L. luctuosum* the mesosoma is depressed at the metanotal suture. Gynes are similar in total size as the gynes of *L. luctuosum*, but are consistently smaller than the gynes of *L. apiculatum*. Males of this species separate from *L. apiculatum* males by being smaller in total length, and having fewer hamuli on the anterior margin of the posterior wing. *Liometopum occidentale* males separate from males of *L. luctuosum* and *L. apiculatum* males by having fewer denticles along the ventral aedeagal margin, which is rounded at the aedeagal apex (notched in *L. microcephalum*). Additionally males of this species have a strong concavity along the posterior margin of the posterior lobe of the volsella (straight in all other species). This species is generally collected at elevations below 1800 m, whereas *L. luctuosum* is normally collected at elevations above 1900 m.

## Caste Descriptions

### *Workers (n=10)*

TL 2.88- 5.06 (4.44), HL 0.81-1.23 (1.09), HW 0.89-1.38 (1.23), EL 0.20-0.25 (0.24), EW 0.15-0.19 (0.16), SL 0.75-1.15 (1.03), PH 0.35- 0.59 (0.49), PL 0.16-0.31 (0.21), CI 96- 125 (112), SI 85- 105 (93), PI 29- 50 (43)

HEAD: Wider than long, posterior medial concavity well defined. Majors rarely with ocelli. Eyes large, longer than wide, medial rather than lateral with 110-125 ommatidia. Antennal scapes short (1.03 mm), surpassing posterior margin of head by less than two times maximum thickness of scape. Funicular segments 1, 2, and 11 longest, all segments longer than wide. Clypeal anterior margin moderately concave. Mandibles punctate, 8-9 teeth on masticatory margin, 2-4 teeth on basal margin. MESOSOMA: convex, most arched at promesonotum, from dorsal view, widest at pronotum 2/3 as wide as maximum head width. Pronotum smooth, convex. Mesonotum straight, weakly indented at sutures. Metanotal suture not depressed. Legs long, slender, femur and tibia equal in length. Propodeum concave, spiracle small, not well defined. Petiole scale-like, sharp petiolar apex, from posterior view, petiole rounded at apex, leaning slightly anteriorly. GASTER: First gastral tergite sometimes covering petiole, other tergites smaller, continuously decreasing in maximum width, rounded at pygidium. COLORATION AND PILOSITY: Bicolored, darker head and gaster, usually dark brown, lighter colored mesosoma usually golden yellow to golden brown. Dense pilosity covering entire cuticular surface. Suberect hairs on dorsal and lateral cephalic margins. Appressed pubescence on lateral cephalic margin. Scape with few short, erect hairs, funicular segments with appressed pubescence. 8-12 erect hairs surpassing anterior clypeal margin. Dorsal surface of mesosoma covered in appressed pubescence, lateral surfaces with few or no hairs. Longest erect hairs (0.26 mm long) on dorsal surface of pronotum. Highest hair density on dorsal surface of gaster. Gaster covered entirely with appressed pubescence and short suberect hairs. Pilosity golden yellow.

### *Gynes (n=7)*

TL 10.5-12.0 (11.03), HL 1.63-1.85 (1.77), HW 2.00-2.38 (2.20), EL 0.38-0.44 (0.39), EW 0.31-0.44 (0.39), SL 1.10-1.40 (1.23), PH 0.83-1.10 (0.95), PL 0.35-0.56 (0.42), CI 112-139 (124), SI 61-79 (70), PI 36-46 (43)

HEAD: Wider than long, posterior cephalic margin weakly concave. Ocelli present, all circular and equal in size. Eyes medial rather than lateral,

large, oval-shaped, with 150-170 ommatidia. Scape short, not surpassing posterior cephalic margin. Frontal lobes protruding anteriorly. First and last funicular segments longest, others continuously decreasing in length. Anterior clypeal margin slightly concave. Mandibles punctate, 8 teeth along masticatory margin, 2-3 reduced teeth along basal margin. MESOSOMA: Strongly convex. Dorsal pronotal surface rounded. Anterior mesonotum convex, posterior mesonotum straight. Metanotal suture touching axillary sclerite. Legs long, slender, femur and tibia equal length. Dorsal posterior propodeal margin rounded. Propodeal spiracle round, medial, not clearly defined. Petiole scale-like, leaning anteriorly, bidentate at apex when seen from posterior view. GASTER: First tergite 1/2 total length, widest, tergites 3-5 continuously decreasing in width. COLORATION AND PILOSITY: Generally concolorous light brown to dark brown, some with lighter colored mesonotum, propodeum, and legs. Dense pilosity covering most cuticular surfaces. Erect to decumbent pilosity along lateral and posterior cephalic margins. Antennae densely covered with short, appressed pubescence. 12 to 18 erect hairs surpassing anterior clypeal margin. Dorsal surface of mesosoma covered in appressed to erect hairs, longest erect hairs on promesonotum. Metanotum and propodeum with few or no hairs. Lacking pubescence on posterior petiolar surface, suberect to decumbent hairs on anterior face of petiole. Appressed pubescence covering entire gastral surface, short suberect and erect hairs on dorsal and ventral gastral surfaces. Pilosity golden yellow to silver.

*Males (n=9)*

TL 8.50-11.25 (9.58), HL 1.00-2.20 (1.20), HW 1.30-2.85 (1.55), EL 0.39-0.44 (0.41), EW 0.31-0.38 (0.34), SL 0.50-0.63 (0.55), PH 0.76-0.94 (0.85), PL 0.23-0.30 (0.22), CI 123-130 (128), SI 26-57 (47), PI 27-32 (31)

HEAD: Wider than long, posterior cephalic margin straight. Ocelli present, medial ocellus wider than long, lateral ocelli longer than wide. Eyes lateral rather than medial, extending past lateral cephalic margins, large with more than 130 ommatidia. Antennal scapes reduced, never surpassing posterior margin of head, reaching only lateral ocular margin. Funicular segments longer than wide, funiculus 4 times longer than scape, 12 segmented. Anterior border of clypeus convex medially. Mandibles with 8-9 teeth on masticatory margin, 3-4 teeth on basal margin, apical teeth largest. MESOSOMA: Strongly convex. Anterior edge of pronotal margin broadly convex. Mesonotum arched, widest (dorsal view) at posterior mesonotum.

Metanotal suture well defined, but not breaking continuous mesosomal margin. Submarginal and discoidal cells closed, first discoidal cell rectangular. Hind wing with 15 or fewer hamuli. Legs long and slender, tibia 3/4 length of femur. Propodeum arched. In lateral view, propodeal spiracle centered, small, oval-shaped. Petiole scale-like, petiolar sclerite keel-shaped, petiole bidentate at apex, upright. GASTER: First gastral segment largest, overhanging petiole. Genital capsule large. Parameres large, ventral margin straight, dorsal margin weakly concave. Volsella large, posterior lobe with concave posterior margin. Aedeagus with 15-18 small, triangular denticles reduced to bumps along posterior ventral margin, posterior apex rounded. Subgenital plate medially notched in U shape along posterior margin. COLORATION AND PILOSITY: Concolorous light brown to dark brown. Dense appressed to erect hairs covering all body surfaces. Suberect to decumbent hairs along posterior and lateral cephalic margin. 18-20 hairs surpassing anterior clypeal margin. Short, erect pilosity on antennal scape. Funiculus covered with dense, appressed pubescence. Dorsal and ventral mesosomal surfaces with erect hairs, lateral surfaces with scarce pilosity. Gaster covered in appressed pubescence, appressed pubescence covering dorsal and ventral surfaces of gaster, lateral surfaces with lower appressed pubescence density, little or no pilosity on genital capsule. Erect to decumbent hairs on parameres. Pilosity golden yellow to silver.

### **Distribution**

Northwestern United States (Washington, Oregon, and California) south to Northwestern Mexico (Baja California).

*Type Material:* No type material was examined

### **Material Examined**

**MEXICO- Baja California:** Tecate, Km 105 Carretera Tecate-Ensenada, Rancho San Ignacio Calamar, 32°30'10.9" N, 116°35'05"W, J. Cortes Aguilar, V. Flores; Tecate, Km 65 Carretera Tecate-Ensenada, 21.vi.2005, 32°11'01" N, 116°29'34.3"W, J. Navarrete-Heredia, E. Lopez.  
**USAU- California:** 06.v.1962, R. Snelling; China Flat, 15.vii.1948, C.D. McNeil; Riverton, 28.ii.1958; Chico 4.ix.1958, Schuster; Chico, 5.iii.1967; Mendocino National Forest, Brittan Ranch, 6 mi WNW of Stonyford, 24.ii.1997, 39°23' 35" N 122° 39'41" W; Tohouse Spring, Westgard Pass,



12.iv.1970; Sequoia National Forest, W. Cedar Grove, 14.v.1976; 2 Km SW Marshal Station, 5.v.1999, 37°N 119°36'W, P.S. Ward; Lakeport, 5.vi.1961; Santa Monica Mts., 30.xi.1963, C.L. Hougue; Tehachapi Mts., 15.v.1976; Santa Monica Mts., Stunt Canyon, 1964; HWY 198, 30 miles W of Coalingas, 10.vi.65; Toll Pence, Ribbonwood, San Jacinto Mts., 20.v.1937, J.G. Shanafelt; Franklin Canyon, 24.iv.1966; Idyllwild, vii.5.1947, W.D. Pierce; Santa Barbara, 28.iv.1944, W.S. Ross; 15 miles N. Bear Lake, 8.x.1963, G.R. Ferguson; Arroyo Seco 10.v.1958; 7 mi S Squaw Tank, 20.iii.1965; 0.5 mi N. Crestline, 7. viii.1967, G.R. Norman; 2. mi E. Cedar Springs; San Gabriel Mts., 7.3 mi West Mt. Brudy Village, 4.ii.1965; 15 mi SE Big Bend, 20.iv.1923; San Juan Canyon, 11.v.68; DeVol, 15.vi.1963, R. Snelling; Pinyon Flat, Bear Creek, 8.viii.1967, T. Bunch; Del Puerto Canyon, 15.ix.1956; Coffee Camp, 7.v.1970; Pine Mt. Top NE Hot Springs, 30.v.1984; Preston, 20.vii.1917; Sta. Lucia Mts., 5.vii.1984, Bryant; 12.7 Miles NNW Happy Camp, vi.1969; Indian Flats, 12.vi.1989; Topanga Co., D. Sheppard; Santa Ynez, 31.x.1962; 5 mi. N. Descano, iv.1972, J.H. Hunt; 12 km ENE Pt. Conception 34°30' N 120° 21'W, 26.iv.1986, J. Longino; Pauma Valley, iv.11.1955; Bayou Rd.; 5.2 miles E. Isabel Cr. 10.viii.1965; Mix Canyon, 11.xii.1960; Del Puerto Canyon 7.v.1970, R. Snelling; Iron Mts., 24 miles E Placerville, 1.vii.1980, R. Mason, H. Paul; Matilija nr. Ojai, 1963 R. Snelling; Borrego Springs, 11.vi.1965; Santa Rosa Plateau Reserve, 3.5 Air Miles WSW Murrieta, 7.8 iv.1985, Donahue; Sespe Canyon, 25.iii.1967, J.A. Honey; 4.5 Miles WNW Jct. Rt. 78, Grapevine Canyon rd., 2.vi.1997, S.P. Cover; Yosemite Valley, 15.vii.1915, W.M. Wheeler; Happy Isles, 30.v.1930, W.M. Wheeler; Stanford University, 1930, Watson; C. Ishida, Camp Ozona; Upper Cuyana, 3 miles N. Rumsey McConnell 14.iii.1983, J. Longino; Arroyo Burro, 19.vii.1987, J. Longino; San Rafael Mountain, 02.ix.1986, J. Longino; Inyo Co, Big Pine, 10.viii.1953; Los Angeles Co., San Gabriel Mts., 14.vii.1965; Riverside Co, San Bernardino Mts. Big Pine Flat. **Oregon:** Takilma, 31.vii.1999, 42°03'N 123°37'W, P.S. Ward; Champoeg State Park, 22.vi.2002, J. Longino. **Washington:** 1 km up road on east bank White Salmon River, 13.v.2001, J. Longino; 10 km E. White Salmon Burdoin Mountain Area, 19.x.200, J. Longino.

### Habitat

This species is commonly collected along coastal regions of southern Oregon, California, south to Northern Mexico. Nesting sites range from lowlands up to 1600 m. More recently this species has been reported in urban

habitats, nesting in homes, underneath insulation or between walls (Gulmahamad, 1995).

### **Biology**

This species is often found nesting in soil and in crevices of trees and underneath bark of dead trees. These ants have been observed on oaks, alders, elms, cottonwoods, creosote, and under rotten logs (Cook, 1953).

These ants have large colonies (up to 60,000 workers) and may be considered pests as they often forage in housing and may cause minor damage to facilities. Foraging trails may reach up to 60 m in length and cover areas of up to 740 m<sup>2</sup>. *Liometopum occidentale* has been observed tending Homoptera, but is also predaceous, and forms massive foraging trails (Gulmahamad, 1995; Ramoselorduy & Levieux, 1992). When they are disturbed they emit pungent disturbing odors and resort to biting for defense. Dinardilla and Sceptobius beetles are often observed alongside foragers or in nests (Danoffburg, 1994). Flights have observed throughout May.

### **Species Summary**

This species is difficult to evaluate, due to the morphological similarities with *L. microcephalum*. Workers, gynes and males of the two species all appear to have a very similar morphological structure. However we are hesitant to synonymize it with *L. microcephalum* for three principal reasons, one due to our limited sample size of *L. microcephalum* specimens, secondly due to the differences in distributional ranges, *L. occidentale* only occurring along the western coast of the United States south to the Northwestern coast of Mexico and *L. microcephalum* having a wide distribution in the European continent, Asia Minor and South into Israel. The different distributions suggest two geographically isolated species. Finally, discriminant function analysis and canonical correlation analysis separate both of these species by a suite of morphometric differences (Fig. 106). Male genitalia dissections were also completed for both species and notable differences were found (Fig. 47-54). Unfortunately only one male of *L. microcephalum* was available for dissection. Descriptions in Wheeler (1905 - workers), (1917 - gyne) were used as the most reliable to identify this species. The males described here were collected in association with workers; therefore we are confident that the identification is correct. Genotypic analyses should be conducted to better determine the relationship between these two species. With the available information we believe they should be recognized as two separate species.

***Liometopum orientale* Karavaiev**

Figs. 29-30

*Liometopum microcephalum* var. *orientalis* Karavaiev 1927: 339, worker, RUSSIA; *Liometopum orientale*: Kupyanskaya 1988: 29, raised to species, male and female, RUSSIA.

**Diagnosis**

Comments: Though similar in morphology to *L. microcephalum*, this species is different in that *L. orientale* lacks decumbent pilosity along the posterior margin of the head, and the scapes of this species present two long, erect hairs at the junction of the scape and the funiculus. The first funicular segment is twice as long as wide in *L. microcephalum*; the first funicular segment is three times longer than wide in *L. orientale*. Perhaps the most obvious difference between the two species is petiolar shape, in *L. microcephalum* the petiole (when seen from posterior view) is spade-like and comes to a sharp apex, however in *L. orientale*, the petiole retains some of the spade-like features, but does not come to a sharp apex (rounded at the apex). In the males of this species, the parameres are triangular-shaped, the ventral margin of the paramere is straight, and lacking the concavity seen in *L. microcephalum*. Due to this suite of morphological character differences, we consider this to be a valid species and retain its current status. For more details on this species refer to Kupyanskaya (1988).

*Type Material*: No type material was examined

**Material Examined**: None

**Species Summary**

Even though type material was not seen, Kupyanskaya's assessment (1988) appears to be thorough and reliable. Cephalic and petiolar characters as well as male genital capsule morphology are the primary reasons for the recognition of this as a separate species from *L. microcephalum*. For future reference, more samples of this species and of *L. microcephalum* should be analyzed to solidify current taxonomic assessments.

***Liometopum sinense* Wheeler**

Figs. 9-10, 74, 101-102

*Liometopum sinense* Wheeler 1921: 541, worker, CHINA: Mokanshan [examined];

*Liometopum sinense* var. *sericatum* Wheeler 1921: 542, worker, CHINA: Mokanshan; **New Synonymy** [examined]

*Liometopum dentimandibulum* Chang & He 2002:110, worker, CHINA: **New Synonymy**

**Diagnosis**

Worker: *Liometopum sinense* is concolorous dark brown to copper in coloration, covered in dense appressed pubescence on all body surfaces, the pubescence is finer on the mesosoma than on the gaster. The antennal scapes reach, but do not surpass the posterior margin of the head, and are covered in appressed pubescence. The anterior clypeal margin is weakly concave, the mandibles are punctate, and the apical tooth is the largest. The majors have a medial ocellus and 8-10 teeth along masticatory margin with 3-4 teeth on the basal margin of the mandible. The pronotum has 8-12 long erect hairs on the dorsal surface. Fine appressed pubescence covers the entire mesosomal surface. The mesosoma is moderately convex, and the highest point is at the mesonotum. The petiole is scale-like with a sharp apex.

Gyne and Male: Unknown

Comments: This species can be separated from the other Old World species by the geographic distribution, as it has only been collected in central China. Morphologically, the petiole differs from those of *L. lindgreeni* and *L. orientale* in that it is scale-like and has a sharp apex; the other two species have a rounded apex. It differs from *L. microcephalum* in that *L. sinense* has fine appressed pubescence on the mesosoma and the *L. microcephalum* mesosomal pubescence is coarse. Additionally, this species is concolorous while *L. microcephalum* is bicolored.

## Caste Description

### *Worker (n=20)*

TL 3.25-5.75 (4.71), HL 0.88-1.36 (1.20), HW 1.00-1.53 (1.33), EL 0.21-0.29 (0.25), EW 0.14-0.21 (0.18), SL 0.90-1.38 (1.07), PH 0.38- 0.51 (0.46), CI 86- 125 (110), SI 80-104 (89), PI 42-73 (63)

HEAD: Wider than long, posterior medial concavity well defined. Majors with one poorly defined medial ocellus. Eyes medial rather than lateral, oval-shaped, 110-115 ommatidia. Scape slender (diameter ~0.14 mm), does not surpass posterior cephalic margin by more than twice maximum thickness of scape. First and last funicular segments longest (0.24 mm) all segments longer than wide. Medial anterior clypeal margin moderately concave. Mandibles punctate, 8-10 teeth on masticatory margin, majors and larger workers with 3-4 teeth on basal margin. MESOSOMA: Strongly convex, pronotal margin convex, from dorsal view widest medially. Dorsum of mesonotum straight. Metanotal suture weakly depressed, not breaking convex dorsal mesosomal margin. Legs long and slender, first tarsus with comb-like pubescence on ventral surface. Propodeum arched, posterior dorsal surface vertical. Propodeal spiracle on posterior lateral surface small, round. Petiole scale-like with sharp angular apex, may or may not lean anteriorly, from posterior view, apex sharp rather than rounded. GASTER: First gastral segment widest, gaster decreasing continuously in size posteriorly. Gaster oval-shaped, pygidium rounded. COLORATION AND PILOSITY: Concolorous light brown to dark brown. Cuticle covered in dense, appressed to erect pilosity. Posterior and lateral cephalic margins lacking erect pilosity, with short subdecumbent to appressed pilosity. Antennae completely covered in appressed pubescence. 24-30 long erect hairs surpassing anterior clypeal margin. Mesosoma completely covered in appressed pubescence. Longest pilosity on propodeal dorsal surface, majors with up to 12 long erect hairs on dorsum (0.20 mm). 4-7 long erect hairs on dorsal mesonotal surface. Long decumbent pubescence on anterior petiolar face. Pubescence on gaster clearly defined, more so than pubescence on head and mesosoma. Pilosity golden yellow.

## Distribution

North Central to South Central China (105°E to 120° E; 20° N to 42°N).

*Type Material:* 6 syntype workers; Lectotype worker (W.M. Wheeler); 1 Paralectotype worker examined: CHINA (MCZC).

### Material Examined

**CHINA- Foochow:** N. Gist Gee. **Guangdong:** 23°25'50" N, 116°12'40"E. **Gangxi:** 22°49' N, 108°19', E, Nanning, Zhou. **Guiyang:** Guiyang, 26°35' N 106°43'E. **Hebei:** Schijashuang, 38°02' 29" N, 114° 28'43"E. **Hunan:** Hengshan, 8.ix.2003, J. Huang leg. **Hupei:** Lichuan Distr. Suisapa, 31.vii.1948, Gressitt & Djou. **Manking:** G.P. Dung. **Mokanshan:** N. Gist Gee, Paralectotype (MCZC). **Soochow:** N. Gist Gee, Syntype (MCZC). **Shannxi:** Xi'an 34°15'44"N, 108°56'16", E, Zhou. **Szechwan:** MTS 4600 ft. above Kuanhsein City, 9.iii.45. **Youluslan:** Silvestri.

**Habitat and Biology:** Unknown

### Species Summary

We consider *L. sinense* var. *sericatum* and *L. dentimandibulum* to be synonyms of *L. sinense*. Discriminant Function analysis revealed significant morphometric variation between *L. sinense* and *L. sinense* var. *sericatum*. However, we believe that such differences are attributed to having a small sample size, covering a limited geographic range. After analyzing the type series of both *L. sinense* and *L. sinense* var. *sericatum*, along with fresh material obtained from Dr. Zhou, we recognize the extreme degree of polymorphism within this species; therefore we consider these two taxa to be synonymous. The second synonymy is that of *L. dentimandibulum*. Even though the type for this species was not seen, the diagnostic characters of *L. dentimandibulum* are consistent with the majors of *L. sinense*. Again, the high degree of polymorphism is to blame for the recognition of the two taxonomic entities. Larger workers and majors of *L. sinense* present the same diagnostic characteristics that were used to define *L. dentimandibulum* as a valid taxon. The principal character is the presence of 3-4 teeth along the basal mandibular margin; this character is present in the majors and larger workers of *L. sinense*.

*Liometopum minimum* Zhou = *Chronoxenus myops* (Forel)  
Figs 55-60

*Liometopum minimum* Zhou 2001: 557, worker; CHINA; Guangxi [10 paratypes Examined], **New Synonymy**

*Bothriomyrmex myops* Forel 1895: 471, workers; [6 Syntypes Examined, MCZC]

*Chronoxenus myops* (Forel 1895):471; Transferred to *Chronoxenus*, Dubovikoff 2005: 93

### **Diagnosis:**

After reviewing paratype material sent from China by Dr. Zhou, we have concluded that this is not a member of *Liometopum*, but rather a member of the genus *Chronoxenus*. Prior to the new combination of Dubovikoff (2005), members of the genus *Chronoxenus* were considered to be part of the genus *Bothriomyrmex*. Syntypes of *B. myops* (now *C. myops*) were examined at the MCZC. Two reported species of *Chronoxenus* have been recorded in China, *C. dalyi* (Forel) and *C. myops* (Forel) (Bolton 1995). We have concluded that *Liometopum minimum* is a synonym of *Chronoxenus myops*. The diagnostic character used in identifying this specimen was the definition of the apical teeth. Specifically, the apical tooth is extremely well defined and large.

*Type material:* 10 paratype workers of *L. minimum* examined: CHINA: 2 deposited at CWEM, 3 deposited at MCZC, 5 deposited at GNUC. 6 syntypes of *Chronoxenus myops* examined: INDIA: Deposited at MCZC.

### **Material Examined**

**CHINA**U- **Guangxi**: Shiwandashan Natural Reserve, 26-ix-2000, Zhou; Shan-Yi; Shiwandashan Natural Reserve, 30.x.2001, Zhou. **INDIA**U- **Smythies**.

## DISCUSSION

### **Species Delineation and Additional Notes**

Differences in morphology, geographic distribution and ecology of the examined taxa infer that the genus *Liometopum* is divided into seven extant species. Three species occur in North America. Using Mayr's Biological

Species Concept, we hypothesize that these three species are valid taxa because of the significant morphological differences, the unique distribution patterns observed, and the ecological differences that occur with each taxon.

The Old World species each follow different evolutionary lineages and constitute reproductively isolated species. No hybrids or clines between species were observed within the seven recognized taxa, which indicate that the seven species are reproductively isolated in their corresponding geographic ranges.

Our results are a hypothesis of the possible structure of the taxonomic species arrangement within the genus *Liometopum*, and are not the final taxonomic assessment of this genus. Our review should be simply viewed as an attempt to arrange a group with a confusing taxonomic past.

Future work should include a deeper examination of the Old World species, including detailed gyne and male caste descriptions for *L. sinense* and *L. lindgreeni* when available to bring more clarity to the taxonomic arrangement of species of the Old World.

The generic level phylogeny of *Liometopum* has been addressed by Shattuck 1992, 1995, Chiotis et al. 2000, Brady et al. 2006, and Moreau et al. 2006. Shattuck's analysis used morphological characters to derive a phylogeny, placing *Tapinoma*, *Technomyrmex*, and *Liometopum* in the same Dolichoderine clade. The molecular analyses presented by Moreau et al. (2006) and Brady et al. (2006) coincide with Shattuck's clades, but place *Liometopum* as a sister genus to *Tapinoma* with *Technomyrmex* as a basal genus (Chiotis, et al. 2000; Brady et al., 2006; Moreau et al., 2006). There are no analyses that consider all *Liometopum* species.

Bolton (1995) and Bolton et al. (2006) indicate that this genus is well represented in the fossil record (9 species of extinct representatives). Taxonomic assessments of the extinct members of this genus remain a possibility for further investigation. No works to date have analyzed the *Liometopum* fossil record. From the available works, it is believed that *Liometopum* is of Early Paleocene origin (Moreau et al. 2006). Such figures are derived from fossil calibrations used in the Moreau et al. (2006) phylogenetic analyses.

## STATISTICAL ANALYSIS

Discriminant analysis and canonical correlation plots were used to evaluate evidence for the separation of species based on morphometric



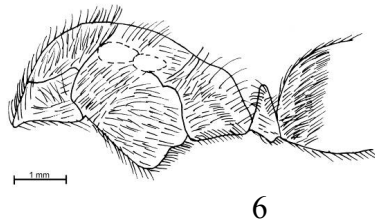
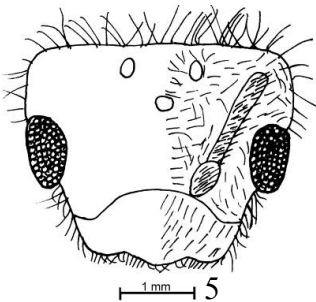
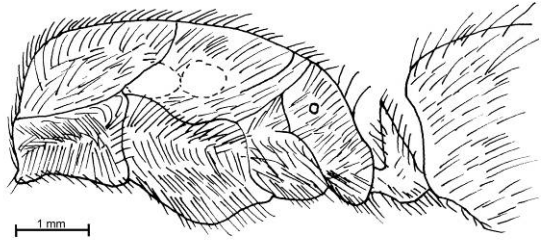
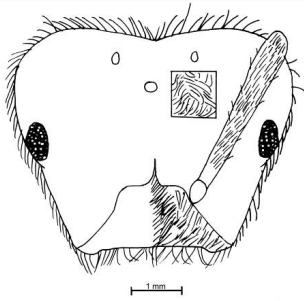
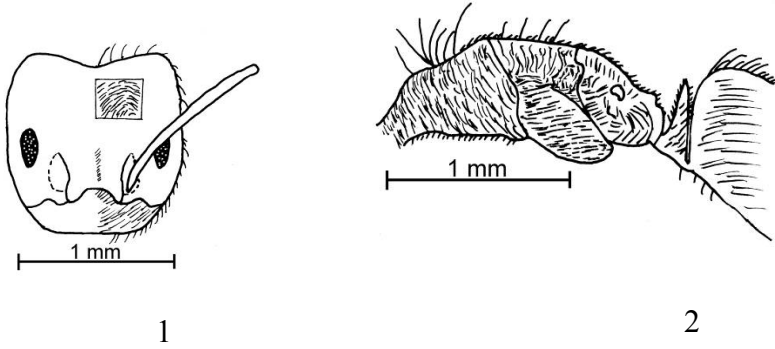
characters. In genera where multiple characters are needed to identify species, discriminant analysis allows us to assign statistical values to morphometric measurements (Seifert, 2003). Consequently, we can better understand morphometric variation within a species and use these characters in species delineation. Using the statistically significant morphometric characters (derived from the discriminant analysis), *L. apiculatum*, *L. luctuosum*, *L. occidentale*, *L. microcephalum*, *L. sinense*, and *L. sinense* var. *sericatum* were separated. Discriminant analysis alone does not yield a clear understanding of species limits, but can offer some resolution to certain species groups (Moder et al. 2007; Schlick-Steiner et al. 2003), but we do not rely completely on morphometric analysis for taxonomic validity. Additional morphological characters yield the strongest evidence for our taxonomic conclusions. For each taxon, a minimum of 10 specimens were measured (when available). Only one specimen of *L. lindgreeni* (holotype) and 8 specimens of *L. sinense* var. *sericatum* (syntypes and lectotypes) were obtained and measured. The lack of data for *L. lindgreeni* yields unreliable results. To assess the species validity of *L. lindgreeni*, meristic characters were used (see *L. lindgreeni* Species Diagnosis).

Our first discriminant analysis and canonical correlation plot (Fig. 106) compared the three recognized species in the New World and one morphologically similar species from the Old World, *L. microcephalum*. Eleven morphometric characters were considered in the Discriminant Analysis. Eye Length, Scape Length and Petiole Height yielded *F* values greater than 4 and were selected for Canonical Correlation Analysis (Table 1). Ninety-five percent confidence intervals were calculated and plotted as ellipses on the figures. All four species separate into individual taxa, supporting our interpretation of the characteristics. Overlap does occur, but we attribute this overlap to the consistent polymorphism of the species and ranges of morphometric data. *Liometopum microcephalum*, of which *L. occidentale* was considered a potential synonym, clearly separates from the New World species and thus *L. occidentale* should retain a valid species status. Overall species definitions based on morphometric character analysis supports our taxonomic assessment.

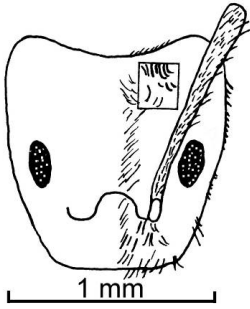
Our second discriminant analysis and canonical correlation plot (Fig. 107) analyzed the four Old World taxa of *Liometopum*. Eleven morphometric characters were considered by the discriminant analysis. Using forward stepwise variable selection, four characters had *F* values greater than 4.0; the three most informative characters were selected. These characters are:

Petiole Index, Scape Length, and Scape Index. The three factors were plotted and 95 percent confidence ellipses were plotted as ellipses on the figures. There is little overlap between *L. microcephalum* and the other Old World species. Some overlap occurs between *L. sinense* and our proposed synonym *L. sinense* var. *sericatum*. The lack of constant overlap between *L. sinense* and *L. sinense* var. *sericatum* may be attributed to the limited sample size of *L. sinense* var. *sericatum*, from the single type locality. In the future, if more specimens are available we suggest a larger sample size to be analyzed. Such results should clarify any taxonomic doubts regarding this proposed synonymy. *Liometopum lindgreeni* groups with *L. sinense*, however, only one specimen of *L. lindgreeni* was available. *Liometopum lindgreeni* appears to be easily separated from *L. sinense* by meristic characters that were not part of the statistical analysis (see *L. lindgreeni* discussion).

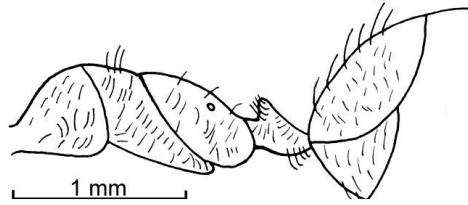
## FIGURES AND TABLES



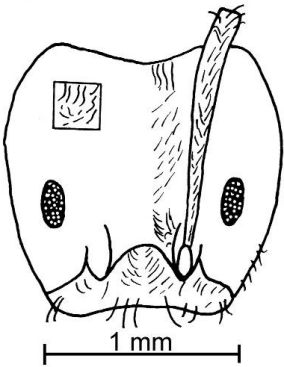
Figures 1-6 *Liometopum apiculatum*; (1,2) Worker head and mesosoma, [MEXICO, Queretaro, Queretaro, La Barreta, 20° 49.35" N 100° 30.94" W (CWEM)]; (3,4) Gyne head and mesosoma, [MEXICO, San Luis Potosi, 41 km SE Sto. Domingo (CWEM)]; (5,6) Male head and mesosoma, [USA, California, San Juan Co. San Juan River mile 165, (CASC)].



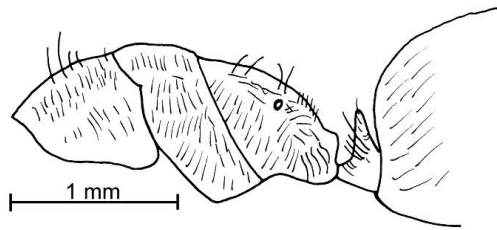
7



8

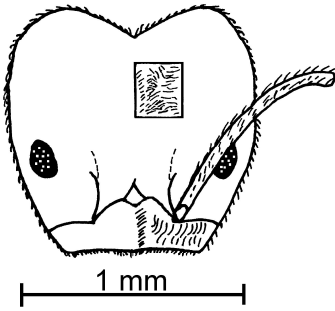


9

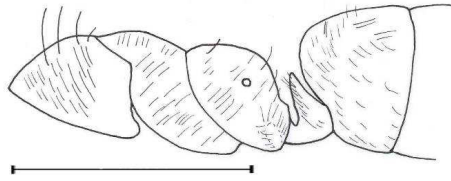


10

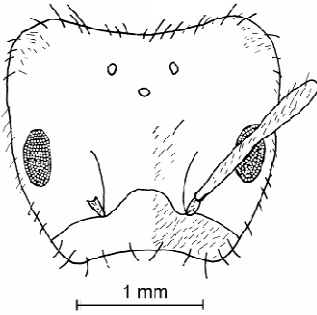
Figures 7-8 *Liometopum lindgreeni*; (7,8) Worker holotype head and mesosoma, [INDIA, Assam, Debrugarh, (MHNG)]; Figures 9-10 *Liometopum sinense*; (9,10) Worker syntype head and mesosoma, [CHINA, Soochow, (MCZC)].



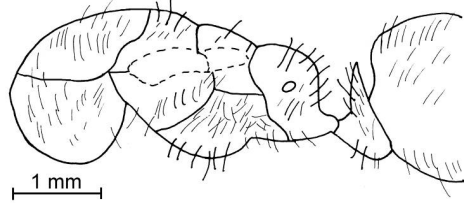
11



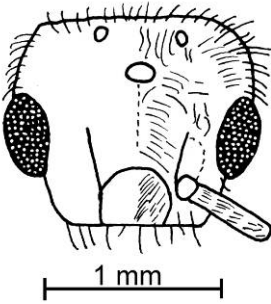
12



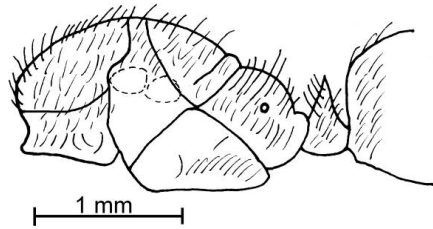
13



14

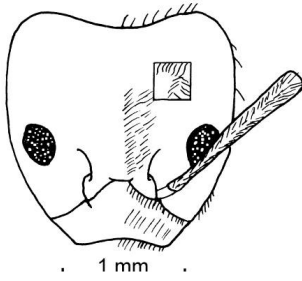


15

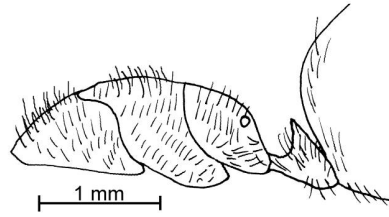


16

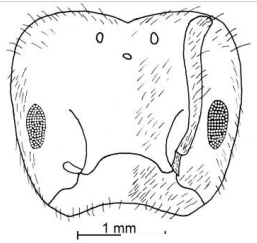
Figures 11-16 *Liometopum luctuosum*; (11, 12) Worker head and mesosoma, [USA, California, San Bernardino Co, Big Pine Flat, (CWEM)]; (13, 14) Gyne head and mesosoma [USA, Arizona, Coconino Co., San Francisco Mts. (MCZC)]; (15, 16) Male syntype head and mesosoma [USA, California, Lake Tahoe (MHNG)].



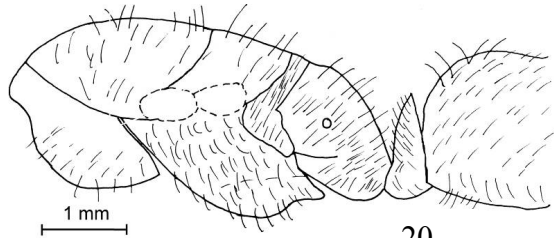
17



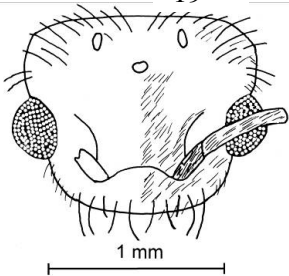
18



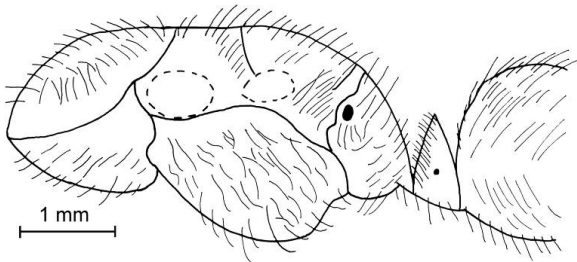
19



20

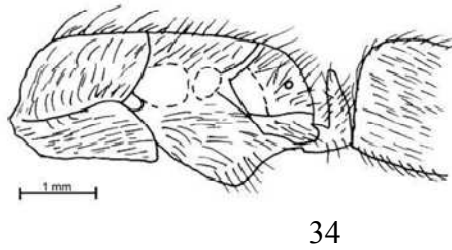
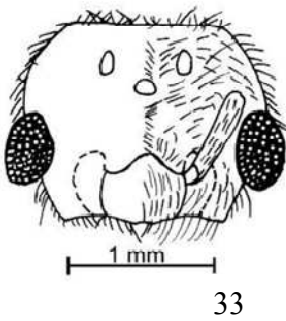
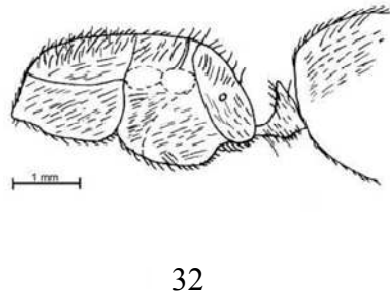
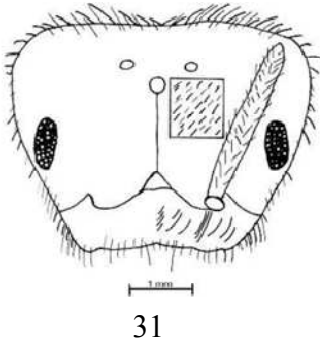
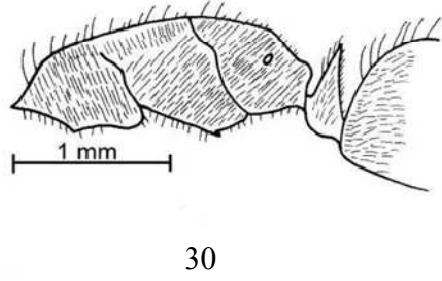
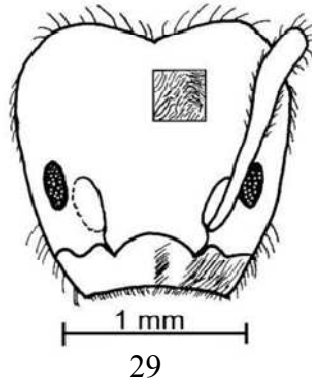


21



22

Figures 17-22 *Liometopum microcephalum*; (17, 18) Worker head and mesosoma, [CZECHOSLOVAKIAU- Moravia, mer. Lednice (CWEM)]; (19, 20) Gyne head and mesosoma, [UROMANIAU, Juderul, Siba, (CASC)]; (21, 22) Male head and mesosoma, [SERBIA, Vojvodina, Vrdnik, Ledniko Jezero (CASC)].



Figs. 29-34. *Liometopum orientale* and *Liometopum microcephalum* (modified from Kupyanskaya 1988). *Liometopum orientale*: (29) Worker head; (30) Worker petiole; (31) *Liometopum microcephalum*: Worker petiole; (32) Gyne head; (33) Male head; (34) Male mesosoma.

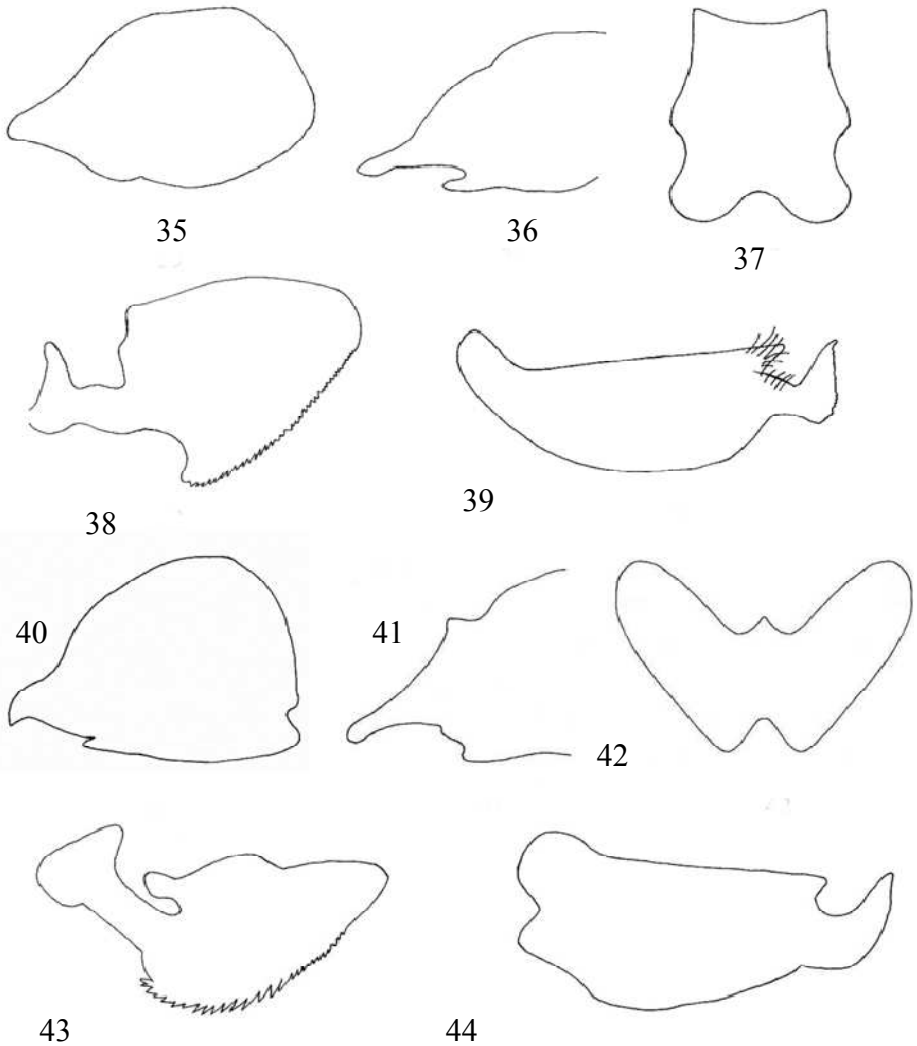


Fig. 35-39 *Liometopum apiculatum* male genitalia, [USA, California, San Juan Co. San Juan River mile 165, (CASC)]; (35) genital capsule; (36) paramere; (37) subgenital plate; (38) aedeagus; (39) volsella.

Fig. 40-44 *Liometopum luctuosum* male genitalia, [USA, Arizona, Yavapai Co, Granite Dells 4 mi. N. Prescott, (CASC)]; (40) genital capsule; (41) paramere; (42) subgenital plate; (43) aedeagus; (44) volsella.



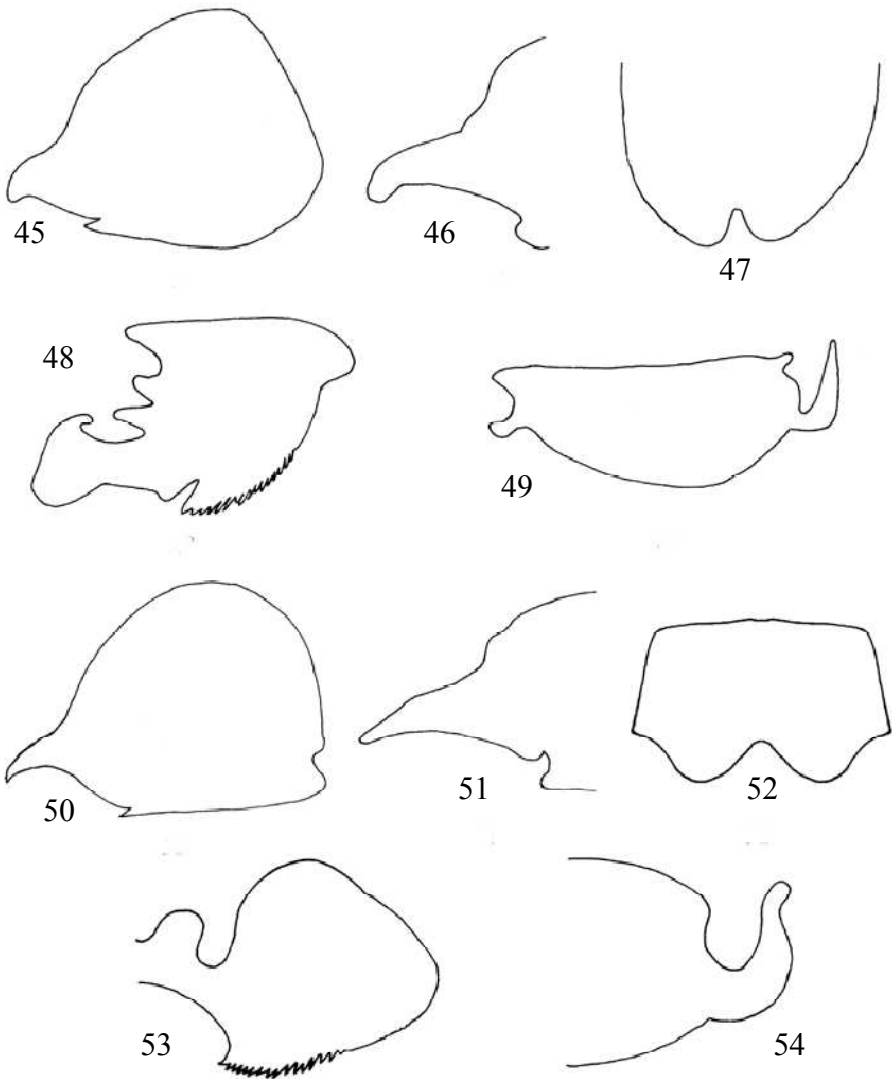
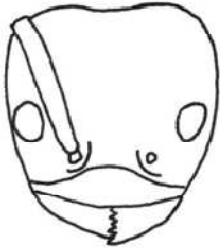
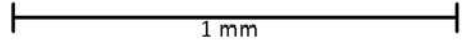
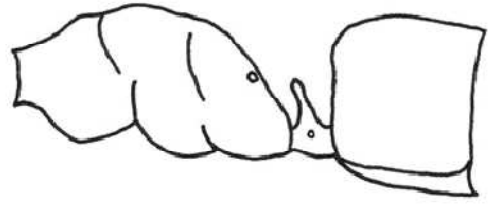


Fig. 45-49 *Liometopum microcephalum* male genitalia, [SERBIA, Vojvodina, Vrdnik, Ledniko Jezero (CASC)] ; (45) genital capsule; (46) paramere; (47) subgenital plate; (48) aedeagus; (49) volsella

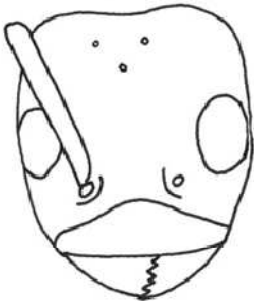
Fig. 50-54 *Liometopum occidentale* male genitalia, [USA, California, Riverside, San Jacinto Mts. (CWEM)]; (50) genital capsule; (51) paramere; (52) subgenital plate; (53) aedeagus; (54) volsella.



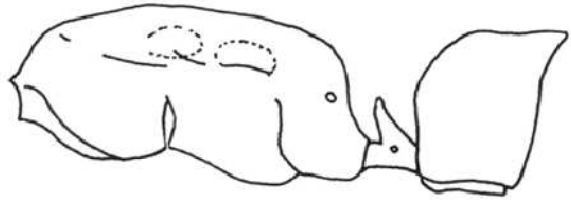
55



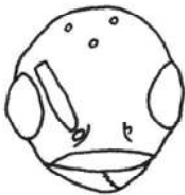
56



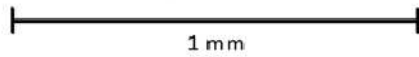
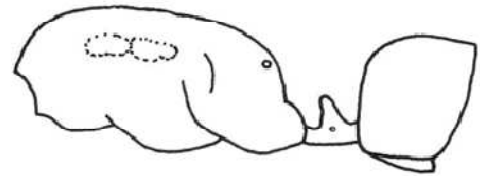
57



58

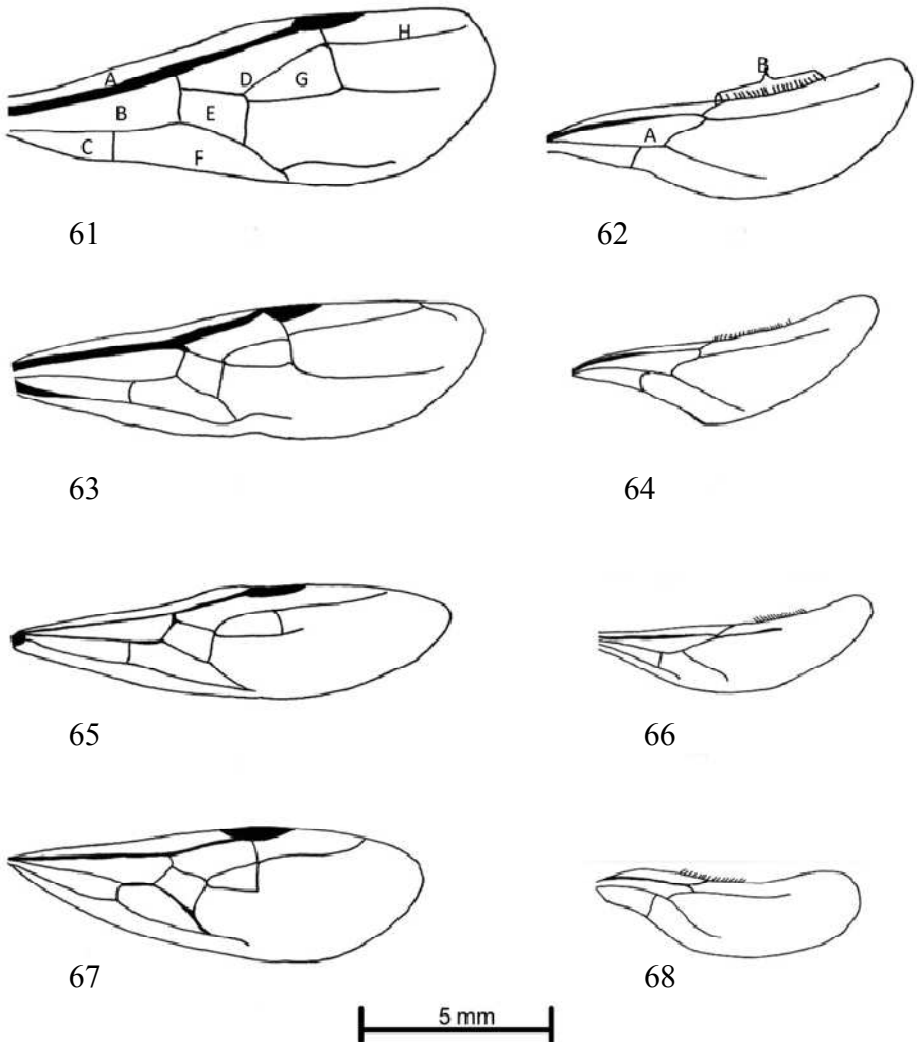


59



59

Figs. 55-60. *Liometopum minimum*= *Chronoxenus myops* (modified from Zhou 2001). (55, 56) Worker head and mesosoma; (57, 58) Gyne head and mesosoma; (59, 60) Male head and mesosoma.



Figs. 61-64. *Liometopum apiculatum*. (61) Gyne anterior wing, (A) Costal Cell, (B) Median Cell, (C) Submedian Cell, (D) First Submarginal Cell (E) First Discoidal Cell, (F) Second Discoidal Cell, (G) Second Submarginal Cell, (H) Marginal Cell; (62) Gyne hind wing, (A) Median Cell, (B) Hamuli; (63) Male anterior wing; (64) Male hind wing.  
 Figs. 65-68. *Liometopum luctuosum*; (65) Gyne anterior wing; (66) Gyne hind wing; (67) Male anterior wing; (68) Male hind wing.

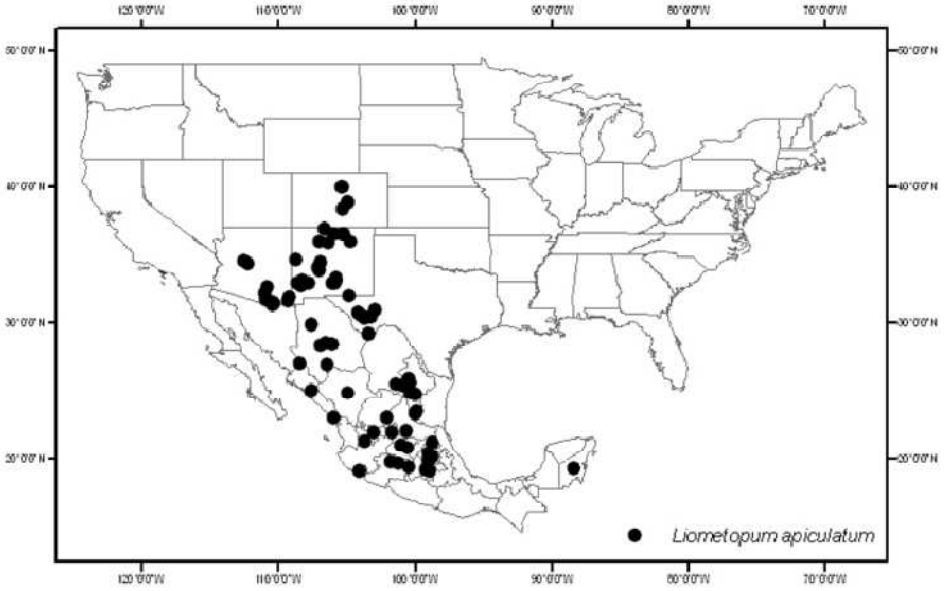


Fig. 69. *Liometopum apiculatum* distribution .

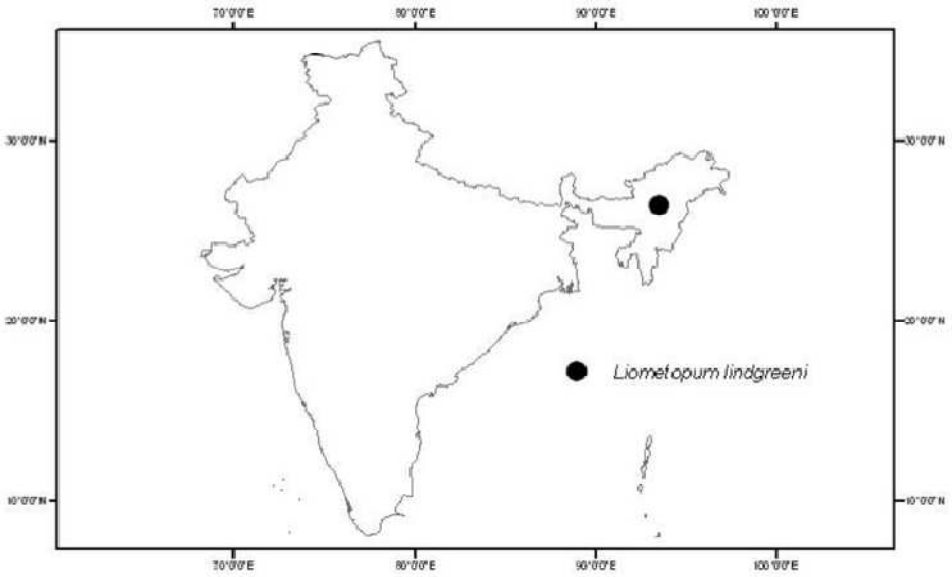


Fig. 70. *Liometopum lindgreeni* distribution.

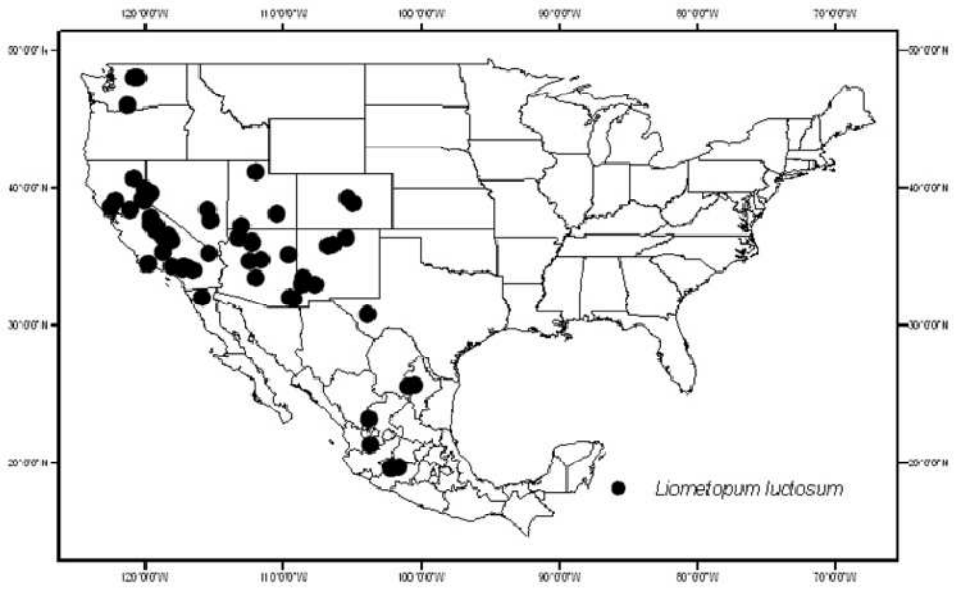


Fig. 71. *Liometopum luctuosum* distribution.

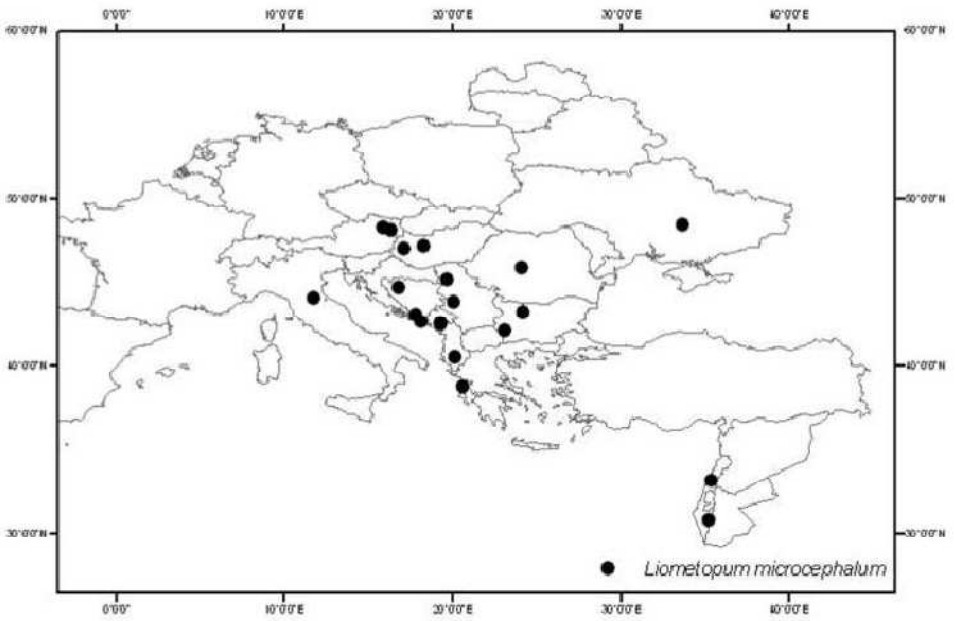


Fig. 72. *Liometopum microcephalum* distribution.

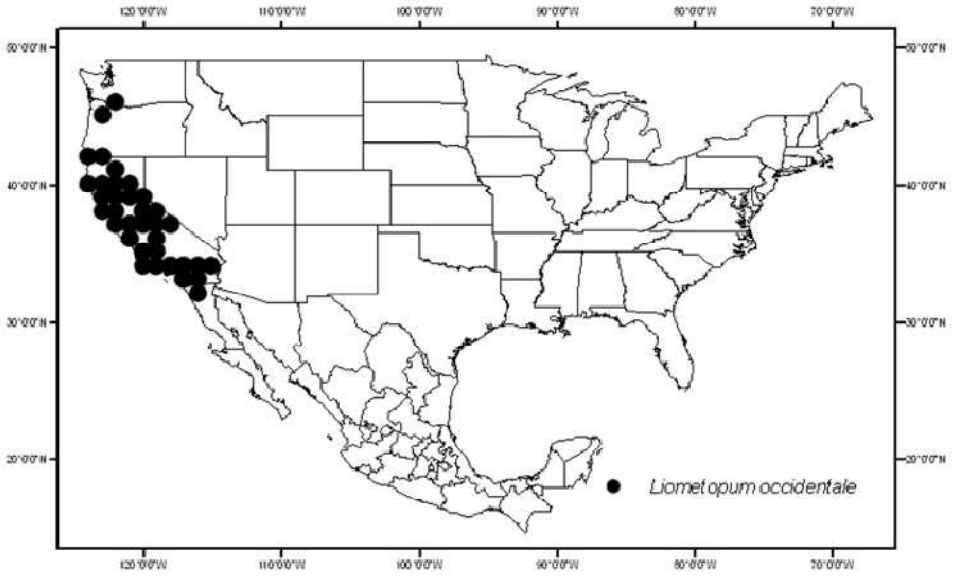


Fig. 73. *Liometopum occidentale* distribution.

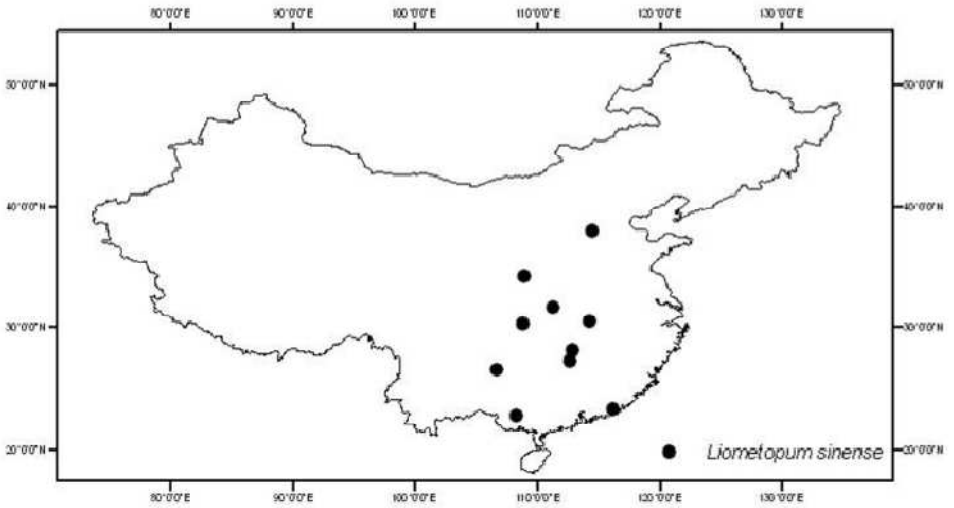


Fig. 74. *Liometopum sinense* distribution.



Figs. 75-80. Digital Micrographs of *Liometopum apiculatum*. (75-76) Worker head and mesosoma [MEXICO , Queretaro, Queretaro, La Barreta, 20° 49.35" N 100° 30.94" W (CWEM)]; (77-78) Gyne head and mesosoma [MEXICO , San Luis Potosi, 41 km SE Sto. Domingo (CWEM)]; (79-80) Male head and mesosoma [US A, Colorado, Colorado Springs, (MCZC)].



Figs. 81-86. Digital Micrographs of *Liometopum luctuosum*. (81-82) Worker head and mesosoma [MEXICO, Coahuila, 13 km E San Antonio, (CWEM)]; (83-84) Gyne head and mesosoma [US A, Arizona, Coconino Co., San Francisco Mts. (MCZC)]; (85-86) Male head and mesosoma [US A, Arizona, Cochise Co., Chiricahua Mts. (MCZC)].





Figs. 87-92. Digital Micrographs of *Liometopum occidentale*. (87-88) Worker head and mesosoma [US A, California, Riverside, San Jacinto Mts. (CWEM)]; (89-90) Gyne head and mesosoma, [US A, Calaveras, Riverside, 4.8 km S. West Point (CASC)]; (91-92) Male head and mesosoma, [US A, California, Riverside, San Jacinto Mts. (CWEM)].

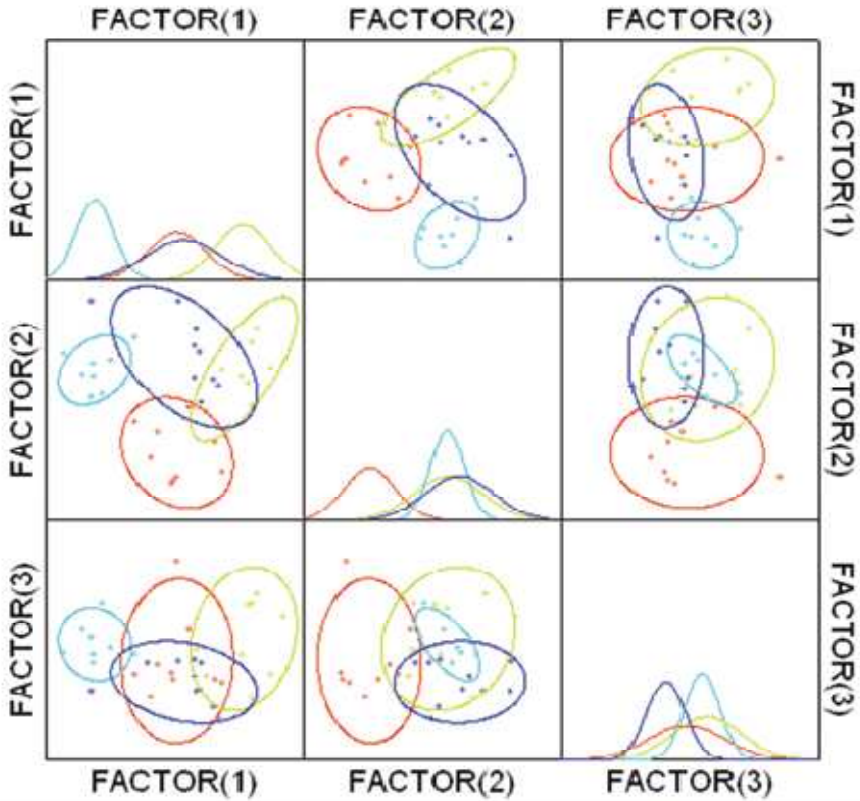


Figs. 93-98. Digital Micrographs of *Liometopum microcephalum*. (93-94) Worker head and mesosoma [CZECHOSLOVAKIA- Moravia, mer. Lednice (CWEM)]; (95- 96) Gyne head and mesosoma [RO MANIA, Juderul, Siba, (CASC)]; (97-98) Male head and mesosoma, [SERB IA, Vojvodina, Vrdnik, Lediniko Jezero (CASC)].



Figs. 99-105. (99-100) *Liometopum lindgreeni* worker head and mesosoma [INDIA, Assam, Debrugarh, (MHNG)]. (101-102) *Liometopum sinense* Worker head and mesosoma [CHINA, Soochow, (MCZC)]; (103) *Sceptobius dispar* (MCZC); (104) *Dinardilla liometopi*, (MCZC); (105) *Liometophilus manni*, (LACM).

## Canonical Scores Plot

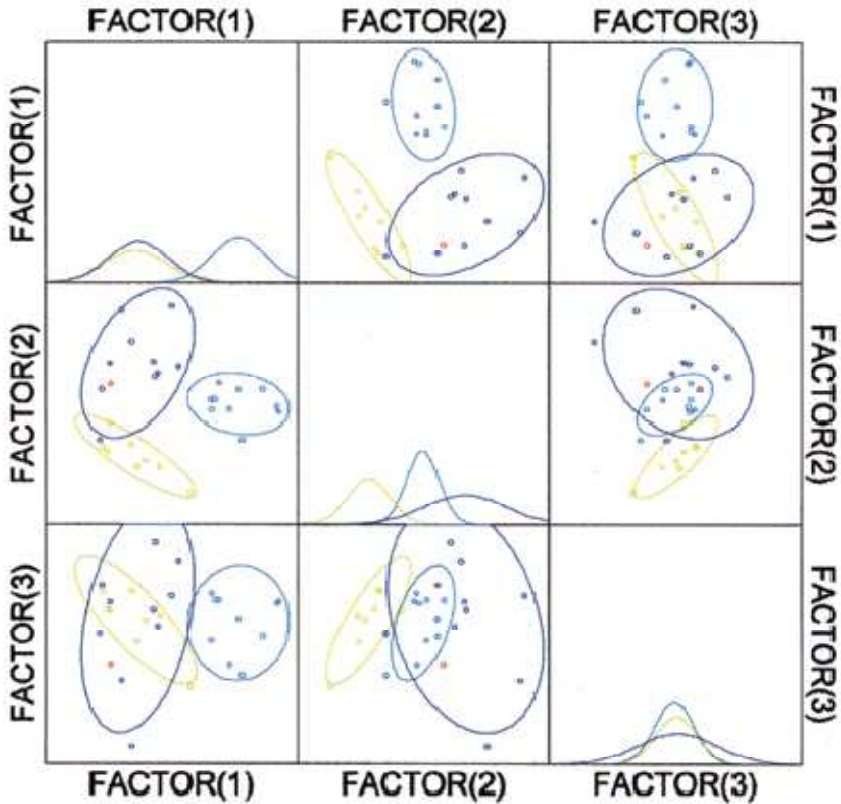


### SPECIES

- *Liometopum apiculatum* Mayr
- *Liometopum luctuosum* Wheeler
- *Liometopum microcephalum* Panzer
- *Liometopum occidentale* Emery

Fig. 106. Three Factor Canonical Analysis Plots: Factor 1= Eye Length; Factor 2= Scape Length; Factor 3= Petiole Height.

### Canonical Scores Plot



### SPECIES

- **Liometopum lindgreeni** Forel
- **Liometopum microcephalum** Panzer
- **Liometopum sinense sericatum** Wheeler
- **Liometopum sinense** Wheeler

Fig. 107. Three factor Canonical Analysis Plots: Factor 1= Petiolar Index; Factor 2= Scape Length; Factor 3= Scape Index.

Table 1. A comparison of the variables selected by discriminant function analysis comparing *L. apiculatum*, *L. luctuosum*, *L. occidentale* and *L. microcephalum*.

Character Selected	F Value Entered	Wilks's Lambda	P value	Eigenvalues	Canonical Correlation
Eye Length	37.527	0.237	0.000	3.796	0.890
Scape Length	18.72	0.089	0.000	1.620	0.786
Petiole Height	5.634	0.059	0.000	0.347	0.508

Table 2. A comparison of the variables selected by discriminant function analysis comparing *L. lindgreeni*, *L. microcephalum* *L. sinense* and *L. sinense* var. *sericatum*.

Character Selected	F Value Entered	Wilks's Lambda	P value	Eigenvalues	Canonical Correlation
Petiole Index	14.744	0.361	0.000	3.490	0.882
Scape Length	6.782	0.195	0.000	2.090	0.822
Scape Index	4.697	0.121	0.000	0.044	0.205

## ACKNOWLEDGEMENTS

We would like to thank Francisco Serna, Shawn T. Dash, Samuel Del Toro, and Paul Lenhart from the University of Texas at El Paso for their valuable input and review of the manuscript. We would also like to extend our appreciation to Dr. Alex Wild, and Dr. John Longino for their review and comments on this manuscript. We thank Dr. Phil Ward for manuscript advice and identification of specimens from California collections. Special thanks are extended to Ms. Rebecca Marin for her help in preparation of distribution maps. Additionally, we would like to thank the instructors Laura Cade and John Wilson for their influence and direction that led to the creation of this manuscript. We would like to thank the various curators of the museum collections including, Stefan Cover and Dr. Gary Alpert (MCZC), Dr. Brian Fisher and April Nobile (CASC), Weiping Xie, Dr. Brian V. Brown and Roy Snelling (LACM), Luis Quiroz (UAGC), Dr. Robert Jones and Maya Rocha (UAQC), Dr. Ted Shultz (USNM), and Dr. Bernhard Merz (MNHG). Additional specimens and distributional data were provided by Dr. Jose-Luis Navarrete-Heredia, and Miguel Vasquez-Bolaños and Georgina A. Quiroz-Rocha. We also would like to thank Dr. Zhou for fresh material collected in China and Dr. John Longino for specimen distribution data. We especially appreciate the help of Dr. Gary Alpert, Stefan Cover, Dr. Brian Fisher and April Nobile for allowing us to utilize imaging equipment. Travel for the MCZC visit was provided by the Ernst Mayr Grant. Funding for this project was provided by NSF Grant DBI 0405470, W. Mackay Principal Investigator, the University of Texas at El Paso Honors Program and NSF Grant, Colorado

Alliance for Graduate Education and the Professoriate; HRDB-639653, NSF06-552.

## REFERENCES

- Andersen, A. N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. *Journal of Biogeography* 24(4): 433-460.
- Atanasov, N. & G.M., Dlusskyi. 1992. Hymenoptera Formicidae. *Fauna Bulgarica* 22: 1-310.
- Baroni Urbani, C. 1971. Catalogo delle specie di Formicidae d'Italia. (Studi sulla mirmecofauna d'Italia). *Memorie della Societa Entomologica Italiana* 50: 5-287.
- Bolton, B. 1995. *A New General Catalogue of the Ants of the World*. Harvard University Press, Cambridge Massachusetts, 504 pp.
- Bolton, B, G. Alpert, P.S. Ward & P. Naskrecki. 2006. Bolton's Catalogue of Ants of the World: 1758-2005. Harvard University Press. Cambridge Massachusetts, London, England (Compact Disc Software).
- Brady, S. G., T. R. Schultz, B.L. Fisher, & P.S. Ward. 2006. Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences* 103(48): 18172-18177.
- Brako, G. 2003. New Species for the ant fauna of Slovenia (Hymenoptera: Formicidae). *Natura Sloveniae* 5: 17-25.
- Buckley, S. B. 1866. Descriptions of new species of North American Formicidae. *Proceedings of the Entomological Society of Philadelphia* 6:152-172.
- Carpenter, F. M. 1930. The fossil ants of North America. *Bulletin of the Museum of Comparative Zoology of Harvard College* 70:1-66
- Chang, Y.D. & D.H. He. 2002. A New Species of *Liometopum* Mayr from Gansu, China (Hymenoptera: Formicidae, Dolichoderinae). *Acta Zootaxonomica Sinica* 45: 110-111.
- Chiotis, M., L. S. Jermin, & R. H., Crozier. 2000. A molecular framework for the phylogeny of the ant subfamily Dolichoderinae. *Molecular Phylogenetics and Evolution* 17(1): 108-116.
- Clark, W. H., & P.E. Blom. 2007. Annotated checklist of the ants on the Idaho National Laboratory (Hymenoptera : Formicidae). *Sociobiology* 49(2): 1-117.
- Creighton, W. S. 1950. The ants of North America. *Bulletin of the Museum of Comparative Zoology of Harvard College* 104:1-585.
- Conconi, R.E.J., P.M.J. Flores, R.A. Perez, G.L. Cuevas, C.S. Sandoval, C.E. Garduno, I. Portillo, T. Delage-Darchen, & B. Delage-Darchen. 1987. Colony structure of *Liometopum apiculatum* M. and *Liometopum occidentale* var. *luctuosum* W. In: Eder, J., & H. Rembold (eds.). *Chemistry and Biology of Social Insects*, Munich:Verlag J. Pepenry. p. 671.

- Conconi, R.E.J., D. Fresneau, & P. Jaisson . 1987. Polytheism of settler queens of *Liometopum apiculatum* M. and *Liometopum occidentale* var. *luctuosum* W. (Hymenoptera-Formicidae-Tapinomini). In: Eder, J. Rembold, H. (Eds.). Chemistry and Biology of Social Insects, Munich:Verlag J. Peperny. p. 109.
- Conconi, R.E.J., R. MacGregor Loaeza, J. Cuadriello Aguilar, & G. Sampedro Rosas. 1983. Quelques données sur la biologie des fourmis *Liometopum* (Dolichoderinae) du Mexique et en particulier sur leurs rapports avec les homopteres. In: Jaisson, P. (ed.). Social insects in the tropics. Proceedings of the first international symposium 2:125-130.
- Cook, T.W. 1953. *The Ants of California*. Pacific Books, Palo Alto California, 462 pp.
- Danoffburg, J. A. 1994. Evolving under myrmecophily - a cladistic revision of the symphilic beetle tribe Sceptobiini (Coleoptera, Staphylinidae, Aleocharinae). Systematic Entomology 19(1): 25-45.
- Dubovikoff, D.A. 2005. The system of taxon *Bothriomyrmex* Emery, 1869 (Hymenoptera: Formicidae) and relative genera. Kavkazskii Entomologicheskii Byulleten 1(1): 89-94.
- Emery, C. 1895. Beiträge zur kenntniss der Nordamerikanischen Ameisenfauna. Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere 8:257-360.
- Forel, A. 1895. Les formicides de l'Empire des Indes et de Ceylan. Part V. Adjonction aux Camponotinae. Journal of the Bombay Natural History Society 9:453-472.
- Forel, A. 1902. Variétés myrmécologiques. Annales de la Societe Entomologique de Belgique 46:284-296.
- Forel, A. 1914. Einige amerikanische Ameisen. Deutsche Entomologische Zeitschrift, 615-620.
- Grabenerger, G., P. Kehrli, B. Schlick-Steiner, F. Steiner, M. Stolz, & S. Bacher. 2005. Predator complex of the horse chestnut leaf miner *Cameraria ohridella*: identification and impact assessment. Blackwell Verlag, Journal of Applied Entomology 129:353-362.
- Gregg, R.E. 1963. *The Ants of Colorado*. University of Colorado Press, Denver Colorado, 792 pp.
- Gulmahamad, H. 1995. The genus *Liometopum* Mayr (Hymenoptera: Formicidae) in California, with notes on nest architecture and structural importance. Pan-Pacific Entomologist 71:82-85.
- Heer, O. 1850. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Zweite Abtheilung: Heuschrecken, Florfliegen, Aderflügler, Schmetterlinge und Fliegen. Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für di gesammten Naturwissenschaften, 11:1-264.
- Hotelling, H. 1936. Relations between two sets of variates. Biometrika. 28: 312-377.
- Karavaiev, W. 1927. Ameisen aus dem paläarktischen Gebiet. Trudy Ukrains'ka Akademiya Nauk Fizichno-Matematichnoho Viddilu 4: 333-348.



- Kistner, D.H., E.A. Jensen, & H.R. Jacobson. 2002. A New Genus and Two New Species of Myrmecophilous Staphylinidae Found with *Liometopum* in California (Coleoptera; Hymenoptera: Formicidae). *Sociobiology* 39 (2): 291-306.
- Kupyanskaya, A. N. 1988. [Far Eastern representatives of the genus *Liometopum* (Hymenoptera, Formicidae).] *Vestnik Zoologii* 1: 29-34.
- H Kupyanskaya, A. N. 1990. [*Ants of the Far East USSR.*] *Akademiya Nauk SSSR, Vladivostok*, 258 pp.
- Kuttner, H. 1977. Hymenoptera, Formicidae. *Insecta Helvetica* 6:1-298.
- Mackay, W. P., D. Lowrie, A. Fisher, E. Mackay, F. Barnes, & D. Lowrie. 1988. The Ants of Los Alamos County, New Mexico (Hymenoptera: Formicidae). In: Trager, J. C. *Advances in Myrmecology*. E. J. Brill, New York, 79-131.
- Mackay, W.P., & E. Mackay. 2002. *The Ants of New Mexico (Hymenoptera: Formicidae)*. Edwin Mellen Press, Lewiston, New York, 400 pp.
- Martinez, D. & A. Tinaut. 2001. About the presence of *Liometopum microcephalum* in the Iberian Peninsula (Hymenoptera: Formicidae). *Boletín de la Asociación Española de Entomología* 25:123-124.
- Mayr, E. 1942. *Systematics and the origin of species from the viewpoint of a zoologist*. Columbia University Press, New York, 334 pp.
- Mayr, E. 1995. Systems of ordering data. *Biology and Philosophy* 10: 419-434.
- Mayr, G. 1853. Einige neue Ameisen. *Verhandlungen des Zoologisch-Botanischen Vereins in Wien* 2:143-150.
- Mayr, G. 1861. *Die europäischen Formiciden*. Vienna. 80 pp.
- Mayr, G. 1867. Vorläufige Studien über die Radoboj-Formiciden, in der Sammlung der k.k. geologischen Reichsanstalt. *Jahrbuch der k.k. Geologischen Reichsanstalt*. 17: 47-62.
- Mayr, G. 1868. Die Ameisen des baltischen Bernsteins. *Beitraege zur Naturkunde Preussens Koeniglichen Physikalisch-Oekonomischen Gesellschaft zu Koenigsberg* 1: 1-102.
- Mayr, G. 1870. Neue Formiciden. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 20: 960-961.
- Merickel, F.W. & W.H. Clark. 1994. *Tetramorium caespitum* and *Liometopum luctuosum* (Hymenoptera: Formicidae): New state records for Idaho and Oregon, with notes on their natural history. *Pan Pacific Entomologist* 70:148-158.
- Miller, T.E.X. 2007. Does having multiple partners weaken the benefits of facultative mutualism? A test with cacti and cactus-tending ants. *Oikos* 116: 500-512.
- Moder, K., B.C. Schlick-Steiner, F.M. Steiner, S. Cremer, E. Christian, & B. Seifert. 2007. Optimal species distinction by discriminant analysis: comparing established methods of character selection with a combination procedure using ant morphometrics as a case study. *Journal of Zoological Systematics and Evolutionary Research* 45(1): 82-87.
- Moreau, C. S., C. D. Bell, R. Vila, S.B. Archibald, & N.E. Pierce. 2006. Phylogeny of the ants: Diversification in the age of angiosperms. *Science* 312(5770): 101-104.

- Moreno-Garcia, A., R.W. Jones, W.P. Mackay, & P. Rojas-Fernandez. 2003. Diversity and habitat Associations of the Ants (Insecta: Formicidae) of El Eden Ecological Reserve. In: Gomez-Pompa, A., Allen, M.F., Fedick, S.L., Jimenez-Osorinio, J.J. (eds.), *The Lowland Maya Area, Three Millennia at the Human-Wildlife Interface*. Food Products Press, New York, pp. 293-304.
- Navarrete-Heredia, J.L., M. Vasquez-Bolanos, & G.A. Quiroz-Rocha. 2007. New Mexican distributional data on the Sceptobiini-*Liometopum* association (Coleoptera : Staphylinidae, Aleocharinae-Hymenoptera : Formicidae, Dolichoderinae). *Sociobiology* 49:221-229.
- Panzer, G. 1798. *Faunae Insectorum Germaniae initia oder Deutschlands Insecten*. p 1652.
- Ramoselorduy, J. & J. Levieux. 1992. *Liometopum-apiculatum* Mayr and *L. occidentale* Wheeler Foraging Areas Studied with Radioisotopes Markers (Hymenoptera, Formicidae - Dolichoderinae). *Bulletin De La Societe Zoologique De France-Evolution Et Zoologie* 117(1): 21-30.
- Roger, J. 1863. Verzeichniss der Formiciden-Gattungen und Arten. *Berliner Entomologische Zeitschrift* 7:1-65.
- Schlick-Steiner, B.C., F.M. Steiner & S. Schödl. 2003. Rote Listen ausgewählter Tiergruppen Niederösterreichs - Ameisen (Hymenoptera: Formicidae). Amt der Niederösterreichischen Landesregierung, Abteilung Naturschutz, St. Pölten. 75pp.
- Siefert, B. 2003. The ant genus *Cardiocondyla* (Insecta:Hymenoptera:Formicidae) - a taxonomic revision of the *C. elegans*, *C. bugarica*, *C. batesii*, *C. nuda*, *C. shuckardi*, *C. stambuloffii*, *C. wroughtonii*, *C. emeryi*, and *C. minutior* species groups. *Annalen des Naturhistorischen Museums in Wien* 104:203-338.
- Shapley, H. 1920. Thermokinetics of *Liometopum apiculatum* Mayr. *Proceedings of the National Academy of Sciences* 6:181.
- Sharma, S. 1996. *Applied Multivariate Techniques*. John Wiley & Sons Inc. New York. 493 pp.
- Shattuck, S.O. 1992. Generic revision of the ant subfamily Dolichoderinae (Hymenoptera: Formicidae). *Sociobiology* 21:1-181.
- Shattuck, S.O. 1992. Higher Classification of the Ant Subfamilies Aneuretinae, Dolichoderinae and Formicinae (Hymenoptera, Formicidae). *Systematic Entomology* 17(2):199-206.
- Shattuck, S.O. 1994. Taxonomic catalog of the ant subfamilies Aneuretinae and Dolichoderinae (Hymenoptera: Formicidae). *University of California Publications in Entomology* 112:1-241.
- Shattuck, S.O. 1995. Generic-Level Relationships within the Ant Subfamily Dolichoderinae (Hymenoptera, Formicidae). *Systematic Entomology* 20(3):217-228.
- Weist, L. 1967. Zur Biologie der Ameise *Liometopum microcephalum*. *Wissenschaftliche Arbeiten Burgenland* 38:136-144.

- Wheeler, G. C., & J. Wheeler. 1951. The ant larvae of the subfamily Dolichoderinae (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington* 53:169-210.
- Wheeler, G. C., J. Wheeler. 1973. *Ants of Deep Canyon*. University of California Press. 162 pp.
- Wheeler, G. C., J. Wheeler. 1986. *The Ants of Nevada*. Natural History Museum of Los Angeles County, Los Angeles. 138 pp.
- Wheeler, W. M. 1905. The North American ants of the genus *Liometopum*. *Bulletin of the American Museum of Natural History* 21:321-333.
- Wheeler, W. M. 1915. The ants of the Baltic amber. *Schriften der Physikalisch-Okonomischen Gellschaft zu Konigsberg* 55:1-142.
- Wheeler, W. M. 1917. The mountain ants of western North America. *Proceedings of the American Academy of Arts & Sciences* 52:457-569.
- Wheeler, W. M. 1921. Chinese Ants. *Bulletin of the Museum of Comparative Zoology of Harvard College* 64: 529-547.
- Zhang J. 1989. [*Fossil insects from Shanwang, Shandong, China.*] Shandong Science and Technology Publishing House, Jinan, China. 459 pp.
- Zhang J., Sun B. and Zhang X. 1994. [*Miocene insects and spiders from Shanwang, Shandong.*] Science Press, Beijing, Beijing. 298 pp.
- Zhou S.Y. 2001. A new species of the ant genus *Liometopum* from Guangxi, China (Hymenoptera: Formicidae). *Acta Zootaxonomica Sinica* 26:557-559.
- Zettel, H., T. Ljumomirov, F.M. Steiner, B.C. Schilck-Steiner, G. Grabenwegner & H. Wiesbauer. 2004. The European ant hunters *Tracheliodes curvitattsus* and *T. varus* (Hymenoptera: Crabronidae): taxonomy, species discriminations, distribution and biology. *Myrmecologische Nachrichten* 6:39-47

