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Description and Ecology of A New Cavernicolous, Arachnophilous Thread-legged Bug (Hemiptera: Reduviidae: Emesini) from Kartchner Caverns, Cochise County, Arizona

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Abstract

A new cavernicolous, arachnophilous thread-legged bug (*Phasmatorcoris labyrinthicus* sp. nov.; Reduviidae: Emesini) is described from Kartchner Caverns, a limestone cavern in Kartchner Caverns State Park near Benson, Arizona, USA. Cavernicolous emesines are recorded from caves in many parts of the world and are distributed across several genera, but are generally uncommon. *P. labyrinthicus* shows no obvious troglomorphy but ecological evidence suggests it is, at minimum, a cave-limited troglophile. The species seems to be low-humidity intolerant, due to its occurrence in a cave within a desert region, effectively confines the population to the cave, and the species may thus actually be troglobitic by default. Arachnophily in emesines is more common, including in *Phasmatorcoris* Breddin, but has been previously documented in only a single cavernicolous species, *Bagauda cavernicola* Paiva, reported from India, Malaysia and Sri Lanka. However, unlike *P. labyrinthicus*, *B. cavernicola* is apparently not morphologically adapted for its arachnophilous association. *P. labyrinthicus* is the only known trogliphilic emesine that is also a morphologically adapted and behaviorally functional arachnophile. The only other known cavernicolous *Phasmatorcoris* (*P. xavieri* Gil-Santana, Alves, Barrett and Costa) is recorded from a sandstone cave in Brazil. *P. xavieri* exhibits morphological features indicative of a potentially arachnophilous habit, but its ecology has not been studied. Adults of *P. labyrinthicus* share characteristics with the species *Phasmatorcoris praecellens* Bergroth, *P. minor* McAtee and Malloch, *P. xavieri*, *P. spectrum* Breddin, and *P. rapax* McAtee and Malloch. *Phasmatorcoris* is primarily a Neotropical genus and the discovery of *P. labyrinthicus* represents a significant range extension for the genus, being the first Nearctic species identified, with its geographically nearest relative an undescribed species from Mazatlan, Mexico, over 1,000 km to the south.

Key words: Heteroptera, Emesinae, new taxon, systematics, *Phasmatorcoris*, trogliphile, troglobite, arachnophile, behavior, cave

Introduction—Regional Setting

Kartchner Caverns is located within Kartchner Caverns State Park (KCSP) near the town of Benson, Cochise County, Arizona. The Park lies within the Basin and Range Province physiographic region of the western United States. The cave is contained within a grouping of small hills situated low on the east flank of the Whetstone Mountains. The cave is formed in Escabrosa limestone of Mississippian age (Jagnow 1999), and dating of speleothems from the cave provide a minimum age for the cave of nearly 200 ka (Ford and Hill 1999). The collapse-sink entrance of the cave is located on a southeasterly-facing slope at an elevation of 1,428 m. The vegetation community in the area is dominantly the Semidesert Grassland biome (Fig. 1) as described by Brown (1982). Average annual precipitation recorded at the Park over the last 20 years is 30.2 centimeters. Less than two percent of this water potentially reaches the cave through infiltration as autogenic meteoric drip waters (Buecher 1999). Compared with earlier, more mesic (wetter) periods, the geologically recent desertification of the southwestern United States, beginning approximately 12–10 kya years ago (Van Devender 1990), resulted in less precipitation being available for the meteoric recharge and maintenance of humid cave environments. As a result, many caves in the region, particularly those with multiple entrances that permit significant air exchange with the

surface, are probably considerably drier than they were prior to desertification. Caves such as Kartchner Caverns, which still support a high humidity environment, may serve as refugia for macro-invertebrates that have been removed regionally from the epigeal environment as a result of the recent desertification.



FIGURE 1. Semidesert Grassland biome at Kartchner Caverns State Park.

History

Presence of this thread-legged bug was first noted in 1990 during an invertebrate faunal survey conducted between May 1989 and May 1991 as one of a series of pre-development studies performed at KCSP, prior to its development as an Arizona state park. The animal was included in the list of invertebrates documented during the survey in a 1992 report to Arizona State Parks (ASP), and in a subsequent paper in the *Journal of Cave and Karst Studies* in 1999 (Welbourn 1992; 1999). The original report and paper contain little information regarding the species, but state that the animals were found in several widely separated areas in the cave, including the Big Room, and a single observation in the Back Section of the cave. The species was considered rare in the cave, and was thought to not be a part of the regular (indigenous) cave fauna. The disposition of the single specimen taken during the original study is not known.

At the request of ASP a two-year study (augmented re-inventory) of the invertebrates of Kartchner Caverns was performed between September 2009 and September 2011 by the author and others. The study ultimately added 58 non-accidental species to the 40 (38¹) non-accidentals that were in the original (1999) faunal survey of the cave. Fourteen of the additions were from specimens sampled by ASP staff between 2002 and 2009, and ten of the added species are troglobites. Seventeen species on the updated list, including the thread-legged bug, were undescribed species (Pape et al. 2012). This is the second paper describing a new macro-invertebrate species resulting from the recent two-year study. The initial paper (Espinasa et al. 2012) described the troglobitic coleopteran (Zygentoma)

1. The text of the original 1999 survey states that 38 macro-invertebrate species were documented in the cave. A review of the paper revealed an actual total of 41 species, 40 of which I determined likely to be integrally connected with the ecology of the cave

Speleonycta anachoretetes Espinasa, Pape, Henneberry and Kinnear. Additional papers are in preparation on the ecology of a troglobitic vaejovid scorpion (*Pseudouroctonus* nr. *apacheanus*) and an undescribed scuttle fly (*Megaselia* sp.), and papers are anticipated for an undescribed scaptiid beetle (*Anaspis* sp.), and an undescribed staphylinid beetle (*Stammoderus* sp.).

Distribution and Ecology of Thread-legged Bugs

Thread-legged bugs constitute a subfamily (Emesinae) of the primarily tropical hemipterous family Reduviidae, which also includes the ambush bugs (Phymatinae). There are currently over 900 described species of emesines from around the world (Capriles 1990), some of which are cosmopolitan in their distribution. Henry and Froeschner (1988) listed fifty two species of emesines from North America.

With their raptorial front legs emesines are effective predators. Some species employ a roaming hunting strategy, while others are stationary predators. Wygodzinsky, in his summary of the dietary records for emesines, concluded that they are essentially opportunistic predators, feeding primarily on insects, but that they commonly prey on spiders and their egg cases. Most species are likely to take any invertebrate that they can subdue.

Most thread-legged bugs are nocturnally active, and species have been recorded from a wide variety of habitats including, in part: among leaves, and on the trunks and undersides of branches of trees; on bark of trees (often among lichens), and under bark of dead snags and fallen tree trunks; on orchids, bromeliads, and Spanish moss high in trees; on fronds of tree ferns and palms; on bushes; on grasses, and among grass roots, and weeds (often near water); among cattails (*Typha* sp.); beneath rocks and other ground debris and in rock piles; on low herbage and in leaf litter; and in flood debris, abandoned bird nests, and aphid galls (Wygodzinsky 1966).

There are several synanthropic emesines, with each species having adopted either a peridomestic or a fully domestic human association. Some synanthropic species live only in human habitations, while others live both in dwellings and associated structures such as barns and other outbuildings. Many of the latter live beneath roofs or under eaves, and in these situations some are associated with spider webs. Other synanthropic species prefer the dark and damp cellars present beneath human dwellings. Some synanthropic emesines (e.g. *Ploiaria domestica* and *P. chilensis*) are global in their distribution (Wygodzinsky 1966). Considering the large number of emesine species, their global distribution and wide variety of habitats occupied, their lineage is probably quite old.

The Emesinae are well represented by species that are partially or entirely cave-inhabiting animals. There are at least 44 species that have been recorded from caves, of which 24 have been found only in caves (Wygodzinsky 1966; McClure et al. 1967; Villiers 1970; Remillet 1973; Gagne and Howarth 1974; Ribes 1977; Oromí et al. 1991; Capriles 1994; Ribes et al. 1998; Rédei 2005; Gil-Santana et al. 2007; Clarke, 2010; Gebauer 2010; Rédei and Tsai 2010; Villiers 1970). Troglaxene, troglophile, and troglobite are three ecological group classifications that are commonly used to describe the degree of association a given species (or species population) has with a cave (or other subterranean) environment. A troglaxene is an animal that enters caves to fill some ecological need, such as obtaining food, water, or shelter, etc., but which cannot survive without returning to the surface to meet some of its life cycle requirements. A troglophile is an animal that is capable of completing its life cycle within caves, but may also do so in non-subterranean habitats. A troglobite is an obligate resident of the cave environment, and which may have evolved physiological and/or morphological traits for survival in such habitats (Barr 1968). Depending on circumstances, different populations of a given species may potentially fit into any of these three ecologic groups.

Troglaxenic species are recorded in the emesine genera *Bagauda* Bergroth, *Lhostella* Villiers, and *Myiophanes* (Wygodzinsky 1966). Troglophilic, or potentially troglophilic, emesines occur in *Mayemesa* (*Amilcaria*) Wygodzinsky, *Bagauda*, *Berlandiana* Villiers, *Gardenoides* Paulian and Grjebine, *Lhostella* Villiers, *Myiophanes* Reuter, *Paramyiophanes* Wygodzinsky, *Phasmatocoris* and *Ploiaria* Scopoli (Wygodzinsky 1966; Capriles 1994; Gil-Santana et al. 2007). Currently, only three fully troglobitic emesine species are known in the world. Two of these species are found in lava tube caves in the Canary Islands: *Collartida anophthalma* Español and Ribes on the southern portion of Isla de Hierro and *C. tanausu* Ribes, Oromi and Ribes on Isla de La Palma. Each of these species is known from two caves on their respective islands. *C. anophthalma* has a bizarrely inflated abdomen that retains no evident external segmentation. *C. tanausu* has its body uniformly covered with short, light brown hairs (Ribes et al. 1998). Both species of *Collartida* are apterous and totally eyeless (Ribes 1977; Ribes et al. 1998). The

third troglobite, *Nesidiolestes ana* Gagné and Howarth, is known from the dark zone of two high-elevation caves on the Mauna Loa Volcano in Hawaii. One of the caves is named Emesine Cave, in honor of the species (Preston et al. 2004). *N. ana* has greatly reduced eyes (Gagné and Howarth, 1974).

Some emesine genera contain both cave and epigeal species in relative proximity. This situation exists with *Nesidiolestes* spp. in Hawaii, which supports four species, with only *N. ana* being cavernicolous (Capriles 1994). It is unknown whether the cavernicolous *Collartida* of the Canary Islands have any extant epigeal relatives (Oromí 2004), and these species may be relictual. The genus is represented elsewhere only in the Near East and Eastern Africa (Capriles 1994).

The only other known cavernicolous *Phasmatorcoris* is *P. xavieri* from Gruta dos Animais, a sandstone cave north of Manaus, Amazonas State, Brazil. The ecology of *P. xavieri* is unknown other than it was found in a dark zone in the cave, about 30 meters from the entrance (Gil-Santana et al. 2007). Other, undescribed, emesines are known from lava tube caves in Tasmania. The ecology of these species is not currently known (Clark 2010). Undescribed species of *Armstrongula* Wygodzinsky are reported as top predators of bat guano deposits in small caves in the Flinders Ranges in South Australia. These species are probably troglomorphic, but their ecology has not been studied in detail (Moulds 2005).

Materials and methods

Structures were examined using a stereoscopic microscope. Measurements were taken using an AmScope MT-1000 digital microscope camera and software.

Phasmatorcoris labyrinthicus Pape

new species

(Figs. 2a–d, 3a–d, 4a–d, 5a–d, 6a, and 6b)

Note: Where they appear in the figures, black lines indicate locations where referenced measurements were taken.

Remarks: *P. labyrinthicus* has the following diagnostic characters of the genus *Phasmatorcoris*: Macropterous; interocular sulcus situated behind middle of eyes; pronotum covering mesonotum, distinctly separated into fore and hind lobes, and not pedunculate; forelobe of pronotum with a median longitudinal furrow; scutellum elevated, but not spined; fore tibia half, or somewhat longer than half length of femur; tarsi three segmented; presence of discal, basal and subbasal cells in the forewing. Exception: tarsus of mid and hind legs with third segment the longest, rather than a longest second segment.

Description: Holotype male body length 11.8 mm; paratype female 12.0 mm. Kartchner Caverns, Kartchner Caverns State Park, Cochise County, Arizona. 31° 50' 16" N 110° 21' 05" W. Both sampled on August 14, 2010; holotype from the upper Tarantula Room, and the paratype from the Jackrabbit Gallery area.

Head testaceous except for a small area postero-laterally near anterolateral pronotal tubercles, and rostrum, which are stramineous (Fig. 2a). Ratios of rostral segments 1–3 using length of first segment (0.391) as the unit of measure = 1/1.115/2.286. Eyes black, of moderate size and sub-circular in profile. Width to height ratio of eye in profile = 0.87. Eyes in profile situated at middle of head, nearly attaining ventral border, but far from dorsal border (Fig. 2a). Interocular sulcus situated just anterior of rear of eye. Sulcus with a small, acute fovea medially, intruding into the anterior lobe of the head. Dorsum and venter of head with many very small papillae supporting short, fine, proclinate hairs. Sides of head with sparse short, proclinate hairs, which are more numerous anterior of eyes. Antennae darker basally, lightening distally; first segment fuscous, second segment testaceous in basal half, becoming stramineous distally, and segments three and four uniformly stramineous. Antennal vestiture short, proclinate and uniformly distributed along length of antennae. Closely-spaced, shallow annulations begin near the proximal end of antennal segment two and continue to the end of segment four. Tip of antennal segment four subtly swollen before an acuminate terminus. Ratios of antennal segments of holotype male 1–4 using length of first segment (6.419 mm) as the unit of measure = 1/0.760/0.161/0.372; paratype female first segment (6.524 mm); 1/0.743/0.252/0.583.

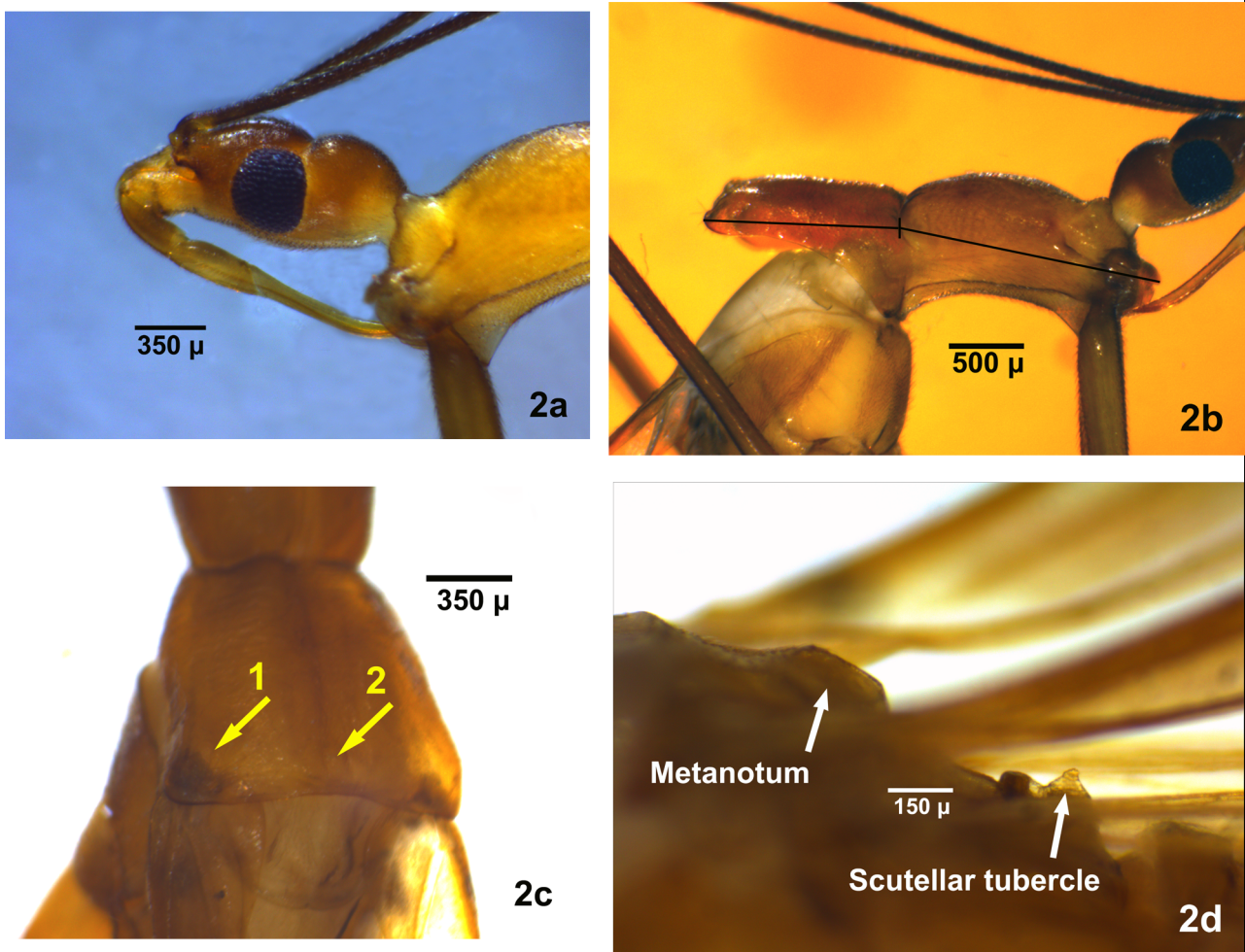


FIGURE 2. *Phasmatorcoris labyrinthicus* sp. nov.; male, holotype, Fig. 2a–profile of head; Fig. 2b–profile of prothorax showing lines used for length measurements; Fig. 2c–dorsal aspect of humeral angle of hind lobe of pronotum showing lack of humeral spinal development at 1 (arrow), and excavated protuberance at 2 (arrow); Fig. 2d–lateral view showing elevated metanotum and scutellar tubercle.

Prothorax uniformly stramineous. Fore lobe 1.38 times length of hind lobe (Fig. 2b). Lobes separated by a distinct, rather deep, transverse sulcus. Fore lobe sub-cylindrical, slightly divergent anteriorly in dorsal aspect, with a distinct, very narrow and shallow, median, longitudinal depression. Anterolateral tubercles salient, but truncate apically. Fore lobe devoid of sculpturing except dorsum with many small papillae medially, similar to those found on the head, except the hairs are shorter and proclinate-appressed. Angles of the collar are salient anteriorly, forming two distinct, truncate-rounded, shallowly convex plates, which cover the dorsal and lateral aspects of the acetabulum. The plates are fully independent anteriorly, with the upper plate slightly overlapping the upper edge of the lower plate, and the pair merging posteriorly into a deep sulcus to just beyond the level of the anterolateral tubercle of the pronotum. Hind lobe of pronotum subquadrate in dorsal aspect, the sides converging slightly anteriorly. The disc microscopically transversely rugose and with a wide, shallow, longitudinal impression medially. Humeri only slightly elevated as a-directional, convex bulges with no indication of spinal development (Fig. 2c–1). Hind lobe also with a very small, low, excavated protuberance at middle of posterior edge (Fig. 2c–2). Metanotum without a spine; posterior half consisting of a broad, low, convex surface. Scutellum with a very small acutely rounded tubercle (Fig. 2d).

Legs with fore coxae ochraceous, four-fifths length of pronotum in lateral view. Remainder of forelegs stramineous. Vestiture uniform, consisting of short, proclinate hairs. Ventral surface of fore-femur with two longitudinal, sub-parallel rows (posteroventral and anteroventral) comprised of a mixture of spiniform setae, spiniferous processes and granules (Fig. 3a). Distance from base of fore femur to insertion of first spiniform seta (Fig. 3b–A) slightly but distinctly shorter than length of fore tarsus (Fig. 3b–1.4A). Posteroventral series of

paratype male composed of 35 (female 39 to 43) slender, spiniform setae, 9 to 11 spiniferous processes (Fig. 3c), and a distal series of approximately 12 short, round-ended granules terminating just short of the distal end of the femur. All elements are inserted on wart-like bases. All spiniferous processes of posteroventral series arise within the first 20 elements of the proximal end of the series. Anteroventral series of paratype male composed of 43 (female 44 to 46) slender, spiniform setae, 7 to 8 spiniferous processes and two sub-terminal granules all inserted on short, wart-like bases. Spiniferous processes of anteroventral series slightly offset anteriorly from setae, and arising within the first 15 elements at the proximal end of the series. A single, isolated spiniform seta present near proximal end of femur basad of anteroventral series interruption (Fig. 3d-1). The gap between the basal end of the anteroventral series and the isolated basal seta allows the fore tarsus to lie in repose against the femur (Fig. 3d-2). Granules located basal to one or a pair of delicate, lighter-colored setae that are the distal terminal elements of the anteroventral series. These setae are offset slightly anterior of the nominal alignment of the series.

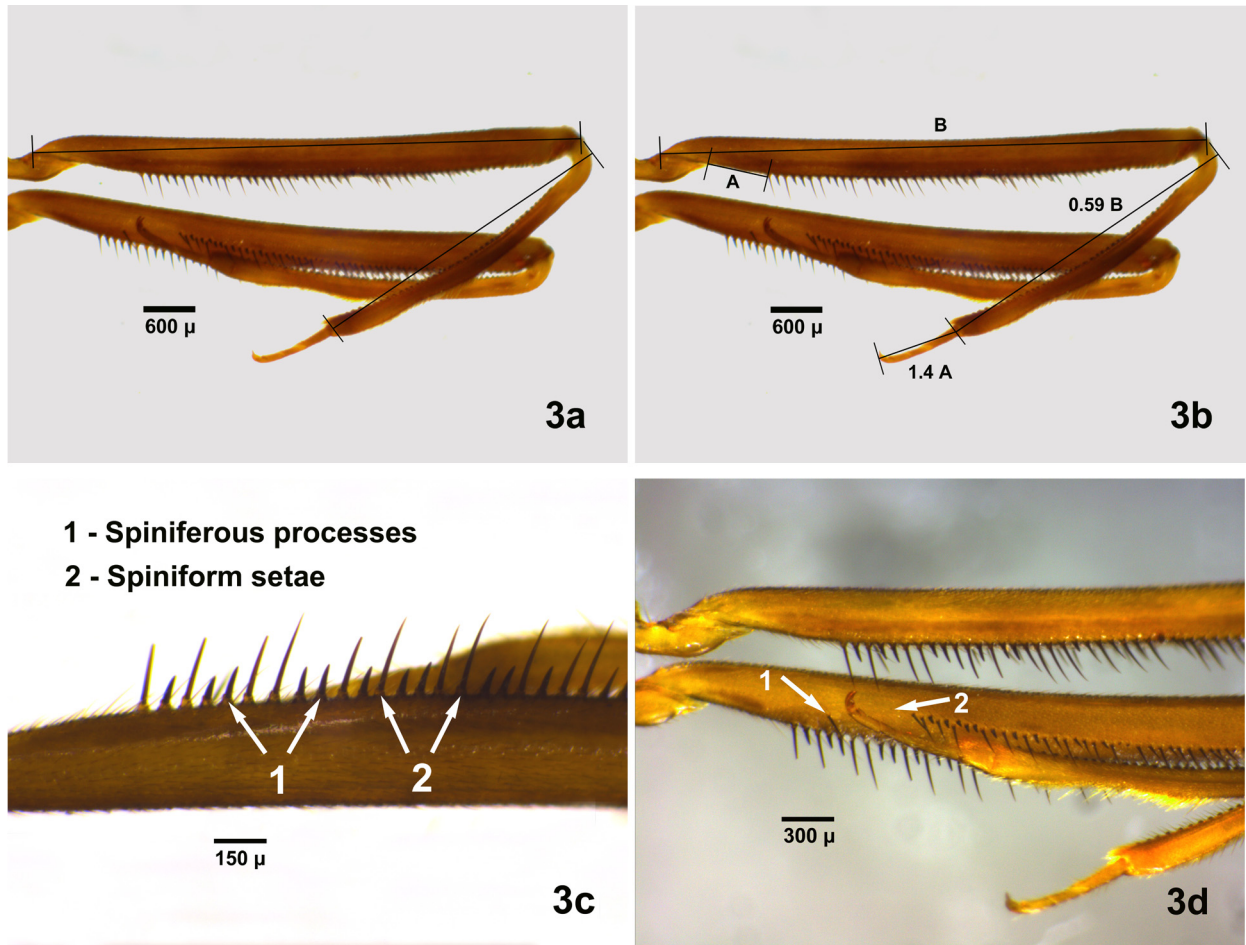


FIGURE 3. *Phasmatocoris labyrinthicus* sp. nov.; male, holotype; forelimb structures; Fig. 3a–ventral aspect of fore-femora showing anterolateral and posterolateral longitudinal rows of spiniferous processes; Fig. 3b–lateral aspect showing lines used for relative length measurements of leg elements discussed in text; Fig. 3c–lateral aspect of fore femur showing armature comprised of spiniferous processes (1; arrows) and spiniform setae (2; arrows); Fig. 3d–lateral aspect of femora showing gap between basal end of anteroventral spine series and isolated basal seta (1; arrow) and gap in spinal series that receives fore tarsus in repose (2; arrow).

Fore tibia 0.59 percent the length of the fore femur (Fig. 3b–0.59B and B); female 0.62 percent. Tibia ventrally with two longitudinal, sub-parallel rows of small, strongly chitinized, apically deflexed, hook-like denticles (Fig. 4a). Each denticle row accompanied laterally by a row of sub-erect bristles. External tibial series continuous, comprised of 38–40 elements, internal series of 16–19 elements interrupted two or three times by relatively long gaps devoid of denticles. Hooks on proximal one or two elements poorly developed. Dorsum of fore tibia with a well-developed linear, calamistrum-like brush distally (Fig. 4b). Brush consisting of clustered stiff, golden bristles that are obliquely and apically inclined. Dorsum of tibia excavated longitudinally at middle of brush, for about half

the total length of the brush (Fig. 4b). Brush with a lateral, parallel auxiliary row of about a dozen setae positioned along the apical 2/3 of the brush (Fig. 4b). Auxiliary setae at least twice the length of the dense brush setae. An isolated small, but dense pre-apical cluster of golden setae, similar to those of the calamistral-like brush, is present on the ventral side of the fore tibia (Fig. 4c). Protibial campaniform sensillae apparently not present.

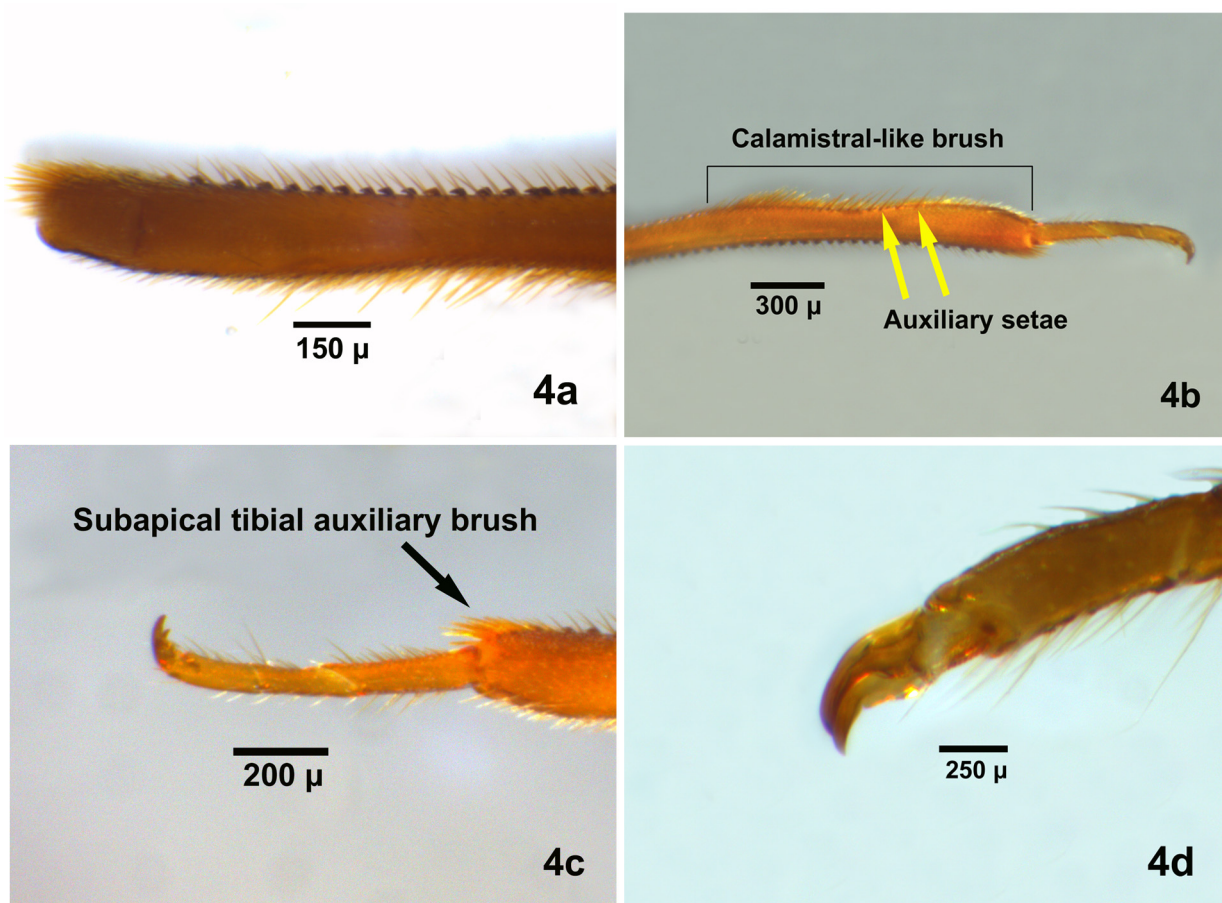


FIGURE 4. *Phasmatocoris labyrinthicus* sp. nov.; male, holotype; additional forelimb details; Fig. 4a–lateral aspect of fore tibia showing ventral, apically deflexed, hook-like denticles; Fig. 4b–calamistral-like setal brush structure on dorsum of fore tibia, with lateral row of auxiliary setae (arrows); Fig. 4c–subapical tibial auxiliary brush; Fig. 4d–foretarsal claws.

Tarsi three segmented, the segments freely articulating (Fig. 4c). Ratios of fore tarsal segments 1–3 using length of first segment as the unit of measure (holotype male 0.266 mm) = 1/0.684/0.876; (paratype female 0.275 mm) = 1/0.622/0.811. Fore tarsus 0.27 percent the length of the fore tibia. Fore tarsi with poorly developed ventral brush of short, golden hairs on all three segments; best developed on segment one. Claws of fore tarsi with a prominent rounded sub-basal projection (Fig. 4d). Ventral lamella poorly developed.

Coxae of middle and hind legs pale yellow, trochanters and femora stramineous, except apex of femora which, along with base of tibiae, are pale yellow. Remainder of middle and hind legs are testaceous. Vestiture as in fore femora consisting of uniformly distributed, short, proclinate hairs. Middle femur nearly attaining apex of abdomen, and hind femur significantly exceeding abdominal apex. Tarsi of middle and hind legs with segments one and two subequal in length and segment three approximately 50 percent longer than either segment one or two (Fig. 5a). Ventral brush present on segments one and two, but even less well developed than on fore tarsi. Claws of middle and hind tarsi with a less well developed basal projection.

Anterior portions of abdomen uniformly pale yellow, posterior edge of segment 7 and all of segments 8 and 9 fuscus. Abdomen keeled laterally and metasternum and abdominal sterna 1–7 slightly carinate medially. Apex of abdomen in lateral aspect similar to that of *P. praecellens*, but with segment 8 slightly longer and pygophore slightly extended dorsally and more rounded posteriorly. Posterior process of pygophore continuous with surface, relatively short and narrow in posterior view, about twice as long as wide and with the tip rounded (Fig. 5b). Parameres of moderate width, slightly widened along their length, with the ends blunt-rounded and the outer angles

very slightly produced, the dorsal corners slightly overlapping, but not fully occluding process of pygophore (Fig. 5c). Phallus not examined. Apex of abdomen of female paratype typical (Fig. 5d), without ventral spine present in *P. xavieri*.



FIGURE 5 . *Phasmatorcoris labyrinthicus* sp. nov.; Fig. 5a—detail of hind tarsus of holotype male showing relative segment proportions differing from foretarsus (Fig. 4c); Fig. 5b—male holotype, postero-dorsal aspect of terminalia showing pygophore process; Fig. 5c—male holotype, postero-lateral aspect of terminalia showing parameres; Fig. 5d—female paratype, lateral aspect of terminalia.

Forewings narrow and rounded apically, attaining apex of abdomen, tucked just under the anterior edge of parameres in male. Discal, basal and subbasal cells, 2.81, 0.86 and 1.36 mm in length respectively (Fig. 6a). Veins stramineous to fuscus. Membrane translucent with minor infuscation of cells in basal half of wing, and less so postero-apically. Hind wing transparent, veins stramineous, cells without infuscation (Fig. 6b). Wings shown in figures are from a paratype female.

Discussion: Due to the presence of spiniferous processes in addition to spiniform setae on the ventral surface of the anterior femora, *P. labyrinthicus* may be most closely related to *P. praecellens* and *P. minor*, the only other species currently known to have that feature. However, Wygodzinsky (1966) suspected another potentially cryptic species among the specimens he included in *praecellens*, which he found not definitively separable by morphologic features. The spiniferous processes in *P. labyrinthicus* are not as robust as those of *P. praecellens*, as shown in Wygodzinsky (1966; figure 86H). Like *P. praecellens*, *P. labyrinthicus* has more than five spiniferous processes in the posteroventral series, but is like *P. minor* in lacking spines on the hind margin of pronotum, which occur on *P. praecellens*. *P. praecellens* is recorded from Panama south to northern South America, while *P. minor* is known only from Argentina. Like *P. labyrinthicus*, both *P. praecellens* and *P. minor* are also arachnophilous species (Wygodzinsky 1966). *P. labyrinthicus* has the portion of the anteroventral series of fore femur situated basad of interruption consisting of a single isolated bristle as in *P. spectrum* and *P. rapax*. The fore tibia in *P. xavieri*, although shorter than in *P. labyrinthicus*, has a similar calamistrum-like structure dorsally, as well as the ventral

pre-apical setal cluster (Gil-Santana et al. 2007; Fig. 6). Because of the presence of these features, *P. xavieri* is suspected to have an arachnophilous association of some kind.

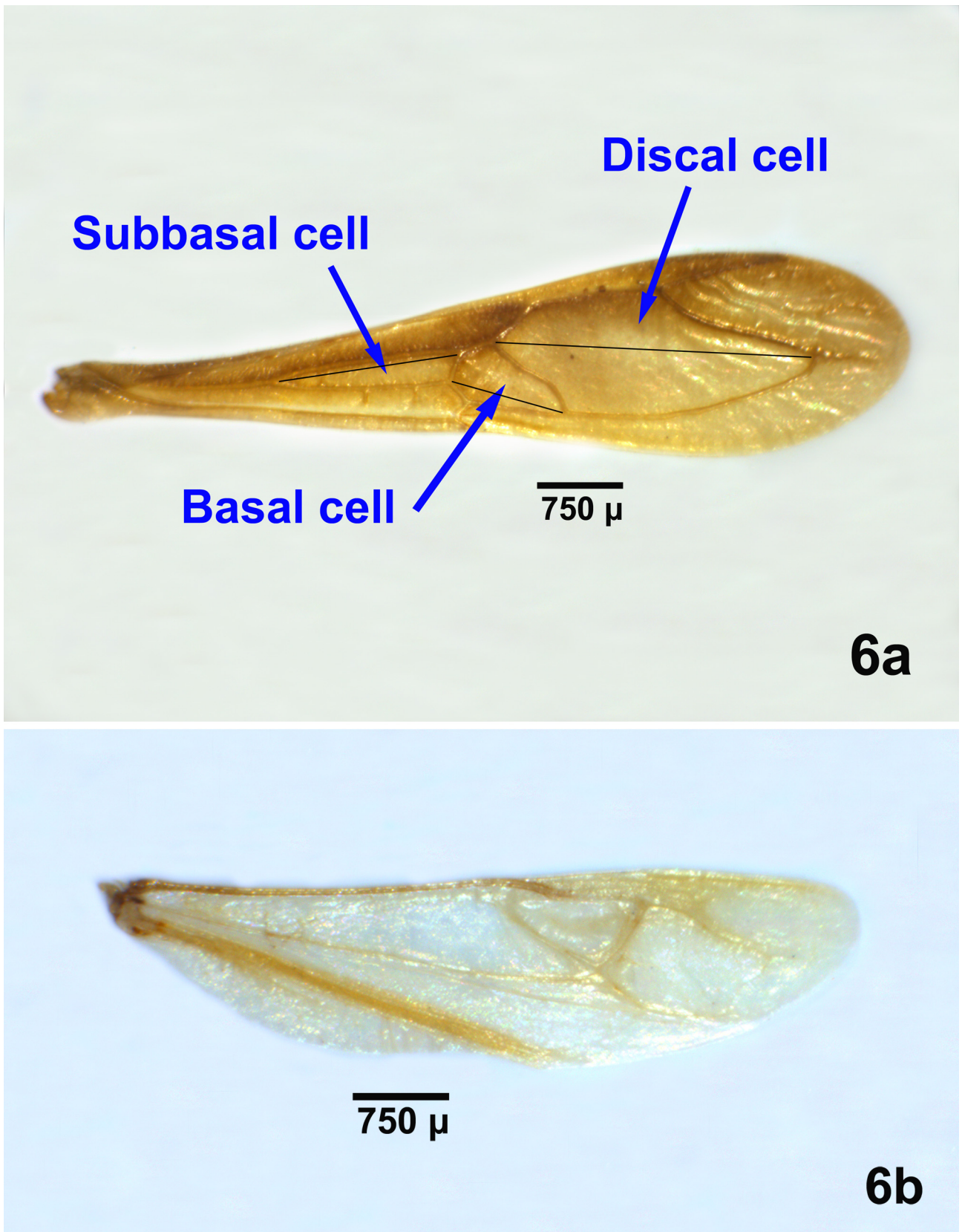


FIGURE 6. *Phasmatocoris labyrinthicus* sp. nov.; Fig. 6a–fore wing; Fig. 6b–hind wing.

A comparative table of the relative position of the calamistrum-like brush on the fore tibia of several emesine species was provided by Wygodzinsky (1966; table 2). The position values in the table were derived by dividing the length of the tibia into 100 units measured from the base of the tibia. The corresponding values for *P. labyrinthicus* are 43–90, which constitutes a brush that is slightly longer than the longest of those given in Wygodzinsky, and significantly longer than the values given for the two listed species of *Phasmatorcoris* (*P. minor*: 60–90, and *P. praecellens*: 70–90). The isolated pre-apical setal cluster of the foretibiae (Fig. 4c) may potentially function, along with the calamistrum-like dorsal brush, in the manipulation of spider silk.

Distribution: *P. labyrinthicus* is known only from the type locality: Kartchner Caverns in Kartchner Caverns State Park, near Benson, Arizona, USA.

Type: Male, and paratype female, American Museum of Natural History (AMNH), New York, New York, USA. The single AMNH accession number for these specimens is 65999.

Material examined: The holotype male and paratype female are currently the only competent specimens of *P. labyrinthicus* available. Three disarticulated specimens (two females and one male) that were sampled as dead individuals were also examined to corroborate the species description. Wygodzinsky (1966) mentioned an undescribed *Phasmatorcoris* from Mazatlan, Mexico. A search for this specimen by the current staff at the American Museum of Natural History in New York, where Wygodzinsky's materials are archived, was unsuccessful, and the determination is that the specimen was either lost or not labeled.

Etymology: the species name *labyrinthicus* is derived from the Greek *labyrinthos*, meaning “a structure of many winding passages”, combined with *-ikos*, also Greek: “belonging to”, in allusion to the labyrinth of passages the animals inhabit in the cave.

Distribution within Kartchner Caverns

P. labyrinthicus is uncommon and localized in the cave. Its distribution appears to be concentrated in proximity to two of the seven known connections the cave has with the surface (Fig. 7). These two surface connections, in the upper Tarantula Room and the Jackrabbit Gallery, are approximately 45 meters apart and are connected by fissures and passage sections, most of which are not negotiable by humans. These areas adjoin the Big Room, which is one of the two large tour sections at Kartchner Caverns. The animals have only rarely been found further than 90 meters distance from these two areas. Since the surface connection in each of these areas is very small there is little air exchanged with the epigeal environment. This results in stable ambient air temperature and relative humidity parameters in this part of the cave. These values are 21.3° C and 96.9 percent respectively in the Jackrabbit Gallery. The small size of the surface connections also limits the movement of animals into and out of the cave to small species such as arthropods.

Two outlier records of the species in the cave, a dead individual found at the Big Room Overlook, and a live animal near the Quartz Divide in the Back Section of the cave during the original study (1990), may be vagrants. The animals may eventually be found in the cave near other surface connections, particularly in the Granite Dells area, where three discrete surface connections have been identified. Should *P. labyrinthicus* be found in Granite Dells, the historic record from the Quartz Divide area would, due to proximity, be reasonably attributable to a distinct sub-population of the species in that part of the cave. All records of the species are from areas within the dark zone of the cave.

Ecology

During the first 11 months of the recent study only dead individuals (all adult) of *P. labyrinthicus* were found in the cave. Using this limited data a concerted effort was made on August 14, 2010 to locate live individuals. A search of the upper portion of the Tarantula Room, above where two of the dead animals were found, immediately revealed several shed skins of juveniles and one additional dead adult. High up in the very upper reaches of the room is a short, narrow fissure passage, where a single live adult male was finally located (Fig. 8). It was tucked beneath a small soil projection that was part of a larger deposit constructed by termites on the limestone bedrock wall. Several termite soil tunnels were also present in the area. The soil tunnels were broken in places, indicating that

they were not currently active. The larger accumulation of soil was left undisturbed, and may have contained termites. It is not known whether the presence of the species in association with termite sign is ecologically significant.

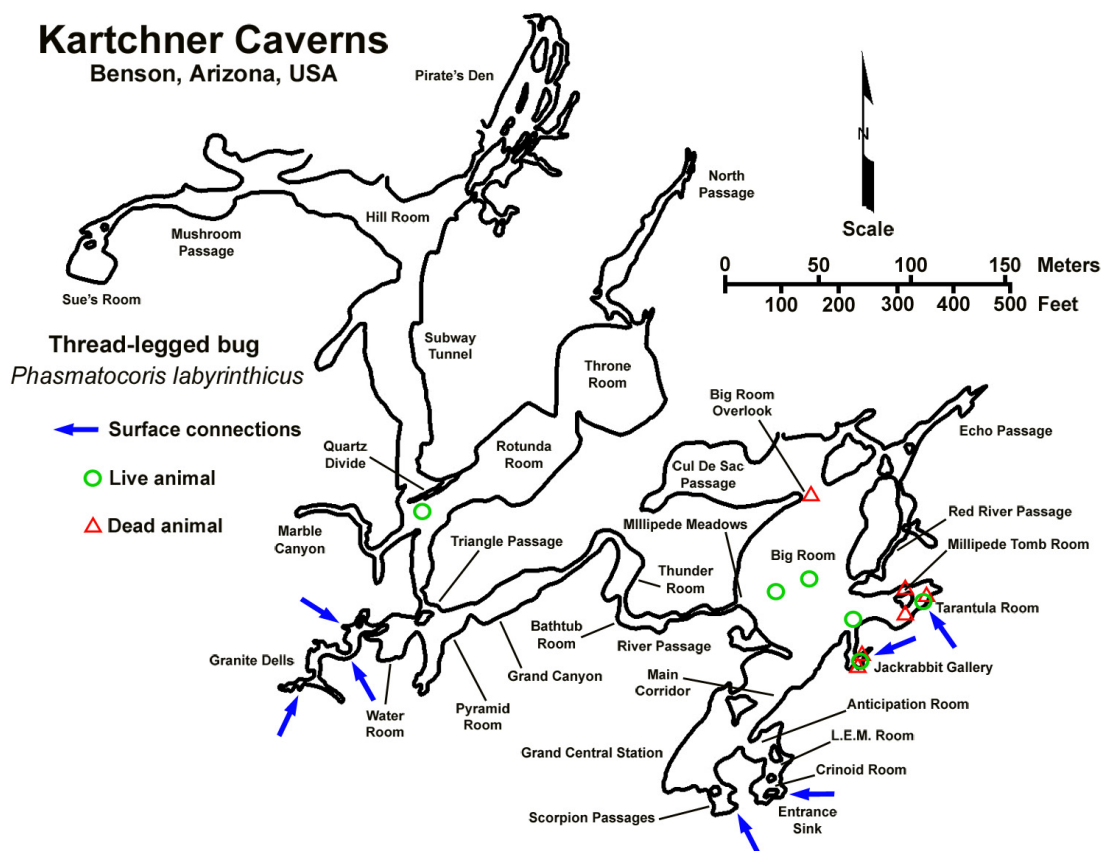


FIGURE 7. Plan map of Kartchner Caverns showing invertebrate-accessible surface connections, and distribution records of *Phasmatocoris labyrinthicus* sp. nov. within the cave.

Carcasses of three species of hymenoptera, all found dead on the floor of the cave directly below where live adult bugs were observed, may be evidence of predation by *P. labyrinthicus*. These included one *Agenioideus biedermani* Banks (Pompilidae) and one undetermined species of Mutillid (or Bradynobaenidae) wasp at the upper Tarantula Room site, and three majors of *Pheidole rhea* (Formicidae) at the Jackrabbit Gallery site. Carcass sizes of the three species were approximately 11, 9, and 4 mm respectively.

The troglomorphic spider *Eidmanella pallida* Emerton (Araneae: Nesticidae) is common in Kartchner Caverns. An adult female *E. pallida* was coaxed into proximity of an adult female *P. labyrinthicus* in the Jackrabbit Gallery on August 14, 2010. The thread-legged bug was stationed on the bedrock wall about three feet above the floor of the cave. The bug appeared to first detect the spider when it approached within about 20 mm. The initial behavior of the bug was defensive, with it shifting its body rearward on its legs as if preparing for retreat, and then slowly stepping backwards a short distance. However, when the spider came into proximity with the bug it appears to have touched the middle left leg of the bug with its front right leg. This stimulated a strike response by the bug. The bug initially grasped the spider from the front with each of its raptorial forelegs securing multiple legs on each side of its prey (Fig. 9). The bug then pierced the coxal-prosomal junction of leg III (left) of the spider dorsally with its rostrum. During feeding the bug re-inserted its rostrum several times and occasionally made minor readjustments to its grasp of the spider. Multiple rostral penetrations and manipulation of prey during feeding have been reported for other emesines (Wignall and Taylor 2008; 2010; Soley et al. 2011). Subsequent rostral penetrations used during the observed feeding event included (in sequence): dorsum of coxal-prosomal junction of leg I (right); ventral aspect of coxal-trochantal junction of leg IV (right); and the anterior part of the sternum..

Many emesines are arachnophilous, either as predators (arachnophagy), or as kleptoparasites, where prey captured in spider webs are stolen (Wygodzinsky 1966; Soley et al. 2011). Some emesines have evolved morphologic features that enhance these associations. One adaptation is expressed as variations in the form of the tarsal claws that are modified for walking on, and possibly also manipulating, spider web strands. *P. labyrinthicus* does not possess such structures on the tarsal claws. Several species have developed an obliquely inclined series of stiff bristles on the dorsal surface of the fore-tibia that are reminiscent of the calamistrum structure on the metatarsi of the hind legs of cribellate spiders (Wygodzinsky 1966). The spider calamistrum is used for combing silk from the cribellum (silk spinning organ), located on the underside of the abdomen anterior to the silk producing spinnerets (Comstock 1940; Ubick et al. 2005). Wygodzinsky (1966) postulated that this evolved structure may serve a comparable silk-manipulating function in emesines. *P. labyrinthicus* has a well developed calamistrum-like structure on the dorsum of its fore-tibiae (Fig. 4b). How this structure is used is not understood, but some association with manipulation of spider silk seems probable. The extremely long legs present in some emesines are certainly advantageous in arachnophilous associations. In addition to facilitating web-walking by distributing the weight of the animals on webs, they also function in keeping the resident spider distant from vital body parts when the bugs are in occupied spiders' webs. However, elongated legs are not necessarily or exclusively an arachnophilous adaptation. Many non-arachnophilous emesines have very long legs, including the free-living *Mayemesa paraensis* Wygodzinsky, which has the proportionally longest legs of any known emesine. And in contrast, some arachnophilous *Stenolemus* Signoret have relatively short legs (Wygodzinsky 1966).



FIGURE 8. Holotype male in habitus in the Tarantula Room, Kartchner Caverns State Park, August 14, 2010.

There is evidence that *P. labyrinthicus* may at least occasionally use spider webs to set up prey capture. While recording a video of the first live adult encountered during the recent study, the animal was observed to circumvent remnants of a spider web that had been constructed within a small (approximately 10 cm diameter) vug in the bedrock wall of the cave. At first it appeared that the animal was avoiding the web, but when it reached the back of the vug it stopped, turned around and proceeded to manipulate silk strands at the periphery of the web. First, it briefly used its left middle leg to move or hook a silk strand, followed by initially hooking a strand located further out with both forelegs. It then performed minor manipulation of another strand with its middle right leg. Both hind legs were apparently the primary anchors for the animal as it performed these maneuvers with its two front pairs of legs. Without moving its anchored hind legs it then swiveled its body counterclockwise about 35 degrees, reached out and grasped another strand(s?) with both forelegs and drew the strand(s?) towards itself as if drawing a bowstring. Once the forward strand(s?) was retracted the animal repositioned its left rear leg and then straightened its body such that there was a uniform alignment of its legs on either side of its body. While maintaining the tension on the forward strands with its forelegs it proceeded to vigorously pump its right rear leg as if to re-secure that anchor point. The animal then remained motionless, apparently set up to await prey that might wander within range. This behavior could represent the construction of a crude snare, but it seems more likely to be the use of a tensioned signal line that alerts the animal to the presence and location of incipient prey. However, the dead spider wasp (*A. biedermani*) found directly below this animal was partially entangled in a few strands of spider silk, and was not wrapped in a manner characteristic of that used by many spiders. The remnants of the web manipulated by the bug appeared to be old, were not attributable to a particular kind of spider, and no spiders were observed in the area. It was not possible to determine from the video whether the calamistral-like brush on the dorsum of the foretibiae of the animal were used in manipulation of the silk strands.

Since the interpretation of this behavior is based on a single episode, it is not known whether this is common behavior for the species, or whether the animals opportunistically utilize old spider webs when they are available. Spiders fabricate their webs in areas where prey are anticipated, and the thread-legged bug may associate the presence of spider webs or their remnants with habitat where invertebrate prey are likely to occur. Use of spider web remnants by *P. labyrinthicus* could be an important element of the prey capture behavior of the species in the totally dark cave environment. Additional study is needed to better understand this behavior.

Most of the spider species present in Kartchner Caverns do not occur in habitat occupied by *P. labyrinthicus*, and the few that do are small, and seem unsuitably matched for an ecological association with the species. The best potential araneid match for *P. labyrinthicus* in the cave would seem to be the pholcid spider (*Physocyclus* sp.), which occurs only in the driest of the cave's entrance areas. *P. labyrinthicus* has so far not been found in this area of the cave, and its apparent absence there is tentatively attributed to the lower humidity in that area. Precedents for arachnophilous associations of emesines with pholcid spiders are recorded for the Australian species *Stenolemus giraffa* Wygodzinsky, which feeds on a variety of spiders, but primarily species in the pholcid genus *Trichocyclus* Simon (Soley et al. 2011), and *Stenolemus bituberus* Stål, which feeds on a variety of spiders, including *Pholcus phalangioides* Fuesslin (Wignall and Taylor 2008).

Other arachnophilous emesines are associated with species of *Achaearana* Strand (Hodge 1984; Wignall and Taylor 2009; 2010). We have a single species of this genus that occurs in the cave (*A. canionis* Chamberlin and Gertsch), but like the *Physocyclus* sp., it occurs only in the relatively dry habitat near the main cave entrance. Because of this, it too is thought to not be a good candidate for an arachnophilous association with *P. labyrinthicus*.

Study of the ecology of *P. labyrinthicus* is aggravated by the apparently small population of the species in the cave. The animal has the calamistrum-like modification of the fore-tibiae, has been observed manipulating old spider silk, and was offered and took a single spider (*E. pallida*) that is a common troglophile in the cave. We do not know if the bug currently has an arachnophilous association with a particular spider species in the cave. The arachnophilous morphology and silk manipulating behavior of the species may be holdovers from earlier times, when the animal may have been associated with a specific spider species either in the cave(s), or in a non-cave, epigeal habitat.

The only previously known cavernicolous emesine with an identified arachnophilous association is *Bagauda cavernicola* reported from India, Malaysia (Malaya), and Sri Lanka (Paiva 1919; Wygodzinsky 1966; Capriles 1990). The record of *B. cavernicola* from Malaysia is apparently in error. On page 54 of his 1966 monograph Wygodzinsky cites Kemp (1924) as a reference for *B. cavernicola* occurring in Batu Cave, Malaya (Malaysia). This should actually be Siju Cave in India (see Paiva 1919 and Kemp in Kemp and China 1924). On page 97 of the

monograph Wygodzinsky correctly lists *B. cavernicola* as occurring in Assam, India, and on page 98 lists *B. lucifugus* McAtee and Malloch as the *Bagauda* present in Batu Cave (Wygodzinsky 1966).

Unlike *P. labyrinthicus*, *B. cavernicola* apparently does not have the tibial modification present in some arachnophilous emesines (see figure 3 in Paiva, 1919). Its arachnophilous association may be strictly predatory with no significant behavioral involvement with the spider web structure. *B. cavernicola* is recorded feeding on the cosmopolitan, troglophilous *Nesticodes (Theridion) rufipes* Lucas (Theridiidae) in Siju Cave near Assam, India (Kemp and China 1924). Interestingly, the population of *B. cavernicola* in Siju Cave is sympatric with a second emesine (*Myiophanes kempii* China) in the cave, with both species occurring in the dark zone at a depth of 400–500 feet (122–125 m) from the entrance (Kemp and China 1924). The only other cave known to support two emesine species is Dark Cave, of the Batu Caves in Selangor, Malaysia, where *Bagauda lucifugus* and *Myiophanes fluitaria* McAtee and Malloch coexist (Wygodzinsky 1966; McClure et al. 1967).

P. xavieri also appears to have a calamistrum-like brush of stiff bristles on the dorsum of the fore-tibiae (Gil-Santana et al. 2007; Fig. 6), which suggests that it may also have an arachnophilous association of some kind. The ecology of *P. xavieri* has not been studied.

No predation of *P. labyrinthicus* has been observed. The only predator that regularly occurs in areas of the cave occupied by the species, and that could effectively capture the bugs, is the endemic vaejovid scorpion *Pseudouroctonus* nr. *apacheanus* Gertsch & Soleglad. There are several spider species recorded from the cave, but they either rarely co-occur with the bugs, or are small enough to present a threat only to small juveniles. *E. pallida* does co-occur with *P. labyrinthicus*, but even adult females of this spider are likely to prey only on small nymphs.



FIGURE 9. Female *P. labyrinthicus* with prey; an adult female *Eidmanella pallida* (Araneae: Nesticidae) in the Jackrabbit Gallery on August 14, 2010.

Advanced troglomorphy in emesines is uncommon, and is apparently limited to a few species, notably those in the lava tube caves of the Canary Islands and Hawaii discussed previously. Few of the cave-inhabiting species, even those apparently successfully troglophilic in the dark zones of caves, exhibit any obvious morphological adaptations associated with their existence in caves. Indeed, some species that live in the dark zones of caves, and

are known only from caves, for example *Bagauda cavernicola*, are colored or patterned similar to many epigeous species (see plate 36; figure 3 in Paiva 1919), and would intuitively seem to not belong in caves. One exception is an undescribed emesine from Wind Tunnel Cave in Australia, which has small reddish eyes (Clarke 2010; fig. 6). All of the obviously morphologically adapted cave emesines currently known occur in lava tube caves. *P. labyrinthicus*, as a cave-inhabiting species, has in common with *P. xavieri* a relatively uniform, generally pale overall coloration. This character may reflect the fact that these species live in caves (Gil-Santana et al. 2007).

P. labyrinthicus has fully developed wings and is probably capable of flight. However, the animals seem reluctant to fly even when threatened, preferring to walk away from perceived danger. They also have retained well-developed eyes and it is assumed that they are fully sighted. Their only morphologic feature that hints at an onset of troglomorphic features is their somewhat light coloration.

Phenology

No eggs of the species have been found in the cave. Single nymphs of *P. labyrinthicus* were observed in the cave on three occasions; January 3, June 11, and September 24, 2011. The first nymph observed was in its third or fourth instar. The second observation five months later on June 11th (Fig. 10) was a fifth (final) instar individual (wing buds were present). The first two observations may have been the same animal. The third nymph was about 5 mm in length, and was probably in its second instar. All nymphs were found in close proximity to the cave side of the Jackrabbit Shaft door. This is also where two adult females were found on August 14, 2010.

A total of six shed exuviae of the species have been found in the cave, all in the upper portion of the Tarantula Room (Fig. 11). Some of the exuviae were the same size, possibly indicating the presence of more than one juvenile of the same age concurrently. Or, they may represent individuals from multiple generations since the residual time of such remains in that part of the cave is quite long. The concentration of the animals and their sign in the upper Tarantula Room-Jackrabbit Gallery area suggests that this area is the core of the population of the species in the cave (Fig. 7). Live adults have so far been observed only in June and August.



FIGURE 10. Fifth instar *P. labyrinthicus* in the Jackrabbit Gallery on June 11, 2011. Arrow shows wing buds.

Based on the limited observations to date, the species is suspected to be univoltine with the animals reaching the adult stage just prior to the summer monsoon rains. An increase in arthropod populations in response to the summer rains, including those that may accidentally or otherwise enter the cave, may provide prey adequate to support annual reproduction of *P. labyrinthicus*. This could explain why the animals seem to be concentrated in

areas of the cave near surface connections. Alternatively, reproduction may be opportunistic, but still dependent on prey availability whenever it occurs.

Ecological Group—Status of *P. labyrinthicus*

Welbourn (1999) stated that individuals of the species “...were found in several widely separated areas (of the cave) in 1990”, and provided a distribution map in an unpublished report to ASP showing three locations where the animals were observed (Welbourn 1992). These original records are included in the location data in Fig. 7 (center of the Big Room and at the Quartz Divide). It is assumed that each observation reported in the original study represents a single animal. No comment was made on the age classes of any of the observed animals. The small number of sightings and the (assumed) presence of only adults in the cave at the time of the original study would intuitively lend credence to the idea that the species might be an accidental in the cave. However, observations of the species in several areas of the cave, including areas remote from surface connections, seems unlikely to be consistent with an accidental status for the species. The presence of the species in the cave spanning twenty years is also inconsistent with an accidental association.

The animal found by Welbourn in the Back Section of the cave was seen near the Quartz Divide (Fig. 7). The animal was presumed to have reached the Back Section by traversing the Triangle Passage from Granite Dells, where we currently know of three discrete surface connections accessible to invertebrates. The distance from the Quartz Divide to the closest of these surface connections is about 100 meters. Thread-legged bugs are not strong fliers, and flight in caves is commonly problematic due to lack of light, passage constrictions, and obstacles. These factors all make the presence of the species relatively deep in the cave problematic for an accidental. However, this is only a single record, and the sighting could be anomalous, representing a vagrant individual. All but one recent record (20 animals) of the species to date (both live and dead animals) are within approximately 30 meters of a surface connection. The furthest recent record from an entrance, at about 90 meters, was a single dead adult found near a floodlight at the Big Room Overlook. Whether this animal walked to that location, or was attracted by the light and flew there, is unknown. This record could also represent a vagrant individual.

Thread-legged bugs are commonly attracted to lights at night. In an effort to confirm that *P. labyrinthicus* is a cave-limited species, ultraviolet (UV) spectrum night lighting was performed near the original cave entrance in late summer of 2011 and 2012, during the summer monsoon season. Dates selected were within the known activity period of the adults in the cave. Nights with no visible moon were selected since the diffuse light of the moon affects nighttime invertebrate activity and competes with the UV lights. Lights were set up on the concrete tram driveway approximately 16 meters northeast of the original cave sink entrance. Presuming that the species is still capable of flight, this distance should be well within the response distance for the insects. The lights were operated for a total of 4.5 hours on two days; August 26, 2011 and August 17, 2012. Weather conditions during the night lighting efforts were considered optimal for potentially attracting the species. None of the animals were found at the lights on either night. While this limited night lighting effort to locate the animals outside of the cave is not by itself conclusive, it does provide evidence that the species may not occur in epigeal habitat. Additional night-lighting efforts should be performed to search for *P. labyrinthicus* elsewhere in the Park, particularly in proximity to other cave surface connections. This will help in confirming the suspected troglotic association of the species.

Environmental change and *P. labyrinthicus* through time

Due to its disjunct distribution from its nearest relative, *P. labyrinthicus* is the geographical outlier of the genus. All other known species of *Phasmatocoris* are Neotropical, but within that region the genus has a good representation in a variety of habitats from dense rain forest, to semidesert, and in caves (Wygodzinsky 1966; Gil-Santana et al. 2007). Regional desertification (drying and warming) of the northern Chihuahuan and Sonoran desert climates began at the end of the Wisconsin glacial episode about 11 kya, and reached its current condition about 4 kya (Van Devender 1990). Prior to that time the area where Kartchner Caverns is located was somewhat cooler and more mesic. Considering that *P. labyrinthicus* seems to prefer the more humid portions of the cave, and is apparently not present near the main cave entrance where conditions are drier, its historic habitat may have been humid rather than

the current arid condition of the epigeal environment. During more mesic times the species may have simultaneously occupied epigeal habitats and cave entrance areas. Upon effective desertification of the region, only the cave population(s) of the species likely remained. *P. labyrinthicus* is likely a relictual population of a once more wide-spread species.

The current drought in the southwestern U.S. has been ongoing for about 14 years (having begun in about 1999; Breshears et al. 2005), and the region may be on the cusp of a significant, anthropogenic-derived permanent change in climate to a warmer and possibly even more xeric habitat (Diffenbaugh and Scherer 2011; Fawcett et al. 2011; Seager et al. 2007).



FIGURE 11. Nymphal exuviae of *P. labyrinthicus* found on a vertical surface in the upper Tarantula Room (August 14, 2010). The head is pointed downward and the dark forelimbs are folded posteriorly beneath the body.

Summary

Only three cavernicolous thread-legged bugs were previously known in the Americas; *Phasmatorcoris xavieri* from Brazil; *Ploiaria umbrarum* McAtee and Malloch from Jamaica; and *P. maya* Wygodzinsky from Yucatan (Wygodzinsky 1966). *P. labyrinthicus* is the fourth and northernmost cavernicolous emesine in the New World (latitude of 31° 50'). *P. labyrinthicus* seems to be a geographic outlier of the genus, occurring in a geologically recent desert, and far from the more typical tropical affinity of its congeners. The population may be relictual, a hold-over from more mesic times, when the species may have also occupied non-cave habitats in the region.

The single previously known cavernicolous species that also has an arachnophilous association is *Bagauda cavernicola* reported from India and Sri Lanka (Paiva 1919; Wygodzinsky 1966; Capriles 1990). Unlike *P. labyrinthicus*, *B. cavernicola* is not morphologically adapted to its arachnophilous association. *B. cavernicola* is recorded feeding on the cosmopolitan, troglophilous *Nesticodes (Theridion) rufipes* (Theridiidae) in Siju Cave at Assam, India (Kemp and China 1924). The precise nature of the arachnophilous association of *P. labyrinthicus* is currently poorly understood.

A significant accumulation of evidence supports, at minimum, a troglophilic habit for *P. labyrinthicus* in Kartchner Caverns. Observations include the presence of shed skins, live juvenile animals, induced feeding on indigenous prey (*E. pallida*) and the presence of carcasses of apparent insect prey at locations occupied by the bugs. There is currently no evidence that the animals ever leave the cave, and they are considered unlikely to disperse to other similar habitats regionally due to the harsh desert climate that has existed in the area for the last 12–10 ka. *P. labyrinthicus* occurs only in humid portions of the cave and avoids drier areas that otherwise seem suitable for the species. If the animals are intolerant of low-humidity environments they may effectively be confined to the cave, in which case the population would be considered troglobitic by default. A lack of obvious morphological adaptations to a cavernicolous existence in the species may be the result of an assumed relatively short duration of the species as a permanent resident in the cave, that is, since the regional desertification of 12–10 ka. Prior to desertification, gene flow between epigean and cave inhabiting individuals of the population would have precluded an evolved morphology for a cavernicolous existence.

Development of Kartchner Caverns as an Arizona State Park required that artificial access to the cave be created to facilitate moving tours into and out of the cave. One of two adits driven into the hill (the Tarantula Tunnel) entered the cave in what we currently consider to be the population center of *P. labyrinthicus* in the cave. The species was considered rare in the cave when the original inventory was conducted over 20 years ago. The status of the species appears to be unchanged, and the development of the cave does not appear to have adversely affected the species. The intermittent operation of the tour lights in the cave could have potential implications for the species if the animals are still volant. The animals could be attracted to the tour lights and fly a considerable distance outside of their normal range in the cave. This could potentially affect their access to localized resources on which they depend. However, at the current time the population of *P. labyrinthicus* at Kartchner Caverns is considered stable and secure, and if the tour lights do have a deleterious effect on the species it is apparently not of consequence at a population level.

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