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FIRST TROGLOBITIC WEEVIL (COLEOPTERA: CURCULIONIDAE) IN NORTH AMERICA? DESCRIPTION OF A NEW EYELESS SPECIES OF *LYMANTES* SCHOENHERR FROM CENTRAL TEXAS CAVES

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ABSTRACT

Recent bio-inventories carried out in Texas caves have led to the discovery of an eyeless weevil *Lymantes nadineae* Anderson, new species (type locality: Texas: Williamson County, Electro-Mag Cave). The species is known only from three specimens from three caves despite intense sampling efforts carried out in a geographic region characterized by narrow endemism of troglobitic animals. *Lymantes nadineae* clearly shows troglobitic adaptations such as complete loss of eyes, reduced pigmentation, and increased length of appendages. The lack of collections on the surface does not exclude the possibility that it is an edaphobite species, but more likely, *L. nadineae* is the first North American troglobitic weevil. Probable evolutionary scenarios hypothesize that *L. nadineae* is a troglobite that has been isolated from its surface ancestor and that survives on roots found on ceilings of shallow caves. The closest known relative appears to be *L. scrobicollis,* a surface species occasionally found in the entrances of caves occurring on the eastern side of the continent, rather than an undescribed species that has recently been collected in leaf litter and at least one cave entrance in Central Texas. *Lymantes nadineae* is likely one of the rarest beetles of North America.

RESUMEN

Los inventarios biológicos recientes realizados en las cuevas de Texas han conducido al descubrimiento de un gorgojo ciego *Lymantes nadineae* Anderson, especie nueva (localidad tipo: Texas: Condado Williamson, Cueva Electro-Mag). La especie se conoce solamente de tres especimenes provenientes de tres cuevas a pesar de los intensos esfuerzos de muestreo realizados en una región geográfica caracterizada por el endemismo de animales troglobios. *Lymantes nadineae* demuestra troglomorfismos tales como pérdida completa de ojos, pigmentación reducida, y alargamiento de los apéndices. La falta de colecciones en la superficie no excluye la posibilidad que sea una especie edáfica, pero lo más probable es que *L. nadineae* sea el primer gorgojo troglobio de América del Norte. El probable escenario evolutivo hipotetiza que *L. nadineae* es una especie troglobia que se ha aislado de su ancestro en la superficie y que sobrevive en las raíces encontradas en los techonadinaes de las cuevas bajas. El pariente más cercano parece ser *L. scrobicollis*, una especie de la superficie encontrada ocasionalmente en las entradas de cuevas en la región oriental del continente, y no una especie sin describir del centro de Texas que se ha colectado recientemente en hojarasca y por lo menos una entrada de cueva. Los *Lymantes nadineae* son probablemente uno del escarabajo más raro de América del Norte.

INTRODUCTION

Central Texas caves have been the object of bio-inventories for about 40 years, and are now known to

harbor one of the richest and most distinctive cave faunas in North America and in the world (Culver, et al., 2003, 2006). More than a thousand cavernicolous taxa have been recorded from the state (Reddell, 1994), including 160 obligatory cave-inhabiting species known in 2008 (J. Reddell, pers. comm.). Such troglobitic species are found in many taxonomic groups, but impressive radiations are well-known for arachnids and Coleoptera, particularly Carabidae (*Rhadine* of the *R. subterranea* group, see Barr, 1974; Reddell and Cokendolpher, 2001, 2004) and Staphylinidae: Pselaphinae (*Batrisodes,* see Chandler, 1992; Chandler and Reddell, 2001; Chandler, et al., 2009). In the last 10 years, the caves of certain areas have been intensely monitored because of conservation issues involving endangered troglobitic species threatened by urban development (see Longacre, 2000; Paquin and Hedin, 2004). Despite important sampling efforts, several of these species are known only from a few specimens or have not been seen since their original collection. Such rarity and/or sampling difficulties result in obvious management problems because of incomplete distributional data, but also demonstrate that knowledge of the diversity is still fragmentary. The distribution and biology of most troglobites remain to be better understood and discoveries of new entities are still likely.

Eyeless weevils are scarce but reported from every continent, except Antarctica (Osella, 1979; Kuschel, 1990). In North America, they are known only from the states of California and Oregon on the west coast and the extreme south of Florida (Osella, 1979; Morrone, et al., 2001). Most eyeless weevil species are associated with deep soil and leaf litter (Gilbert, 1956; Howden, 1992; Osella, 1977, 1989), and are usually collected by sifting and washing deep humus or soil (Morrone, et al., 2001). None of the North American eyeless weevils are cave obligates although leaf litter inhabiting species with reduced eyes are sometimes collected in cave entrances. The present paper describes a new eyeless weevil known from three Texas caves, hypothesized to be a troglobite rather than an edaphobite. The tenuous distinction between troglophiles and troglobites is addressed, particularly for Texas Coleoptera, and evolutionary scenarios concerning the existence of what appears to be the first troglobitic weevil in North America are briefly explored.

METHODS

Specimens were collected in cave bio-inventories and preserved in 80% ethanol. These were air dried and mounted on a point for morphological examination and description. They were examined with a WILD M5 stereoscope at magnifications of up to 200X. Dissections were made by gently boiling the specimens in water with subsequent separation of the abdomen and placement of the latter in hot 5-10% KOH solution to clear away musculature. Habitus photographs were taken using Automontage™. For other illustrative purposes, specimens were examined under a SMZ-U Nikon dissection microscope. A Nikon Coolpix 950 digital camera attached to the microscope was used to take photographs of the different structures to be illustrated. The digital photo was then used to trace proportions, and the illustration was detailed and shaded by referring back to the

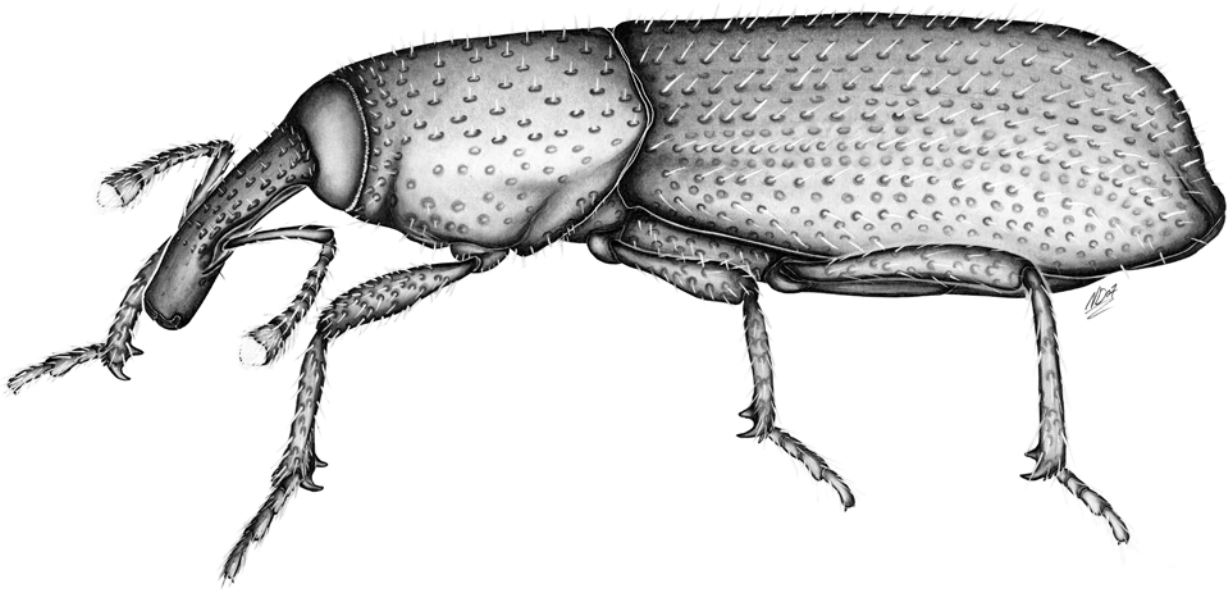


Fig. 1.-Female allotype *Lymantes nadineae*, n.sp., habitus.

specimen under the microscope. Genitalia were photographed and illustrated under an AmScope XSG Series T-500 compound microscope as explained above. Specimens are deposited in the Canadian Museum of Nature (CMNC), Ottawa, Canada, and the Texas Memorial Museum, The Universitty of Texas at Austin (TMMC).

TAXONOMY

Family Curculionidae
Lymantes Schoenherr

Lymantes nadineae **Anderson**, new species
Figs. 1-6

Diagnosis.—Eyes fully lacking, with no external trace of eye facets or ocular swelling (Fig. 1). Punctures of body generally small, widely spaced, those of pronotal disc shallow, small, widely spaced, the distance between punctures much greater than diameter of a puncture (Figs. 2-4). Punctures of striae of elytral disc small, shallow, and linearly arranged, intervals distinct, much wider than width of a strial puncture, disc with more or less 30 punctures along each complete strial length. Dorsal vestiture short and very fine, each seta about as long as basal puncture. Legs long and spindly, hind femora about 6X as long as wide, apex reaching slightly beyond suture between ventrites 2 and 3. Aedeagus as in Fig. 5.

Type-data.—Holotype male (CMNC), Texas: Williamson County, Electro-Mag Cave, 27 Dec. 2006 (P. Paquin, C. Crawford, K. White), found dead on a flowstone. Allotype female (CMNC), Texas: Travis County, Tooth Cave, 19 May 1965 (T. C. Barr). Paratype female (TMMC), Texas: Williamson County, Phraetica Cave, 20 June 2002 (M. Warton).

Etymology.—This species is named after Nadine Dupérré for her outstanding contributions to systematics in providing many taxonomists with beautiful illustrations to describe and document arthropod diversity.

Description.—Male, length 3.5 mm, width 1.1 mm. Color pale orange brown throughout. Head globose, minutely finely punctuate. Eyes fully lacking, ocular swelling not evident. Rostrum with antennae inserted slightly beyond apical third of length, slightly wider in dorsal view beyond antennae insertion, scrobes narrowly visible at point of antennal insertion in dorsal view. Rostrum about 0.7X length of pronotum, slightly arcuate in lateral view, dorsally moderately deeply, moderately densely punctuate, punctures separated by about their own diameter, row of punctures above scrobe coalescent, forming shallow groove. Ventrally irregularly punctulate, most punctures coalescent, with median posterior extension represented by narrowly separated lateral cariniform ridges, extended to base of rostrum. Antennae with scape almost reaching base of rostrum, funicle with articles 1 and 2 elongate, subequal in length, articles 3-6 monilliform, article 7 longer and wide and wider towards apex. Pronotum with width about 0.7X length, lateral margins slightly arcuate, widest at about midlength, subapical constriction not evident dorsally, distinctly impressed laterally, bordered posteriorly by 2-3 crenulae, disc with punctures shallow, small, widely spaced, distance between punctures much greater than diameter of a puncture, each puncture with small, fine erect seta. Elytra about twice as long as wide, lateral margins subparallel from behind humeri to apical fourth, humeri not pronounced, disc with striae with small, shallow and linearly arranged punctures numbering about 30 per complete discal stria, intervals impunctate, shining, much wider than width of a strial puncture, punctures each with fine, very short erect seta. Striae 1-6 complete to base, 7 and 8 fused opposite metacoxae, not continuous to base, stria 10 terminated opposite metacoxa. Venter uniformly shallowly, sparsely, regularly punctuate, punctures well-spaced, except punctures larger, deeper and more closely spaced on ventrite 5. Abdominal ventrites 1 and 2 very long, each about as long as ventrites 3-5 combined, ventrites 3 and 4 very short, subequal in length, ventrite 5 about twice as long as 3 and 4 combined. Legs sparsely shallowly punctuate, punctures well-spaced, long and slender, femora extended slightly beyond suture between ventrites 2 and 3, about 6X as long as wide, tibiae straight, slender, about 3/4 as long at femora. Tarsi slender, ventrally with a few scattered setae, tarsal claws absent (broken?). Aedeagus with body short, very slightly longer than wide; internal sac present with extensive internal sclerotization in form of a pair of basal arciform sclerites one (darker) situated more dorsally, distally with pair of laterally situated helical (twisted) band-like sclerites surrounding an irregularly shaped median apical complex; struts long, about 3X length of aedeagal body.

Female differing from male as follows. Female, length 3.8-4.2 mm, width 1.25-1.30 mm. Rostrum with antennae inserted slightly proximad of apical third of length. Pronotum more elongate, width about 0.6X length, individual punctures less evident, particularly on disc. Elytral striae not as deeply impressed. Tarsi with claws. Female not dissected.

Distribution.—Known only from two caves in Williamson County, and one in Travis County, Texas (Fig. 6).

Comments.—Sleeper (1965) and Howden (1992) were the last authors to treat *Lymantes*. Sleeper redescribed *L. scrobicollis* Gyllenhal and *L. puteolatum* (Dury), and described two new species and one subspecies. Howden's review consisted of a condensation of Sleeper's treatment, with some new distributional data. No dissections of genitalia were made by these authors.

In addition to *L. nadineae* described herein, two undescribed species are also known: one from the Edwards Plateau (and surrounding regions) of Central Texas, and one from the Davis and Guadalupe Mountains of West Texas. Additional specimens recently collected throughout the southeastern United States need to be assigned to species. The treatment of Sleeper (1965) needs reconsideration using additional morphological characters as well as characters of genitalia. A preliminary assessment suggests that all eastern specimens may be members of a single, widely distributed species, which would go under the name *L. scrobicollis* Gyllenhal. The genus is currently under revision by R.S.A.

The three known specimens of *L. nadineae* collected in different but proximal caves, are here considered conspecific, being the only known *Lymantes* that fully lack any external traces of eye facets and an ocular swelling as well as sharing the unique feature of smaller, shallower and more widely spaced body punctation and longer dorsal vestiture. Among other *Lymantes*, only *Lymantes scrobicollis* Gyllenhal (known from "Am. Borealis") is noted as lacking eye facets although a distinct ocular swelling was noted (Sleeper, 1965; Howden,





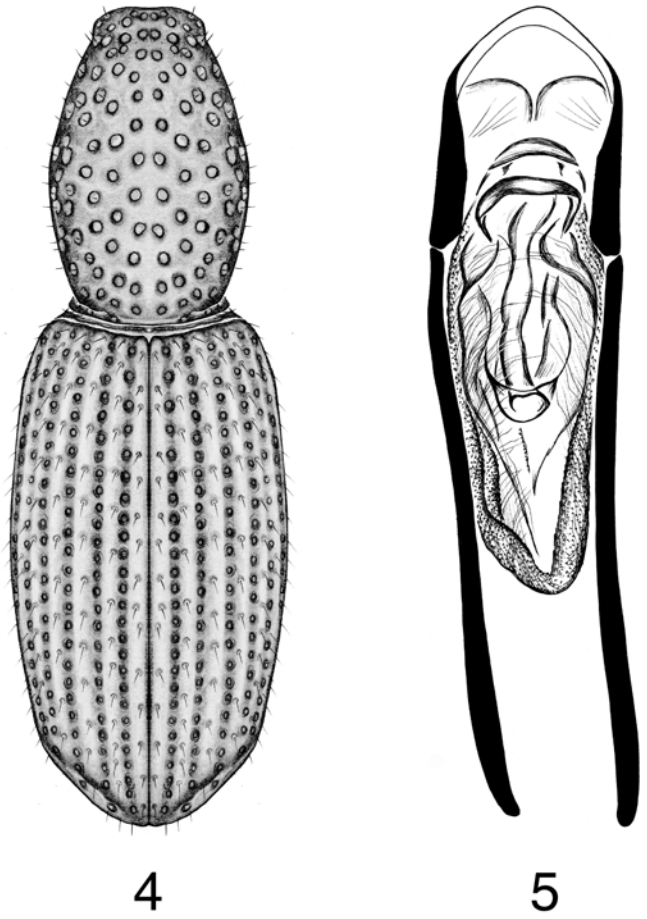
Figs. 2, 3.- Male holotype *Lymantes nadineae*, n.sp. 2, dorsal view; 3, lateral view.

1992). One of us (R.S.A.) has examined the holotype of *L. scrobicollis* (on loan from the Naturhistorika riksmuseet, Stockholm, Sweden), and both an ocular swelling and 4-6 linearly arranged eye facets are present. As for punctation, all other *Lymantes* possess large, deep, closely spaced (generally subcontiguous) dorsal and ventral punctures. For example, *L. nadineae* has more or less 30 punctures along the complete length of any elytral stria, whereas in other *Lymantes* the number of punctures does not exceed 20 and is generally less than 20. Tarsal claws are apparently lacking in the male which was collected already dead. They may have been broken but the undamaged nature of all other parts of all legs, including the apical tarsomere, suggests they may be truly absent. The other specimens of *L. nadineae* also show the characteristic cave adaptations to subterranean life of reduced pigmentation, more so than in most other *Lymantes*, and have longer, more slender legs (hind tibia l/w = 5.73, N=3 compared with l/w = 4.19, N=5 for *L. scrobicollis*).

Lymantes nadineae appears to be closely related to the widespread eastern species *L. scrobicollis,* which is sometimes found in leaf litter at cave entrances, and not to an additional undescribed species from Central Texas. The latter species has been collected in leaf litter and at least one cave entrance and has obvious eye facets at the base of the rostrum. With *L. scrobicollis*, *L. nadineae* shares the character states of longer dorsal vestiture and a very similar structure of the internal sac of the aedeagus.

DISCUSSION

Some beetles associated with Texas caves are well-known troglophiles. For example, the widespread species *Ptomaphagus cavernicola* Schwartz (Leiodidae) does not display morphological adaptations for cave life despite clear behavioral affinities for this habitat (Peck, 1973). Thanks to sound taxonomy and adequate sampling, the species is also known from surface habitats (Peck, 1982), leaving no doubts of its ecological status as a troglophile. However, the distinction between a troglophile (affinities for living in a cave) and a troglobite (obligate inhabitant of caves) could be difficult to delineate because morphological adaptations such as eye reduction, lost of pigmentation and leg elongation are also observed for species associated with other types of habi-



Figs. 4, 5.- Male holotype *Lymantes nadineae*, n.sp. 4, details of punctation on pronotum and elytra; 5, aedeagus, ventral view.

tats - such as deep litter and soil. Aalbu (2005) reported tenebrionid species [*Schizillus nunenmacheri* Blaisdell and *Asbolus mexicanus* (Champion)] from West Texas and Mexican caves that display morphological adaptations for cave habitats – morphological elongation and reduction in the number of eggs – but these species are also known from surface records and are better categorized as troglophiles. For these species, caves may simply constitute a refuge from extreme environmental conditions (Aalbu, 2005).

In other cases, the assignment as a troglobite or a troglophile is very tenuous because of incomplete knowledge. For instance, three eyeless species of Anillina (Carabidae) are known from Central Texas [*Micranillodes depressus* Jeannel, *Anillodes debilis* LeConte and *Anillodes minutus* Jeannel]. The labels of the only published records (the three female holotypes) do not provide any details about habitat of collection, but all subsequent collections of eyeless Anillina in Texas (about 70 specimens known, Paquin and Bousquet, in prep.) are from caves. The lack of surface sampling in Central Texas does not exclude the possibility that these species could survive outside of the cave environment despite their total lack of eyes. Affinities of Anillina for surface soil (non-cave) habitats and deep litter has been recently documented by Sokolov, et al. (2004, 2007) for Appalachian species, but none of these display eye reduction comparable to the Texas species. Due to the few data available, in addition to taxonomic problems that hamper species-level identification, the ecological status of Texas anillines remains undetermined.

The recognition of dependence on cave habitats and the discrimination of this trait from a lack of sampling in other surface habitats – such as deep litter, soil, or talus slopes that could also harbor eyeless species – are particularly difficult for species that are known only from a few specimens. While high numbers of specimens and morphological adaptations support the troglobitic status of the members of *subterranea* group of *Rhadine* or *Batrisodes* spp., the three known specimens of *L. nadineae* do not allow any level of certainty about their ecological status. Because no troglobitic weevils are known yet from North America, it does not mean that *L. nadineae* is an edaphobite. Coincidently, in a review of Staphylinidae associated with caves (exclusive of Pselaphinae and Aleocharinae), Peck and Thayer (2003) concluded that there are no troglobitic Staphylinidae in North America. However, they did not account for *Cylindropsis* sp. an eyeless rove-beetle known only from one specimen collected from Tooth Cave in Travis County (Central Texas), because the species has never been described due to its poor condition (S. B. Peck, pers. comm.). Nonetheless, it has been considered for listing as an endangered species (see Chambers, 1988), but the procedure was aborted due to the lack of a formal species identity. It is remarkable that two eyeless species, *L. nadineae* and *Cylindropsis* sp., which may both constitute the only troglobitic members of their families (excluding Pselaphinae for Staphylinidae) in North America, are known only from the same area in Central Texas. While it could be a coincidence, it may also suggest that evolutionary pressure that resulted in the unique and well-known area of narrow endemism for cave life in Central Texas (Culver, et al., 2006), may have affected some taxa in a unique manner in this particular region.

It is generally admitted that evolutionary processes behind cave adaptations may be a reaction to adverse conditions (glaciations, extreme temperatures, etc.) (Barr, 1968; Culver, et al., 2007). However, the discovery of a troglobitic fauna in the relatively young lava-tube caves of Hawaii (Howarth, 1972) challenged these hypotheses. Howarth (1986) suggested that cave adaptations could also be the result of adaptative shifts towards empty ecological niches (Howarth, 1980, 1993). This alternative hypothesis supports well the interpretation of the radiation of Cixiidae (Hemiptera) that are feeding on plant roots in Hawaiian caves (Hoch, 1999; Wessel and Hoch, 1999). In a world review of eyeless weevils, Osella (1979) stated that specimens of eyeless weevils collected in caves are not true cave-dwellers as they likely came into caves following the roots of trees, and could not survive, let alone breed, in this environment. This interpretation is arguable as roots found on cave ceilings are a part of the cave ecosystem, as are other food sources on which much cave life depends (cave guano, cricket droppings, etc.). However, affinities for moist and cool conditions, as well as food source availability (roots), might be a driving force behind the evolution of an edaphobite weevil towards troglobitism, echoing the principles proposed by Barr (1968) and Howarth (1986). Curiously however, although we know nothing of *Lymantes* biology, the genus belongs in Molytinae, a subfamily apparently saproxylic (feeding on dead wood) rather than rhizophagous (feeding on roots) (Osella, 1979). In the case of *L. nadineae*, we know nothing about food habits, but feeding on woody roots found on cave ceilings is perhaps the best available hypothesis. Its ecological status as a troglobite is possible under both the scenarios of Barr (1968) and Howarth (1986) and its association with caves may well represent an invasion of an empty niche, or that adverse conditions isolated the species from its surface ancestor long enough to allow development of morphological modifications to cave life. A combination of both scenarios is also possible. Given that the only known specimens were not found in entrances but in true cave conditions (total darkness along with other troglobitic spiders, millipedes, and beetles), and that survival and evolution

is possible as a root feeder in a cave context, this species is proposed as the first North American troglobitic weevil. Additional data will hopefully confirm this hypothesis or suggest an alternative evolutionary scenario.

The known distribution of *L. nadineae* is comparable to that of other troglobitic species: *Texella reyesi* Ubick and Briggs (Opiliones, Phalangodidae, see Ubick and Briggs, 2004), *Anapistula* sp. (Araneae: Symphytognathidae, Paquin, et al., in prep.), *Speodesmus bicornourus* Causey (Diplopoda, Polydesmidae, see Elliott, 2004), *Batrisodes* spp. (Coleoptera: Staphylinidae: Pselaphinae, see Chandler, 1992; Chandler and Reddell, 2001; Chandler, et al., 2009), and *Rhadine* spp. (Coleoptera: Carabidae, see Barr, 1974) that are known exclusively from Travis and Williamson Counties. Such narrow distributions raise important evolutionary/ecological questions, for which we still do not have any firm answers: are these distributions the result of an initial cave invasion and subsequent subterranean dispersion through the mesocavern; or are these distributions the result of independent vicariant events leading to complex population structure and/or speciation

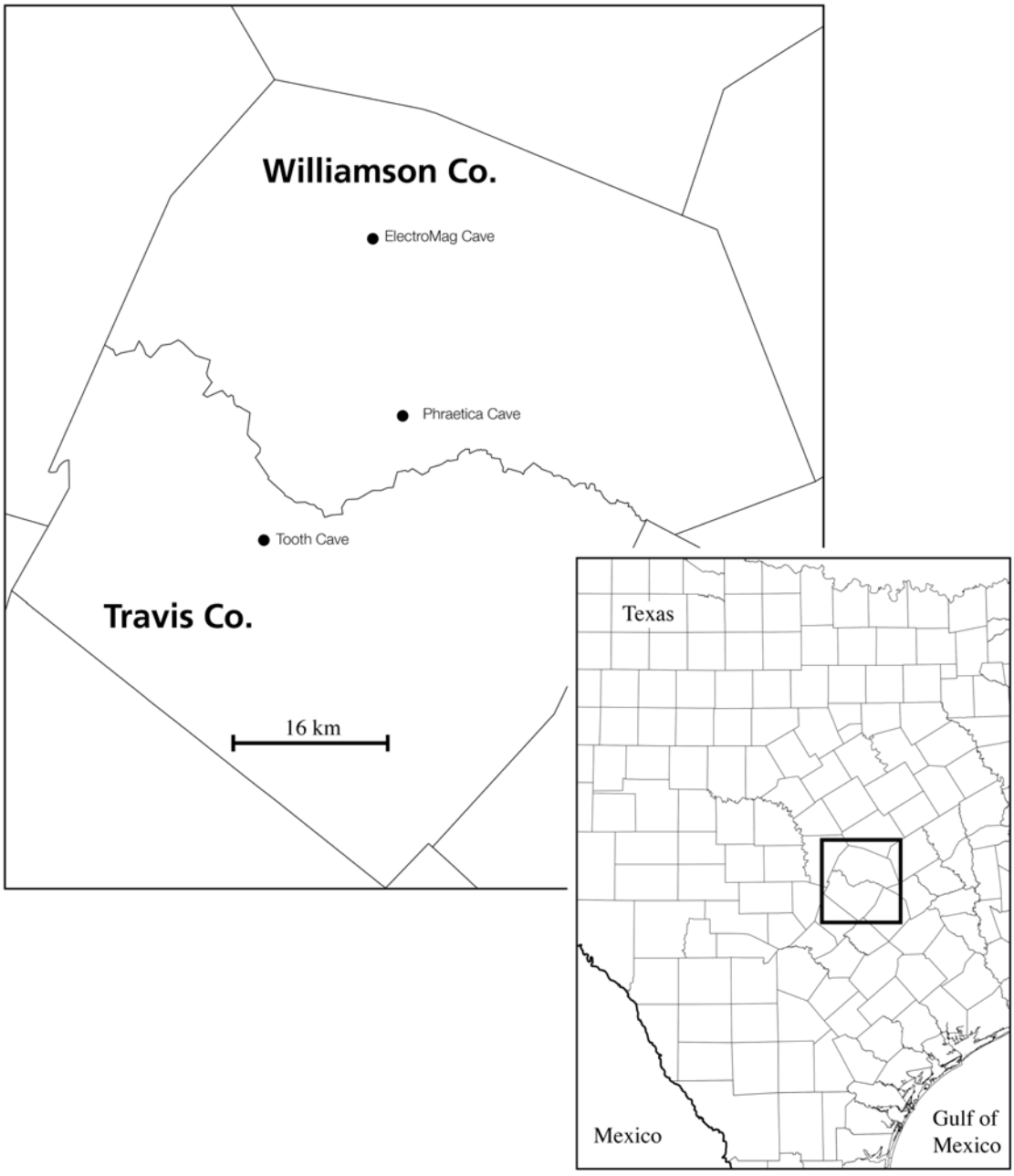


Fig. 6.-Distribution map of *Lymantes nadineae*, n.sp. known only from Travis and Williamson Counties, Central Texas.

patterns; or something else? Recent genetic data on *Cicurina* (Araneae: Dictynidae) show a high level of connection between caves of this area (Paquin and Hedin, 2007). However, this does not allow one to discriminate between evolutionary scenarios that are linked into a complex geological history which resulted in a cave network that evolved since its formation about 10 million years ago to its present condition. Hedin (1997a, b) concluded that vicariance has been a driving force behind the diversification of Appalachian *Nesticus* (Araneae: Nesticidae), but in Texas, the apparently higher degree of connection between caves and the complexity of the subterranean network related to the aquifer evolution may have driven the diversification of life differently.

It is remarkable that the closest relative of *L. nadineae* is not an undescribed *Lymantes* species found in leaf litter and at least one cave entrance in Central Texas, but rather *L. scrobicollis* a species found in leaf litter and cave entrances in the eastern U.S.A., east of Texas. Comparable relationships are observed for some *Batrisodes* and *Cicurina* species, which suggests an isolation of the Texas troglobites from their related species that shifted towards the east. In these cases, other congeneric surface species are found in Texas caves and these are not the closest known relatives (*Cicurina varians*, *Batrisodes uncicornis, Lymantes* sp.), suggesting broader affinities for cave habitats in each genus.

One of the three known localities, Phraetica Cave, has unfortunately been altered by urban development and the entrance is presently sealed by concrete. Given the proximity of the known locations and the suspected connectivity between caves of Central Texas (see Paquin and Hedin, 2007), it is likely that *L. nadineae* also inhabits other caves of this area. However, intensive monitoring by J. Reddell and his collaborators have yet failed to yield additional specimens, but eyeless weevils are typically rare, even for litter species. Collecting efforts in caves are rarely oriented towards ceilings where roots are found, and a careful examination of this microhabitat may increase chances of future collections. Given the monitoring intensity of the caves in the distribution area and that only three specimens have been found in more than 40 years of collection, *L. nadineae* is likely one of the rarest beetles in North America.

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