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The importance of ants in cave ecology, with new records and behavioral observations of ants in Arizona caves

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Abstract: The importance of ants as elements in cave ecology has been mostly unrecognized. A global list of ant species recorded from caves, compiled from a review of existing literature, is presented. This paper also reviews what is currently known about ants occurring in Arizona (USA) caves. The diversity and distribution represented in these records suggests ants are relatively common cave visitors (trogloxenes). A general utilization of caves by ants within both temperate and tropical latitudes may be inferred from this combined evidence. Observations of ant behavior in Arizona caves demonstrate a low level and sporadic, but persistent, use of these habitats and their contained resources by individual ant colonies. Documentation of *Neivamyrmex* sp. preying on cave-inhabiting arthropods is reported here for the first time. Observations of hypogeic army ants in caves suggests they may not penetrate to great vertical depth in search of prey, but can be persistent occupants in relatively shallow, horizontal sections of caves where they may prey on endemic cave animals. First cave records for ten ant species are reported from Arizona caves. These include two species of *Neivamyrmex* (*N. nigrescens* Cresson and *Neivamyrmex* sp.; Formicidae: Dorylinae), four myrmecines (*Pheidole portalsensis* Wilson, *Pheidole* cf. *porcula* Wheeler, *Solenopsis aurea* Wheeler and *Stenammas* sp. Westwood), one dolichoderine (*Forelius keiferi* Wheeler) and three formicines (*Lasius arizonicus* Wheeler, *L. sitiens* Wilson, and *Camponotus* sp. Mayr).

Keywords: ants, cave ecology, Formicidae, troglaxene

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INTRODUCTION

The importance of ants as elements in the ecology of caves has been mostly unrecognized (Bellés, 1987; Tinaut & Lopez, 2001; Sendra et al., 2011) and historically, research has focused on determining if there are any truly troglotrophic ant species (Kempf, 1961; Wilson, 1962; Tinaut, 2001; Roncin & Deharveng, 2003). Due, in part, to the search for cave-adapted ants, the importance of individual ant colonies utilizing caves has not received adequate attention. The few researchers that have treated ants generally as potentially important elements in cave ecology include Peck, in his studies of caves in the Caribbean (Peck, 1974; 1981a; 1981b; 1982; 1992), Reddell & Cokendolpher (2001) and Cokendolpher et al. (2009) in similar studies in Belize, Mexico, and California and Texas in the USA, and Roncin & Deharveng (2003) in Laos. The great majority of ants occurring in caves probably function as troglaxenes, and it is in this capacity that their importance in cave ecology lies.

Arizona (USA) has a significant cave resource, with approximately 1,500 known caves, but our knowledge of arthropods in caves in the state is very limited (Pape, 2014; Pape & OConnor, 2014). This paper reviews what is currently known about ants occurring in Arizona caves. The first record of an ant in an Arizona cave was not reported until 1999, when Muchmore & Pape (1999) mentioned a *Monomorium* sp. Mayr from Arkenstone Cave near Vail, Arizona. This record is now known to actually be *Pheidole* cf. *porcula* Wheeler (this paper). Ten years passed before a second ant record appeared in Shear et al. (2009), for *Camponotus ocreatus* Emery from Cathedral Cave in northern Arizona. Wynne & Voyles (2014) reported four ant species from caves in the Grand Canyon-Parashant National Monument in Mohave County, Arizona. And most recently, studies in Kartchner Caverns at Kartchner Caverns State Park (KCSP) near Benson, Arizona added an additional five species to the list of ants found in Arizona caves (Pape & OConnor, 2014).

This paper provides a literature summary of ant species recorded from caves around the World, with

new data from Arizona. Important elements of this data are the records and ecology of *Neivamyrmex* found in caves, including their predation on endemic cave arthropods. The sum of this data demonstrates the importance of individual ant colonies in the cave ecology, behavior that is probably global in extent.

MATERIALS AND METHODS

Literature review

A list of ant species recorded in caves was compiled from a review of existing literature, and is presented in [Appendix A](#). Multiple cave records for species (such as the hundreds of records for *Solenopsis invicta* Buren from caves in Texas) have not all been included. Rather, the list was constructed with the intent of listing all genera and species reported from caves, and to assemble the known distribution of cave occurrences for each species. The cave ecological group assigned to these occurrences, when provided by the recording author(s), is included in Appendix A using their original terminology.

There is a long history of efforts to define the ecological associations of terrestrial cave animals, which have been summarized by several authors including Vandel (1965), Camacho (1992) and Sket (2008). To date the issue seems to not be satisfactorily resolved to the satisfaction of all (Romero, 2009, 2011; Lunghi et al., 2014; Pape, this paper), but the definitions proposed by Sket (2008) seem to be gaining greater acceptance among biospeleologists. I use the following definitions (modified after Sket, 2008) in the body of this paper. A troglóbiont is an obligate cave animal, which cannot live outside of the cave environment. A eutroglóphile is a facultative cave animal that is capable of completing its life cycle within caves, but may also do so in similar habitats. A subtroglóphile is an animal that has a proclivity for regularly using caves to meet one or more of its ecological needs, such as food, water, shelter, etc., but must return to the epigeal environment to meet some required life cycle need(s). A troglóxene is an animal that opportunistically uses cave resources that occur within its territory. The term incidental (rather than "accidental") is reserved for animals that randomly enter a cave, and that derive no ecological benefit from their presence in these habitats.

Taxonomy follows ANTCAT (Bolton, 2014) and phylogenetic sequence follows Ward (2014).

Field studies

Field studies for this paper consisted of in-cave biological surveys conducted in 35 caves in Arizona spanning 25 years. Surveys were conducted to document all macrobiotic resources, and did not specifically target ants. Search effort varied considerably, ranging from a couple of hours during a single visit to an individual cave (as at Porcupine Cave) to more extensive efforts involving numerous visits to a single cave over many years (as at Arkenstone Cave, with approximately 500 in-cave hours during 124 visits over 14 years, and supplemented by observations at the cave entrance during related studies). Surveys consisted of searching human-accessible portions of

caves, turning over floor debris including small rocks, broken cave formations, and organic debris, and searching dead animals, scat and bat guano deposits. No pitfall traps were employed. Baits, consisting of raw wood blocks, were used only during the recent two-year Kartchner Caverns study (Pape & O'Connor, 2014). Since field studies in most of the caves were concerned primarily with establishing baseline biological inventories, no quantitative measurements of available nutrients were performed.

Most caves in Arizona contain sensitive archaeological, paleontological, biological or mineralogical resources, or some combination of these constituents. Few of these sites have adequate protections in place to protect these resources. Due to the presence of sensitive resources and the limited value of the negative findings at 29 of the studied caves, many of which were only visited once, they are not named in this paper. Descriptions are provided below for the six caves where ants were found during the field studies and for one previous record (at Cathedral Cave), for which such information was available.

Cave descriptions

- Arkenstone Cave is a designated research site located within Colossal Cave Mountain Park 37 km southeast of Tucson, near Vail, Arizona. The cave is situated in Arizona Upland Subdivision Sonoran Desertscrub (Turner & Brown, 1982) at 1,112 m asl. The cave is formed in Paleozoic age (370-260 mya) limestone strata, and is approximately 1,000 m in length. The cave supports several endemic troglóbiont arthropods (Muchmore & Pape, 1999).
- Kartchner Caverns State Park, near Benson, Arizona, lies within the Basin and Range Province physiographic region of the western United States, and is situated in the Semidesert Grassland biotic community (Brown & Makings, 2014). Kartchner Caverns is contained within a grouping of small hills situated low on the east flank of the Whetstone Mountains, and is formed in the Mississippian age (359-318 mya) Escabrosa Limestone (Jagnow, 1999). The cave is 1,428 m above sea level (asl), and is approximately three kilometers in length (Fig. 1). Kartchner Caverns supports a maternity colony of the cave myotis (*Myotis velifer* Allen) and a large and diverse suite of invertebrates, including several endemic troglóbionts (Welbourn, 1999; Pape & O'Connor, 2014).
- Hidden Cave is a small cave on the east side of the Santa Rita Mountains in Santa Cruz County, Arizona. The cave is situated in Madrean Evergreen Woodland (Brown, 1982a), at 1,613 m asl, and its entrance overlooks a small, ephemeral riparian drainage. The cave is developed in the Mississippian age Escabrosa Limestone.
- Porcupine Cave is situated in Petran Montane Conifer Forest (Pape & Brown, 1982) on the Mogollon Rim in central Arizona, at approximately 2,180 m asl. The cave is formed in Permian age (270 mya) Kaibab Limestone, and is 1,585 m long.

- Nugget Cave is a small cave situated in Semidesert Grassland (Brown & Makings, 2014) at an elevation of 1,500 m asl in the Santa Catalina Mountains north of Tucson, Arizona.
- Cathedral Cave is a limestone cave located near Ash Fork, Arizona in Great Basin Conifer Woodland (Brown, 1982b) at an elevation of 1,621 m asl (Shear et al., 2009).

Vertical subsurface depths reported for ant observations in the study caves were determined by surveying using Suunto brand hand held compass and clinometer, Leica DISTO™ lite⁵ laser meter and a 100-foot Keson fiberglass tape. Survey data was reduced using Fountain Computer Product's 2003 version of Compass cave survey software.

Voucher specimens have been placed in the University of Arizona Insect Collection (UAIC), Tucson, Arizona.

Portions of these studies were conducted under an Arizona State Parks permit dated 10 September 2009 (Kartchner Caverns), and United States Forest Service Permits SUP0065, dated 5 April 1993, Extension dated 23 August 1995 and SUP0065-01, dated 30 April 2014.

RESULTS

Literature review

This paper is the first effort to consolidate records of ants from caves (Appendix A). The included data provides support for the discussion on the importance of these animals in cave ecology. Records of ants occurring in caves are numerous, dispersed among a variety of taxa, and include approximately 300 species in 80 genera (Wheeler, 1938; Wilson, 1962; Reddell & Mitchell, 1971a, b; Decu et al., 1998; Reddell & Cokendolpher, 2001; Framenau & Thomas, 2008). The records are distributed globally, with the majority occurring in tropical regions or adjacent low latitudes (Appendix A). The list likely includes the great majority of available records, but it is probable that a few have eluded my search efforts.

Over half (56%) of ant subfamilies and nearly one quarter (24.4%) of currently valid genera have been recorded from caves (Appendix A). This broad representation across the family is evidence for a persistent presence of these animals in caves. It also speaks to the ubiquitous presence of ants globally, where they opportunistically occupy most available habitats. Hypogaeic species would intuitively be anticipated to occur more commonly in caves, but this is not evident in the available records. None of the genera appearing in the records are represented disproportionate to their species richness, and thus no affinity for cave use by any group is readily apparent. Since many of the records are ancillary, and not the result of targeted surveys for ants, attaching significance to any apparent prominence of a taxon among this data is problematic. Such analysis would require a review of all records of each species recorded from caves and is beyond the scope of this paper. Additionally, existing records are almost certainly clustered due to variability of search

efforts regionally. Some regions have received focused attention, while others remain almost completely unstudied. This complicates any analysis using current records, and much additional data from ant-focused research is needed before meaningful analyses can be performed.

Less than half of the records include an author-assigned ecological association (ecological group) for the ants with the caves where they were found. And, nearly half of the records providing an association are considered incidental (accidental) occurrences by the record author(s). Ants are thus seldom included in ecological discussions that accompany cave biological inventories. Since authors often fail to provide specific definitions to assigned ecological groups for reported occurrences (Sket, 2008), comparisons between records are problematic. A proliferation of classification systems for ecologically stratifying cave biota has, over the years, introduced considerable confusion into the biospeleological literature (Sket, 2008), and this further aggravates record comparisons. Thus, no effort has been made in this paper to adjust or correlate the record authors' intent for ecological categories they assigned.

Field studies

Observed nutrient resources in the studied caves varied significantly in quantity. Six of the caves have a long history of use by bats, and contain significant, annually refreshed bat guano deposits (Hoffmeister, 1986; Cockrum 1991; Cockrum & Petryszyn, 1991; Mizutani et al. 1992; Buecher & Sidner 1999; USFWS, 1995; Pape, 2014; Pape & OConnor, 2014). However, ants were found in only two of these caves, and only at Patagonia Bat Cave were ants observed actively foraging at a bat guano deposit. Dead vertebrate and invertebrate remains contributed to overall nutrient resources in several of the studied caves. Ringtail scats (*Bassariscus astutus* Lichtenstein) are important nutrient sources for many cave invertebrates (Muchmore & Pape, 1999; Pape, 2014; Pape & OConnor, 2014), and were present in many of the caves in this study. Cave crickets and their guano are sometimes important nutrient sources in caves (Barr, 1967; Hubbell & Norton, 1978; Muchmore & Pape, 1999; Lavoie et al., 2007), particularly where cricket populations are significant, such as in Arkenstone Cave (Poulson, 1992; Muchmore & Pape, 1999; Lavoie et al., 2007).

Plant materials found in the caves were generally quite limited, particularly in lower elevation desert caves, and were almost always concentrated near surface connections where such debris cascades into cave entrances. Only Porcupine Cave contained significant plant material in the cave interior. This cave occasionally takes a significant quantity of water directly into the entrance from the adjacent drainage during large hydrologic events, resulting in organic materials being transported into the cave. None of the studied caves contain a perennial vadose stream that provides a regular source of allochthonous nutrient input. However, a few of

the caves occasionally receive small to moderate quantities of vadose flow that enters the caves through the alluvium of adjacent surface drainages during spring runoff or stochastic precipitation events. These waters are usually devoid of coarse organic materials, which are apparently filtered out during passage through the alluvium. The raw wood blocks used as bait in the Kartchner Caverns study did not attract any of the five ant species found in that cave.

Ants were recorded in six of the 35 caves studied. These new records increase the number of species recorded from Arizona caves from 10 to 20 species (Table 1). The distribution of these records is shown in Fig. 3. The following species accounts provide information on each of the ant records from Arizona caves, and assign an ecological group to the subject colony. The discussion section following the species accounts addresses how these findings support the importance of ants in cave ecology.

Table 1. Summary of ant species recorded from caves in Arizona and the ecological associations for observed colonies.

Species	Cave Name	Cave Entrance Elevation (m)	Ecological Group (Source Author)	Source
Dorylinae				
<i>Neivamyrmex graciellae</i>	Kartchner Caverns	1,428	Subtroglophile*	Pape & OConnor, 2014
<i>Neivamyrmex leonardi</i>	Kartchner Caverns	1,428	Subtroglophile*	Pape & OConnor, 2014
<i>Neivamyrmex nigrescens</i>	Arkenstone Cave	1,112	Trogloxene	This paper
<i>Neivamyrmex</i> sp.	Arkenstone Cave	1,112	Subtroglophile	This paper
Dolichoderinae				
<i>Forelius keiferi</i>	Arkenstone Cave	1,112	Trogloxene	This paper
Formicinae				
<i>Lasius arizonicus</i>	Hidden Cave	1,613	Subtroglophile	This paper
<i>Lasius sitiens</i>	Porcupine Cave	2,140	Subtroglophile?	This paper
<i>Nylanderia</i> cf. <i>hystrix</i>	PARA 1801	3,540	Incidental	Wynne & Voyles, 2014
<i>Camponotus ocreatus</i>	Cathedral Cave	1,621	Unknown	Shear et al., 2009
<i>Camponotus</i> sp.	Hidden Cave	1,613	Incidental	This paper
Myrmicinae				
<i>Pheidole</i> cf. <i>porcula</i>	Arkenstone Cave	1,112	Trogloxene	This paper
<i>Pheidole portalensis</i>	Arkenstone Cave	1,112	Subtroglophile	This paper
<i>Pheidole rhea</i>	Kartchner Caverns	1,428	Trogloxene	Pape & OConnor, 2014
<i>Pheidole rhea</i>	Patagonia Bat Cave	1,592	Trogloxene	This paper
<i>Pheidole vistana</i>	PARA 2602	736	Incidental	Wynne & Voyles, 2014
<i>Pheidole</i> sp.	Kartchner Caverns	1,428	Incidental [†]	Pape & OConnor, 2014
<i>Pheidole</i> sp.	PARA 2204	1,272	Incidental	Wynne & Voyles, 2014
<i>Solenopsis aurea</i>	Arkenstone Cave	1,112	Trogloxene?	This paper
<i>Solenopsis xyloni</i>	PARA 2602	736	Incidental	Wynne & Voyles, 2014
<i>Stenammina</i> sp.	Nugget Cave	1,518	Trogloxene?	This paper
<i>Trachymyrmex arizonensis</i>	Kartchner Caverns	1,428	Trogloxene	Pape & OConnor, 2014

*Originally listed as a troglophile in Pape & OConnor, 2014.

[†]Originally listed as a troglaxene in Pape & OConnor, 2014.

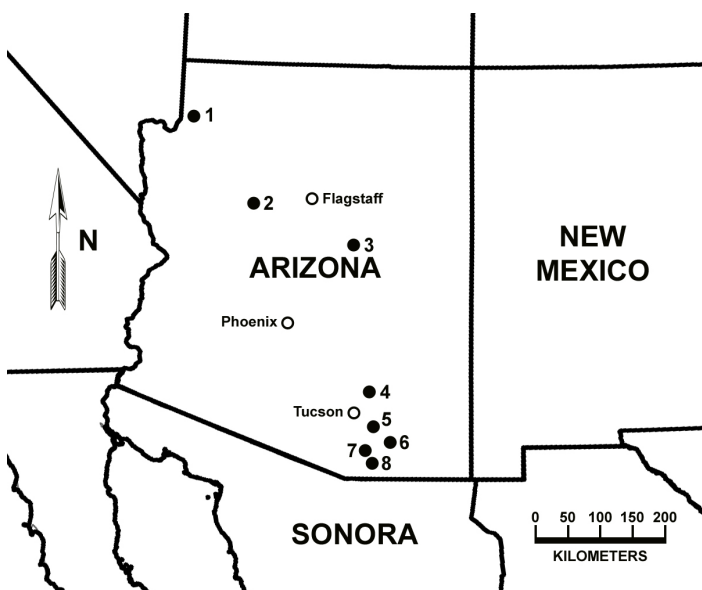


Fig. 3. Regional map showing location of caves discussed in this paper.

1) Grand Canyon-Parashant National Monument caves; 2) Cathedral Cave; 3) Porcupine Cave; 4) Nugget Cave; 5) Arkenstone Cave; 6) Kartchner Caverns; 7) Hidden Cave; 8) Patagonia Bat Cave.

Species accounts

Neivamyrmex graciellae

Neivamyrmex graciellae Mann was previously known only from the states of Jalisco and Oaxaca in central and southern Mexico, and from a single occurrence in southern Arizona at Florida Canyon, on the west flank of the Santa Rita Mountains (Snelling & Snelling, 2007). A recent study at Kartchner Caverns revealed a long-term presence of this species associated with that cave (Pape & OConnor, 2014). *N. graciellae* has been observed active in the cave at depths ranging from 15 to 24 m below the surface.

During an earlier study at KCSP Welbourn (1999) reported the presence of what appeared to be old ant trails in the soil substrate (Fig. 4) near the entrance to the Red River Passage (Fig. 1). However, no ants were observed associated with the trails, or anywhere else in the cave during his study. Subsequent to Welbourn's study and commercial development of the cave as a state park, KCSP personnel had observed and sampled ants in the cave on several occasions. My review of these materials revealed the presence of

two army ant species; *N. graciellae* and *Neivamyrmex leonardi* Wheeler.

During the recent study we found contemporary evidence of ant trail building in the same area of the cave that Welbourn mentioned (Figs. 5 & 6). One of the trails (Fig. 5A) entered an access turret (Fig. 5B) atop a mud-covered calcite bridge that spans the Red River Passage in the cave. It is presumed that this natural bridge structure contained a bivouac of *N. graciellae* at one time. There are very few records of ant trails found in caves. The ant trails in Kartchner Caverns are similar to those of *Labidus coecus* Latreille, which have rarely been reported in caves in Texas and Mexico (Fig. 8 in Reddell & Cokendolpher, 2001). There are currently no Arizona records for *L. coecus*. *Nomamyrmex* (*N. esenbecki wilsoni* Santschi), a deep subterranean doryline (Schneirla, 1971), has been recorded in the United States only from south central Texas (Watkins, 1985), and has so far not been recorded in caves.

A raiding column of *N. graciellae* was observed in the Red River Passage on 3 October 2013. Hundreds of ants, consisting of both minor and major workers, were moving in both directions along the approximately

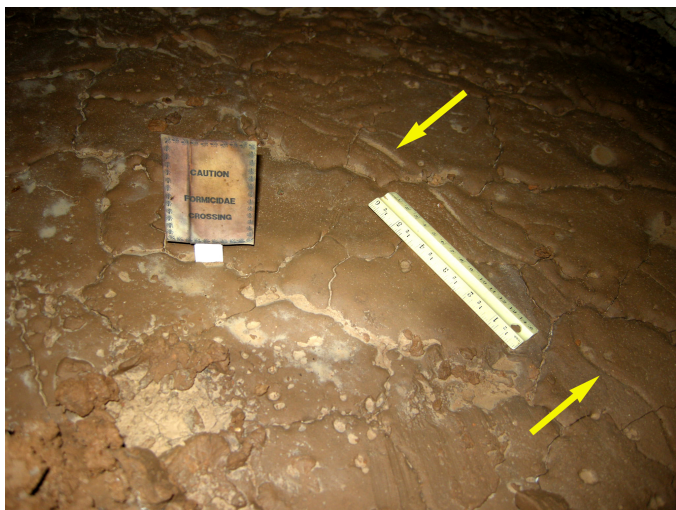


Fig. 4. Old, eroded army ant trail (arrows) in cave mud substrate near the entrance to the Red River Passage in Kartchner Caverns. The scale is 15 cm. The sign is from the original study conducted in the cave (Welbourn, 1999), and reads Caution – Formicidae Crossing.

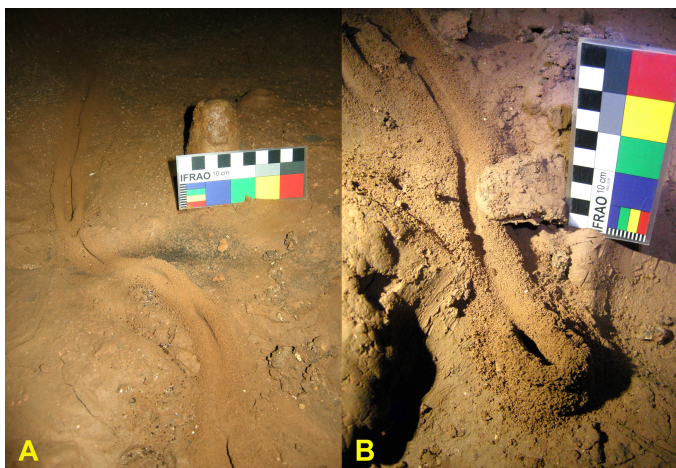


Fig. 5. Recent army ant trail in the Red River Passage at Kartchner Caverns (A), which leads to the old bivouac access turret, situated atop a mud-covered calcite bridge that spans the ephemeral Red River Passage stream (B). The scale is 10 cm.



Fig. 6. Multiple recent, parallel trails of *Neivamyrmex graciellae* in the Red River Passage at Kartchner Caverns. The right trail cross-cuts the previous trails at the top of the image. Scale is 10 cm.

11 m of their trail that was visible. The ants were transporting prey, including pupae and workers of *Crematogaster opuntiae* Buren (Fig. 7). They entered the old bivouac site via the turret but emerged from the far side of the bridge and continued to the northeast. The old bivouac site was apparently not actively being used at the time. Two meters beyond the turret the column went beneath the east wall of the passage at the contact of the bedrock with the floor soil fill. The southwest arm of their trail entered a humanly inaccessible area of breakdown blocks on the cave floor. Small numbers of *N. graciellae* are occasionally observed in other areas of the cave by park staff or researchers.

An old waste midden consisting of hundreds of undigestible cuticular elements of *C. opuntiae* (Fig. 8) was found immediately adjacent to the raiding column trail, four meters southwest of the calcite bridge access turret. The midden is presumed to be the remains of an old *N. graciellae* bivouac site, where the undigestible parts were dropped out of the bivouac. The only other army ant bivouac records from caves are of *L. coecus*, found in at least three caves in Texas, including: Beck Crevice Cave, Beck Sewer Cave and Testudo Tube (Reddell & Cokendolpher, 2001).



Fig. 7. Minor workers of *Neivamyrmex graciellae* on their raiding trail in Kartchner Caverns, October 3, 2013. The ant at the center of the image is carrying a *Crematogaster opuntiae* pupa.

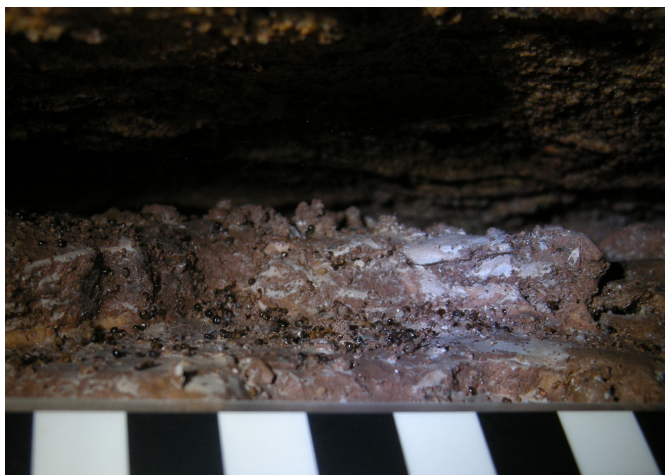


Fig. 8. Remains of *Crematogaster opuntiae* prey in the waste midden at the Red River Passage in Kartchner Caverns. The midden was likely associated with a previous *Neivamyrmex graciellae* bivouac.

It is not known whether *N. graciellae* feeds exclusively on ants, or may opportunistically prey on other arthropods in the cave, including those associated with the bat guano deposits. The absence of ant trails in the vicinity of the guano deposits suggests that *N. graciellae* does not forage at those sites.

Welbourn (1999) reported that some of the ant trails he observed were constructed over human footprints in the cave. Since the cave was not discovered until 1974, those trails would have been no older than 17 years in age at the time of his study (1989-1991). The old trails are still visible today (Fig. 4), and are now between 27 and 42 years in age. The old trails are approximately 1.5 m above the current hydrologic flow level of the ephemeral stream in the adjacent Red River Passage, and are unlikely to have been affected by flowing or pooled water. The degeneration of the trails probably results from a gradual equalization slumping of the clay soil substrate due to repeated changes in soil moisture content. Repeated expansion and contraction of the soil over long periods of time would gradually obliterate the trails. Entrenched ant trails have so far been found only in the vicinity of the Red River Passage.

C. opuntiae, has not been found in the cave, and is considered unlikely to occur there. *N. graciellae* probably leaves the cave to forage, and likely also during alate dispersal. Neither active bivouacs nor reproductives of *N. graciellae* have been observed in the cave, but the presence of the old bivouac access turret, the waste midden, active prey transport and multiple trails of varying age are ample evidence supporting a long-term use of the cave by this species. Based on this evidence *N. graciellae* is considered a subtroglophile in Kartchner Caverns.

Neivamyrmex leonardi

N. leonardi is a small, pale-yellow, eyeless army ant, for which there were previously only two Arizona records, one each, from Nogales and Tucson (Snelling & Snelling, 2007). The species is also known from Oklahoma, Texas, Nevada and California in the U.S., and from Baja California and northern Baja California Sur, Mexico (Cokendolpher, 1990; Snelling & Snelling, no date; 2007), with the majority of records from

southern California (Snelling & Snelling, 2007). There are no previous cave records for the species.

There is currently only a single record of this species from Kartchner Caverns, from 19 December 2006, when one major and three minor workers were sampled (Pape & OConnor, 2014). The ants were found obtaining water from a leaking faucet along a tour trail deep within the cave near one of the main bat guano deposits in the Big Room (Fig. 1). It is not known whether *N. leonardi* may forage at the nearby bat guano deposit, but none of the ants were observed there during numerous visits to the location during the recent two-year study (Pape & OConnor, 2014). Bat guano samples taken monthly at this location during that study did not include any of the ants, and the species is apparently rare in the cave. *N. leonardi* is certainly a subtroglophile in the cave. The potential for the colony being eutroglophilic is reviewed in the discussion section.

Neivamyrmex nigrescens

While performing field observations at the entrance to Arkenstone Cave on 12 November 2000, I observed a small leader column of several *N. nigrescens* exiting the cave beginning at 10:26 hrs. About two-dozen ants were in the column, going upslope a distance of about 20 cm. They remained in the shade beneath a shallow overhang of the bedrock fault along which the cave is developed, and did not venture beyond the point where the bedrock was visibly damp. The ants appeared to want to continue further from the cave, but were apparently discouraged by daylight and/or moisture conditions (surface dryness) they encountered, and periodically returned to the cave. The rock surface temperature was 8°C in the shade of the cave entrance sink at the time. The area the ants were traversing was approximately 0.9 m from the sun-shade interface at the north side of the cave entrance sink. The ants were intermittently active here between 10:26 and 14:10, a total of just over three hours. No prey was observed being transported along this short, exploratory column. Based on current knowledge, this colony is considered a troglonexene in the cave.

Neivamyrmex sp.

During a visit to Arkenstone Cave on 23 October 1999 a raiding column of *Neivamyrmex* sp. was observed actively foraging in the cave. The ants were first observed in the First Antechamber, which is just within the cave aphotic zone (Fig. 9). This location is 33 m from the cave entrance and 36 meters vertically below the surface of the cave hill.

The leading edge of the foraging column was somewhat dispersed. About two meters closer to the front of the cave, where the ants were more numerous, they had scavenged a tachinid fly and were transporting it back along the column in two pieces consisting of its left wing and the co-joined thorax and abdomen. The ant column was traced back towards the front of the cave where they were observed entering the cave directly from the epikarst into a breakdown-choked area approximately seven

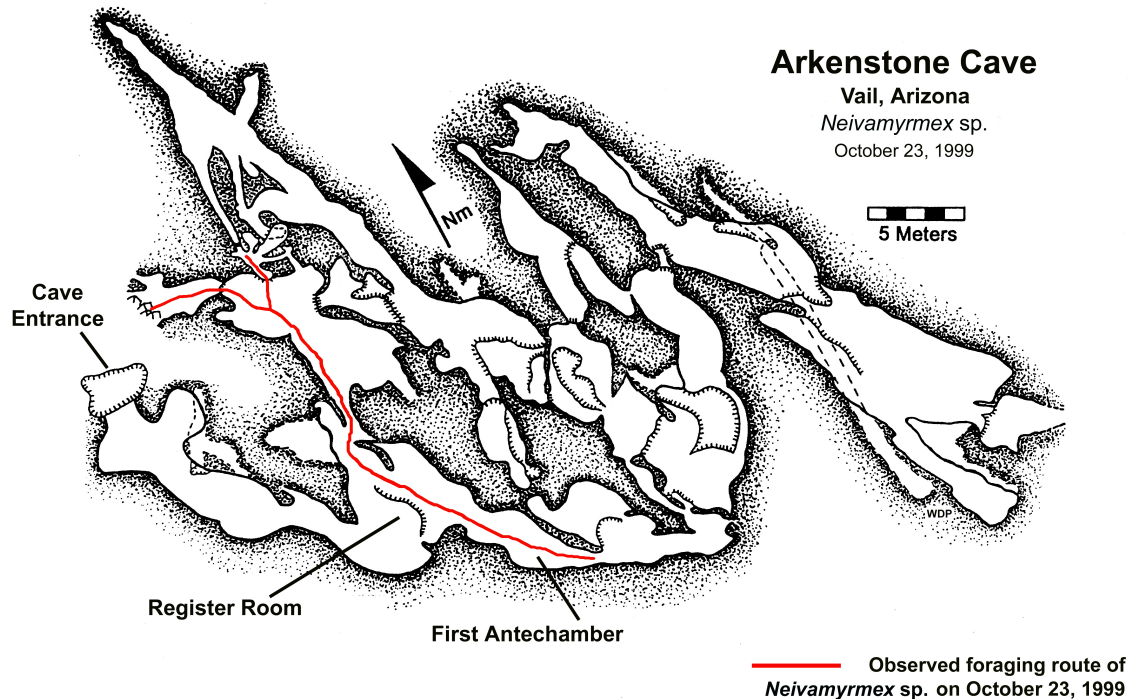


Fig. 9. Plan view map of Arkenstone Cave showing foraging route of *Neivamyrmex* sp. observed on October 23, 1999.

meters east of the gated human entrance. From this point the ants had a single column, which was observed to divide only once. The left branch headed up a parallel passage a distance of at least two meters. The main foraging column extended for a distance of 24 m through the Register Room and into the adjacent First Antechamber (Fig. 9, red line). The linear extent of the column observed within the cave was approximately 34 m. The foraging ants averaged about 60 per decimeter along the column, resulting in an estimated 20,000 observed individuals.

Along the length of the column several invertebrates had been attacked by the ants, including two adult cave cricket (*Ceuthophilus* cf. *pinalensis* Hubbell: Rhaphidophoridae) (Fig. 10). Due to their large size, the crickets had not been moved along the column, but were being processed by the ants into smaller pieces for easier transport. The crickets had evidently been taken down where they stood when they were overcome by the advancing ant column. Several cave millipedes *Colactis utorum* Chamberlin (Diplopoda: Dorypetalidae) had also been subdued by the ants (Fig. 11). The millipedes are not highly mobile and were easily overcome by the advancing ant column.

This occurrence of *Neivamyrmex* sp. in Arkenstone Cave was the only time that the species was observed during more than 130 visits (including the 124 visits that had a biological survey component) to the cave between October 1987 and September of 2002. This is the first instance reporting an army ant colony preying on cave animals. *Neivamyrmex* sp. is a subtroglophile in the cave.

Forelius keiferi

Forelius keiferi Wheeler was observed entering and leaving Arkenstone Cave on 16 April 2013. Five ants were seen removing a small, round piece of debris from the cave, which may have been a piece of a

ringtail scat. The species is a troglaxene that forages in the cave entrance area.



Fig. 10. Raiding column of *Neivamyrmex* sp. dismembering a live-captured adult female cave cricket (*Ceuthophilus* cf. *pinalensis*) in Arkenstone Cave, October 23, 1999.



Fig. 11. Raiding column of *Neivamyrmex* sp. attacking a dorypetalid millipede (*Colactis utorum*) in Arkenstone Cave, October 23, 1999.

Lasius arizonicus

During a visit to Hidden Cave on 11 January 2013 a single ant nest access soil turret and an adjacent tunnel surface breach were observed on the cave floor 30 m from the cave entrance. No ants were present at the time of this visit. Several subsequent visits to the cave revealed additional digging activity of the ants in the front part of the cave, but the ants (*Lasius arizonicus* Wheeler) were not found and sampled until 27 June 2015. During this visit two colonies of *L. arizonicus* were found active in the cave. Approximately a dozen ants were roaming over the cave floor and beneath debris in proximity to their nest in the front part of the cave, in the area where their diggings had previously been observed. An abundance of white fungus is present on fine plant rootlets in the soil substrate where the ants occur in this area. It is not known if the fungus is significant in the ecology of the species. A second colony was found at the very back of the cave. Here, a small cluster of approximately 20 individuals were assembled in a concentrated group on the floor of the cave. A nest entrance was not evident in the soft floor sediments at this location. Due to the nesting activity and persistent use of Hidden Cave by *L. arizonicus*, the colonies occurring in the cave are assigned the status of a subtroglophile.

Lasius sitchensis

A few workers of *Lasius sitchensis* Wilson were found in the front part of Porcupine Cave in northern Arizona on 15 May 1999, approximately 6 m in from the cave entrance. The association of this colony with the cave was not readily apparent, but Wilson (1955) made the following comments regarding this species: "The light coloration, small eyes, and shortened appendages of *sitchensis* constitute a remarkable morphological convergence to the species of the subgenus *Cautolasius*, and specifically to the primitive species *L. (C.) alienoflavus* Bingham. There can be little question that the characters shared by these two species are the mark of a subterranean mode of life." The cave is subject to occasional flooding during significant precipitation events. The presence of organic materials adhered to the ceiling in the interior of the cave indicates that the cave totally fills with water on occasion. The colony of *L. sitchensis* in Porcupine Cave may be subtrogliphilic.

Nylanderia (Paratrechina) cf. hystrix

There is a single record of this species from a cave (PARA 1801) in the Grand Canyon-Parashant National Monument in northern Arizona. The cave is located at an elevation of 3,540 m. The occurrence was considered incidental (accidental) by the authors. Ants for all the PARA cave records included in this paper were taken in baited pitfall traps in the cave entrances (Wynne & Voyles, 2014). There is only one previous record of *N. hystrix* from Arizona, collected in 2003 from beneath a stone in a desert wash at Matkatamiba Canyon in Grand Canyon National Park (AntWeb). The Matkatamiba Canyon specimens are archived in the collection at the California Academy of Sciences (CASENT 0056873).

Camponotus ocreatus

This species is recorded from Cathedral Cave in northern Yavapai County, Arizona (Shear et al., 2009). The Shear paper addressed new cave millipede species from the southwestern United States, and there was no ecological information specific to *C. ocreatus* included in the work, thus its ecological status is unknown.

Camponotus sp.

During a visit to Hidden Cave on 7 January, 2015 a single *Camponotus* sp. major was found approximately 30 m into the cave. This individual was alive, but mostly immobile, and barely able to stand. It is assumed that this individual is an isolated, vagrant from the surface that could not find its way out of the cave. Regular human traffic in the cave may easily have obliterated its chemical trail, causing the animal to become lost in the cave. This species is not *C. ocreatus*. This record is considered an incidental occurrence in the cave.

Pheidole cf. porcula

This small, uniformly brownish-yellow ant has a fairly regular presence within Arkenstone Cave, where they forage on nutrients in the twilight zone. Unfortunately only minors have ever been found. This species was incorrectly reported as *Monomorium* sp. in Muchmore and Pape (1999). This ant seems most similar to *Pheidole porcula* Wheeler, but may be an undescribed species. The species has been found no deeper than 27 m from the entrance, and they rarely enter the aphotic zone. They have been observed in the cave during most months of the year, with seldom more than a couple dozen foraging individuals present at any given time.

They have been observed scavenging a variety of dead invertebrates from the cave, including a lithobiid centipede, an epigeal grasshopper (*Phrynotettix tshivavensis* Haldeman) and cave crickets (*C. cf. pinalensis*). They dismember larger carcasses, and cooperatively remove pieces from the cave to their nest outside the cave (Fig. 12). A large number (50-75) of the ants were observed scavenging at ringtail urine on the floor of the Register Room. The species is a troglaxene in Arkenstone cave.

Pheidole portalensis

Pheidole portalensis Wilson was recorded from Arkenstone Cave on 16 November 2003, when at least ten ants were seen foraging from the cave entrance. One ant was carrying the abdomen of a small beetle (*Hyporhagus* sp.; Zopheridae) into the cave. The ants did not go any further than about 30 cm outside the cave, and it is presumed that their nest was in the front portion, and not deep within the cave. According to Stefan Cover (as cited in Wilson, 2003), *P. portalensis* regularly nests in cracks in rock walls, from which they forage. In this instance apparently, the ants selected a cave for their nest site. This colony is assigned a subtrogliphile status based on the presence of their nest within the cave.



Fig. 12. Several *Pheidole* cf. *porcula* inside Arkenstone Cave transporting a leg of *Ceuthophilus* cf. *pinalensis* out of the cave, July 19, 1992.

Pheidole rhea

P. rhea was occasionally found in Kartchner Caverns during the recently completed two-year study (Pape & OConnor, 2014). They were usually found in the Jackrabbit Shaft and the adjacent portion of the Jackrabbit Gallery (Fig. 1). There is one additional record of the species taken from a tour trail curb deeper in the cave, in the Rotunda Room. This latter record likely represents a vagrant animal, which may have been transported deep into the cave on a tour visitor. *P. rhea* is relatively common on the hill above the cave.

There is evidence that *P. rhea* in Kartchner Caverns is occasionally preyed upon by the endemic thread-legged bug *Phasmatorcoris labyrinthicus* Pape (Pape, 2013). Three ants, including one major, were found lying dead on the cave floor in the Jackrabbit Gallery near the Jackrabbit Shaft door below where the predatory thread-legged bugs have been found on several occasions. We do not know why this ant species comes into the cave. Their presence could be a simple case of proximity to a nest in the soil horizon near the top of the Jackrabbit Shaft. A variety of invertebrates occur in this area of the cave, and *P. rhea* could possibly be preying on some of these species, although this has not been observed. Due to its somewhat regular presence and a suspected nexus with the ecology of the cave, the *P. rhea* colony at Kartchner Caverns is presumed to be a troglaxene.

A second *P. rhea* colony was observed at Patagonia Bat Cave in southern Arizona on 17 August 1996. The ants accessed the cave through the lower entrance, and a steady column of minor workers was busily removing arthropods and other materials from the main bat guano deposit at the rear of the cave (Fig. 2). Among the prey were larvae of a dermestid beetle (*Dermestes carnivorous* Fabricius; Fig. 13; arrow 1) and two species of bat flies (Diptera: Streblidae); *Trichobius major* Coquillett (Fig. 13; arrow 2) and *T. sphaeronotus* Jobling. Live bat flies are highly unlikely to occur on the guano deposit on the

floor of the cave. Possibly the ants were retrieving flies that had died of natural causes, or that may have been injured or killed by grooming bats. Flies dispatched in this manner would fall to the guano deposit where they could be scavenged by the ants. Because *Pheidole* commonly forage on the ground, and seldom climb very high in vegetation even when harvesting seed (Wilson, 2003), it seems improbable that the ants would capture live flies since they would have to forage on the cave ceiling where the flies typically occur in the bat roost.

Leptonycteris primarily feed on nectar and pollen of cacti and agaves during nocturnal foraging forays, and return to the roost to digest their meal and groom. Pollen in their guano, combined with remnants groomed from their faces, accumulates below the

roost into a thin, consolidated yellow cake. The ants were seen removing rather large pieces of this material from the cave. The ants were also removing cactus fruit seeds from the bat guano deposit. These were identified as seeds of the organpipe cactus (*Stenocereus thurberi* Engelman) by W.D. Peachey (personal communication, 24 October 2013). The site was revisited on 30 August 2014 but no ants were found foraging in the cave. The nearest *Pheidole* nest located during this second visit was approximately 235 m south of the cave. The *P. rhea* colony documented foraging in the cave is assigned the status of a troglaxene.

Pheidole vistana

Three *P. vistana* were sampled in the entrance area of a cave (PARA 2602) in the Grand Canyon-Parashant National Monument in northern Arizona by Wynne & Voyles (2014). The cave is located at an elevation of 736 m. This occurrence of *P. vistana* in the cave was considered incidental (accidental) by the authors.

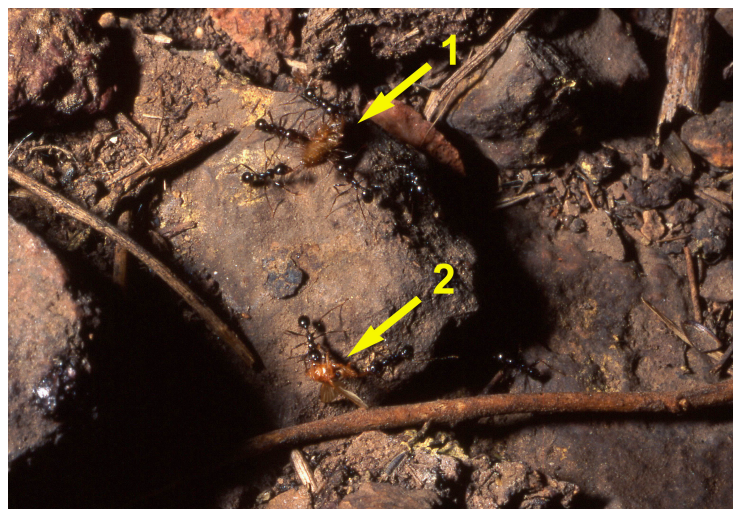


Fig. 13. Foraging *Pheidole rhea* in Patagonia Bat Cave, 16 August 1996. Prey include larvae of the dermestid beetle *Dermestes carnivorous* (arrow 1) and the streblid fly *Trichobius major* (arrow 2). Faint, yellow pollen guano splatters of the lesser long-nosed bats (*Leptonycteris yerbabuena*) that occupy the cave can be seen on the rock in the upper left portion of the photograph.

Pheidole sp.

A single minor of this species was found on 27 May, 2007 in the Throne Room, deep within Kartchner Caverns. However, because there is only this single record, and the sample location was on the tour trail, this individual is most likely an incidental that came into the cave with one of the commercial tours.

Pheidole sp.

A single unidentifiable minor worker of this species was taken in the entrance to PARA cave 2204 (Wynne & Voyles, 2014). This species was considered an incidental (accidental) by the authors.

Solenopsis aurea

At least one species of *Solenopsis* (the invasive *S. invicta*) is known to forage within caves (Elliott, 1992, 2000; Longacre, 2000; Taylor et al., 2005; Cokendolpher et al., 2009). A single worker of the desert fire ant (*Solenopsis aurea* Wheeler) was found just inside the entrance to Arkenstone Cave on 14 January 2012. The ants could potentially prey on invertebrates that occupy the cave. The association of this species with the cave is not known, but it is a presumed troglaxene.

Solenopsis xyloni

Five *S. xyloni* were taken in the entrance of PARA cave 2602 (Wynne & Voyles, 2014). The ants were considered incidentals (accidentals) by the authors. As the numbers of an ant species found in an individual cave increases, either at one time, or cumulatively during separate events, there is an implied greater potential that their presence has some ecological significance. Normally, the presence of five ants would suggest foraging behavior within the cave. However, since the ants were taken in baited traps this confounds the question, since the ants may have been attracted to the bait from outside of the cave. This record should continue to be considered incidental until further evidence suggests otherwise.

Stenamamma sp.

Three *Stenamamma* were sampled at Nugget Cave in the Santa Catalina Mountains north of Tucson on 21 July 1993. Unfortunately the specimens have been lost, and had not been identified to species. An attempt to relocate this species at Nugget Cave was made on 17 August 2014, but the ants were not present at that time. The association of this colony with the cave is suspected to be that of a troglaxene.

Trachymyrmex arizonensis

T. arizonensis was recorded from Kartchner Caverns during the recent two-year macro-invertebrate study of the cave (Pape & OConnor, 2014). Most observations of the species were in the Jackrabbit Shaft (Jackrabbit Gallery area; Fig. 1). The ants were observed moving chaff from their fungus garden to a refuse midden near the top of the shaft. The chaff had overflowed this repository and had cascaded down into the shaft. The fungus garden was not visible, but was likely present

immediately adjacent to the shaft in a fracture in the pediment, or in the adjacent soil profile.

During a visit to the cave on 31 May 2012 the species was observed excavating a nest in a crack in the bedrock wall about 2.5 m. below the top of the shaft. There were about two dozen ants actively working the hole and removing soil particles. A soil spoils pile had accumulated on part of the metal framework for the shaft ladder structure. This nest was still active two years later, on 19 October 2014.

Army ants (*Neivamyrmex* spp.), many of which are primarily ant predators, have been recorded preying on *T. arizonensis* in southern Arizona (LaPolla et al., 2002; Rabeling et al., 2007). *Neivamyrmex* have not been found in proximity to the Jackrabbit Shaft. If *N. graciellae* does prey on *T. arizonensis*, this likely occurs outside the cave, in the epikarst or the overlying soil profile. *N. leonardi* is probably too small a species to successfully predate *Trachymyrmex* spp., and the single record for the species is deep within the cave, far from where *T. arizonensis* has been found.

The presence of *T. arizonensis* in the cave is opportunistic in that they have incorporated this small portion of the cave as a part of their occupied habitat. Since their nest is not technically within the cave and the ants forage outside the cave, this colony of *T. arizonensis* is assigned the status of a troglaxene.

DISCUSSION

There are currently over 13,000 recognized species of ants (Formicidae) in the World, possibly representing only about one half to one third of the actual number of extant species (Bolton, 2014; Ward, 2014). Considering their impressive species diversity, global distribution, and integration into nearly every terrestrial ecotope, it seems intuitive that ants should have a significant presence in the ecology of caves.

Obstacles to recognition of the role that ants play in cave ecology have included: the apparently low level or relative infrequency of their presence in these environments; the fact that many cave biological studies are limited in extent; and an apparent misalignment of the presence of observers with the peak activity periods of ants in caves. That is, researchers commonly visit caves during daylight hours, due to convenience, and may miss crepuscular or nocturnal ant activity, particularly some of the subterranean species, such as *Neivamyrmex*. Additionally, perceptions of what constitutes "typical" behavior for a given ant species should not preclude recognition of individual colony behavior associated with use of cave nutrients.

The number of ant species recorded in individual caves was to a great extent a function of search effort expended. Six ant species were recorded from Arkenstone Cave, where cumulative search time was approximately 500 hours over 14 years. The five species of ants found in Kartchner Caverns were documented during 210 hours of searching during a two-year study (Pape & OConnor, 2014). Search efforts in the remaining caves were considerably less intense, often involving only a few hours during

a single visit. Only one of the caves (Hidden Cave) yielded more than a single ant species (two), one of which was considered an incidental occurrence. No ants were found in 29 of the study caves. Since ants seem to have a low level and sporadic, but persistent presence in caves, their detection may require extensive searching. Thus the negative findings from the low-effort sites are inconclusive, and the apparent absence of ants in these caves in no way precludes their use of those sites.

Observations of cave invertebrates in Arizona have revealed a low level and sporadic, but persistent use of cave habitats and their contained resources by ants. That is, an ant species may be present in a cave irregularly or occasionally (sporadic), and yet is persistent over time, with repeated occurrences separated by months or years. The importance of ants in cave ecology is supported, in part, by observations of colonies of 13 ant species exploiting resources in Arizona caves (this paper). The majority of these observations are from two caves in southeast Arizona, Kartchner Caverns and Arkenstone Cave, which have been extensively studied. It is assumed that similar use of cave resources by ants occurs elsewhere, particularly in the lowland humid tropics where ants have a more pronounced presence, and where nutrients are generally more available in both epigeal and hypogeal environments (Romero, 2009, 2011). This is supported by the numerous records of ants reported from caves in these regions (Appendix A).

Subterranean terrestrial habitats

Subterranean terrestrial habitats have in common their humid, aphotic environments and spatial proximity. Subterranean profiles in karst regions typically include the following habitats, from top to bottom: soil, epikarst, bedrock fissures, and caves (Juberthie, 1980; Camacho, 1992; Juberthie, 2000; Culver & Pipan, 2014). Each of these habitats supports its own unique biota (Howarth, 1983; Camacho, 1992; Culver & Pipan, 2009a, 2014), but due to proximity and microclimatic similarity there is much biotic movement across their boundaries (Howarth, 1983; Culver & Pipan, 2014; Pape, personal observation). Cave entrances serve as movement corridors that are readily accessible to animals occupying both epigeal and subterranean habitats (Howarth, 1983; Romero, 2009; Prous et al., 2015; Pape, personal observation). Thus, caves are often intimately connected with habitats occupied by edaphic ant species, and nutrients present in caves are commonly within the foraging range of their colonies.

Nutrients in caves

Caves have long been recognized as comparatively oligotrophic environments, with most nutrients being transported into caves from photic epigeal ecosystems by hydrologic movement, gravity or animal transport (Camacho, 1992; Polis et al., 1997; Culver & Pipan, 2009a; Romero, 2009; Pape & OConnor, 2014; Prous et al., 2015). Bacteria and fungi are important decomposers of organic materials in caves, and the role of bacteria and archaea in

chemolithoautotrophic primary production in these environments is only beginning to be understood and appreciated (Cunningham et al., 1995; Ortiz et al., 2013). Nutrient sources commonly found in caves include plant debris, small vertebrates, macro-invertebrates, animal carcasses, and feces (Howarth, 1983; Ferreira & Martins, 1999; Hüppop, 2000; Culver & Pipan, 2009; Trajano & Bichuette, 2009; Prous et al., 2015; Pape, personal observation). Bat and bird guano deposits in caves are occasionally extensive, and often support their own diverse invertebrate fauna (Ferreira & Martins, 1999; Deharveng & Bedos, 2000; Moulds, 2004; 2006; Ferreira et al., 2007; Pape, 2014; Pape & OConnor, 2014). Animals, including ants, forage at these guano deposits, where they scavenge materials and/or prey on invertebrates integral to the guano food web. The guano of cave-roosting frugivorous bats commonly includes the seeds of fruits on which they feed, and may be gathered by seed harvesting ants, such as *Messor*, *Monomorium*, *Pheidole*, *Pogonomyrmex*, and others. So it is not only scavenging and predatory ants that forage at cave guano deposits, but seed harvesting species may also be present. The Oil Bird (*Steatornis caripensis* Humboldt), or Guacharo, nests in caves in northern South America and the Caribbean region. Oil Birds are also frugivorous and regurgitate fruit parts, including seeds, from their diet in their nesting caves (Polis et al., 1997; Holland et al., 2009; Romero, 2009). The seeds of fruits consumed by Oil Birds are too large to be scavenged directly by ants, but fruit parts or arthropods associated with these deposits may provide nutrients for ants foraging in these caves.

Cave foraging ants

Cave foraging ants are either epigeal species, which may include adventitious foraging in caves among their primarily epigeal provisioning activities, or hypogean species that live in the soil profile or epikarst, but that include caves that are integrated into their occupied habitat. The use of caves by ant colonies is primarily in the role of a troglodene, where the ants include foraging in caves only as a portion of their overall provisioning behavior. This was recognized early on by Kempf (1961) and Wilson (1962). These colonies return their cave-garnered provisions to their nests located outside caves. Obviously, cave nutrients must be within the foraging range of the colony. Because of this, use of a given cave by ants may vary from year to year depending on the areal distribution of the colonies over time. This was evident for the *P. rhea* colony at Patagonia Bat Cave discussed previously.

Some of the more important ant genera using caves, such as *Labidus*, *Neivamyrmex*, and (probably) *Nomamyrmex*, already possess an innate hypogean life style. Living in the soil profile or epikarst, these ants occupy thermally moderated, humid, aphotic habitats that are very similar to the cave environment. The New World tropical *Cheliomyrmex*, which are distinctly subterranean (Schneirla, 1971), have so far not been recorded from caves. This may be due to these ants being generally uncommon (Holldobler & Wilson, 1990) or the lack of a proactive search effort,

rather than an indication of their absence from caves.

The genus *Neivamyrmex* currently contains 131 described species (Kronauer, 2009; HOL), making it the largest group among the New World Dorylinae. There are currently 20 *Neivamyrmex* species known to occur in Arizona (AntWeb), four of which have been documented from caves in the state (Pape & OConnor, 2014; this paper). As a group *Neivamyrmex* is predominantly hypogeic, with their bivouacs and predatory hunting activities mostly confined to subterranean habitats (Schneirla, 1971; Ryder Wilkie et al., 2007; Pacheco & Vasconcelos, 2012). Surface activity levels vary among *Neivamyrmex* species, and are limited primarily to predatory raids, emigrations and reproductive flights conducted at night or on overcast days (Smith, 1942; Rettenmeyer, 1963). *Neivamyrmex* are primarily predators of other ant species or termites, but some species also take other arthropod prey including both soft and hard-bodied forms (Rettenmeyer, 1963; Schneirla, 1971; Miranda et al., 1980; Holldobler & Wilson, 1990; this paper).

Due to their nomadic, subterranean life style, *Neivamyrmex* may commonly intersect caves as they migrate through the soil and epikarst in karst terrains, and are probably more common in these environments than existing records might suggest. The earliest cave record for *Neivamyrmex* (*N. fallax* Borgmeier) was from Cotterell Cave in Travis County, Texas, where its occurrence was presumed to be incidental (accidental) (Reddell & Cokendolpher, 2001). Adding to the *N. fallax* record, two additional *Neivamyrmex* (*N. graciellae* Mann, *N. leonardi* Wheeler) were recorded at Kartchner Caverns (Pape & OConnor, 2014), and two more (*N. nigrescens* and *Neivamyrmex* sp.) in Arkenstone Cave (this paper). These last four species records are the first evidence demonstrating the association of *Neivamyrmex* with the ecology of caves.

The ant that appears most prominently in cave records, the red imported fire ant (*S. invicta*), is considered one of the 14 worst invasive alien insect species in the World (Lowe et al., 2004). *S. invicta* has been documented preying on a variety of arthropods in Texas caves, and is a significant threat to endemic cave animals (Elliott, 1992, 2000; Longacre, 2000; Taylor et al., 2005; Cokendolpher et al., 2009). *S. invicta* occurs in Texas as a non-native, invasive species, and has been recorded from well over 200 caves within a relatively small area in the central portion of the state (Reddell & Cokendolpher, 2001). The large number of cave records for the species is mostly the result of extensive surveys in caves that are known to (or potentially) support more than a dozen endemic cave invertebrates that are listed as endangered under the ESA. While the Texas records for *S. invicta* are a special circumstance, in that they resulted from an extensive and concerted search effort, they demonstrate the potential for ants to affect the ecology of caves, in this case in a negative manner.

Hypogeic ants and foraging depth in caves

Subterranean army ants are a potentially significant threat to cave animals, particularly invertebrates, as documented for *Neivamyrmex* sp. at Arkenstone Cave

(Figs. 10 & 11). Army ant attacks on endemic cave invertebrates that have small populations or a limited distribution within a cave could result in adverse population-level impacts or extirpation of these animals. Since hypogeic army ants are at home in the subterranean environment, it would seem reasonable that they are capable of penetrating deeply into caves. The limited evidence we have so far, however, suggests that while they may travel substantial horizontal distances within caves, their movements seem to be vertically constrained.

Many army ant species prey primarily on other ant species, or on termites (Schneirla, 1971; Holldobler & Wilson, 1990). Deep substrate penetration is used by termites to obtain water or clay in areas where these resources are scarce. Termites have been found as deep as 70 m, and are suggested to possibly seek water sources as deep as 100 m (Yakushev, 1968; Lee & Wood, 1971; Cloud et al., 1980). However, the bulk of individuals within termite colonies typically occur in the top couple of meters of the soil horizon, where food resources are most abundant (Lee & Wood, 1971; Matsumoto, 1976; Sheikh & Kayani, 1982), and their numbers decrease significantly with depth (Yakushev, 1968). Ant nest depth varies among species and is, to a degree, a function of colony size (Buhl et al., 2004; Mikheyev & Tschinkel, 2004; Tschinkel, 2004). Schneirla (1958) describes his excavation of a *N. nigrescens* bivouac within the galleries of a fungus ant in southern Arizona, which did not exceed one meter in depth. The larger, more permanent foraging trunk trails of the hypogeic *Dorylus laevigatus* Smith (Dorylinae) were found to typically occur at depths between 8 and 12 cm in the soil horizon in Malaysia (Berghoff et al., 2002). Other *Dorylus* nest at depths between 1 and 4 m (Gotwald, 1995). Other species, which are more hypogeous by nature, may excavate to somewhat greater depths. Nests of some larger ant colonies (e.g. *Atta texana* Buckley) have been recorded reaching as deep as 7.6 m within the soil horizon (Moser, 2006). These huge nest structures, which occur in several genera, are supported by colonies that may contain several million individuals (Holldobler & Wilson, 1990). A majority of ant colonies are considerably smaller in scale and are typically concentrated much closer to the surface, usually within the upper three meters or so of the soil horizon (Antoniali & Giannotti, 2001; Berghoff et al., 2002; Tschinkel, 2004, 2005, 2009; Bollazzi et al., 2008).

Foraging behavior of the more hypogeous army ant species likely co-evolved over time in concert with their mostly subterranean prey, and the habitats that these prey occupy. Since army ant prey abundance likely attenuates with depth in the soil horizon and epikarst, the evolved predatory foraging behavior of army ants may have become depth constrained to the approximate limits normally occupied by their prey.

Army ants periodically occupy prey nests between foraging episodes (Schneirla, 1958, 1971; Gotwald, 1995). While prey nest sites initially provide food for army ants, they also provide shelter, and minimize the need for them to construct nests. It is not known if,

or to what extent, army ants may modify prey nests. Since such bivouacs are temporary for these nomadic animals, it seems likely that they would not make extensive modifications to these structures. This suggests that army ants may not excavate beyond the pre-existing limits of prey nests.

Another factor that may have molded army ant behavior over time, and may affect the vertical depth they will pursue prey, is the air chemistry within prey nests. The percentage of O₂ and CO₂ in the air within ant nests is normally in balance. Some ants have been observed to partition their age classes vertically within nests based on atmospheric concentrations of CO₂, which increases significantly with depth in the nest, and furthest from surface connections where air exchange occurs (Kleineidam & Roces, 2000; Tschinkel, 2004). When large numbers of marauding army ants enter their prey nest, activity of both the invaders and prey is increased to a high level of vigor. Oxygen is consumed at higher rates and carbon dioxide is increased in the atmosphere through respiration. The likely significant increase in CO₂ concentration resulting from these struggles may make conditions in the deeper reaches of the nest marginally suitable during the brief times the invaders are present. The presence of inhospitable atmospheric conditions in the deeper reaches of prey nests, along with diminishing numbers of prey with vertical depth, may inhibit downward vertical predatory foraging in hypogeic ants.

Cave entrances allow animal movements into and out of caves, and are thus avenues of nutrient input to caves. These cave-surface interfaces commonly support a greater species richness and animal abundance than normally occur in cave interiors (Prous et al., 2004; Culver & Pipan, 2014; Pape & OConnor, 2014; Prous et al., 2015). One would expect ant colonies that occupy networks of cave passages to concentrate their activities near surface connections, where nutrients are likely to be more abundant.

This appears to be how *N. graciellae* is distributed within Kartchner Caverns (Fig. 1). Because of this, cave systems with multiple, closely-spaced surface connections should be a potentially ideal environment for cave-inhabiting army ant colonies.

N. graciellae has been observed active at depths ranging from 15 to 24 m below the surface at Kartchner Caverns. Measured depths include 16 m in the Tarantula Room area (C in Fig. 14), 24 m in the Red River Passage (B in Fig. 14), and 15 m in the Anticipation Room. *N. graciellae* is currently known to prey only on other ant species (Watkins & Coody, Pape, 1986; this paper). The presence of this predator at depths well below where its prey is likely to occur, within the top couple of meters of the surface, would seem to be ineffectual behavior. However, an analysis of the structure of the cave relative to ant activities reveals that these in-cave depths are functionally artificial, and that the ants are not accessing the cave in a precipitous, vertical descent. *N. graciellae* probably primarily occupies the late Pleistocene alluvial deposits that overlie the lower portions of the bedrock pediment of the cave hill. Their activities within the cave are associated with sub-horizontal access zones that are discontinuously situated at the periphery of the cave (Figs. 1 & 14; access zone). These access zones are comprised of the shallow surface alluvium and the contiguous consolidated soil sediments that were emplaced by gravity and autogenic meteoric waters in collapse, fault and fracture structures, and cave passages. Activities of *N. graciellae* in the cave seem to be concentrated in the vicinity of the Red River Passage, which is approximately 40 m from the surface of the cave hill along the presumed access zone shown in Fig. 14. This is the shortest distance from the cave that would allow the ants to reach the zone where their prey is presumed to occupy the alluvium overlying the cave. This suggests that army ants, even in a karst situation, do not normally penetrate

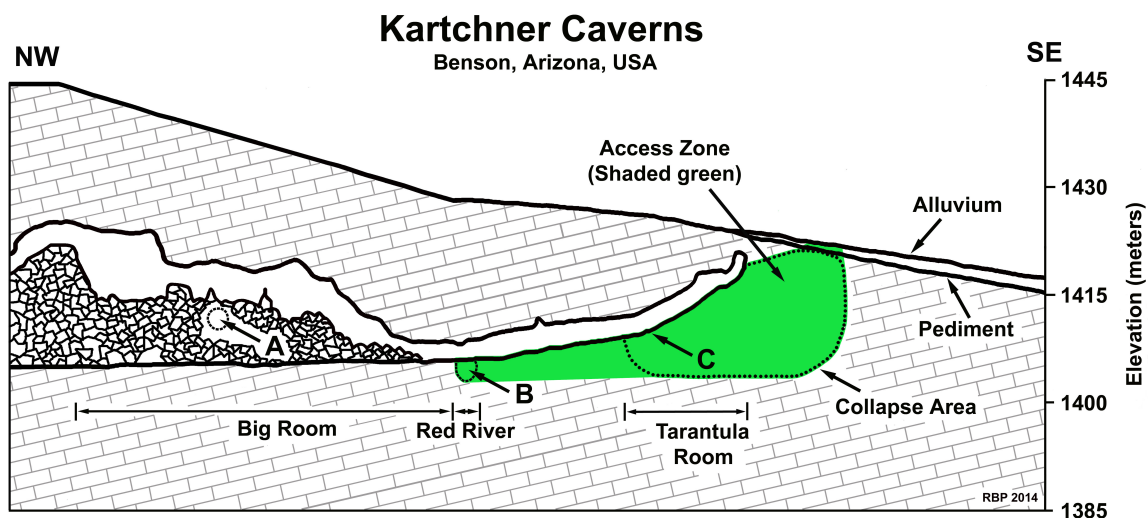


Fig. 14. Cross section of a portion of Kartchner Caverns (modified from Jagnow, 1999; with permission) showing relative depths for occurrences of *Neivamyrmex leonardi* and *Neivamyrmex graciellae*. The location for *N. leonardi* (A) in the Big Room, is the only record for the species in the cave. A typical access zone used by *N. graciellae* to enter the cave from the soil horizon is shown in green. Such access zones occur where incompetent areas of the cave hill pediment (collapse area in this figure; dotted line) are in contact with the overlying alluvium occupied by the ants. Two locations where *N. graciellae* has been observed in the cave are the Red River Passage (B) and the vicinity of the Tarantula Room (C). The Red River Passage is the center of activity for *N. graciellae* in the cave.

to great vertical depth in search of prey, and that their activities may be mostly confined to horizontal underground movements.

N. leonardi is a small, delicate, pale and blind species, which probably has small colonies. The species is certainly less mobile than the larger, longer-legged *N. graciellae*, and probably has a smaller foraging range. *N. leonardi* was found deep within Kartchner Caverns, 28 m vertically and 130 m horizontally from the surface of the cave hill (Fig. 14). The combination of a presumed low mobility of this species, and its location deep within the cave suggests some potential exists that the colony may be eutroglophilic. A combination of small body size along with small colony size in ants occurring in caves was suggested by Tinaut & Lopez (2001) as a possible evolutionary solution that might compensate for the large deme requirement in social insects that is usually unsupported within oligotrophic cave habitats.

Ecological groups, troglomorphy, and troglobiotic ants

The ecological group assigned to ant colonies using caves should be a function of the nature and level of their association with these habitats, and not contingent on the presence of troglomorphy. Eutroglophiles and troglobionts do not always exhibit a readily apparent adaptive morphology (Romero, 2009, 2011; Pipan & Culver, 2012; Pape, 2013). This is particularly true for those that have only recently adopted a cavernicolous existence (Pape, 2013). Isolation of animal populations in caves, which may eventually result in troglomorphy, can occur due to a variety of causes, including vicariance resulting from geophysical or hydrologic changes, changes in climate, or partitioning due to resource availability, competition, or predation (Coineau & Boutin, 1992; Holsinger, 2000; Culver & Pipan, 2009, 2014). Advanced troglomorphy is more evident in some other cave-occupying terrestrial arthropod taxa (Scorpionida, Pseudoscorpiones, Araneae, Opiliones) but, based on existing evidence, appears to be generally not well expressed in ants.

The reduced eyes and shortened appendages in primitive ants such as *Amblyopone* spp. suggest adaptation to aphotic environments early in ant evolution (Holldobler & Wilson, 1990; Wilson & Holldobler, 2005). However, few ant species exhibit significant loss of pigmentation, and even fewer show significant attenuation of the body, limbs or sensory structures present in many troglobionts. No known ant species exhibits extreme troglomorphy, as occurs in troglobionts in other taxonomic groups, where these morphologies co-evolved.

The fascination with troglomorphic, troglobiotic species gathers much attention from cave biologists (Pipan & Culver, 2012; Prous et al., 2015), and the search for troglobiotic ant species has a long history. Very few ant species have been suggested as true cavernicoles, particularly where the association implies a troglobiotic life style. Most that have been eventually found to also occur in epigeal habitats (Roncin & Deharveng, 2003), and thus at most have

occasional subtroglophilic colonies. Some of these are: *Aphaenogaster cardenai* Espadaler in Spain, *Carebara (Oligomyrmex; Erebotomyrma; Spelaeomyrmex) urichi* Wheeler in Trinidad, and *Hypoponera ragusai* Santschi in Granada (Wilson, 1962; Tinaut, 2001; Tinaut & Lopez, 2001; Roncin & Deharveng, 2003). More recently, Ortuño et al. (2014) presented information regarding *A. cardenai* as an inhabitant of the mesovoid shallow substratum. They precluded *A. cardenai* as a eutroglophile (troglophile) based on its epigeal reproductive dispersal behavior. This is likely a limiting factor for most ant colonies residing in caves, which could otherwise be considered eutroglophiles. Reddell suggested that *Nylanderia (Paratrechina) pearsei* Wheeler might be a troglobiotic species. This pale yellow, microphthalmic species is poorly known and has been recorded only from cave aphotic zones, typically found on moist flowstone or rock surfaces, or associated with drip pools (Reddell, 1977). Wheeler (1938), in his description of the species, referred to it as belonging to a small group of cavernicolous species. There have been no ecological studies of this species and its status is thus not currently established. The species may have subtroglophilic colonies.

Ant nesting activities have rarely been reported occurring in caves. Tinaut & Lopez (2001) report three records of ants nesting in caves from the literature: *Carebara urichi* in Trinidad (Wilson, 1962); *Lasius umbratus* Nylander in Spain (Lopez Gomez, 1988); and *Hypoconerops ragusai* in southern Spain (Tinaut, 2001). The bivouac records for *L. coecus* in Texas caves (Reddell & Cokendolpher, 2001) could possibly also include stary phase bivouacs, which are the reproductive phase nests of army ants.

Wilson (1962) proposed that limitations are imposed on the evolution of troglobiotic forms in social insects by their need to form very large demes to support genetic viability and stability comparable with that found in non-social insects. He suggested that large demes would seldom be sustainable in cave environments due to the compounding factors of limitations on available nutrients and physical space (suitable habitat) present in these ecotopes. This likely explains why the preponderance of observations of ants found in caves has, until recently, not revealed any potentially troglobiotic forms.

The only ant species currently known that exhibits both a complex troglomorphy and an apparently strict cavernicolous habit is *Leptogenys khammouanensis* Roncin & Deharveng, which lives deep within large caves in Laos (Roncin & Deharveng, 2003). The species has reduced eyes with 15-20 ommatidia, the body color is a pale, orange-yellow, and the entire body form, including the legs and antennae, is moderately attenuated. *L. khammouanensis* is larger than other *Leptogenys* species, some of which have a morphology that suggests a subterranean evolution, but not necessarily a strict cavernicolous, or troglobiotic existence (Roncin & Deharveng, 2003). Both dwarfism and gigantism occur occasionally in troglobiotic species (Vandel, 1965; Culver & Pipan, 2009b; Trontelj et al., 2012), and the larger size of

L. khammouanensis, compared with its congeners, may be additional evidence of troglomorphy. While the ecology of this species has not been studied, it is possible that it may be the first truly troglolithic ant species that has been found.

SUMMARY

The literature review revealed a diversity of ant subfamilies and genera occurring in caves globally, demonstrating their persistent presence in these habitats. The nature of the existing records, consisting of a high percentage of ancillary data, and likely skewed by an unintended emphasis of studies regionally, currently precludes meaningful analyses regarding any affinity for caves by discrete ant taxa, or regional prominence for the use of caves by ants.

This paper consolidates the 10 previously reported records of ants from five Arizona caves and adds 11 new records, for ten additional species, from five other Arizona caves. The new records are elements from a larger data set of biological surveys of macrobiotic fauna in 35 Arizona caves over a 25 year period. Ants were found in only six of the 35 caves studied. Survey efforts ranged from a single visit (Porcupine Cave) to 124 visits to a single cave over a 25-year period (Arkenstone Cave). Considering that the known cave resource in Arizona includes over 1,500 caves, the 35 caves visited represent a very small data set. Yet, based on this limited information it is apparent that ants play an important role in the ecology of some caves. It seems reasonable that similar behavior probably occurs on a global scale. This is particularly anticipated for the tropics, where ants are more diverse and there are greater available nutrient resources to support the animals in both epigeal and cave environments. While the presence of ants in caves seems to generally occur at low levels, and may be sporadic, they are persistent in their presence in these habitats over time. The significance of cave habitats in providing both a suitable environment and nutrient sources for edaphic ant colonies is no longer in question. Observations of ant behavior in caves in Arizona ranged from simple foraging by scavenging species, such as *Pheidole*, to the large-scale marauding by *Neivamyrmex* sp. observed at Arkenstone Cave. Behavioral analysis of *N. graciellae* in Kartchner Caverns and *Neivamyrmex* sp. in Arkenstone Cave suggests that hypogeic army ants may not penetrate to great depth to search for prey, but can be persistent occupants of relatively shallow, horizontal sections of caves, where they may prey on endemic cave animals (*Neivamyrmex* sp.). Information contained within this paper will hopefully encourage researchers to reconsider the role of ants in cave ecosystems.

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Appendix A. List of ant records from caves, record source, and record author-assigned ecological group.

SPECIES	CAVE	LOCATION	COUNTRY	RECORD SOURCE	AUTHOR-ASSIGNED ECOLOGICAL GROUP
AMBLYOPONINAE					
<i>Amblyopone australis</i> (Erichson, 1842)	Jenolan Caves	New South Wales	Australia	Wheeler 1927	None
<i>Amblyopone</i> sp.	Bayliss Cave	Queensland	Australia	Clarke 2010	None
PONERINAE					
<i>Anochetus mayri</i> (Emery, 1884)	Cueva Tuna	Cabo Rojo	Puerto Rico	Peck 1981b	Troglophile
<i>Anochetus</i> sp.	Actun Xpukil	Yucatan	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Brachyponera (Pachycondyla) christmasi</i> (Donisthorpe, 1935)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Brachyponera (Pachycondyla) obscurans</i> (Walker, 1859)	Davao Cave 1 & 2	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Hypoponera confinis</i> (Roger, 1860)	Farm Caves	Mawlamyine (Moulmein, Burma)	Myanmar	Annandale et al., 1913	None
<i>Hypoponera (Ponera) dulcis</i> (Forel, 1907)	Caves	Tanga and Shimoni	Tanzania and Kenya	Alluaud & Jeannel 1914 (in Wilson 1962)	None
<i>Hypoponera eduardi</i> (Forel, 1894)	Caves	Iberian Peninsula	Europe	Espadaler 1983	Accidental
<i>Hypoponera (Ponera) ergatandria</i> (Forel, 1893)	San Bulha Cenote	Motul, Yucatan	Mexico	Wheeler 1938	None
<i>Hypoponera inexorata</i> (Wheeler, 1903)	Hold Me Back Cave	Bexar Co., Texas	USA	Cokendolpher et al., 2009	Accidental
<i>Hypoponera opaciceps</i> (Mayr, 1887)	Oxford Cave	Manchester	Jamaica	Peck 1992	Troglophile
<i>Hypoponera opaciceps</i> (Mayr, 1887)	Stealth Cave	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Hypoponera opaciceps</i> (Mayr, 1887)	Cenote de Sambula Motul	Yucatan	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Hypoponera (Ponera) opaciceps</i> (Mayr, 1887)	San Isidro Cave	Merida, Yucatan	Mexico	Wheeler 1938	None
<i>Hypoponera opacior</i> (Forel, 1893)	Eagles Nest Cave	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Hypoponera opacior (H. opacipes)</i> (Forel, 1893)	Caves	Not listed	Jamaica	Decu et al., 1998	None
<i>Hypoponera punctatissima</i> (Roger, 1859)	Daniel Roux Cave Upper	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Hypoponera punctatissima</i> (Roger, 1859)	Grutas de Monte Bravo	Campeche	Mexico	Reddell & Cokendolpher 2001	None
<i>Hypoponera punctatissima</i> (Roger, 1859)	Caves	Yucatan	Mexico	Reddell 1977	None
<i>Hypoponera punctatissima</i> (Roger, 1859)	Cove Bermejales	Cadiz	Spain	Espadaler 1983	Accidental
<i>Hypoponera ragusai</i> (Emery, 1894)	Grotta della Sabbia	Sciacca, Sicily	Italy	Baroni Urbani 1962a	Troglophile
<i>Hypoponera ragusai</i> (Emery, 1894)	Grotta di Calafarina Pachino	Syracuse	Italy	Baroni Urbani 1962a	Troglophile
<i>Hypoponera ragusai</i> (Emery, 1894)	Grotta delle Stalattiti	Igadi Island, Sicily	Italy	Mei 1992	Troglophile
<i>Hypoponera ragusai (H. gleadowi)</i> (Emery, 1894)	Cueva del Guano	Buena Vista, Falcon	Venezuela	Peck 1982	Troglophile
<i>Hypoponera ragusai</i> (Emery, 1894)	Cueva del Barranco Iñate	Lobres, Granada	Spain	Tinaut 2001	Troglophile
<i>Hypoponera</i> sp. 2	Cueva Los Chorros; Cueva El Convento	Arecibo; Guayanilla	Puerto Rico	Peck 1981b	Troglophile
<i>Hypoponera</i> sp. 2	Cousins Cove Cave #1	Hanover	Jamaica	Peck 1992	Troglophile
<i>Hypoponera</i> sp. 3	Bambribo Cave	St. Ann	Jamaica	Peck 1992	Troglophile

<i>Hypoconera</i> sp.	Coles Cave	Welchman Hall	Barbados	Peck 1981a	Troglophile
<i>Hypoconera</i> sp.	Cueva de Corozal	Corozal	Puerto Rico	Peck 1974	Troglophile?
<i>Hypoconera</i> sp.	Caves	Brazilia	Brazil	Trajano & Bichuette 2009	Trogloxene
<i>Hypoconera</i> sp.	Actun Huachap	Campeche	Mexico	Reddell & Cokendolpher 2001	None
<i>Hypoconera</i> sp.	Three-Holer Cave	Travis Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Leptogenys diminuta</i> (Smith, 1857)	Batu Caves	Selangor	Malaysia	Wilson 1962	None
<i>Leptogenys elongata</i> (Buckley, 1866)	Backhole	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Leptogenys jeanneli</i> (Santschi, 1914)	Caves	Tanga and Shimoni	Tanzania and Kenya	Alluaud & Jeannel 1914 (in Wilson 1962)	None
<i>Leptogenys khammouanensis</i> (Roncin & Deharveng, 2003)	Tham Nam Non	Ban Boc, Khammouane	Laos	Roncin & Deharveng 2003	None
<i>Leptogenys khammouanensis</i> (Roncin & Deharveng, 2003)	Tham Thé	Ban Nakok, Khammouane	Laos	Roncin & Deharveng 2003	None
<i>Leptogenys</i> sp. 1	Cueva del Lencho Virgen	Acatlán, Oaxaca	Mexico	Reddell & Cokendolpher 2001	None
<i>Leptogenys</i> sp. 2	Cenote de Juan Coh	Quintana Roo	Mexico	Reddell & Cokendolpher 2001	None
<i>Leptogenys</i> sp. 3	Cenote Amil	Abalá, Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Leptogenys</i> sp. 4	Judge's Chamber Cave	Val Verde Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Leptogenys</i> sp.	Davao Cave 1	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Leptogenys</i> sp.	Grutas de Xkalumkin	Campeche	Mexico	Reddell & Cokendolpher 2001	None
<i>Mayaponera</i> (<i>Mesoponera</i> ; <i>Pachycondyla</i>) <i>constricta</i> (Mayr, 1884)	Oropouche Cave	Not listed	Trinidad	Wilson 1962	Trogloxene
<i>Neoponera</i> (<i>Pachycondyla</i>) <i>apicalis</i> (Latreille, 1802)	Caves	Yucatan	Mexico	Reddell 1977	None
<i>Neoponera</i> (<i>Pachycondyla</i>) <i>apicalis</i> (Latreille, 1802)	Grutas de Xtacumbilxunam	Campeche	Mexico	Reddell & Cokendolpher 2001	None
<i>Neoponera</i> (<i>Pachycondyla</i>) <i>apicalis</i> (Latreille, 1802)	Cenote de Juan Coh	Quintana Roo	Mexico	Reddell & Cokendolpher 2001	None
<i>Neoponera</i> (<i>N. latreillei</i>) <i>apicalis</i> (Latreille, 1802)	Cinco de Mayas Cave	Tekax, Yucatan	Mexico	Wheeler 1938	None
<i>Neoponera</i> (<i>N. latreillei</i>) <i>apicalis</i> (Latreille, 1802)	Puz Cave	Oxkutzcab, Yucatan	Mexico	Wheeler 1938	None
<i>Neoponera</i> (<i>Pachycondyla</i>) <i>carinulata</i> (Roger, 1861)	Cebada Cave	Chiquibul Cave System	Belize	Reddell & Veni 1996	Accidental
<i>Neoponera</i> (<i>Pachycondyla</i>) <i>unidentata</i> (Mayr, 1862)	Sotano de Tampamache	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	None
<i>Neoponera villosa</i> (Fabricius, 1804)	Sotano de El Molino	Tamaulipas	Mexico	Reddell & Mitchell 1971b	None
<i>Neoponera</i> (<i>Pachycondyla</i>) <i>villosa</i> (Fabricius, 1804)	Grutas de San Antonio	Campeche	Mexico	Reddell & Cokendolpher 2001	None
<i>Neoponera</i> (<i>Pachycondyla</i>) <i>villosa</i> (Fabricius, 1804)	Caves	Yucatan	Mexico	Reddell 1977	None
<i>Odontomachus bauri</i> (Emery, 1892)	Peru Cave	St. Elizabeth	Jamaica	Peck 1992	Troglophile
<i>Odontomachus bauri</i> (Emery, 1892)	Caves	Not listed	Trinidad	Decu et al., 1998	Accidental or Trogloxene
<i>Odontomachus brunneus</i> (Patton, 1894)	Cueva Tuna	Cabo Rojo	Puerto Rico	Peck 1981b	Troglophile
<i>Odontomachus clarus</i> (Roger, 1861)	Platypus Pit	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Odontomachus haematodus</i> (Linnaeus, 1758)	Oropouche Cave	Not listed	Trinidad	Wilson 1962	Trogloxene
<i>Odontomachus haematodus</i> (Linnaeus, 1758)	Caves	Tanga and Shimoni	Tanzania and Kenya	Alluaud & Jeannel 1914 (in Wilson 1962)	None

<i>Odontomachus haematodus</i> (Linnaeus, 1758)	Caves	Not listed	Cuba	Decu et al., 1998	Accidental or Troglaxene
<i>Odontomachus haematodus</i> (Linnaeus, 1758)	Second cave on San Roque Rd.	Oxkutzcab, Yucatan	Mexico	Wheeler 1938	None
<i>Odontomachus insularis</i> (Guérin-Meneville, 1844)	Caves	Not listed	Cuba	Decu et al., 1998	Accidental or Troglaxene
<i>Odontomachus opaciventris</i> (Forel, 1899)	Caves 1 & 3	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Odontomachus ruginodis</i> (Smith, 1937)	Cueva de los Alfaros	Mora	Puerto Rico	Peck 1974	Troglophile
<i>Odontomachus ruginodis</i> (Smith, 1937)	Cueva del Azufre	Tabasco	Mexico	Reddell & Cokendolpher 2001	None
<i>Odontomachus</i> sp.	Kitaotao Cave 1, 2 & 3	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Odontomachus</i> sp.	Million-bat Cave; Patag Cave; Guano Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Troglophile
<i>Odontomachus</i> sp.	Actun Xpukil	Yucatan	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Odontoponera</i> sp.	Davao Cave 1	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Pachycondyla harpax</i> (Fabricius, 1804)	Actun Halmensura	Campeche	Mexico	Reddell & Cokendolpher 2001	None
<i>Pachycondyla harpax</i> (Fabricius, 1804)	Weynand Cave	Medina Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Pachycondyla harpax</i> (Fabricius, 1804)	Caves	Yucatan	Mexico	Reddell 1977	None
<i>Pachycondyla harpax</i> (<i>P. h. montezumia</i>) (Fabricius, 1804)	Sotano del Arroyo and Cueva Chica	San Luis Potosi	Mexico	Reddell & Mitchell 1971a	None
<i>Pachycondyla harpax</i> (<i>P. h. montezumia</i>) (Fabricius, 1804)	Sotano de la Joya de Salas	Tamaulipas	Mexico	Reddell & Mitchell 1971b	None
<i>Pachycondyla harpax</i> (<i>P. h. montezumia</i>) (Fabricius, 1804)	Gongora Cave	Oxkutzcab, Yucatan	Mexico	Wheeler 1938	None
<i>Pachycondyla impressa</i> (Roger, 1861)	Pedra Suspensa Cave	Bahia	Brazil	Trajano 2000	None
<i>Pachycondyla (Euponera)</i> sp.	Ventana Jabali	San Luis Potosi	Mexico	Reddell & Mitchell 1971a	None
<i>Pachycondyla</i> sp. 1	Actun Kaua	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Pachycondyla</i> sp.	Sumiyot Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Accidental
<i>Pachycondyla</i> sp.	Grutas de Xtacumbilxunam	Campeche	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Pachycondyla</i> sp.	Upper Daniel Roux Cave	Christmas Island	Australia	Humphreys & Eberhard 2001	None
<i>Pachycondyla</i> sp.	Salawao Cave	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Parvaponera (Pachycondyla) darwinii</i> (Forel, 1893)	19th Hole Cave	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Platythyrea parallela</i> (Smith, 1859)	Davao Cave 2	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Platythyrea punctata</i> (Smith, 1858)	Brandon Hill Cave	St. James	Jamaica	Peck 1992	Troglophile
<i>Platythyrea</i> sp. (<i>parallela</i> group)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Ponera coarctata</i> (Latreille, 1802)	Av. Ancosa	Barcelona	Spain	Espadaler 1983	Accidental
<i>Ponera coarctata</i> (Latreille, 1802)	Grotta dell' Acqua Presso	Canicattini Bagni, Sicily	Italy	Baroni Urbani 1962b	None
<i>Ponera coarctata</i> (Latreille, 1802)	Caves	Not listed	Switzerland	Espadaler 1983	None
<i>Ponera swezeyi</i> (Wheeler, 1933)	Grants Well Cave	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Ponera</i> sp.	Batu Caves	Selangor	Malaysia	McClure et al., 1967	None
<i>Pseudoneoponera (Bothroponera) rufipes</i> (Jerdon, 1851)	Batu Caves	Selangor	Malaysia	McClure et al., 1967	None
<i>Pseudoneoponera (Pachycondyla; Bothroponera) tridentata</i> (Smith, 1858)	Batu Caves	Selangor	Malaysia	Wilson 1962	None
<i>Pseudoponera (Euponera) stigma</i> (Fabricius, 1804)	Sotano de Gomez Farias	Tamaulipas	Mexico	Reddell & Mitchell 1971b	None

<i>Pseudoponera (Pachycondyla) stigma</i> (Fabricius, 1804)	Cueva de San Pedro	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Pseudoponera (Pachycondyla) stigma</i> (Fabricius, 1804)	Mocho Cave	St. James	Jamaica	Peck 1992	Troglophile
<i>Rasopone (Pachycondyla) ferruginea</i> (Smith, 1858)	Sotano de Guadalupe	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	None
PROCERATIINAE					
<i>Proceratium compitale</i> (Ward, 1988)	Cueva de los Lagos	Coahuila	Mexico	Reddell & Cokendolpher 2001	None
<i>Proceratium compitale</i> (Ward, 1988)	Caverns of Sonora	Sutton Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Proceratium micrommatum (Sysphincta cavernicola)</i> (Roger, 1863)	Chilibrillo Caves	Not listed	Panama	Borgmeier 1937	None
<i>Proceratium pergandei</i> (Emery, 1895)	Cross the Creek Cave	Bexar Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Proceratium (Sysphincta) sp.</i>	Cueva de los Lagos	Coahuila	Mexico	Reddell 1982	None
DORYLINAE					
<i>Cerapachys (edentatus?)</i> (Forel, 1900)	Bat Cave	Naracoorte	Australia	Moulds 2006	Accidental
<i>Dorylus fimbriatus</i> (Shuckard, 1840)	Caves	Tanga and Shimoni	Tanzania and Kenya	Alluaud & Jeannel 1914 (in Wilson 1962)	None
<i>Dorylus fulvus (Typhlopone clausii)</i> (Westwood, 1839)	San Servolo Cave	Trieste	Italy	Müller 1923	None
<i>Dorylus fulvus (Typhlopone clausii)</i> (Westwood, 1839)	Cave	Carniola	Slovenia	Packard 1888	None
<i>Eciton burchellii</i> (Westwood, 1842)	Actun Xpukil	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Eciton sp. 1</i>	Cave 7	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Labidus coecus</i> (Latreille, 1802)	Cuevas de las Bellotas	Oaxaca	Mexico	Reddell & Cokendolpher 2001	Trogloxene
<i>Labidus coecus</i> (Latreille, 1802)	A Guacharo Cave	San Andres	Peru	Kempf 1961	Trogloxene
<i>Labidus coecus</i> (Latreille, 1802)	Cueva del Guacharo	Caripe Valley, Monagas	Venezuela	Kempf 1961	Trogloxene
<i>Labidus coecus</i> (Latreille, 1802)	Beck Sewer Cave	Williamson Co., Texas	USA	Reddell & Cokendolpher 2001	Trogloxene
<i>Labidus praedator</i> (Smith, 1858)	Sotano de Yerbaniz	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	None
<i>Neivamyrmex graciellae</i> (Mann, 1926)	Kartchner Caverns	Cochise Co., Arizona	USA	Pape & OConnor 2014	Subtroglophile
<i>Neivamyrmex leonardi</i> (Wheeler, 1915)	Kartchner Caverns	Cochise Co., Arizona	USA	Pape & OConnor 2014	Subtroglophile
<i>Neivamyrmex nigrescens</i> (Cresson, 1872)	Arkenstone Cave	Pima Co., Arizona	USA	Pape - this paper	Trogloxene
<i>Neivamyrmex opacithorax</i> (Emery, 1894)	50 Bucket Cave	Bexar Co., Texas	USA	Cokendolpher et al., 2009	Accidental
<i>Neivamyrmex sp.</i>	Arkenstone Cave	Pima Co., Arizona	USA	Pape - this paper	Trogloxene
<i>Neivamyrmex swainsonii (N. fallax)</i> (Shuckard, 1840)	Cotterell Cave	Travis Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Nomamyrmex esenbeckii (N. e. wilsoni)</i> (Westwood, 1842)	Cueva de Kopoil	Quintana Roo	Mexico	Reddell & Cokendolpher 2001	None
<i>Nomamyrmex hartigii</i> (Westwood, 1842)	Cueva de Juan Sanchez	Oaxaca	Mexico	Reddell & Cokendolpher 2001	Accidental
DOLICHODERINAE					
<i>Azteca sp.</i>	Cebada Cave (Chiquibul Cave System)	Cayo	Belize	Reddell & Veni 1996	Accidental
<i>Dolichoderus bispinosus</i> (Olivier, 1792)	Cueva de Abispa	Quintana Roo	Mexico	Reddell & Cokendolpher 2001	None
<i>Dolichoderus bispinosus</i> (Olivier, 1792)	Xconsacab Cave	Tizamin, Yucatan	Mexico	Wheeler 1938	None

<i>Dolichoderus thoracicus</i> (Smith, 1860)	Buho Cave; Million-bat Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Accidental
<i>Dolichoderus thoracicus</i> (Smith, 1860)	Kariis; Salawao; Kitaotao 1, 2 & 3	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Dolichoderus</i> sp. 1	Cave 23	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Dolichoderus</i> sp.	Bulod Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Accidental
<i>Dorymyrmex</i> sp.	Lucky Hill Farm Cave	St. Ann	Jamaica	Peck 1992	Troglophile
<i>Forelius keiferi</i> (Wheeler, 1934)	Arkenstone Cave	Pima Co., Arizona	USA	Pape - this paper	Trogloxene
<i>Forelius mccooki</i> (McCook, 1880)	Cenote de San Isidro	Merida, Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Forelius mccooki</i> (McCook, 1880)	San Isidro Cave	Merida, Yucatan	Mexico	Wheeler 1938	None
<i>Forelius pruinosus</i> (Roger, 1863)	Pain in the Glass Cave	Bexar Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Iridomyrmex</i> sp.	Barkers Cave	Queensland	Australia	Clarke 2010	None
<i>Linepithema humile</i> (Mayr, 1868)	Cave	Sao Miguel, Azores	Portugal	Wetterer et al., 2004	None
<i>Linepithema humile</i> (<i>Iridomyrmex humilis</i>) (Mayr, 1868)	Cove Petita	Robids, Mallorca	Spain	Espadaler 1983	Accidental
<i>Liometopum apiculatum</i> (Mayr, 1870)	Cueva del Salitre	Chihuahua	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Liometopum apiculatum</i> (Mayr, 1870)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Liometopum luctuosum</i> (Wheeler, 1905)	Fern Frond Cave	Amador Co., California	USA	Reddell & Cokendolpher 2001	Accidental
<i>Liometopum occidentale</i> (Emery, 1895)	Confluence Cave	Toulumne Co., California	USA	Reddell & Cokendolpher 2001	Accidental
<i>Liometopum</i> sp.	ELMA 008	Cibola Co., New Mexico	USA	Wynne 2013	None
<i>Tapinoma melanocephalum</i> (Fabricius, 1793)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Tapinoma melanocephalum</i> (Fabricius, 1793)	Batu Caves	Selangor	Malaysia	McClure et al., 1967	None
<i>Tapinoma sessile</i> (Say, 1836)	McNamee's Cave	Toulumne Co., California	USA	Reddell & Cokendolpher 2001	Accidental
<i>Tapinoma sessile</i> (Say, 1836)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Tapinoma</i> sp.	Sumidero de Fantasmas	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	None
<i>Tapinoma</i> sp.	Kariis Cave	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Technomyrmex albipes</i> (Smith, 1861)	Kitaotao 1	Mindanao	Philippines	Figueras & Nuneza 2013	None
PSEUDOMYRMECINAE					
<i>Pseudomyrmex gracilis</i> (Fabricius, 1804)	Drip Cave	Trelawny	Jamaica	Peck 1992	Accidental
<i>Pseudomyrmex</i> sp.	Cenote de Las Ruinas	Quintana Roo	Mexico	Reddell & Cokendolpher 2001	Accidental
FORMICINAE					
<i>Acropyga</i> sp.	Cueva de Tancah	Tancah, Quintana Roo	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Anoplolepis gracilipes</i> (Smith, 1857)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Brachymyrmex cavernicola</i> (Wheeler, 1938)	Balaam Canche Cave	Chichen Itza, Yucatan	Mexico	Wheeler 1938; Wilson 1962	Troglophile
<i>Brachymyrmex cavernicola</i> (Wheeler, 1938)	Cueva de las Maravillas	Oaxaca	Mexico	Reddell & Cokendolpher 2001	Troglophile
<i>Brachymyrmex cavernicola</i> (Wheeler, 1938)	Chac Mol Cave	Tohil, Yucatan	Mexico	Wheeler 1938	None
<i>Brachymyrmex cavernicola</i> (Wheeler, 1938)	Caves	Yucatan	Mexico	Wheeler 1938	None
<i>Camponotus aethiops</i> (Latreille, 1798)	Ledenika cave	Vratsa	Bulgaria	Lapeva-Gjonova et al., 2010	None
<i>Camponotus aethiops</i> (Latreille, 1798)	Avenc Quatretonda	Xativa, Valencia	Spain	Espadaler 1983	Accidental

<i>Camponotus americanus</i> (Mayr, 1862)	Rich Mountain Blowhole Cave	Great Smoky Mtns. N.P., Tennessee	USA	Reeves 2000	Accidental
<i>Camponotus atriceps</i> (Smith, 1858)	Cebada Cave	Cayo	Belize	Reddell & Cokendolpher 2001	None
<i>Camponotus atriceps</i> (Smith, 1858)	Caves: 4, 11, 14, 15 & 26	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Camponotus consobrinus (obniger ?)</i> (Erichson, 1842)	Bat Cave	Naracoorte	Australia	Moulds 2006	Accidental
<i>Camponotus cruentatus</i> (Latreille, 1802)	Avenc Ferla	Barcelona	Spain	Espadaler 1983	Accidental
<i>Camponotus decipiens</i> (Emery, 1893)	Simons Road Side Sink No. 1	Burnet Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Camponotus festinatus</i> (Buckley, 1866)	Felton Cave	Sutton Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Camponotus herculeanus</i> (Linnaeus, 1758)	Cave	Not listed	Italy	Espadaler 1983	Trogloxene
<i>Camponotus melichloros</i> (Kirby, 1889)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Camponotus mina</i> (Forel, 1879)	Shelter Cave	Dona Ana Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Camponotus nearcticus</i> (Emery, 1893)	Backhole	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Camponotus ocreatus</i> (Emery, 1893)	Cathedral Cave	Yavapai Co., Arizona	USA	Shear et al., 2009	None
<i>Camponotus piceus</i> (Leach, 1825)	Avenc Quatretonda	Xativa, Valencia	Spain	Espadaler 1983	Accidental
<i>Camponotus picipes</i> (Olivier, 1792)	Cueva del Camino	Tamaulipas	Mexico	Reddell & Cokendolpher 2001	None
<i>Camponotus pilicornis</i> (Roger, 1859)	Avenc Pla	Bassioles, Barcelona	Spain	Espadaler 1983	Accidental
<i>Camponotus planatus</i> (Roger, 1863)	Actun Xpukil	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Camponotus rectangularis</i> (Emery, 1890)	Actun Loltun	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Camponotus sansabeanus</i> (Buckley, 1866)	Ezell's Cave	Hays Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Camponotus sansabeanus (C. s. torrefactus)</i> (Buckley, 1866)	Hidden Cave	Eddy Co., New Mexico	USA	Cokendolpher & Polyak 2004	Accidental
<i>Camponotus semitestaceus</i> (Snelling, 1970)	Yearwood Gold Mine Cave	Williamson Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Camponotus texanus</i> (Wheeler, 1903)	Nolan Creek Cave	Ft. Hood, Bell Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Camponotus truncatus</i> (Spinola, 1808)	Cove Pinta	Callosa d'ensarria, Alicante	Spain	Espadaler 1983	Accidental
<i>Camponotus turkestanus</i> (André, 1882)	Cave	Not listed	Afghanistan	Decu et al., 1998	None
<i>Camponotus vagus</i> (Scopoli, 1763)	Ledenika cave	Vratsa	Bulgaria	Lapeva-Gjonova et al., 2010	None
<i>Camponotus vicinus</i> (Mayr, 1870)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Camponotus vittatus</i> (Forel, 1904)	Cave 10	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Camponotus</i> sp. 1	Cave 5	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Camponotus</i> sp. 2	Cave 12	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Camponotus</i> sp. 3	Cave 9	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Camponotus</i> sp.	Million-bat Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Troglophile
<i>Camponotus</i> sp.	Batu Caves	Selangor	Malaysia	McClure et al., 1967	None
<i>Camponotus</i> sp.	Hidden Cave	Santa Cruz Co., Arizona	USA	Pape - this paper	Incidental
<i>Camponotus</i> sp.	Sotano del Profesor	Veracruz	Mexico	Reddell & Mitchell 1971c	None
<i>Echinopla vermiculata</i> (Emery, 1898)	Salawao Cave	Mindanao	Philippines	Figueras & Nuneza 2013	None

<i>Formica abdominalis</i> (Latreille, 1802) incertae sedis (<i>Camponotus abdominalis</i>)	Cebada Cave	Chiquibul Cave System	Belize	Reddell & Veni 1996	Accidental
<i>Formica cunicularia</i> (Latreille, 1798)	Cave	Not listed	Italy	Espadaler 1983	Trogloxene
<i>Formica gagates</i> (Latreille, 1798)	Cove Espluguèll	Serradell, Lleida	Spain	Espadaler 1983	Accidental
<i>Formica gagates</i> (Latreille, 1798)	Avenc Pedres	Can Sallent, Barcelona	Spain	Espadaler 1983	Accidental
<i>Formica gnava</i> (Buckley, 1866)	Harrison Cave	Sutton Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Formica lasioides</i> (Emery, 1893)	Cave	Vancouver Is., BC	Canada	Roth 2001	None
<i>Formica lemani</i> (Bondroit, 1917)	Cave	Not listed	Italy	Espadaler 1983	Trogloxene
<i>Formica limata</i> (Wheeler, 1913)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	Troglophile
<i>Formica moki</i> (Wheeler, 1906)	Barren Cave	Calaveras Co., California	USA	Reddell & Cokendolpher 2001	Accidental
<i>Formica rufibarbis</i> (Fabricius, 1793)	Grotto Martino	Matteria	Slovenia	Müller 1923	None
<i>Formica</i> sp. (<i>fusca</i> group)	Campsey Cave	Hardeman Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Formica</i> sp. (<i>rufibarbis</i> group)	Sotano del Profesor	Tequila, Veracruz	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Iberoformica</i> (<i>Formica</i>) <i>subrufa</i> (Roger, 1859)	Avenc Erminies	Mura, Barcelona	Spain	Espadaler 1983	Accidental
<i>Iberoformica</i> (<i>Formica</i>) <i>subrufa</i> (Roger, 1859)	Avenc Quatretonda	Xativa, V	Spain	Espadaler 1983	Accidental
<i>Lasius arizonicus</i> (Wheeler, 1917)	Hidden Cave	Santa Cruz Co., Arizona	USA	Pape - this paper	Subtroglophile
<i>Lasius distinguendus</i> (Emery, 1916)	Dimnice Cave	Marcovsina	Italy	Müller 1923	None
<i>Lasius emarginatus</i> (Olivier, 1792)	Cave	Not listed	Italy	Espadaler 1983	Trogloxene
<i>Lasius emarginatus</i> (Olivier, 1792)	Cove del Mamut	Barcelona	Spain	Espadaler 1983	Accidental
<i>Lasius grandis</i> (Forel, 1909)	Grutas dos Anjos	Santa Maria, Azores	Portugal	Wetterer et al., 2004	None
<i>Lasius mixtus</i> (Nylander, 1846)	Cove d'en Janet	Tarragona	Spain	Espadaler 1983	Troglophile
<i>Lasius mixtus</i> (Nylander, 1846)	Avenc Ancosa	Barcelona	Spain	Espadaler 1983	Troglophile
<i>Lasius mixtus</i> (Nylander, 1846)	Forat Borau	Arinsol	Andorra	Espadaler 1983	Troglophile
<i>Lasius mixtus</i> (Nylander, 1846)	Cave	Not listed	Spain, Italy & Greece	Decu et al., 1998	Trogloxene
<i>Lasius niger</i> (Linnaeus, 1758)	Cove Mescar	Tarragona	Spain	Espadaler 1983	Accidental
<i>Lasius niger</i> (Linnaeus, 1758)	Cardano de Abajo	Cardano de Abajo	Spain	Lopez Gomez 1988	Troglophile?
<i>Lasius pallitarsis</i> (Provancher, 1881)	Caves	Oregon & Washington	USA	Roth 2001	Trogloxene
<i>Lasius sitiens</i> (Wilson, 1955)	Porcupine Cave	Coconino Co., Arizona	USA	Pape - this paper	Subtroglophile?
<i>Lasius umbratus</i> (Nylander, 1846)	Cardano de Abajo	Cardano de Abajo	Spain	Decu et al., 1998	Troglophile
<i>Lasius</i> sp.	Caves	Not listed	Switzerland	Espadaler 1983	None
<i>Nylanderia</i> (<i>Paratrechina</i>) <i>bourbonica</i> (Forel, 1886)	Caves-North Kona area	Hawai'i, Hawai'i	USA	Howarth et al., 2007	Trogloxene
<i>Nylanderia</i> (<i>Paratrechina</i>) <i>bourbonica</i> (Forel, 1886)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Nylanderia</i> (<i>Paratrechina</i>) cf. <i>hystrix</i> (Trager, 1984)	Parashant (PARA) 1801	Grand Canyon-Parashant National Monument, Arizona	USA	Wynne & Voyles 2014	Accidental
<i>Nylanderia</i> (<i>Paratrechina</i>) <i>jaegerskioeldi</i> (Mayr, 1904)	Caves	Tanga and Shimoni	Tanzania and Kenya	Alluaud & Jeannel 1914 (in Wilson 1962)	None
<i>Nylanderia</i> (<i>Paratrechina</i>) <i>myops</i> (Mann, 1920)	Caves	Not listed	Cuba	Wilson 1962	None
<i>Nylanderia myops</i> (<i>N. troglodytes</i>) (Mann, 1920)	Caves	Not listed	Cuba	Wheeler 1938	None
<i>Nylanderia</i> (<i>Paratrechina</i>) <i>pearsei</i> (Wheeler, 1938)	Caves	Yucatan	Mexico	Wheeler 1938; Reddell 1977	Troglophile

<i>Nylanderia (Paratrechina) pearsei</i> (Wheeler, 1938)	Grutas de Xkalumkin	Campeche	Mexico	Reddell & Cokendolpher 2001	Troglophile
<i>Nylanderia pearsei</i> (Wheeler, 1938)	Muruztun Cave	Tizamin, Yucatan	Mexico	Wheeler 1938	Troglophile
<i>Nylanderia (Paratrechina) terricola</i> (Buckley, 1866)	Caverns of Sonora	Sutton Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Nylanderia (Paratrechina) terricola</i> (Buckley, 1866)	Cueva de Empalme	Coahuila	Mexico	Reddell & Cokendolpher 2001	Accidental?
<i>Nylanderia vividula</i> (Nylander, 1846)	Baker's Crossing Cave	Kinney Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Nylanderia</i> sp. (<i>Paratrechina</i> sp.) (<i>caeciliae</i> group)	Actun Dxibi	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Nylanderia</i> sp.	Guano Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Troglophile
<i>Paratrechina arenivaga</i> (Wheeler, 1905)	Canyon Ranch Shelf Cave	Bexar Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Paratrechina longicornis</i> (Latreille, 1802)	Lucky Hill Farm Cave	St. Ann	Jamaica	Peck 1992	Troglophile
<i>Paratrechina longicornis</i> (Latreille, 1802)	Command Hill Cave	Ascension Island	British Territory	Wetterer et al., 2007	None
<i>Paratrechina longicornis</i> (Latreille, 1802)	Davao Cave 1	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Paratrechina longicornis</i> (Latreille, 1802)	Batu Caves	Selangor	Malaysia	McClure et al., 1967	None
<i>Paratrechina</i> sp. 1	Cueva de Potrerillos	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	None
<i>Paratrechina</i> sp. 2	Cueva de los Viet Cong	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	None
<i>Paratrechina</i> sp.	Cave KNI-9	Ningbing Range; Kimberley, W. Australia	Australia	Humphreys 1998	Troglophile?
<i>Paratrechina</i> sp.	Cave C-29	Cape Range; Carnarvon Basin, W. Australia	Australia	Humphreys 1998	Troglophile?
<i>Paratrechina</i> sp.	Rope Ladder Cave	Queensland	Australia	Weinstein & Slaney 1995	Trogloxene
<i>Paratrechina</i> sp.	Cebada Cave	Chiquibul Cave System	Belize	Reddell & Veni 1996	Accidental
<i>Plagiolepis pygmaea</i> (Latreille, 1798)	Avenc Getru	Barcelona	Spain	Espadaler 1983	Accidental
<i>Plagiolepis pygmaea</i> (Latreille, 1798)	Avenc Refoia	Prat de Compte, Tarragona	Spain	Espadaler 1983	Accidental
<i>Polyrhachis bellicosa</i> (Smith, 1859)	Gomantong Caves	Sandakan Residency	Borneo	Hung 1970	None
<i>Polyrhachis hector</i> (Smith, 1857)	Davao Cave 1; Kitaotao 1 & 3	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Polyrhachis illaudata</i> (Walker, 1859)	Davao Cave 2	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Polyrhachis mindanaensis</i> (Emery, 1923)	Davao Cave 1; Kitaotao 1, 2 & 3	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Polyrhachis olybria</i> (Forel, 1912)	Davao Cave 2	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Polyrhachis</i> sp. 1	Bulod Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Accidental
<i>Polyrhachis</i> sp. 2	Bulod Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Accidental
<i>Polyrhachis</i> sp. 3	Patag Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Accidental
<i>Polyrhachis</i> sp. 4	Guano Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Troglophile
<i>Polyrhachis</i> sp.	Davao Cave 1; Salawao Cave	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Prenolepis imparis</i> (Say, 1836)	Connie's Cave	Amador Co., California	USA	Reddell & Cokendolpher 2001	None
<i>Prolasius</i> sp.	Pinwill Cave	Queensland	Australia	Clarke 2010	None
ECTATOMMINAE					
<i>Ectatomma brunneum</i> (Smith, 1858)	Cave 22	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Gnamptogenys continua</i> (Mayr, 1887)	Mt. Plenty Cave	St. Ann	Jamaica	Peck 1992	Troglophile

<i>Gnamptogenys striatula</i> (Mayr, 1884)	Cousins Cove Cave	Hanover	Jamaica	Peck 1992	Troglophile
<i>Gnamptogenys striatula</i> (Mayr, 1884)	Cave 9	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Gnamptogenys strigata</i> (Norton, 1868)	Cueva de la Sala de Agua Grande	Veracruz	Mexico	Reddell & Cokendolpher 2001	None
<i>Gnamptogenys</i> sp., (<i>striatula</i> complex).	Coles Cave	St. Thomas Parish	Barbados	Peck 1981a	Troglophile
<i>Gnamptogenys</i> sp.	Kitaotao 1 & 3	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Rhytidoponera metallica</i> (Smith, 1858)	Bat Cave	Naracoorte	Australia	Moulds 2006	Accidental
MYRMICINAE					
<i>Acromyrmex echinator</i> (<i>A. octospinosus</i> var. <i>echinator</i>) (Forel, 1899)	Puz Cave; Gongora Cave	Oxkutzcab, Yucatan	Mexico	Wheeler 1938	Accidental
<i>Acromyrmex echinator</i> (<i>A. octospinosus</i> var. <i>echinator</i>) (Forel, 1899)	Ziz Cave	Yucatan	Mexico	Wheeler 1938	Accidental
<i>Acromyrmex echinator</i> (<i>A. octospinosus</i> var. <i>echinator</i>) (Forel, 1899)	San Bulha Cave	Merida, Yucatan	Mexico	Wheeler 1938	Accidental
<i>Acromyrmex echinator</i> (<i>A. octospinosus</i> var. <i>echinator</i>) (Forel, 1899)	Xkyc Cave	Calcehtok, Yucatan	Mexico	Wheeler 1938	Accidental
<i>Acromyrmex hystrix</i> (Latreille, 1802)	Cave 27	Estreito, Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Acromyrmex octospinosus</i> (Reich, 1793)	Caves	Yucatan	Mexico	Reddell 1977	Trogloxene
<i>Acromyrmex octospinosus</i> (Reich, 1793)	Cenote Aka Chen	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Aphaenogaster cardenai</i> (Espadaler, 1981)	Caves	Not listed	Spain	Tinaut & Lopez 2001	Troglophile
<i>Aphaenogaster crocea</i> (André, 1881)	Grotta dell' Acqua Presso	Canicattini Bagni, Sicily	Italy	Baroni Urbani 1962b	None
<i>Aphaenogaster senilis</i> (Mayr, 1853)	Grotta di S. Giovanni	Domusnovas, Carbonia-Iglesias, Sardinia	Italy	Rigato & Toni 2011	None
<i>Aphaenogaster subterranea</i> (Latreille, 1798)	Grotta dell' Acqua Presso	Canicattini Bagni, Sicily	Italy	Baroni Urbani 1962b	None
<i>Aphaenogaster subterranea</i> (Latreille, 1798)	Cave	Matteria	Slovenia	Müller 1923	None
<i>Aphenogaster texana</i> (Wheeler, 1915)	O.T.L. Cave	Brewster Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Aphenogaster</i> cf. <i>texana</i>	Sistema Purificacion	Tamaulipas	Mexico	Reddell & Cokendolpher 2001	None
<i>Aphenogaster</i> sp. 1	Cueva 8 de Julio	Morelos	Mexico	Reddell & Cokendolpher 2001	None
<i>Aphenogaster</i> sp. 2	Loop-Around Cave	Ft. Hood, Bell Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Apterostigma</i> sp.	Cueva del Ojo de Agua Grande	Veracruz	Mexico	Reddell & Cokendolpher 2001	None
<i>Atta cephalotes</i> (<i>A. c.</i> var. <i>opaca</i>) (Linnaeus, 1758)	Muruztun Cave	Tizamin, Yucatan	Mexico	Wheeler 1938	None
<i>Atta cephalotes</i> (<i>A. c.</i> var. <i>opaca</i>) (Linnaeus, 1758)	Cueva Muruztun	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Atta mexicana</i> (Smith, 1858)	Cueva de las Lagunitas	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	None
<i>Atta texana</i> (Buckley, 1860)	Fog Fissure	Bandera Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Atta</i> sp.	Gruta Fradinhos	Altinopolis, Sao Paulo	Brazil	Trajano 1987	None
<i>Atta</i> sp.	Actun Toh	Yucatan	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Carebara (Oligomyrmex) longii</i> (Wheeler, 1903)	Viper Den Cave	Coryell Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Carebara silenus</i> (Smith, 1858)	Bat Cave	Sarawak	Malaysia	Chapman 1982	Trogloxene

<i>Carebara (Spelaeomyrmex; Oligomyrmex; Erebomyrma) urichi</i> (Wheeler, 1922)	Oropouche (Guacharo) Cave	Not listed	Trinidad	Wheeler 1922; Wilson 1962; Cover 1989	Troglophile
<i>Carebara (Spelaeomyrmex) urichi</i> (Wheeler, 1922)	San Bulha Cenote	Motul, Yucatan	Mexico	Wheeler 1938	Troglophile
<i>Carebara (Oligomyrmex) urichi</i> (Wheeler, 1922)	Cenote de Sambula Motul	Yucatan	Mexico	Reddell & Cokendolpher 2001	Troglophile
<i>Cephalotes atratus</i> (Linnaeus, 1758)	Caves 16 & 23	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Crematogaster emeryana</i> (Creighton, 1950)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Crematogaster hespera</i> (Buren, 1968)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Crematogaster laeviuscula</i> (Mayr, 1870)	Wildflower Cave	Travis Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Crematogaster scutellaris</i> (Olivier, 1792)	Avenc dels Trigassos	Baget, Girona	Spain	Espadaler 1983	Accidental
<i>Crematogaster scutellaris</i> (Olivier, 1792)	Tana da Bazura	Savona	Italy	Franciscolo 1955	Accidental
<i>Crematogaster sordidula</i> (Nylander 1849)	Tana da Bazura	Savona	Italy	Franciscolo 1955	Accidental
<i>Crematogaster</i> cf. <i>steinheili</i> (Forel, 1881)	Cueva Tuna	Cabo Rojo	Puerto Rico	Peck 1981b	Troglophile
<i>Crematogaster subdentata</i> (C. s. <i>kaschgariensis</i>) (Mayr, 1877)	Caves	Not listed	Afghanistan	Decu et al., 1998	None
<i>Crematogaster sumichrasti</i> (Mayr, 1870)	Cebada Cave	Chiquibul Cave System	Belize	Reddell & Veni 1996	Accidental
<i>Crematogaster</i> sp. 1	Cave 24	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Crematogaster</i> sp. 2	Cave 25	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Crematogaster</i> sp. 3	Cave 13	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Crematogaster</i> sp.	Runaway Bay Caves	St. Ann	Jamaica	Peck 1992	Troglophile
<i>Crematogaster</i> sp.	Million-bat Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Troglophile
<i>Crematogaster</i> sp.	Campsey Cave	Hardeman Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Crematogaster</i> sp.	Davao Cave 1 & 2; Kitaotao Cave 1, 2 & 3	Mindanao	Philippines	Figueras and Nuneza 2013	None
<i>Crematogaster</i> sp.	Bat Cave	Sarawak	Malaysia	Chapman 1982	Trogloxene
<i>Crematogaster</i> sp.	Balam's Cave	Cayo	Belize	Reddell & Cokendolpher 2001	None
<i>Cyphomyrmex rimosus</i> (Spinola, 1851)	Aguas Buenas Cave	Aguas Buenas	Puerto Rico	Peck 1974	Troglophile
<i>Cyphomyrmex rimosus</i> (Spinola, 1851)	Mt. Plenty Cave	St. Ann	Jamaica	Peck 1992	Troglophile
<i>Cyphomyrmex rimosus</i> (Spinola, 1851)	Up the Creek Cave	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Eurhopalothrix pilulifera</i> (Brown & Kempf, 1960)	Cenote Chen Mul	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Goniomma blanci</i> (André, 1881)	Avenc Toni	Sot del Bac, Barcelona	Spain	Espadaler 1983	Accidental
<i>Leptothorax</i> sp.	Cove de la Torre	Sant Feliu de Pallarols, Girona	Spain	Espadaler 1983	Accidental
<i>Messor minor</i> (M. m. <i>maurus</i>) (André, 1883)	Sima Robada	Tenerife, Canary Islands	Spain	Martín et al., 1985	Trogloxene
<i>Monomorium carbonarium</i> (Smith, 1858)	Grutas dos Anjos	Santa Maria, Azores	Portugal	Wetterer et al., 2004	None
<i>Monomorium cyaneum</i> (Wheeler, 1914)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Monomorium (cyaneum?)</i> (Wheeler, 1914)	Bullis Hole	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Monomorium minimum</i> (Buckley, 1866)	Gorman Cave	San Saba Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Monomorium minimum</i> (Buckley, 1866)	Hidden Cave	Eddy Co., New Mexico	USA	Cokendolpher & Polyak 2004	Accidental
<i>Monomorium pharaonis</i> (Linnaeus, 1758)	Batu Caves	Selangor	Malaysia	McClure et al., 1967	None

<i>Monomorium rhopalocerum</i> (<i>M. r. speluncarum</i>) (Emery, 1895)	Caves	Tanga and Shimoni	Tanzania and Kenya	Alluaud & Jeannel 1914 (in Wilson 1962)	None
<i>Monomorium</i> cf. <i>subcoecum</i> (Emery, 1894)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Monomorium</i> sp.	Davao Cave 1	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Monomorium</i> sp.	Bat Cave	Sarawak	Malaysia	Chapman 1982	Trogloxene
<i>Monomorium</i> sp.	Cueva de la Cerca de Piedra	Nuevo Leon	Mexico	Reddell & Cokendolpher 2001	None
<i>Myrmecina americana</i> (Emery, 1895)	Big Crevice	Fort Hood, Bell Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Myrmecina americana</i> (Emery, 1895)	Newsome Gap Cave	Dade Co., Georgia	USA	Reeves et al., 2000	None
<i>Myrmecina americana</i> (Emery, 1895)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Myrmecina graminicola</i> (Latreille, 1802)	Cove de la Torre	Sant Feliu de Pallarols, Girona	Spain	Espadaler 1983	Accidental
<i>Myrmica rubra</i> (<i>M. laevinodis</i>) (Linnaeus, 1758)	Cave	Marcovsina	Italy	Müeller 1923	None
<i>Myrmica rubra</i> (Linnaeus, 1758)	Cave	Not listed	Italy	Espadaler 1983	Trogloxene
<i>Myrmica rubra</i> (Linnaeus, 1758)	Cove de la Torre	Sant Feliu de Pallarols, Girona	Spain	Espadaler 1983	Accidental
<i>Myrmica striolagaster</i> (Cole, 1953)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Myrmicaria brunnea</i> (Saunders, 1842)	Sumiyot Cave; Patag Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Accidental
<i>Myrmicaria brunnea</i> (Saunders, 1842)	Davao Cave 1; Kitaotao Cave 1	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Nesomyrmex</i> (<i>Leptothorax</i>) <i>anduzei</i> (Weber, 1943)	Caves	Carabobo	Venezuela	Weber 1943	None
<i>Octostruma</i> sp.	Actun Siete Aguas	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Pheidole absurda</i> (Forel, 1886)	Actun Xpukil	Yucatan	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Pheidole biconstricta</i> (Mayr, 1870)	Caves	Not listed	Trinidad	Decu et al., 1998	None
<i>Pheidole crassinoda</i> (Emery, 1895)	Lanner Gorge Cave	Kruger National Park	South Africa	Braack 1989	None
<i>Pheidole dentata</i> (Mayr, 1886)	Sotano del Molino	Tamaulipas	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Pheidole dentata</i> (Mayr, 1886)	Cave of the Bearded Tree	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Pheidole fervens</i> (<i>P. javana</i>) (Smith, 1858)	Dark Cave of the Batu Caves	Kuala Lumpur, Selangor	Malaysia	McClure et al., 1967	None
<i>Pheidole hyatti</i> (Emery, 1895)	Streak Cave	Bell Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Pheidole longipes</i> (Latreille, 1802)	Bat Cave	Sarawak	Malaysia	Chapman 1982	Trogloxene
<i>Pheidole megacephala</i> (Fabricius, 1793)	Sima Robada	Tenerife, Canary Islands	Spain	Martín et al., 1985	Trogloxene
<i>Pheidole megacephala</i> (Fabricius, 1793)	Caves - East Maui Cave Reserve	Maui, Hawai'i	USA	Howarth et al., 2007	Trogloxene
<i>Pheidole megacephala</i> (Fabricius, 1793)	Grotte de Shimoni	Not listed	Kenya	Decu et al., 1998	None
<i>Pheidole obscurithorax</i> (Naves, 1985)	Caves 2 & 19	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Pheidole pallidula</i> (Nylander, 1849)	Cove Santa	Algodonales, Cadiz	Spain	Espadaler 1983	Accidental
<i>Pheidole pallidula</i> (Nylander, 1849)	Graller de Gurb	Sa. de Lleras, Lleida	Spain	Espadaler 1983	Accidental
<i>Pheidole pallidula</i> (Nylander, 1849)	Cove Figuerot	Sant Llorenç del Munt, Barcelona	Spain	Espadaler 1983	Accidental
<i>Pheidole pallidula</i> (<i>P. p. arenarum</i>) (Nylander, 1849)	Caves	Not listed	Afghanistan	Decu et al., 1998	None

<i>Pheidole pallidula</i> (<i>P. p. arenarum orientalis</i>) (Nylander, 1849)	Caves	Not listed	Afghanistan	Decu et al., 1998	None
<i>Pheidole porcula</i> (Wheeler, 1908)	Vera Cruz Shaft	Bexar Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Pheidole</i> cf. <i>porcula</i>	Arkenstone Cave	Pima Co., Arizona	USA	Pape - this paper	Trogloxene
<i>Pheidole portalensis</i> (Wilson, 2003)	Arkenstone Cave	Pima Co., Arizona	USA	Pape - this paper	Trogloxene
<i>Pheidole punctatissima</i> (Mayr, 1870)	Cebada Cave	Chiquibul Cave System	Belize	Reddell & Veni 1996	Accidental
<i>Pheidole punctatissima</i> (Mayr, 1870)	Spukil Cave	Calcehtok, Yucatan	Mexico	Wheeler 1938	None
<i>Pheidole punctatissima</i> (Mayr, 1870)	San Bulha Cenote	Motul, Yucatan	Mexico	Wheeler 1938	None
<i>Pheidole rhea</i> (Wheeler, 1908)	Patagonia Bat Cave	Patagonia, Arizona	USA	Pape - this paper	Trogloxene
<i>Pheidole strator</i> (Forel, 1910)	Grotte de Shimoni	Not listed	Kenya	Decu et al., 1998	Accidental or Trogloxene
<i>Pheidole tolteca</i> (Forel, 1901)	Cueva del Diablo	Morelos	Mexico	Reddell & Cokendolpher 2001	None
<i>Pheidole vistana</i> (Forel, 1914)	Parashant (PARA) 2602	Grand Canyon-Parashant National Monument, Arizona	USA	Wynne & Voyles 2014	Accidental
<i>Pheidole</i> sp. 1	Caves 17 & 21	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Pheidole</i> sp. 2	Cave 8	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Pheidole</i> sp. 3	Cave 18	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Pheidole</i> sp. 4	Cave 9	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Pheidole</i> sp. 5	Cave 3	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Pheidole</i> sp. 1	Cenote de Juan Coh	Quintana Roo	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Pheidole</i> sp. 2	Ventana Jabali	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	None
<i>Pheidole</i> sp. 3	Cenote Amil	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Pheidole</i> sp. 4 (<i>flavens</i> group)	Cenote Chen Mul	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Pheidole</i> sp. (<i>bicarinata</i> group)	Cueva Grande	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Pheidole</i> sp. (<i>variabilis</i> group)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Pheidole</i> sp.	Cueva de Cerro San Jose	Santa Barbara	Puerto Rico	Peck 1974	Troglophile
<i>Pheidole</i> sp.	Moseley Hall Cave	St. Ann	Jamaica	Peck 1992	Troglophile
<i>Pheidole</i> sp.	Cave Two	Siargao Island	Philippines	Batucan & Nuneza 2013	Accidental
<i>Pheidole</i> sp.	Parashant (PARA) 2204	Grand Canyon-Parashant National Monument, Arizona	USA	Wynne & d Voyles 2014	Accidental
<i>Pheidole</i> sp.	ELMA 008	Cibola Co., New Mexico	USA	Wynne 2013	None
<i>Pheidole</i> sp.	Awesome Entrance Cave	Bell Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Pheidole</i> sp.	Caves	Aripo Valley	Trinidad	Weber 1943	None
<i>Pheidole</i> sp.	San Bulha Cave	Merida, Yucatan	Mexico	Wheeler 1938	None
<i>Pheidologeton maccus</i> (Wheeler, 1929)	Kitaotao Cave 1, 2 & 3	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Pheidologeton</i> sp.	Buho Cave; Million-bat Cave; Naugon Cave	Siargao Island	Philippines	Batucan & Nuneza 2013	Troglophile
<i>Pheidologeton</i> sp.	Kariis and Salawao Caves	Mindanao	Philippines	Figueras & Nuneza 2013	None
<i>Pogonomyrmex barbatus</i> (Smith, 1858)	Dunbar Cave	Edwards Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental

<i>Pogonomyrmex comanche</i> (Wheeler, 1902)	Fossil Cave	Travis Co., Texas	USA	Reddell & Cokendolpher 2001	Accidental
<i>Pristomyrmex</i> sp.	Batu Caves	Selangor	Malaysia	McClure et al., 1967	None
<i>Rogeria inermis</i> (Mann, 1922)	Monawa Cave	Westmorland	Jamaica	Peck 1992	Troglophile
<i>Solenopsis aurea</i> (Wheeler, 1906)	Arkenstone Cave	Pima Co., Arizona	USA	Pape - this paper	Trogloxene?
<i>Solenopsis fugax</i> (Latreille, 1798)	Privorac Cave	Brusje, Hvar Island	Croatia	Müller 1923	None
<i>Solenopsis geminata</i> (Fabricius, 1804)	Oxford Cave	Manchester	Jamaica	Peck 1992	Troglophile
<i>Solenopsis geminata</i> (Fabricius, 1804)	Cueva de Corozal	Corozal	Puerto Rico	Peck 1974	Troglophile
<i>Solenopsis geminata</i> (Fabricius, 1804)	Volcan de los Murcielagos	Campeche	Mexico	Reddell & Cokendolpher 2001	Trogloxene
<i>Solenopsis geminata</i> (Fabricius, 1804)	Cebada Cave	Chiquibul Cave System	Belize	Reddell & Veni 1996	Accidental
<i>Solenopsis geminata</i> (Fabricius, 1804)	Cebada Cave	Cayo	Belize	Reddell & Cokendolpher 2001	None
<i>Solenopsis geminata</i> (Fabricius, 1804)	Puz Cave; Gongora Cave	Oxkutzcab, Yucatan	Mexico	Wheeler 1938	None
<i>Solenopsis geminata</i> (Fabricius, 1804)	Kamikazi Cricket Cave	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Solenopsis geminata</i> (Fabricius, 1804)	San Isidro Cave	Merida, Yucatan	Mexico	Wheeler 1938	None
<i>Solenopsis geminata</i> (Fabricius, 1804)	California Cave and Pedra Suspensa Cave	Bahia	Brazil	Trajano 2000	None
<i>Solenopsis globularia</i> (Smith, 1858)	Comfortless Crevices	Ascension Island	British Territory	Wetterer et al., 2007	None
<i>Solenopsis globularia</i> (Smith, 1858)	Rupert's Cave	St. Helena	British Territory	Wetterer et al., 2007	None
<i>Solenopsis invicta</i> (Buren, 1972)	B. J. Pit	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	Trogloxene
<i>Solenopsis invicta</i> (Buren, 1972)	Big Red Cave	Fort Hood	Texas	Taylor et al., 2005	None
<i>Solenopsis tenuis</i> (Mayr, 1878)	Oropouche Cave	Not listed	Trinidad	Wilson 1962	Trogloxene
<i>Solenopsis texana</i> (Emery, 1895)	Big Crevice	Fort Hood, Bell Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Solenopsis wolfi</i> (Emery, 1915)	Privorac cave	Brusje, Hvar Island	Croatia	Bracko 2006	None
<i>Solenopsis xyloni</i> (No authors, 1879)	Bracken Bat Cave	Bexar Co., Texas	USA	Reddell & Cokendolpher 2001	None
<i>Solenopsis xyloni</i> (No authors, 1879)	Parashant (PARA) 2602	Grand Canyon-Parashant National Monument, Arizona	USA	Wynne & Voyles 2014	Accidental
<i>Solenopsis</i> sp. 1	Cave 14	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Solenopsis</i> sp. 2	Caves 6 & 20	Maranhão	Brazil	Dáttilo et al., 2012	None
<i>Solenopsis</i> sp. 1	Cenote de Sihunchen	Yucatan	Mexico	Reddell & Cokendolpher 2001	Trogloxene
<i>Solenopsis</i> sp. 2	Actun Xpukil	Yucatan	Mexico	Reddell & Cokendolpher 2001	Trogloxene
<i>Solenopsis</i> sp.	Cueva Pajita	Lares	Puerto Rico	Peck 1974	Troglophile
<i>Solenopsis</i> sp.	Sotano de las Piedras	San Luis Potosi	Mexico	Reddell & Cokendolpher 2001	Trogloxene
<i>Solenopsis</i> sp.	Caves-North Kona area	Hawai'i, Hawai'i	USA	Howarth et al., 2007	Trogloxene
<i>Stenamma debile</i> (Foerster, 1850)	Grotta di S. Giovanni	Sardinia	Italy	Rigato & Toni 2011	None
<i>Stenamma</i> sp.	Nugget Cave	Pinal Co., Arizona	USA	Pape - this paper	Trogloxene?
<i>Stenamma</i> sp. (probable undescribed sp.)	Cenote de Santo Domingo	Quintana Roo	Mexico	Reddell & Cokendolpher 2001	None

<i>Strumigenys languinosa</i> (Wheeler, 1905)	Actun Xpukil	Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Strumigenys ludovici</i> (<i>S. alluaudi</i>) (Forel, 1904)	Grotte de Kulumuzi	Tanga	Tanzania	Decu et al., 1998	None
<i>Strumigenys ludovici</i> (<i>S. alluaudi</i>) (Forel, 1904)	Grotte de Shimoni	Not listed	Kenya	Decu et al., 1998	None
<i>Strumigenys</i> (<i>Miccostruma</i> ; <i>Smithistruma</i>) <i>marginata</i> (Santschi, 1914)	Caves	Tanga and Shimoni	Tanzania and Kenya	Alluaud & Jeannel 1914 (in Wilson 1962)	None
<i>Strumigenys rogeri</i> (Emery, 1890)	Oxford Cave	Manchester	Jamaica	Peck 1992	Troglophile
<i>Strumigenys stygia</i> (Santschi, 1913)	Caves	Tanga and Shimoni	Tanzania and Kenya	Alluaud & Jeannel 1914 (in Wilson 1962)	None
<i>Strumigenys</i> sp.	Caves	Aripo Valley	Trinidad	Weber 1943	None
<i>Temnothorax</i> (<i>Leptothorax</i>) <i>affinis</i> (Mayr, 1855)	Av. Clast	Coll Cassot, Barcelona	Spain	Espadaler 1983	Accidental
<i>Temnothorax</i> (<i>Leptothorax</i>) <i>cokendolpheri</i> (Mackay, 2000)	Hidden Cave	Eddy Co., New Mexico	USA	Cokendolpher & Polyak 2004	Accidental
<i>Temnothorax</i> (<i>Leptothorax</i>) <i>nevadensis</i> (Wheeler, 1903)	Oregon Caves	Oregon Caves Ntl. Mon.	USA	Roth 2001	Trogloxene
<i>Temnothorax nevadensis</i> (<i>Paratrechina terricola</i>) (Wheeler, 1903)	Caverns of Sonora	Sutton Co., Texas	USA	Reddell & Cokendolpher 2001	Trogloxene
<i>Temnothorax obturator</i> (no authors, 1903)	Runoff Cave	Bell Co., Texas	USA	Cokendolpher et al., 2009	None
<i>Temnothorax</i> (<i>Leptothorax</i>) <i>rugatulus</i> (Emery, 1895)	Hidden Cave	Eddy Co., New Mexico	USA	Mackay & Mackay 2002	None
<i>Temnothorax</i> (<i>Leptothorax</i>) <i>unifasciatus</i> (Latreille, 1798)	Algar do Carvão	Terceira, Azores	Portugal	Wetterer et al., 2004	None
<i>Tetramorium bicarinatum</i> (Nylander, 1846)	Actun Nohcacab	Santa Elena, Yucatan	Mexico	Reddell & Cokendolpher 2001	None
<i>Tetramorium insolens</i> (Smith, 1861)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Tetramorium lanuginosum</i> (Mayr, 1870)	Cenote de Hochtun	Yucatan	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Tetramorium lanuginosum</i> (<i>Triglyphothrix striatidens</i>) (Mayr, 1870)	Siju Cave	Garo Hills, Assam	India	Wheeler 1924	None
<i>Tetramorium lucayanum</i> (Wheeler, 1905)	Caves	Not listed	Antillies	Decu et al., 1998	Trogloxene
<i>Tetramorium lucayanum</i> (Wheeler, 1905)	Caves	Not listed	Africa	Decu et al., 1998	None
<i>Tetramorium lucidulum</i> (Menozi, 1933)	Caves	Not listed	Afghanistan	Decu et al., 1998	None
<i>Tetramorium semilaeve</i> (André, 1883)	Calypso Cave	Gozo Island	Malta	Schembri & Collingwood 1981	None
<i>Tetramorium simillimum</i> (Smith, 1851)	Cousins Cove Cave	Hanover	Jamaica	Peck 1992	Troglophile
<i>Tetramorium simillimum</i> (Smith, 1851)	Caves	Christmas Island	Australia	Framenau & Thomas 2008	None
<i>Tetramorium</i> sp.	Kariis Cave; Salawao Cave; Kitaotao 1, 2 & 3	Mindanao	Philippines	Figueras and Nuneza 2013	None
<i>Trachymyrmex arizonensis</i> (Wheeler, 1907)	Kartchner Caverns	Cochise Co., Arizona	USA	Pape & OConnor 2014	Trogloxene
<i>Trachymyrmex</i> sp.	Grutas de Tzab-Nah	Yucatan	Mexico	Reddell & Cokendolpher 2001	Accidental
<i>Wasmannia auropunctata</i> (Roger, 1863)	Coles Cave	Welchman Hall	Barbados	Peck 1981a	Troglophile
<i>Wasmannia auropunctata</i> (Roger, 1863)	Oxford Cave	Manchester	Jamaica	Peck 1992	Troglophile
<i>Wasmannia auropunctata</i> (Roger, 1863)	Cebada Cave	Chiquibul Cave System	Belize	Reddell & Veni 1996	Accidental
<i>Wasmannia auropunctata</i> (Roger, 1863)	Cebada Cave	Cayo	Belize	Reddell & Cokendolpher 2001	None
<i>Wasmannia auropunctata</i> (Roger, 1863)	Oropouche (Guacharo) Cave	Not listed	Trinidad	Wheeler 1922; Cover 1989	None
<i>Wasmannia</i> (<i>Ochetomyrmex</i>) <i>auropunctata</i> (Roger, 1863)	Aguas Buenas Cave	Aguas Buenas	Puerto Rico	Peck 1974	Troglophile