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Publication Date
2011

Peer reviewed|Thesis/dissertation

Studies on the Cave- Spider Family Leptonetidae in North America

By

Joel Matthew Ledford

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor George R. Roderick, Chair
Professor Charles E. Griswold, Co- Chair
Professor Rosemary G. Gillespie
Professor Brent D. Mishler

Spring 2011

Abstract

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The spider family Leptonetidae Simon, 1890 includes 17 genera and 213 species worldwide. They are broadly distributed in the Holarctic and typically associated with cool, moist habitats such as leaf litter, moss, rotting logs, and caves. The North American fauna is divided into two subfamilies, the Archoleptonetinae and Leptonetinae, with representatives in California through the Southern U.S. and Mexico. Five genera are currently recognized (Platnick, 2010), the most diverse of which is *Neoleptoneta* Brignoli, 1972 with a center of diversity in Texas where most species are known only from caves (Gertsch, 1974). Their restricted distributions and specialized biology have made them conservation priorities and two Texas species, *Neoleptoneta microps* (Gertsch, 1974) and *N. myopica* (Gertsch, 1974), are listed under the U.S. Endangered Species Act.

The impetus for this study was a series of collections produced over the past thirty years which have dramatically increased the number of records for the family, including the discovery of several unknown sexes and new species. Additionally, detailed morphological study using scanning electron microscopy (SEM) has revealed a wealth of new characters many of which have implications for relationships within the family and among spiders as a whole. Lastly, fresh collections for several genera in Alabama, California, Mexico, and Texas have facilitated the use of molecular data to develop phylogenetic hypotheses within the family for the first time. The primary objective for the study is to revise the systematics of the North American genera, with particular emphasis on the taxonomy and relationships within the Archoleptonetinae and the Texas cave fauna. The study is divided into three chapters, the results of which are briefly summarized below.

In the first chapter, a detailed morphological study of the genus *Archoleptoneta* revealed the presence of a cribellum an calamistrum representing the first cribellate member of the Leptonetidae. The morphology and relationships for the family are reviewed and the genus *Darkoneta* is described to include the ecribellate archoleptonetines. Three new species are also described from California, Mexico, and Guatemala.

The second chapter uses molecular sequence variation from three genes to produce a phylogeny for the North American Leptonetidae, with emphasis on the relationships of *Neoleptoneta* Brignoli, 1972. The placement of two *incertae sedis* species, *Leptoneta brunnea* (Gertsch, 1974) and *Leptoneta sandra* (Gertsch, 1974) are also considered and four new genera are described. Morphological data are traced on the molecular phylogeny and patterns of cave evolution are discussed.

The third chapter revises the taxonomy of the genus *Tayshaneta*, including the descriptions of ten new species from Texas. All *Tayshaneta* species are diagnosed and keyed, and comparative images using scanning electron and compound light microscopy are provided. Relationships among *Tayshaneta* are also discussed, including detailed descriptions of their morphology. Lastly, the karst faunal region (KFR) conservation strategy in Central Texas is evaluated using revised species distributions.

Dedication

Dedicated to my wife Karin Ledford, and the Lindstrom and Ubick families who always believed in me.

Acknowledgements

This study would not have been possible without consistent care, guidance, and support from my family, advisors, and friends. I thank the members of my advising committee, Charles Griswold, George Roderick, Rosemary Gillespie, Brent Mishler, and Marshal Hedin for their patience, encouragement, and advice. Several individuals have been especially supportive and inspiring throughout my education, especially Charles Griswold and Darrell Ubick both whom have guided my studies for over a decade. The California Academy of Sciences has been instrumental to my education and the curators, postdocs, staff, and collections have been a source of constant inspiration. Rosemary Gillespie and George Roderick provided excellent research resources and support in the Evolab at U.C. Berkeley. Josh Campbell, James Cokendolpher, Sarah Crews, Nadine Dupérré, Mark Harvey, Marshal Hedin, Rick Lapoint, Jeremy Miller, Brent Mishler, Pierre Paquin, Norman Platnick, Carles Ribera, Brian Simison, Darrell Ubick, and Kip Will were invaluable sources of discussion about spiders, systematics, and phylogenetic methods. Several arachnologists have inspired me throughout my studies, many of which are my spider heroes: Paolo Brignoli, Fred Coyle, Willis Gertsch, Brent Opell, and Vincent Roth.

I thank the following individuals, organizations, and institutions for specimen loans: Pierre Paquin and Kemble White, SWCA Environmental Consultants; Mark Sanders, City of Austin, Texas; Andy Gluesenkamp, Texas Parks and Wildlife; Norman Platnick and Louis Sorkin, American Museum of Natural History; Darrell Ubick, California Academy of Sciences; James Cokendolpher, Museum of Texas Tech University; James Reddell, Texas Memorial Museum; Peter Sprouse, Jean Krejca, and Kathleen O'Connor, Zara Environmental. Collecting permits were facilitated by Kathleen O'Connor, Zara Environmental, Cyndee Watson, U.S. Fish and Wildlife, David Riskind, Texas Parks and Wildlife, and Mark Sanders, City of Austin, Texas.

Several members of the Evolab at U.C. Berkeley and the California Academy of Sciences provided helpful discussions and technical assistance in the lab: Fernando Alvarez-Padilla, Brad Balukjian, Gordon Bennett, Anthea Carmichael, Sarah Crews, Kari Goodman, David Hembry, Jennifer Immamura, Rick Lapoint, Steve Lew, Alma Saucedo, Sean Schoville, Scott Serata, Matthew VanDam, and Hannah Wood. Jennifer Yang was an invaluable assistant in the lab as part of the URAP program at U.C. Berkeley. Many Texas cavers contributed to this project and I was honored by each of their efforts, including: Craig Crawford, Andy Gluesenkamp, Jim "Crash" Kennedy, Jean Krejca, Niki Lake, Krista McDermid, Kathleen O'Connor, James Reddell, William Russell, Mark Sanders, Peter Sprouse, and Kimble White. Jeremy Brown and the Bodega Phylogenetics Workshop helped tremendously with analyses and understanding phylogenetic methods. Wayne Pfeiffer generously provided computer resources and technical expertise.

The following individuals and institutions provided financial support: the National Science Foundation, Harriet Exline- Frizzel fund, California Academy of Sciences, Walker Fund, University of California, Berkeley, National Speleological Society, Western Cave Conservancy, and the University of California.

Family and friends were instrumental to my success and I am grateful to each of them for their support and care: Brad Balukjian, Gordon Bennett, Sarah Crews, David Hembry, Rick and Crystal Lapoint, and Pierre Paquin. Anthea Carmichael provided me with a home away from home, entertaining morning commutes, and an endless supply of

canine companionship. Jim Ledford taught me the value of education, hard work, and perseverance. Tom and Linda Lindstrom encouraged my studies from the beginning and gave me a wonderful wife and family.

Lastly, I thank my patient and caring wife Karin Ledford and our dogs Howie and Seymour without whom I would never have made it.

Chapter 1:

A Study of the Subfamily Archoleptonetinae with a Review of the Morphology and Relationships for the Leptonetidae

Abstract

Detailed examination of the spinning organs and legs of *Archoleptoneta schusteri* Gertsch (1974) has revealed a cribellum and calamistrum, which represents the discovery of the first cribellate member of the Leptonetidae. Subsequent examination of all other described *Archoleptoneta* species has confirmed the presence of a rectangular colulus similar to other leptonetids. A comparative review of the characters used to support the Leptonetidae is presented, including a discussion of their phylogenetic implications. The distribution of several features of the spinning organs, respiratory system, and genitalia suggests that the phylogenetic position of the Leptonetidae needs to be reevaluated, and makes their position within the Haplogynae uncertain. Illustrations and detailed discussion of characters in the Archoleptonetinae and Leptonetinae are provided. *Archoleptoneta schusteri* Gertsch is redescribed including detailed images of its spinning organs and genitalia. All ecribellate archoleptonetines are transferred to the new genus *Darkoneta* **gen. nov.** based on the loss of the cribellum, giving the following new combinations: *Darkoneta arganoi* (Brignoli, 1974). **comb nov.**, *Darkoneta garza* (Gertsch, 1974) **comb nov.**, *Darkoneta obscura* (Gertsch, 1974) **comb nov.**, and *Darkoneta stridulans* (Platnick, 1994) **comb nov**. Three new species are described: *Archoleptoneta gertschi* **sp. nov.** from Eastern California, *Darkoneta reddelli* **sp. nov.** from Puebla, Mexico, and *Darkoneta quetzal* **sp. nov.** from San Lorenzo, Guatemala. Dichotomous keys are provided with a discussion of problems with the diagnosis of females. Distribution maps for each species are shown with a discussion of areas that require additional sampling in order to resolve species limits.

Introduction

California is renowned for biodiversity, particularly with respect to its endemic plants and invertebrates (Myers et al., 2000). Several recent studies highlight the evolutionary significance of the Californian spider fauna (Bond et al., 2001; Hedin, 2001; Ramirez & Chi, 2004), which contains a large number of relatively ancient lineages often characterized by morphological homogeneity and the retention of ancestral character states, such as the cribellum. The Californian leptonetid fauna is no exception, and until recently (Ledford, 2004; Ledford et al., 2005), has remained largely unexplored.

In this paper, we report on the discovery of a cribellum in *Archoleptoneta schusteri* Gertsch, a spider from California that is recognized as a basal leptonetid (Brignoli 1979; Gertsch, 1974; Platnick 1986, 1994). The phylogenetic implications of the leptonetid cribellum are addressed in the context of a review of the characters used to support relationships within the Leptonetidae. *Archoleptoneta schusteri* is redescribed including detailed images of its spinning organs and genitalia. We provide detailed discussions of the Archoleptonetinae and Leptonetinae, and illustrate *Leptoneta infuscata* Simon 1872 as an exemplar of the latter subfamily. Ecribellate archoleptonetines are transferred to the new genus *Darkoneta* **gen. nov.** based on the loss of the cribellum giving the new combinations: *Darkoneta arganoi* (Brignoli, 1974). **comb nov.**, *Darkoneta garza* (Gertsch, 1974) **comb nov.**, *Darkoneta obscura* (Gertsch, 1974) **comb nov.**, and *Darkoneta stridulans* (Platnick, 1994) **comb nov**. Three new species are described, *Archoleptoneta gertschi* **sp. nov.** from Eastern California, *Darkoneta reddelli* **sp. nov.** from Puebla, Mexico, and *Darkoneta quetzal* **sp. nov.** from San Lorenzo, Guatemala. Dichotomous keys are provided with a discussion of problems with the diagnosis of females. We also provide distribution maps for each species, highlighting areas that need additional sampling to resolve species limits.

Taxonomic background: Gertsch (1974) revised the North American leptonetids and described the genus *Archoleptoneta* to contain four species diagnosed by having six eyes in a single group (Figs. 7, 13, 25) and characteristics of the male genitalia (Figs. 76-78). Although the genus was only based on symplesiomorphies, he argued that this suite of characters placed *Archoleptoneta* as the sister group of all other leptonetids for which he erected the new subfamily Archoleptonetinae. Platnick (1986) corroborated Gertsch's hypothesis through an examination of the tibial and patellar glands, and described a new species, *Archoleptoneta stridulans,* from Panama (Platnick, 1994). Whereas images of the spinning organs and male genitalia for *A. stridulans* are provided in Platnick (1994), no comparative images for other *Archoleptoneta* species exist aside from the simple line drawings in Gertsch (1974). The small size and delicate nature of *Archoleptoneta*, and leptonetids in general, requires the use of compound microscopy and, preferably, scanning electron microscopy in order to resolve the fine structures of the spinning organs and genitalia. Not surprisingly, a wealth of informative characters has remained unexplored, including structures such as the cribellum, which went undiscovered for over thirty years.

Diagnostic challenges: Morphological homogeneity among the Leptonetidae is well- documented (Gertsch, 1974; Ledford, 2004) and presents significant challenges to species diagnosis, especially in the absence of male specimens. Archoleptonetine females show little interspecific variation, their genitalia are difficult to prepare, and preparations are often ambiguous. Furthermore, most species are known from single collections and in two cases (*D. arganoi* and *D. obscura*) from single specimens, which prevents the assessment of intraspecific variation. While this is not a problem unique to leptonetids, their morphological subtlety and relative rarity makes species delimitation especially challenging. Both Gertsch (1974) and Platnick (1994) encountered similar problems and prepared no diagnostic keys, instead relying on features which, admittedly, are likely to be inconsistent, i.e., the relative sizes of eyes, cheliceral teeth, pigmentation, etc. While these diagnostic issues may eventually result in synonymies, especially for species known only from females, we take a conservative approach in this paper and make no taxonomic changes in the absence of male specimens.

Materials and Methods

Species descriptions refer to a single adult individual for each sex, which is identified as a type or by the locality at which it was collected. Descriptions of females were based on specimens collected in association with males from or near the type locality. All measurements are in millimeters and quantify the size of a structure at its widest or longest point. A section reporting the variation in the most conspicuous and variable features follows each description and represents two to nine individuals (*n*), encompassing the full range in overall size.

Prior to examination with a Leo 1450VP Scanning Electron Microscope, all structures were cleaned with a fine brush and critical point dried. Spinneret preparations followed the methods of Coddington (1983), consisting of a brief cleaning in an ultrasonicator and a gentle squeeze of the abdomen using forceps in order to extend and separate the spinnerets. Large structures were examined using a Leica MZ 12.5 microscope.

Vulvae were carefully excised and placed in a pancreatin solution for 24- 48 hours to digest extraneous tissue (Alvarez- Padilla and Hormiga, 2007) then placed in water and manually cleaned. Best results were obtained by removing the cuticle from the dorsal surface of the abdomen and digesting the entire structure. If the vulva remained unclear, it was stained with Chlorazol Black and reexamined. Images of each species were prepared using a Syncroscopy Automontage system attached to a Leica MZ 16 stereomicroscope or a Leica DM 4000 compound microscope. Genitalia and small structures were placed in glycerin and examined in well slides or temporary mounts following the procedure described by Coddington (1983).

Abbreviations used in the text are standard for the Araneae and are as follows: ALS, anterior lateral spinnerets; PMS, posterior median spinnerets; PLS, posterior lateral spinnerets; AC, aciniform gland spigots; CY, cylindrical gland spigots; MAP, major ampullate gland spigot(s); mAP, minor ampullate gland spigot(s); MSp, "modified spigot" (a possible homologue of pseudoflagelliform and flagelliform gland spigots, i.e., Griswold et al., 2005); Nu, nubbin (an aborted spigot); PI, piriform gland spigots; TP, tartipore (scar left from cuticular penetration by a silk gland duct from a previous instar); AME, anterior median eyes; ALE, anterior lateral eyes; PME, posterior median eyes; PLE, posterior lateral eyes. Structures for archoleptonetine male genitalia are as follows: E, embolus; MS, median sclerite; PRS, prolateral sclerite; RLS, retrolateral sclerite.

The specimens on which this study is based were kindly provided by Norman Platnick and Louis Sorkin, American Museum of Natural History (AMNH), the

California Academy of Sciences (CASC), Darrell Ubick, personal collection (DU), Petra Sierwald and James Boone, Field Museum of Natural History (FMNH), and James Cokendolpher, Museum of Texas Tech University (TTUZ).

Distribution

Archoleptoneta schusteri is widespread in California (Fig. 115), and known from Sonoma County south to Monterey County and east to Fresno County. Several regions, including the North and South Coast and the Eastern Sierras, are poorly sampled and most collections are represented by females or juveniles which have few diagnostic characters. Even in relatively well- sampled areas, many county records are for females which may represent distinct species (Fig. 115). Several records for *Archoleptoneta gertschi* **sp. nov.** are from caves in Amador, Calaveras, and El Dorado counties, but specimens show no obvious signs of troglomorphy. It is interesting to note that only a single troglobitic leptonetid is known from California (*Calileptoneta briggsi* Ledford) despite the diversity of cave- adapted species in North America (Gertsch, 1974).

Efforts to recollect *Darkoneta garza* (Gertsch, 1974) at the type locality in Justiceburg, Texas (Fig. 116) have been unsuccessful and the precise locality for this species is ambiguous. A juvenile specimen has been collected from the Davis Mountains in Jeff Davis County, Texas and may belong to this species (D. Ubick, pers. comm.). Three female specimens from Bill's Cave near Tucson, Arizona may represent a new species based on the distributional disjunction but are not diagnosable from *D. garza*. Given the diversity of leptonetids found in the American Southwest (Gertsch, 1974; Cokendolpher & Reddell, 2001; Cokendolpher, 2004), it is likely that additional species await discovery.

Mexico has a rich and largely undescribed leptonetid fauna, several species of which are known only from a single sex. As mentioned by Platnick (1991) both *D. araganoi* and *D. obscura* are known from adjacent localities in Chiapas, near Comitán (Fig. 116) which makes them likely synonyms. In the absence of males for either species, however, we prefer to make no taxonomic changes. The new species *Darkoneta reddelli* is the first known troglobitic archoleptonetine and given the abundance of caves and troglobites in the area (Reddell, 1977), suggests the possibility of a much more diverse fauna.

Comparative morphology

Leptonetidae

Synapomorphies. Synapomorphies for the Leptonetidae include an unusual iridescence, especially on the legs and carapace (Figs. 1- 3), autospasy at the patella- tibia joint, the presence of tartipores on the ALS (Fig. 50, 58, 62, 70), male palpi with a fused tegulum and subtegulum but with an expandable basal haematodocha, and a respiratory system consisting of a pair of short median branches with long laterals that open to a single spiracle anteriad of the ALS (Fig. 114).

Respiratory system. (Fig. 114) The respiratory system is unlike other Haplogynae in that there is a single tracheal spiracle anteriad of the anterior lateral spinnerets, which opens to a pair of long lateral branches with a pair of short median branches, similar to that found in many Entelegynae (Ramirez, 2000). The tracheae are restricted to the abdomen. Anteriorly, the respiratory system consists of a pair of book lungs.

Expandable palpi. Brignoli (1979) was the first to note the expandable morphology of leptonetid male palpi. While it is tempting to make comparisons with the palpi of some Entelegynae, homology between these structures is difficult to assess. Leptonetid palps are generally far less expandable, i.e. the bulb twists up to 180° from a basal hemotadocha with some accessory sclerites and the embolus slightly changing orientation but not ballooning out as in typical entelegynes.

Archoleptonetinae

Synapomorphies. Platnick (1986) proposed the oval to elongate patellar- tibial glands (Fig. 31) as a synapomorphy for *Archoleptoneta*, which is confirmed by this study, including for the ecribellate species placed in the new genus *Darkoneta*. We also note that the glands are sparsely distributed on the legs in contrast to Telemidae and Ochyroceratidae which have the glands more densely distributed. The tarsal organ is unique in having a long central receptor flanked by two shorter lobes (Fig. 37, 39). Male palpi bear 3 accessory sclerites attached to the bulb via a flexible base with a tapering embolus (Figs. 76, 80- 83, 86, 89, 92, 96, 98, 101- 102, 104- 107) that bears a ventral groove apically. The endites each bear a pair of stout setae on their ventrolateral surfaces (Fig. 35). The PLS are cylindrical and apically produced to a point with two cylindrical gland spigots in females both of which are absent in males (Figs. 52, 56, 60, 64).
Cephalothorax. The carapace (Figs. 6- 8, 11- 13, 23, 25, 29, 32) has minimal setation and is gently to sharply sloped in lateral profile (Figs. 9- 10, 16- 17). The color is pale yellow to orange in living specimens, but is often depigmented in alcohol. There are six eyes (Figs. 6- 8, 11- 13, 23, 25- 26) in a single cluster with dark or dusky markings surrounding the ocular area and raised in lateral view, except for *D. reddelli* which is eyeless (Fig. 32). The endites each bear a pair of stout setae ventrally (Fig. 35) and an exposed serrula that occupies approximately half their length. Males of *Darkoneta stridulans* (Platnick, 1994) and *Darkoneta quetzal* **sp. nov.** have a deep invagination on the posterior margin of the carapace with a lateral pair of stridulatory picks that strike a file on the dorsoapical surface of the abdomen (Figs. 29- 30).
Legs. The legs are long and thin, with scattered setae and few spines. The patellar and tibial glands are elongate and oval with single small pores (Fig. 31). In *A. schusteri*, the calamistrum occurs dorsoapically on metatarsus IV and is composed of 4- 5 elongate setae (Figs. 45, 48). There are three tarsal claws on all legs and a single claw on the palpi of females. The exposed tarsal organ of females (Fig. 37) and males (Fig. 39) has three receptors, one of which is elongate, and partially enclosed by a shallow hood.
Abdomen. (Figs. 6, 8, 9- 10, 11- 17) The abdomen is covered in fine setae, oval in shape, and lacks a pattern. As in other leptonetids, the abdomen and legs are iridescent in life (Fig. 1). Males and females of *Darkoneta quetzal* **sp. nov.** and *D. stridulans* have the abdomen curved dorsoapically in lateral profile (Figs. 16, 17).
Spinning organs. (Figs. 43- 44, 46- 47, 49- 56, 57- 64) The anterior lateral spinnerets are cylindrical and bear spigots of a variety of sizes, which makes interpretation of spigot type difficult. Females bear two spigots larger than others, probably major ampullate gland spigots, 3- 4 tartipores, and 3- 4 probably piriform gland spigots. One or more of these probable piriform gland spigots may lack a base (PI* in Fig. 58). Male ALS are similar but have fewer piriform gland spigots. Epiandrous spigots were not observed in archoleptonetine males, but are present in leptonetines. The posterior median spinnerets

of *Archoleptoneta* females bear 3- 4 spigots: the anterior 2 are on stout, cylindrical bases, the posterior 2 arise from low bases, with a large tartipore nearby (Fig. 51). The PMS of males (Fig. 55) has only the two posterior spigots, which we interpret as aciniform gland spigots. The ontogeny of the anterior spigots that are found only in females suggest that they may be cylindrical gland spigots, as have previously been reported for leptonetines (Platnick et al, 1991). *Darkoneta* female PMS differ: there is an anterior spigot on a squat base, a nubbin behind this, and two posterior spigots with elongate shafts (Fig. 59). The male has only the anterior spigot, which we interpret as a minor ampullate gland spigot, and the accompanying nubbin. The posterior spigots occurring only in the female are probably cylindrical gland spigots. The posterior lateral spinnerets are cylindrical and produced to a point apically. Females have two posterior spigots with stout shafts and cylindrical bases, which resemble the possible cylindrical gland spigots on the PMS (Figs. 52, 60). These are absent in males (Figs. 56, 64). The female basal spigots, which have no counterpart in males, may be cylindrical gland spigots. A single large spigot arises at the pointed apex of the PLS of female *Archoleptoneta*; this spigot has a narrow shaft (Fig. 52, MSp?) and is replaced by a nubbin in males (Fig. 56 NuMSp?). No spigots occur on the PLS of males. Interpretation of the female apical spigot is problematic. Replacement by a nubbin in males suggests that it may be an aborted aciniform gland spigot, or perhaps a “modified spigot”, which has not yet been reported for haplogynes (Griswold et al, 2005). In cribellate species, the cribellum is divided and composed of numerous strobilate spigots. Paracribellar spigots are absent. The cribellum (Figs. 43- 44, 47, 49, 53) is represented by a rectangular colulus (Fig. 46, 57, 61) in *Darkoneta* **gen. nov**. Platnick (1994) reported on the spigots of *Archoleptoneta* (now *Darkoneta*) *stridulans* and reported a single major ampullate gland spigot on the ALS (Platnick, 1994, figs. 13, 16), but his figures reveal a variety of sizes and shapes of ALS spigots, including at least one lacking a base, and therefore we suggest that *D. stridulans* may also have multiple major ampullate gland spigots on the ALS. The presence of multiple major ampullate gland spigots on the ALS may be an additional synapomorphy for the Archoleptonetinae.

Male Genitalia. (Figs. 76- 78, 79- 84, 85- 90, 91- 96, 97- 102, 103- 108) The palpal tarsus of males is elongate and cylindrical, without obvious modifications or constrictions. The bulb is oval with a fused tegulum and subtegulum. The embolus is tapered and with a ventroapical groove (Figs. 76, 80, 84, 86, 89, 92, 95, 98, 104, 108). The embolus and all accessory structures are flexibly attached to the bulb at its base. Three accessory sclerites are present in conjunction with the embolus: two sclerites straddle the embolus at the base (PRS, MS, Fig. 76) and are rounded or pointed apically. A single sclerite situated prolaterally (RLS, Fig. 76) is variable in shape, and produced to a fine or blunt point. The basal haematodocha is expandable and capable of rotating the bulb up to 90° with the embolus protruding retroventrally and perpendicular to the tarsus. The males of *Darkoneta quetzal* **sp. nov.** have a distinctive gonopore anteriad of the epigastric furrow (Fig. 34), similar to some Telemidae, but this character has not been widely surveyed.

Female Genitalia. (Figs. 109- 112) The vulva of females consists of a pair of simple spermathecae with little appreciable variation, lacking the atrium and lateral twisted spermathecae present in leptonetines.

Web. Several specimens of *Archoleptoneta schusteri* were observed in the field and maintained for extended periods in the lab. Aside from a few scattered strands, no web was ever produced. A single unidentified female specimen of *Darkoneta* **gen. nov.** from Bill's cave, Arizona produced a small sheet web similar to other leptonetids.

Eggsac. The eggsac of *A. schusteri* is a flattened disc which is attached to the underside of rocks and contains 4- 6 eggs (n= 2).

LEPTONETINAE

Synapomorphies. Ocular arrangement with PME displaced behind the ALE and PLE, AME lost (Figs. 18- 22, 24, 27, 28); metatarsus III with apical preening comb (Fig. 12- 13 from Ledford, 2004); female genitalia consisting of a large central atrium with a pair of twisted lateral spermathecae (Fig. 113).

Exemplars. Morphological observations are based on the European species *Leptoneta infuscata* Simon, 1872 which is a typical leptonetine. Several Asian, European, and North American genera were also examined; any deviations from the morphology of *L. infuscata* are noted below.

Cephalothorax. (Figs. 18- 20, 24) Leptonetines share a unique ocular arrangement among spiders where the AME are lost and the PME are displaced posteriad of the anterior eye group. The chelicerae of some *Appaleptoneta* and *Neoleptoneta* have a retrolateral stridulatory file (Fig. 42) but no stridulatory picks have been located on the legs or palpi.

Legs. All leptonetine genera examined have a ventroapical preening comb on tibia III (Figs. 12- 13 from Ledford, 2004). The patellar and tibial glands or 'Emerit's glands' (Emerit, 1981; Platnick, 1986) are variable in shape and largely consistent within genera. Some species of *Calileptoneta*, however, have multiple gland types on the same leg segment that match the descriptions provided by Platnick (1986). A comprehensive review of these glands is necessary in order to address this variation, especially in the context of higher- level relationships among the Leptonetidae. The tarsal organ of females is exposed and has two small lobes on a slightly elevated base (Fig. 38). Male tarsal organs are on a distinctly elevated and cylindrical base with two lobes (Fig. 40). Considerable morphological variation in tarsal organs is present among leptonetine genera and further study will likely prove phylogenetically informative.

Abdomen. (Figs. 18, 21- 22) Most endogean species have dusky markings dorsally with or without scattered elongate setae.

Spinning organs. (Figs. 65- 72) The anterior lateral spinnerets of both sexes are cylindrical and bear a single major ampullate gland spigot, much larger than the other spigots, 1- 4 tartipores, and several piriform gland spigots. The posterior median and posterior lateral spinnerets are comb- like and bear a linear row of 12 or more aciniform gland spigots. In females there may be 1 or 2 larger spigots inside the line of aciniform gland spigots: we interpret these as cylindrical gland spigots, as suggested by Platnick et al. (1991). Other genera examined, i.e., *Appaleptoneta* (Platnick et al. 1991, figs. 216- 221) and *Calileptoneta* (Ledford, 2004, figs. 24- 27) are similar. In males 4- 5 epiandrous spigots occur anteriad of the epiandrum (Fig. 28 from Ledford, 2004).

Male Genitalia. (Figs. 73- 75) The palpal tarsus is dorsally constricted (Fig. 75) and often modified apically and retrolaterally, usually bearing chemosensory and a variety of other specialized setae. The lateral surfaces of the tibia typically have a variety of spines and twisted setae which in many genera are produced into large spine- like apophyses. The apical portion of the bulb is weakly sclerotized and bears a variety of accessory sclerites that change orientation when the bulb is expanded. The embolus is situated ventroapically and is broad in most genera but may be reduced to a simple pore on a short base (*Neoleptoneta*).

Female Genitalia. (Fig. 113) The vulva has a large, central atrium with a pair of lateral twisted spermathecae bearing numerous flagellate pores. Short, twisted tubes connect the spermathecae laterally to the atrium.

Web. (Figs. 2, 4) The web is a finely woven sheet with a messy retreat, usually constructed among layered rocks or breakdown areas in caves. Close inspection of the web reveals a pattern of parallel lines of silk similar to that recorded for the Ochyroceratidae (Hormiga et al., 2007). Similar lines of silk have also been noted for the Telemidae (pers. obs.). Males may be found either in webs with females or as vagrants (Fig. 3).

Eggsac. (Fig. 5) The eggsac of *Neoleptoneta* and *Calileptoneta* is spherical, covered in soil, and suspended from a few silk lines near the edges of the sheet web. Eggsacs of *Calileptoneta helferi* contained 10- 16 eggs, while the eggsac of *Neoleptoneta anopica* (a strongly cave- adapted species) contained 2 relatively large eggs. Cokendolpher (2004) reported 1 egg per sac for *Neoleptoneta bullis*.

Discussion

Leptonetids have figured prominently in the most recent phylogenetic analyses of haplogyne spiders (Platnick et al., 1991; Ramirez, 2000), where they are weakly supported as sister to the Telemidae. This relationship is based on the modified PMS and PLS that bear a linear brush of aciniform gland spigots (Figs. 65- 72) and the patellar and tibial glands or ‘Emerit’s glands’. Leptonetids are remarkable in these studies due to several instances of homoplasy with the Entelegynae; specifically, the presence of cylindrical gland spigots (Figs. 51, 55, 59, 63, 68- 69, 71- 72) (shared with Telemidae) and tartipores (Figs. 50, 54, 58, 62, 59, 63, 70), and the absence of a cheliceral lamina (also like Telemidae), a classic synapomorphy for the Haplogynae (but also present in dysderoids). Indeed, the only synapomorphy that leptonetids share with other Haplogynae is the fusion of the tegulum and subtegulum. This rampant homoplasy, especially when coupled with the discovery of a cribellum in *Archoleptoneta,* further challenges the current classification.

Brignoli (1979) was the first to review the morphology and relationships of leptonetids, using data from his work on the European fauna as well as observations from the families Telemidae and Ochyroceratidae. He concluded that support for a relationship among these families was dubious and largely based on their similarity in ecology. Furthermore, he suspected that the combination of non “haplogyne” characters found in leptonetids (absence of a cheliceral lamina, expandable and structurally complex palpal bulb) might ally them more closely with entelegynes. This intriguing hypothesis was again briefly discussed by Platnick et al. (1991) in relation to the spinning organs, due to their apparent cylindrical gland spigots. They suggested that “leptonetids and telemids might be more closely related to entelegynes than to other haplogynes” but this suggestion was ultimately not supported by their analyses. The subsequent reanalysis by Ramirez (2000) did not incorporate additional leptonetid exemplars, nor examine their respiratory system directly, but recent work (Ramirez, pers. comm.) has shown that the tracheae of *Appaleptoneta* are similar to some entelegynes in having a pair of short interior branches and long laterals connected to a single spiracle. This morphology has since been confirmed for all North American leptonetid genera and *Leptoneta infuscata* from Spain.

Given the distribution of leptonetid characters, one may wonder why they are included in the Haplogynae and, more importantly, where they belong in the context of araneomorph relationships? A recent analysis of Entelegynae relationships (Griswold et al., 2005) moved Haplogynae (admittedly underrepresented in the analysis by only two filistatids and one segestriid) to the base of the Neocribellatae, uniting the Entelegynae with the Austrochiloidea on the basis of serrate claw setae, true median tracheae, tartipores, cylindrical gland spigots, cribellate silk fibrils with nodules, and "type II" cribellate silk carding behavior (in which the two legs IV are braced and move together). At least the true median tracheae, tartipores, and cylindrical gland spigots of leptonetids are remarkably similar to this clade. Observations of *Archoleptoneta schusteri* cribellate silk and silk carding behavior will be telling indeed.

The obvious reason for maintaining their current position would be the presence of haplogyne female genitalia. However, if one considers the families Tetragnathidae and Oonopidae, the former of which has lost the entelegyne condition (Hormiga et al., 1995) and the latter that has independently evolved it (Fannes & Jocque, 2008), the argument is not very satisfying. The fusion of the tegulum and subtegulum becomes the single synapomorphy for leptonetids plus other Haplogynae. Other evidence placing Leptonetidae in the Haplogynae consists of characters shared with other haplogyne families, i.e., tibial glands and apparent cylindrical gland spigots with Telemidae and densely packed PLS aciniform gland spigots with Telemidae and Ochyroceratidae. Both of these families lack tartipores, and at least ochyroceratids have the cheliceral lamina, a classic synapomorphy for Haplogynae. However, the patellar and tibial glands, or at least structures very similar to them morphologically, are known in the families Cybaeidae and Salticidae, which suggests the potential for a much broader distribution of this character among spiders (Bennett, 1989). If the current classification of spiders is accepted at face value (Coddington, 2005), we are not only faced with the same issues of homoplasy discovered by Platnick et al. (1991), but also the *bête noire* of spider character distributions, the unique derivation of the cribellum. While the suggestion of independent evolution of the cribellum is not without precedent (Silva Davila, 2003), it seems unlikely given the presence of several entelegyne synapomorphies in the Leptonetidae. Two scenarios are thus presented: 1) leptonetids are proto- entelegynes and belong in their own superfamily or, 2) leptonetids are sister to the remaining Haplogynae. While we have a preference for the former hypothesis, a formal test will inevitably require a comprehensive reanalysis, including multiple exemplars from the Haplogynae and Entelegynae, which is beyond the scope of this study but currently underway by the Assembling the Tree of Life project.

While the analyses of Platnick et al. (1991) and Ramirez (2000) are landmarks in the understanding of relationships and character distributions among haplogyne spiders, both studies suffer from sparse taxon sampling, especially within the Leptonetidae and potential outgroups. We also find it interesting that the largely intuitive predictions made by Brignoli, despite his lack of modern microscopy resources and a less evolved but very broad understanding of spider relationships, may be closer to reality than shown by modern studies. More importantly, however, these studies reflect how much our understanding of haplogyne spiders has grown, and highlight the need for a comprehensive review of their phylogeny.

Diagnostic Keys

In the absence of males, most archoleptonetines may only be confidently assigned to genus. Three species, *D. arganoi, D. obscura,* and *D. garza* are known from females and are currently not diagnosable except by geography. Both Gertsch (1974) and Platnick (1986, 1994) recognized diagnostic problems within the subfamily and neither prepared diagnostic keys. The key presented here specifically targets male specimens, except for *A. schusteri* and *D. stridulans*, which have diagnostic female genitalia.

Key to the genera of Archoleptonetinae

1- Cribellum and calamistrum present (Figs. 43- 45, 47- 48); males with a sinuous and elongate embolus (E, Fig. 98), a straight prolateral sclerite (PRS, Fig. 98, 101- 102), and lacking stridulatory structures on the carapace and abdomen. Known only from California (Fig. 115) ... Genus *Archoleptoneta* Gertsch

Colulus present (Figs. 46, 57, 61); males with an enlarged prolateral sclerite (PRS, Figs. 80, 83, 86, 89, 92, 94, 96) and with or without stridulatory structures on the carapace and abdomen (Figs. 12, 13, 29, 30, 32). Known from Arizona and Texas south to Panama (Fig, 116) ... Genus *Darkoneta*

Key to the species of *Archoleptoneta*

1- Embolus straight to sinuate, running the length of the tarsus (E, Figs. 76, 98); median sclerite narrow and pointed apically (MS, Figs. 97- 102); females with elongate spermathecae, three times as long as wide and with narrow bases (Fig. 109) ... A. *schusteri* Gertsch
Embolus distinctly curved to the prolateral side of the tarsus (E, Figs. 104, 105, 108); median sclerite broad and rounded apically (MS, Figs. 104, 107); females with spermathecae no more than twice as long as wide, with wide bases (Fig. 110) ... *A. gertschi* **sp. nov.**

Key to the species of *Darkoneta*

1- Males with a distinct stridulatory process on the posterior margin of the carapace and the anterior surface of the abdomen (Figs. 11- 13, 29- 30) ... 2

Without a stridulatory process or females only (Fig. 32- 33) ... 3

2- Male palp with a broad, spoon shaped prolateral sclerite (PRS, Figs. 80, 83) and an elongate embolus extending to the apex of the tarsus (E, Figs. 80, 84) ... *D. stridulans* Platnick (part)

Male palp with a broad, apically pointed prolateral sclerite (PRS, Figs. 86, 89) and a short embolus extending no more than 2/3 the length of the tarsus (E, Figs. 86, 89) ... *D. quetzal* **sp. nov.**

3- Eyes and pigmentation absent (Fig. 32), femur I length 2.2- 2.8x carapace width, male palp with an enlarged prolateral sclerite (PRS, Figs, 92, 96) and a short, stout embolus extending no longer than 1/2 the length of the tarsus ... *D. reddelli* **sp. nov.**

Eyes present, femur I length 1.0- 1.8x carapace width ... 4

4- Females with apically curved spermathecae (Fig. 111), Panama ... *D. stridulans*

Females with spermathecae that are as long as wide, oval to quadrate, not apically curved (Fig. 112, Fig. 5B from Brignoli, 1975), Mexico and Texas ... *D. aranoi*, *D. garza*, *D. obscura*, *D. quetzal*

Taxonomy

Genus *Archoleptoneta* Gertsch, 1974

Type species. *Archoleptoneta schusteri*, Gertsch 1974.
Archoleptoneta Gertsch 1974: 198 (type species *Archoleptoneta schusteri* Gertsch 1974: 199); Platnick 2008.
Archoleptoneta (part): Brignoli 1974: 210- 212; Brignoli 1977: 215- 217; Ledford 2004: 122; Platnick 1994.

Diagnosis. Small (1.16- 1.82 mm), three- clawed, cribellate, six- eyed spiders separated from other leptonetids except *Darkoneta* **gen. nov.** by having the eyes contiguous (Figs. 6- 8, 23, 25); male palpal tarsus cylindrical, lacking a dorsal groove (Fig. 78); bulb suboval with three accessory sclerites (Figs. 76- 77, 98, 101, 104, 107); females with simple, paired receptacula (Figs. 109). Separated from *Darkoneta* **gen. nov.** by having a cribellum, males with a long, tapering embolus that extends to the tip of the tarsus (Fig. 76- 78, 98, 99, 104, 105, 108), and a straight, unmodified prolateral sclerite (PRS, Figs. 98- 99, 101- 102, 104- 105, 107- 108). Females with spermathecae that are longer than wide (Figs. 109- 110).
Synapomorphies. *Archoleptoneta* species are united by features of the male palpal bulb, including the presence of a straight prolateral sclerite (PRS, Figs. 98, 101- 102, 104- 105, 107) and a straight median sclerite (MS, Figs. 98, 101, 104, 107).
Description. Total length 1.16- 1.82. Carapace pale to light- brown, round to oval in dorsal view (Figs. 6- 8, 23), length 1.14- 1.30 x width; smooth; thoracic fovea inconspicuous; rounded along posterior margin in both sexes; six eyes, AME absent; ALE and PME with dark to dusky markings, u- shaped at posterior margin (Figs. 7, 25); OA wider than long, with a single seta anteriad of ALE, two setae posteriad of PLE; chelicerae unmodified, fang promargin with a single large proximal tooth and 6- 8 denticles. Sternum smooth, oval, tapering posteriorly, as long as wide. Abdomen (Figs. 6, 8) oval, pale to light- brown, covered with fine setae; spinning organs (Figs. 43- 44, 47,

49- 56); cribellum oval, divided, with uniformly distributed strobilate spigots, reduced in males (Fig. 53); ALS cylindrical, with 3- 4 tartipores, with at least two major ampullate gland spigots and 3- 5 piriform gland spigots; PMS tetrahedral, females with 2 anterior cylindrical gland spigots, 2 aciniform gland spigots posteriorly (Fig. 51), males retain 2 aciniform gland spigots; female PLS with 2 posterior cylindrical gland spigots and a single spigot on an elongate pointed base, which is replaced by a nubbin in males. Leg formula IV, I, II, III or I, IV, II, III; legs elongate and thin, sparsely covered with fine setae and lacking spines; male femur I 1.50- 1.90 x carapace width, females 1.50- 1.89 x carapace width; middorsal integumentary glands elongate, with single, small pores (Fig. 31). Male palpal femur length 0.57- 0.77 x carapace width; palpal tarsus cylindrical in dorsal view (Fig. 78). Basal haematodocha expandable, bulb suboval, bearing three ventral accessory sclerites at base (Figs. 76, 98, 101, 104, 107) embolus straight to sinuous, extending to the tip of the tarsus (Fig. 76, 98, 104- 105, 108); tarsal organ trilobed (Figs. 37, 39). Female genitalia (Figs. 109- 110) haplogyne, consisting of simple, paired spermathecae.

Composition. Two species, *A. schusteri* Gertsch, 1974 and *A. gertschi* **sp. nov.**

Distribution. Restricted to California (Fig. 115).

Archoleptoneta schusteri **Gertsch, 1974**

(Figs. 1, 6- 10, 23, 25- 26, 33, 35, 37, 39, 41, 43- 45, 47- 48, 49- 56, 76- 78, 97- 102, 109)

Types. Male holotype from 6 miles Southeast of Half Moon Bay, San Mateo County, California, USA (AMNH, examined).

Other Material Examined. USA: California: **Alameda County:** Berkeley, 2.iii.1958, L. M. Smith, 37.87N, 122.26W, 4 females (AMNH); Castro Valley, 24.iii.1941, W. M. Pearce, 37.71N, 122.07W, 1 female (AMNH); Oakland, 30.ii.1953, W. O. Bentinck, 37.77N, 122.21W, 1 female (AMNH); Sinbad Creek, West of Pleasanton, 27.iii.1992, D. Ubick, 37.61N, 121.88W, 1 female (DU); **Contra Costa County**: 1mi. West Orinda, 12.xii.1953, V. Roth, 37.88N, 122.20W, 1 male, 3 females (AMNH); Mt. Diablo State Park, North Gate Road, 22.ii.1991, D. Ubick, 37.88N, 121.98W, 1 female (DU); **Fresno County**: 0.3 mi. South Highway 180 along Highway 63, 29.iii.1991, D. Ubick, 36.72N, 119.28W, 3 males, 2 females, 2 juveniles (DU); **Marin County**: Carson Ridge, 1.i.1961, C. W. O'Brien, 37.96N, 122.63W, 1 male (AMNH); Inverness, xi.1953, V. Roth, 38.083N, 122.83W, 1 female (AMNH); Novato, 7.i.1987, D. Ubick, 38.12N, 122.57W, 1 male, 1 female, 2 juveniles (DU); Novato, Burdell Mountain, 16.iii.1990, D. Ubick and T. S. Briggs, 38.12N, 122.57W, 2 males (DU); Novato, San Marin Drive, 2.i.1986, D. Ubick, 38.12N, 122.57W, 1 male, 3 females (DU); Novato, San Marin Drive, 18.iv.1992, D. Ubick and J. Boutin, 38.12N, 122.57W, 2 males (DU); South Slope of Burdell Mtn., North of Novato, 28.xi.1992, D. Ubick, J. Boutin, C. Griswold, and T. Meikle, 38.12N, 122.57W, 2 males, 8 females, 3 juveniles (CASC); 3mi. NW San Rafael, Terra Linda, 7.iii.1982, D. Ubick and T . S. Briggs, 38.00N, 122.55W, 2 males (DU); Novato, San Marin Drive, 14.iii.1982, D. Ubick, 38.12N, 122.57W, 1 male, 2 females (DU); Novato, San Marin Drive, 7.xii.1985, D. Ubick, 38.12N, 122.57W, 1 male, 3 females (DU); Tiburon, Ring Mtn., 19.iii.1994, D. Ubick, 37.90N, 122.48W, 1 male, 1 female (DU); **Monterey County**: Coast Ridge Trail, 1.vi.1991, D. Ubick, 35.97N, 121.43W, 1 female (DU); Point Cypress, 4mi. NE of Carmel, 23.ii.1957, G. A. Marsh, 36.56N, 121.82W, 1 female (AMNH); **Napa County**: 3mi. North Calistoga, 31.xii.1953, G. A. Marsh, R. O.

Schuster, and V. Roth, 38.62N, 122.57W, 2 females (AMNH); Mt. St. Helena, 31.xii.1953, G. Marsh, R. Schuster, and V. Roth, 38.66N, 122.63W, 1 female (AMNH); **San Benito County:** 12.7mi. SE of Pacines on Panoche Rd., 1.xii.1984, D. Ubick, 36.66N, 121.05W, 1 male, 2 females (DU); **San Francisco County**: Potrero Hill, 18.i.1990, D. Ubick, 37.75N, 122.39W, 1 male (DU); Potrero Hill, 23.xii.1988, T. S. Briggs, 37.75N, 122.39W, 1 female (DU); **San Mateo County**: Belmont, 5.iii.1961, R. O. Schuster, 37.51N, 122.29W, 1 female (AMNH); Canada College, 23.x.1988, T. S. Briggs, 37.44N, 122.26W, 2 females (DU); Edgewood Park, 2.i.1987, D. Ubick, 37.47N, 122.28W, 1 female, 2 juveniles (DU); Edgewood Park, 24.xii.1987, D. Ubick, 37.47N, 122.28W, 1 male (DU); Polhemus Rd., 2.i.1983, D. Ubick, 37.52N, 122.34W, 3 females (DU); San Bruno Mountain, 1.iii.1992, D. Ubick, 37.68N, 122.43W, 1 female (DU); San Bruno Mountain, 18.i.1992, D. Ubick, 37.68N, 122.43W, 1 female (DU); Sharp Park, 29.iii.1960, S. F. Bailey, 37.63N, 122.47W, 1 male (AMNH); Jasper Ridge Biological Reserve, 30.xii.1988, D. Ubick, 37.40N, 122.24W, 3 females, 2 juveniles (DU); **Santa Clara County:** Henry Coe State Park, 31.iii.1989, D. Ubick, 37.21N, 121.51W, 1 female (DU); Mt. Madonna, 2.i.1954, R. Burdick, 37.01N, 121.70W, 1 male, 6 females (AMNH); San Antonio Valley Rd., 7.iv.1991, D. Ubick, 37.35N, 121.54W, 1 female (DU); Santa Teresa County Park, South end, serpentine grassland, 10.ii.1989, 37.21N, 121.78W, D. Ubick, 1 female (DU); Shaeirn Ranch, 5.2mi. North Bell Station, 10.ii.1991, D. Ubick, W. Rauscher, 37.11N, 121.31W, 6 females (DU); Stevens Creek, 2.vi.1957, R. O. Schuster, 37.27N, 122.07W, 2 males, 6 females (AMNH); Stevens Creek, 27.vii.1957, G. A. Marsh, 37.27N, 122.07W, 1 female (AMNH); **Santa Cruz County**: 9.5mi. NE of Soquel, 31.xii.1956, S. M. Fidel, 37.11N, 121.95W, 6 males, 1 female, 8 juveniles (AMNH); Ben Lomond, 21.vi.1953, C. D. MacNeill, 37.07N, 122.08W, 1 male (AMNH); Santa Boulder Creek, 22.i.1955, Burdick and Wasbauer, 37.13N, 122.12W, 1 female (AMNH); Cave Gulch, 18.vi.1984, D. Ubick, 36.99N, 122.07W, 1 female (DU); Shasta County: outside Potter Creek Cave, 8.vi.1995, D. Ubick, 40.78N, 122.28W, 1 female (DU); **Sonoma County**: 1.5mi. East Healdsburg, 29.iii.1981, D. Ubick, 38.62N, 122.83W, 1 female (DU); Mark West Springs, 31.xii.1953, Roth, Schuster, and Marsh, 38.54N, 122.72W, 1 female (AMNH); **Tulare County**: Bacon Hill, 24.iii.1991, D. Ubick, T. Briggs, and W. Rauscher, 36.45N, 119.18W, 1 male (DU); Sequoia/ Kings Cyn. National Park, Clough Cave, 27.iv.2004, J. Krejca, P. Sprouse, S. Fryer, D. Ubick, P. Paquin, 36.35N, 118.76W, 2 females (CASC).

Diagnosis. Separated from *Archoleptoneta gertschi* **sp. nov.** by having males with an embolus that runs the length of the tarsus (Figs. 76, 98) and an apically pointed median sclerite (Figs. 98, 101). Females with elongate spermathecae on narrow bases, approximately three times as long as wide (Fig. 109).

Description. Male (holotype)**.**

Total length 1.36. Specimen yellow- orange; missing left leg II and patella- tarsus of legs III & IV.

Carapace 0.55 long, 0.48 wide, height at fovea 0.23 x carapace width; clypeus 0.08 high, chelicerae 0.23 long. Ocular area 0.04 long, 0.06 wide. Sternum 0.4 long, 0.35 wide; labium 0.03 long, 0.09 wide; palpal coxae 0.19 long, 0.11 wide.

Legs covered with fine setae. Leg formula IV, I, II, III. Measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 0.76 + 0.21 + 0.20 + 0.58 + 0.40 = [2.15]; II: 0.64 + 0.20 + 0.53 + 0.47 + 0.28 = [2.12]; III: 0.58 + 0.18 + 0.46 + 0.43 + 0.34

= [1.99]; IV: 0.76 + 0.18 + 0.69 + 0.52 + 0.38 = [2.53]; pedipalpus: 0.32 + 0.08 + 0.15 + 0.29 = [0.84]. Femur I 1.58 x carapace width, palpal femur 0.66 x carapace width.

Palpal bulb 0.17 long, 0.13 wide; embolus sinuous and extending to the tip of the tarsus. Prolateral sclerite straight, produced to a blunt point apically; median sclerite with a slight retrolateral bend and tapering to a fine point; retrolateral sclerite tapering to a fine point.

Abdomen pale, without pattern, 0.81 long, 0.50 wide.

Variation (*n* = 8). Total length 1.23- 1.77; carapace length 1.15- 1.23 x carapace width; OAL 0.50- 0.66 x OAW; length femur I 1.58- 1.90 x carapace width, palpal femur 0.59- 0.67 x carapace width. Embolus straight (Fig. 98) to sinuous (Fig. 76).

Female (Soquel).

Total length 1.45. Coloration and markings identical to male.

Carapace 0.60 long, 0.48 wide, height at fovea 1.4 × carapace width; clypeus 0.09 high, chelicerae 0.24 long. Ocular area 0.40 long, 0.70 wide. Sternum as long as wide; labium 0.03 long, 0.08 wide; palpal coxae 0.18 long, 0.06 wide.

Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 0.73 + 0.21 + 0.65 + 0.55 + 0.39 = [2.53]; II: 0.61 + 0.18 + 0.55 + 0.47 + 0.35 = [2.16]; III: 0.58 + 0.19 + 0.47 + 0.44 + 0.32 = [2.0]; IV: 0.73 + 0.19 + 0.69 + 0.50 + 0.37 = [2.48]; pedipalpus: 0.23 + 0.11 + 0.16 + 0.24 = [0.74]. Femur I 1.5 × carapace width, palpal femur 0.47 × carapace width.

Abdomen 0.85 long, 0.73 wide. Spermathecae longer than wide and with narrow bases (Fig. 109) .

Variation (*n* = 5). Total length 1.45- 1.82; carapace length 1.20- 1.27 × carapace width; OAL 0.57- 0.67 × OAW; length femur I 1.50- 1.72 × carapace width, palpal femur 0.42- 0.61 × carapace width.

Distribution. Widespread in California (Fig.115) from Sonoma County south to Monterey County and east to Fresno County.

Natural History. *Archoleptoneta schusteri* occurs in a variety of habitats but are most commonly encountered under moist stones and leaf litter. Several populations in the Bay Area are abundant on serpentine soils. The eggsac is a flattened disc, which contains 4- 6 eggs, adhered to the bottom of stones. Specimens maintained in captivity produced minimal silk and cribellate carding behavior has not been observed.

Archoleptoneta gertschi, **sp. nov.**

(Figs. 103- 108, 110)

Type material. Male holotype from 3 miles South- Southeast Jackson, Amador County, California, USA (CASC).

Other material examined. Amador County: 0.5mi. North of Mokelumne on Hwy 49, 5.iii.1958, L. M. Smith and R. O. Schuster, 38.30N, 120.70W, 3 females (AMNH); 3mi. SSE Jackson, 27.xii.1965, J. S. Buckett, M. R. and R. C. Gardner, 38.32N, 120.73W, 2 females (CASC); Connie's Cave, 0.5 mi. N. Volcano, 15.iv.1979, Rudolph, Winterath, Van Ingen, and Cowan, 38.44N, 120.63W, 1 female (AMNH); Pardee Reservoir, Chrome Cave Area, 24.i.1981, D. Ubick, 38.28N, 120.86W, 2 females (DU); 2mi. Northeast of Jackson, 16.iv.1957, L. M. Smith and R. O. Schuster, 38.37N, 120.75W, 1 male, 3 females (AMNH); near Buckeye Root Cave, Volcano City, 6.i.2007, N. Dupérré, J. Ledford, and P. Paquin 38.44N, 120.63W, 1 male, 6 females (CASC); near Humming

Bird Cave, Volcano city, 6.i.2007, N. Dupérré, J. Ledford, and P. Paquin 38.44N, 120.63W, 6 females (CASC); **Calaveras County:** 2mi. West San Andreas, 25.iii.1958, L. M. Smith and R. O. Schuster, 38.19N, 120.71W, 1 female (AMNH); 6.0mi. NW Columbia, Peruvian Gulch, 10.v.1980, D. Ubick, 38.08N, 120.49W, 1 female (DU); Grapevine Gulch Cave, 7mi. ESE Angels Camp, 27.iv.1977, A. G. Grubbs, S. Hewson, M. McEachern, and J. Montre, 38.09N, 120.42W, 2 females (AMNH); Moaning Cave, 6.4km East Angels Camp, 6.xii.1977, W. R. Elliott, A. G. Grubbs, and S. A. Winterath, 38.06N, 120.46W, 6 females (AMNH); Peruvian Gulch, Speleogen Cave, 24.iii.2000, D. Ubick and S. Ubick, 38.04N, 120.47W, 1 female (DU); Airola Rd., 05.i.2007, N. Dupérré, J. Ledford, and P. Paquin, 38.04N, 120.48W, 1 female (CASC); El Dorado County: Crystal Cosumnes Cave, 07.i.2007, N. Dupérré, J. Ledford, and P. Paquin, 1 female (CASC); 6mi. SW Highway 49 on Rattlesnake Bar Road, 4.ii.1995, D. Ubick, 38.78N, 121.08W, 4 females (DU); **Placer County:** 4 mi. West Newcastle, 10.iii.1959, R. O. Schuster and L. M. Smith, 38.87N, 121.20W, 1 female (AMNH); 4 mi. West Newcastle, 10.iii.1959, L. M. Smith and R. O. Schuster, 38.87N, 121.20W, 2 females (AMNH); 4mi. West Newcastle, 3.i.1959, F. Raney and R .O. Schuster, 38.87N, 121.20W, 2 females (AMNH);

Diagnosis. Separated from *A. schusteri* by having males with the embolus distinctly bent perpendicular to prolateral side of the tarsus (Figs. 104, 105, 108) and with a broad median sclerite (Fig. 104, 107). Females with spermathecae that are approximately twice as long as wide and with broad bases (Fig. 110).

Description. Male (holotype)

Total length 1.31. Specimen pale, lacking any distinctive markings.

Carapace 0.55 long, 0.45 wide, height at fovea 0.46 x carapace width; clypeus 0.08 high, chelicerae 0.21 long. Ocular area 0.05 long, 0.11 wide. Sternum as long as wide; labium 0.05 long, 0.08 wide; palpal coxae 0.15 long, 0.10 wide.

Legs sparsely setose and lacking spines. Leg formula I, IV, II, III. Measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 0.71 + 0.21 + 0.68 + 0.58 + 0.35= [2.63]; II: 0.60 + 0.19 + 0.52 + 0.48 + 0.31 = [2.1]; III: 0.53 + 0.15 + 0.44 + 0.40 + 0.32 = [1.84]; IV: 0.74 + 0.16 + 0.66 + 0.52 + 0.34 = [2.42]; pedipalpus: 0.26 + 0.10 + 0.15 + 0.27 = [0.78]. Femur I 1.57 x carapace width, palpal femur 0.57 x carapace width.

Palpal bulb 0.24 long, 0.11 wide. Prolateral sclerite straight, produced to a blunt point apically; median sclerite broad with a shallow central depression; retrolateral sclerite broad at its base and tapering to a fine point apically.

Abdomen pale, without pattern, 0.76 long, 0.45 wide.

Variation (*n* = 2). Total length 1.30- 1.32; carapace length 1.21- 1.30 x carapace width; OAL 0.43- 0.57 x OAW; length femur I 1.57- 1.69 x carapace width, palpal femur 0.57- 0.65 x carapace width.

Female (paratype)

Total length 1.35. Coloration identical to male, missing patella- tarsus of leg I. Carapace 0.56 long, 0.47 wide, height at fovea 0.38 × carapace width; clypeus 0.08 high, chelicerae 0.21 long. Ocular area 0.06 long, 0.11 wide. Sternum 0.34 long, 0.26 wide; labium 0.05 long, 0.09 wide; palpal coxae 0.15 long, 0.11 wide.

Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 0.69 + missing + missing + missing + missing = [N/A]; II: 0.56 + 0.18 + 0.58 + 0.44 + 0.32 = [2.08]; III: 0.52 + 0.18 + 0.42 + 0.39 + 0.31 = [1.82]; IV: 0.71 + 0.19 + 0.63 +

0.47 + 0.34= [2.34]; pedipalpus: 0.26 + 0.10 + 0.15 + 0.29 = [0.8]. Femur I 1.48 x carapace width, palpal femur 0.55 x carapace width.

Abdomen pale, without pattern, 0.79 long, 0.56 wide. Spermathecae slightly longer than wide and with wide bases (Fig. 110).

Variation ($n = 3$). Total length 1.16- 1.31; carapace length 1.20- 1.30 × carapace width; OAL 0.42- 0.45 × OAW; length femur I 1.30- 1.89 × carapace width, palpal femur 0.45- 0.51 × carapace width.

Etymology. This species is named in honor of Willis Gertsch, who discovered and described many species of North American Leptonetidae and was a pioneer of North American arachnology.

Natural History. Several records for *A. gertschi* **sp. nov.** are from caves in the Mother Lode region of California. Some specimens from caves (particularly Grapevine Gulch Cave) have longer legs than surface populations but no additional troglomorphic morphology. Specimens are most commonly encountered at cave entrances or in the twilight zone under moist stones.

Distribution. Known from localities in Amador, Calaveras, El Dorado, and Placer counties (Fig. 115).

***Darkoneta*, gen. nov.**

(Figs. 11- 17, 29, 30, 32, 34, 46, 57- 64, 79- 84, 85- 90, 91- 96, 111, 112, 116)

Type species. *Archoleptoneta stridulans* Platnick, 1994, here designated.

Etymology. This genus is named in honor of Darko Ljubić (Darrell Ubick), a trusted friend, colleague, and collector of many leptonetids throughout North America and Europe.

Diagnosis. Small (0.87-1.28 mm), three- clawed, ecribellate, six- eyed or blind spiders separated from all other leptonetids except *Archoleptoneta* by having the eyes contiguous (Figs. 11- 13); male palpal tarsus cylindrical; bulb suboval with three accessory sclerites and a tapering embolus (Figs. 80, 83, 86, 89, 92, 95); females with simple, paired receptacula (Fig. 111- 112). Separated from *Archoleptoneta* by having a rectangular colulus (Fig. 46, 57, 61) and males with a stout prolateral accessory sclerite (PRS, Figs. 80, 83, 86, 89, 92, 94).

Synapomorphies. *Darkoneta* **gen. nov.** species are united by the presence of a colulus (Figs. 46, 57, 61) and an enlarged, modified prolateral sclerite on the male palpal bulb (PRS, Figs. 80, 83, 86, 89, 92, 94).

Description. Total length 0.87- 1.28. Carapace pale to orange, round to oval in dorsal view (Figs. 6- 8, 16), elevated in lateral profile (Fig. 16- 17), length 1.10- 1.33 x width; smooth; thoracic fovea inconspicuous; carapace rounded along posterior margin in females, males of *D. stridulans* and *D. quetzal* **sp. nov.** with posterior stridulatory structures (Fig. 12- 13, 29- 30), all other species unmodified; six eyes (Fig. 29) or blind (Fig. 32), AME absent; ALE and PLE with dark to dusky markings (Fig. 11- 13); OA wider than long, with a single seta anteriad of ALE, two setae posteriad of PLE; fang furrow with 5- 6 teeth on the promargin and 0- 2 teeth on the retromargin. Sternum smooth, tapering posteriorly, as long as wide. Abdomen (Figs. 11- 12, 14- 17) oval, pale to light- brown, covered with fine setae; stridulatory files present anteriorly in males of *D. stridulans* and *D. quetzal* **sp. nov.**; spinning organs (Figs. 46, 57- 64); colulus recatangular (Fig. 46, 57, 61); ALS cylindrical, with 1- 3 tartipores, a single elongate spigot anteriorly, and 4 spigots of varying size on short, circular bases, and at least one spigot lacking a base; PMS tetrahedral, females with 2- 4 spigots on short, circular bases, 1- 2 spigots on a thickened base anteriorly (Fig. 59), with or without a single nubbin (Fig. 59), male PMS with 1- 2 spigots on short, circular bases; PLS with 1- 2 spigots on an elongate pointed base in females, absent in males. Leg formula I, IV, II, III or IV, I, II, III; legs elongate and thin, sparsely covered with fine setae and lacking spines; male femur I 1.19- 2.80 x carapace width, females 1.13- 2.3 x carapace width; middorsal integumentary glands elongate, with single, small pores (Figs. 7- 8 in Platnick, 1994). Male palpal femur length 0.50- 0.78 x carapace width. Basal haematodocha expandable, bulb suboval, bearing three flexibly attached accessory sclerites at base (Figs. 80, 83, 86, 89, 92, 95), embolus tapered or broad. Female genitalia (Fig. 111- 112) haplogyne, consisting of simple, paired recaptacula.

Composition. Six species; *D. arganoi* (Brignoli, 1975) **comb. nov**, *D. garza* (Gertsch, 1974) **comb. nov**, *D. obscura* (Gertsch, 1974) **comb. nov**, *D. quetzal* **sp. nov.**, *D. reddelli* **sp. nov.**, and *D. stridulans* (Platnick, 1994) **comb. nov**.

Distribution. Known from localities in Arizona, Mexico, Panama, Guatemala, and Texas (Fig. 116).

Darkoneta quetzal, **sp. nov.**

(Figs. 11- 17, 29- 30, 34, 57- 64, 85- 90, 112)

Type material. Male holotype from Sierra de Las Minas, 9 km North of San Lorenzo, Dep. Zacapa, Guatemala (AMNH).

Other material examined. Guatemala: Dep. Zacapa, Sierra de Las Minas, 9 km North of San Lorenzo, 17.xi.1986, E. Lindquist, 3 females, 2 males (AMNH).

Diagnosis. Separated from all *Darkoneta* species except *D. stridulans* (Figs. 79- 84) by having males with a posterior stridulatory mechanism on the carapace and abdomen (Figs. 29- 30). Separated from *D. stridulans* by details of the male palpal bulb, including: a prolaterally bent embolus extending no more than 2/3 the length of the tarsus (E, Figs. 86, 89) and a broad, sharply pointed prolateral sclerite (PRS, Figs. 86, 89).

Description. Male (holotype)

Total length 0.9. Specimen pale orange, darker around carapace margins and gradually lighter towards fovea.

Carapace 0.47 long, 0.36 wide, height at fovea 0.50 x carapace width; clypeus 0.08 high, chelicerae 0.22 long. Ocular area 0.05 long, 0.09 wide. Sternum 0.34 long, 0.28 wide; labium 0.05 long, 0.08 wide; palpal coxae 0.15 long, 0.08 wide.

Legs covered in fine setae. Leg formula I, IV, II, III. Measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 0.43 + 0.15 + 0.39 + 0.30 + 0.25 = [1.52]; II: 0.36 + 0.14 + 0.29 + 0.27 + 0.23 = [1.29]; III: 0.30 + 0.12 + 0.23 + 0.24 + 0.21 = [1.10]; IV: 0.43 + 0.14 + 0.37 + 0.30 + 0.24= [1.48]; pedipalpus: 0.18 + 0.08 + 0.11 + 0.19 = [0.56]. Femur I 1.19 x carapace width, palpal femur 0.5 x carapace width.

Palpal bulb 0.11 long, 0.09 wide. Prolateral sclerite broad, triangular and with a retrolateral bend; median sclerite procurved and sharply tapering retrolaterally; retrolateral sclerite similar to median sclerite and sharply tapering retrolaterally; embolus short, thin, and tapering apically.

Abdomen pale, without pattern, 0.43 long, 0.31 wide.

Female (paratype)

Total length 0.93. Coloration and markings identical to male. Carapace 0.44 long, 0.36 wide, height at fovea 0.61 × carapace width; clypeus 0.8 high, chelicerae 0.23 long. Ocular area 0.06 long, 0.10 wide. Sternum 0.29 long, 0.23 wide; labium 0.5 long, 0.8 wide; palpal coxae 0.18 long, 0.10 wide.

Leg measurements (Femur + Patella + Tibia + Metatarsus + Tarsus = [Total]): I: 0.41 + 0.14 + 0.30 + 0.23 + 0.21 = [1.29]; II: 0.31 + 0.11 + 0.24 + 0.21 + 0.21 = [1.29]; III: 0.27 + 0.14 + 0.31 + 0.20 + 0.17 = [1.09]; IV: 0.38 + 0.15 + 0.32 + 0.25 + 0.21 = [1.31]; pedipalpus: 0.16 + 0.06 + 0.11 + 0.17 = [0.5]. Femur I 1.13 x carapace width, palpal femur 0.44 x carapace width.

Abdomen pale, without pattern, 0.49 long, 0.37 wide. Spermathecae as long as wide (Fig. 112).

Variation (*n* = 2). Total length 0.93- 1.10; carapace length 1.22- 1.24 × carapace width; OAL 0.55- 0.60 × OAW; length femur I 1.05- 1.14 × carapace width, palpal femur 0.44- 0.49 × carapace width.

Etymology. This species is named for Quetzalcoatl, the feathered serpent diety worshipped throughout Mesoamerica as the patron god of knowledge and learning; also the quetzal, the national symbol of Guatemala.

Distribution. Known only from the type locality in the Sierra de Las Minas, Guatemala.

Darkoneta reddelli, **sp. nov.**

(Figs. 32, 46, 91- 96)

Type material. Male holotype from Cueva de Tasalolpan, 5 km southwest of Cuetzalan, Puebla, Mexico (AMNH).

Other material examined. Mexico: Puebla: Cueva de Tasalolpan, 5 km southwest Cuetzalan, 20.02N, 97.54W, 22.xii.1976, J. Reddell, A. Grubbs, C. Soileau, D. McKenzie, 2 females, 6 juveniles (AMNH).

Diagnosis. Pale, eyeless troglobite (Fig. 32) separated from other *Darkoneta* species by having males with a stout embolus that extends 1/2 the length of the tarsus (Fig. 92, 95) and a proventrally curved and thickened prolateral sclerite (Fig. 96).

Description. Male (holotype). Total length 0.87. Specimen pale, eyeless; missing patella- tarsus for all legs.

Carapace 0.38 long, 0.32 wide, height at fovea 0.56 x carapace width; clypeus 0.04 high, chelicerae 0.21 long, fang furrow with three small teeth on retromargin and a single large proximal tooth. Sternum 0.26 long, 0.28 wide; labium .05 long, .06 wide; palpal coxae .12 long, .07 wide.

Femora elongate and covered with fine setae. Leg measurements (Femur only): I: 0.9; II: 0.58; III: 0.73; IV: 0.93; pedipalpus: 0.25 + 0.09 + 0.11 + 0.25 = [0.7]. Femur I 2.8 x carapace width, palpal femur 0.78 x carapace width.

Palpal bulb 0.15 long, 0.08 wide; Prolateral sclerite enlarged and with a retrolateral bend; median sclerite long and thin, tapering retrolaterally; retrolateral sclerite sharply tapering retrolaterally; embolus short, enlarged, and extending 1/2 the length of the tarsus.

Abdomen pale, without pattern, 0.49 long, 0.34 wide.

Remarks. This series of specimens includes eight individuals, two of which are adult males. Most of the specimens are missing leg segments and their abdomens. While a female individual is almost certainly a part of the series, the absence of abdomens makes it impossible to identify a mature specimen, therefore no female is described.

Etymology. This species is named in honor of James Reddell, collector of this and many other species of leptonetids throughout North America.

Distribution. Known only from Cueva de Tasalolpan, Puebla, Mexico.

Acknowledgements

We thank James Cokendolpher, Pierre Paquin, Norman Platnick, Martin Ramirez, and Darrell Ubick for many insightful discussions about leptonetid siders. Martín Ramírez and Norm Platnick critically read a draft of the manuscript. The personal collection of Darrell Ubick was invaluable to the project, and has added numerous records since Gertsch (1974). Jillian Cowles and Bill Savary provided the first specimens known from Arizona. We also thank the following for loaning specimens: Norman Platnick and Louis Sorkin, American Museum of Natural History, Petra Sierwald and James Boone, Field Museum of Natural History, and James Cokendolpher, Museum of Texas Tech University. Rolf Aalbu, Nadine Duperre, Martin Haye, Karin Ledford, Dan Snyder, and Steve Synhorst provided assistance in the field. Members of the Mother Lode Grotto facilitated access to caves. Marlee Phillips assisted in the construction of distribution maps as part of the 2007 Pinhead Institute Fellows Program. Peter Sprouse provided precise localities for Mexican caves. Lou Sorkin at the AMNH kindly packed several loans of leptonetids. Martín Ramírez (MJR) generously provided the image of the tracheal system of *Appaleptoneta*. We also thank the members of the Evolab at U.C. Berkeley, especially Rosemary Gillespie and George Roderick, for financial support. This project was funded by awards from the National Science Foundation (DDIG-0909872 and EAR- 0228699), the Western Region of the National Speleological Society, the National Speleological Society, the Walker Fund at the University of California, Berkeley, and the Harriet Exline- Frizzell Fund at the California Academy of Sciences.

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Captions

Figures 1- 5: Images of living Leptonetidae.
1. *Archoleptoneta schusteri* female, Marin County, CA, USA; 2. *Neoleptoneta myopica* female, Tooth Cave, Travis County, TX, USA; 3. *Neoleptoneta myopica* male, Tooth Cave, Travis County, TX; 4. Web of *Neoleptoneta myopica*, Tooth Cave, Travis County, TX; 5. Eggsac of *Neoleptoneta anopica*, Corn Cobb's Cave, Williamson County, TX.

Figures 6- 10: *Archoleptoneta schusteri*, Burdell Mountain, Marin County, CA, USA.
6. Female habitus, dorsal; 7. Female carapace, dorsal; 8. Male habitus, dorsal; 9. Female habitus, lateral; 10. Male habitus, lateral.

Figures 11- 17: *Darkoneta quetzal* **sp. nov.**, Sierra de Las Minas, Guatemala. 11. Female habitus, dorsal; 12. Male habitus, dorsal; 13. Male carapace, dorsal; 14. Female habitus, ventral; 15. Male habitus, ventral; 16. Female habitus, lateral; 17. Male habitus, lateral.

Figures 18- 22: *Leptoneta infuscata,* Cova de l'avenc del Pla de Comes, Spain.
18. Female habitus, dorsal; 19. Female carapace, dorsal; 20. Male carapace, dorsal; 21. Female habitus, lateral; 22. Male habitus, lateral.

Figures 23- 28: Eyes of Leptonetidae
23. *Archoleptoneta schusteri* female carapace, dorsal, Burdell Mountain, Marin County, CA, USA; 24. *Leptoneta infuscata* female carapace, dorsal, Cova de l'avenc del Pla de Comes, Spain; 25. *A. schusteri* female, eyes, dorsal, Burdell Mountain; 26. *A. schusteri* female, eyes, lateral, Burdell Mountain; 27. *L. infuscata* female, eyes, dorsal, Cova de l'avenc; 28. *L. infuscata* female, eyes, lateral, Cova de l'avenc.

Figures 29- 34: Archoleptonetinae general morphology
29. *Darkoneta quetzal* **sp. nov.**, male carapace, dorsal, arrows to stridulatory picks; 30. *Darkoneta quetzal* **sp. nov.**, stridulatory structures, dorsal; 31. *Archoleptoneta schusteri*, female, Burdell Mountain, Marin Co., CA, patella III, dorsal, showing gland; 32. *Darkoneta reddelli* **sp. nov.**, juvenile carapace, dorsal; 33. *Archoleptoneta schusteri*, female, Burdell Mountain, Marin Co., CA, carapace, posterior; 34. *Darkoneta quetzal* **sp. nov.**, male abdomen, ventral, showing gonopore anteriad of epigastric furrow.

Figures 35- 42: General Morphology, SEM
35. *Archoleptoneta schusteri*, female, right endite, ventral, Burdell Mountain, Marin County, CA, USA, arrows to paired stout setae; 36. *Leptoneta infuscata*, female, left endite, ventral, Cova de l'avenc, Spain; 37. *A. schusteri*, female, tarsal organ, right tarsus, leg I, Burdell Mountain; 38. *L. infuscata*, female, tarsal organ, right tarsus, leg I, Cova de l'avenc, Spain; 39. *A. schusteri*, male, tarsal organ, right tarsus, leg I, Burdell Mountain; 40. *L. infuscata*, male, tarsal organ, right tarsus, leg I, Cova de l'avenc, Spain; 41. *A. schusteri*, female, left chelicera, Burdell Mountain; 42. *Neoleptoneta myopica*, female, right chelicera, Gallifer Cave, Travis County, TX, USA.

Figures 43- 48: Archoleptonetinae spinnerets and calamistra, SEM

43. *Archoleptoneta schusteri*, female, spinnerets, ventral, Burdell Mountain, Marin County, CA, USA; 44. *A. schusteri*, female, cribellum, Burdell Mountain; 45. *A. schusteri*, female, calamistrum, right metatarsus IV, Burdell Mountain; 46. *Darkoneta stridulans*, female, spinnerets, ventral, Chiriqui, Panama; 47. *A. schusteri*, female, cribellum, spigots, Burdell Mountain; 48. *A. schusteri*, female, calamistrum, right metatarsus IV, Burdell Mountain.

Figures 49- 56: *Archoleptoneta schusteri*, spinnerets, Burdell Mountain, Marin County, CA, USA.
49. Female spinnerets, ventral; 50. Female right ALS; 51. Female PMS; 52. Female right PLS; 53. Male spinnerets ventral; 54. Male left ALS; 55. Male PMS; 56. Male left PLS. AC, aciniform gland spigots; CY, cylindrical gland spigots; MAP, major ampullate gland spigot(s); mAP, minor ampullate gland spigot(s); MSp, possible modified spigot; Nu MSp, nubbin of possible modified spigot; PI, piriform gland spigots; TP, tartipore.

Figures 57- 64: *Darkoneta quetzal* **sp. nov.**, spinnerets, Sierra de Las Minas, Guatemala
57. Female spinnerets, ventral; 58. Female right ALS; 59. Female PMS; 60. Female right PLS; 61. Male spinnerets, ventral; 62. Male right ALS; 63. Male PMS; 64. Male left PLS. CY, cylindrical gland spigots; MAP, major ampullate gland spigot(s); mAP, minor ampullate gland spigot(s); Nu, nubbin; PI, piriform gland spigots; PI*, piriform gland spigots lacking a base; TP, tartipore.

Figures 65- 72: *Leptoneta infuscata*, spinnerets, Cova de l'avenc, Spain.
65. Female spinnerets ventral; 66. Male spinnerets, ventral; 67. Female right ALS, 68. Female PMS; 69. Female PLS; 70. Male left ALS; 71. Male left PMS and PLS; 72. Male left PLS. CY, cylindrical gland spigots; MAP, major ampullate gland spigot(s); TP, tartipore.

Figures 73- 78: Comparative views of archoleptonetine and leptonetine palps.
73- 75: *Leptoneta infuscata*, right palp, Cova de l'avenc, Spain. 73. Ventral, 74. Retrolateral, 75. Dorsal. 76- 78: *Archoleptoneta schusteri*, right palp, Burdell Mountain, Marin County, USA. 76. Ventral, 77. Retrolateral, 78. Dorsal. E, embolus; MS, median sclerite; PRS, prolateral sclerite; RLS, retrolateral sclerite.

Figures 79- 84: Microstructure views of *Darkoneta stridulans*, male right palp, Chiriqui, Panama.
79. Retrolateral; 80. Ventral; 81. Prolateral; 82. Bulb, retrolateral; 83. Accessory sclerites, ventral; 84. Accessory sclerites, ventral. E, embolus; MS, median sclerite; PRS, prolateral sclerite; RLS, retrolateral sclerite.

Figures 85- 90: Microstructure views of *Darkoneta quetzal* **sp. nov.**, male right palp, Sierra de Las Minas, Guatemala.
85. Retrolateral; 86. Ventral; 87. Prolateral; 88. Bulb, retrolateral; 89. Accessory sclerites, ventral; 90. Accessory sclerites, prolateral. E, embolus; MS, median sclerite; PRS, prolateral sclerite; RLS, retrolateral sclerite.

Figures 91- 96: Microstructure views of *Darkoneta reddelli* **sp. nov.**, male right palp, Cueva de Tasalolpan, Mexico.
91. Retrolateral; 92. Ventral; 93. Prolateral; 94. Bulb, ventral; 95. Embolus, ventral; 96. Accessory sclerites, prolateral. E, embolus; MS, median sclerite; PRS, prolateral sclerite; RLS, retrolateral sclerite.

Figures 97- 102: Microstructure views of *Archoleptoneta schusteri*, male right palp, Soquel, Santa Cruz Co., California, USA.
97. Retrolateral; 98. Ventral; 99. Prolateral; 100. Bulb, prolateral; 101. Accessory sclerites, ventral; 102. Accessory sclerites, prolateral. E, embolus; MS, median sclerite; PRS, prolateral sclerite; RLS, retrolateral sclerite.

Figures 103- 108: Microstructure views of *Archoleptoneta gertschi* **sp. nov.**, male right palp, Calaveras Co., California, USA.
103. Retrolateral; 104. Ventral; 105. Prolateral; 106. Bulb, prolateral; 107. Accessory sclerites, ventral; 108. Accessory sclerites, prolateral. E, embolus; MS, median sclerite; PRS, prolateral sclerite; RLS, retrolateral sclerite.

Figures 109- 114: Leptonetidae female genitalia and respiratory system.
109. *Archoleptoneta schusteri* female genitalia, dorsal, Soquel, Santa Cruz Co.; 110. *Archoleptoneta gertschi*, **sp. nov.**, female genitalia, dorsal, Calaveras Co.; 111. *D. stridulans* female genitalia, dorsal, Panama; 112. *Darkoneta quetzal* **sp. nov.**, female genitalia, dorsal, Guatemala; 113. *L. infuscata* female genitalia, dorsal; 114. *Appaleptoneta* sp. female tracheae, dorsal (image from MJR).

Figures 115- 116: Distribution maps for North American Leptonetidae.
115. Distribution of *Archoleptoneta* in California. *A. schusteri* localities outlined in orange, *A. gertschi* **sp. nov.** localities highlighted in red. Localities for which there are no known males and are in need of additional sampling are outlined in black. 116. Distribution of *Darkoneta*.


1


2
2 mm


3
2 mm


4
0.5 cm


5
3 mm


6


7


8


9


10


11

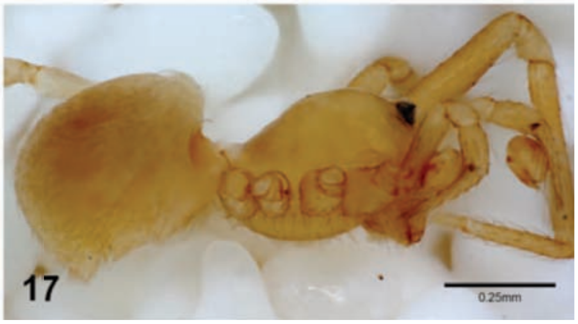

12


13


14


15


16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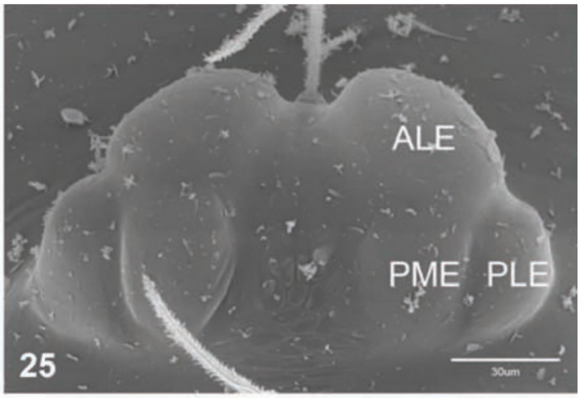
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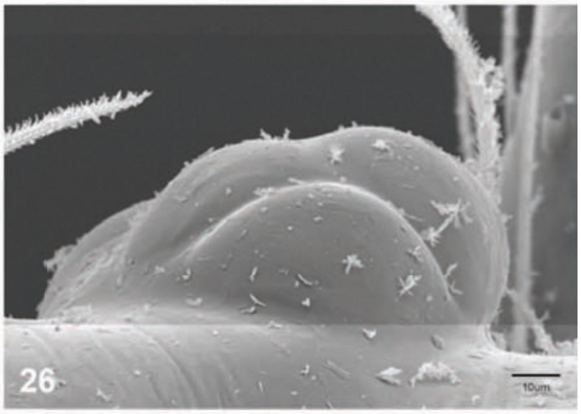
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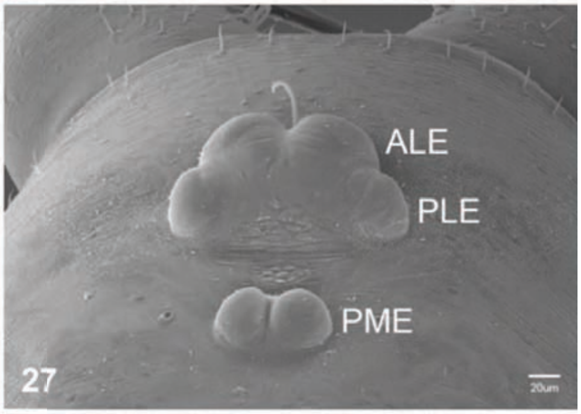
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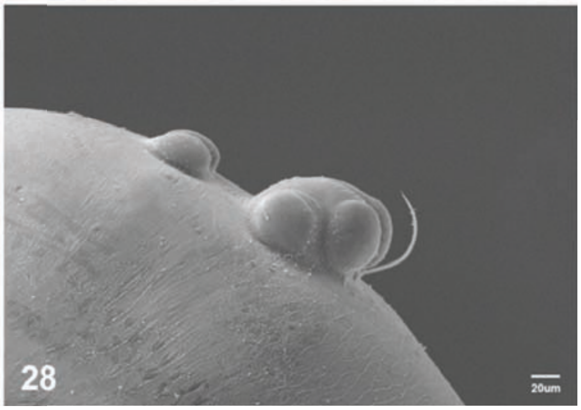
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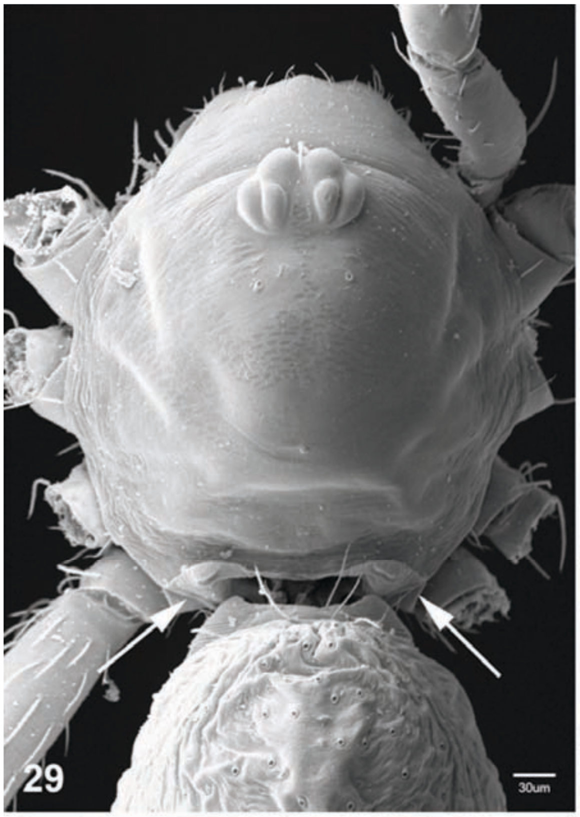
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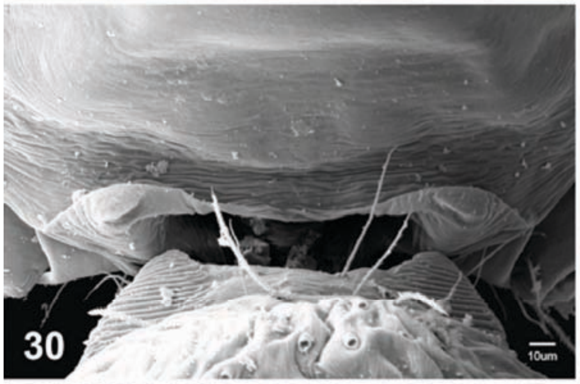
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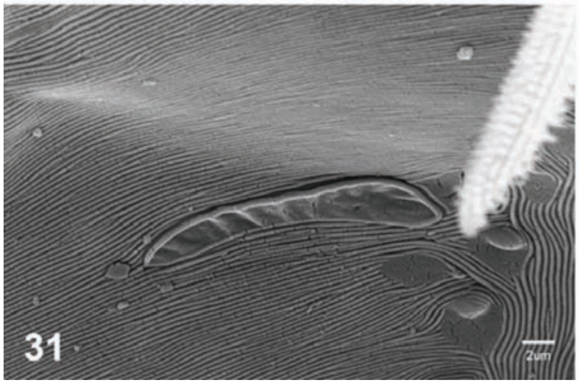
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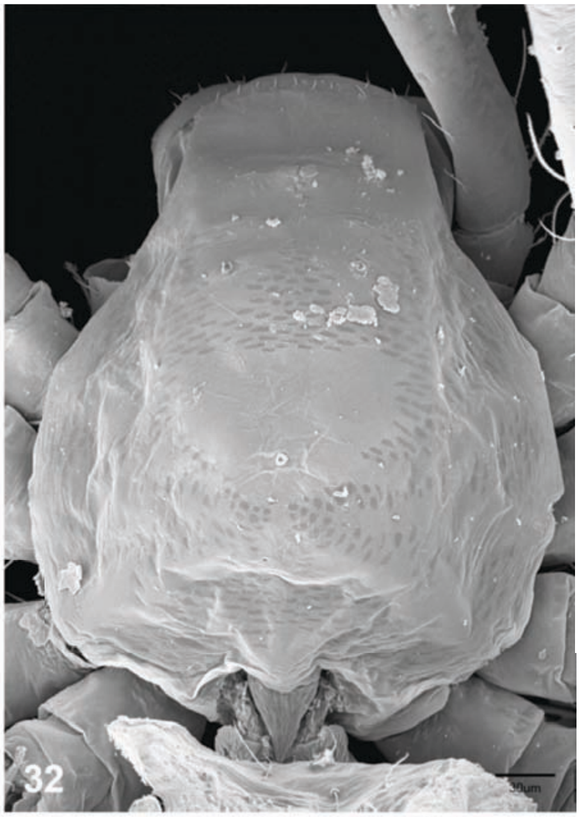
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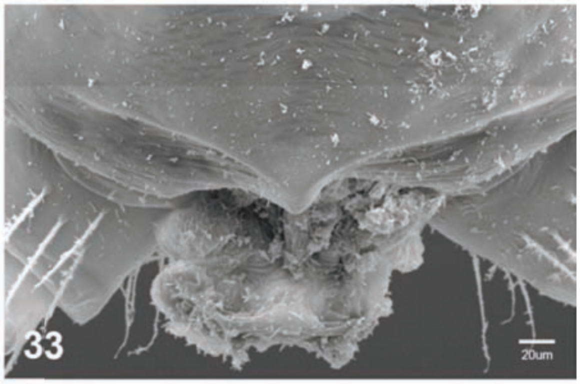
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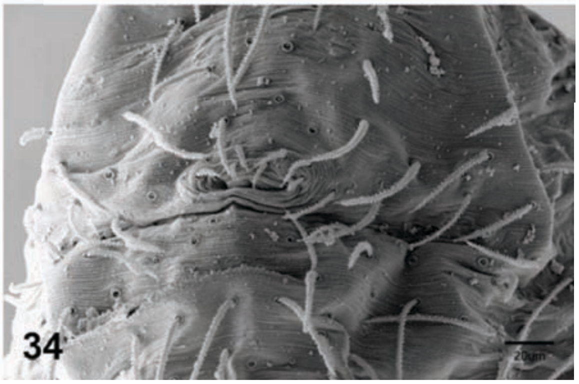
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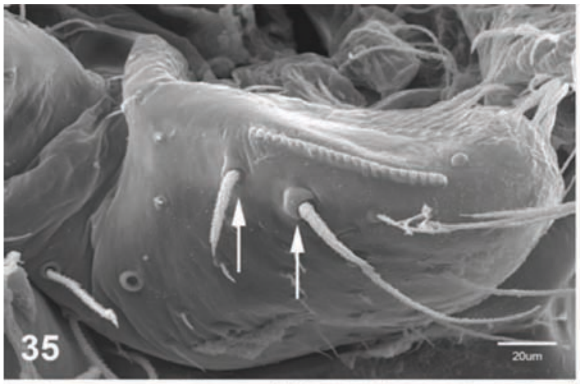
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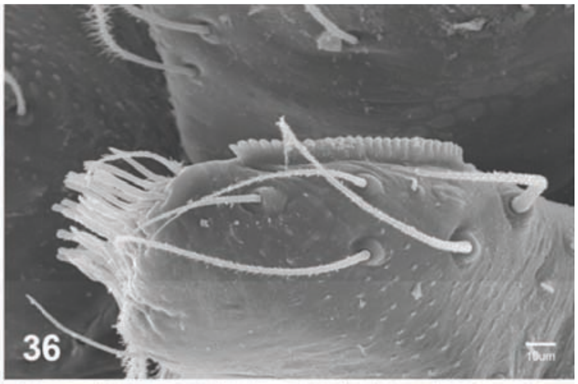
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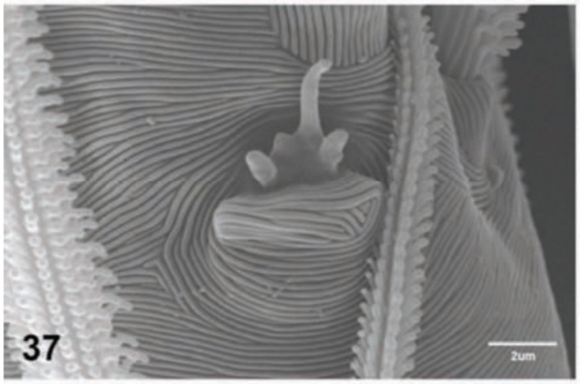
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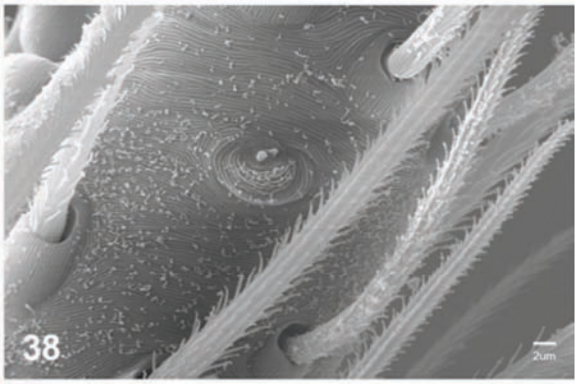
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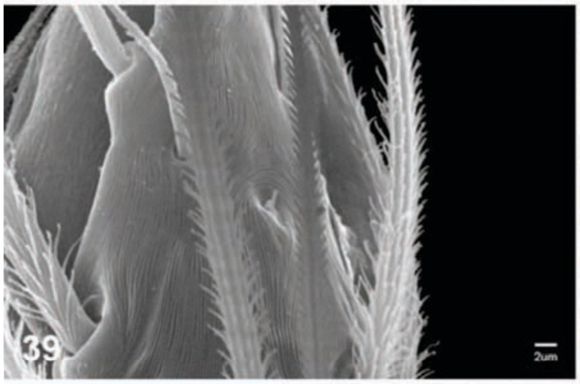
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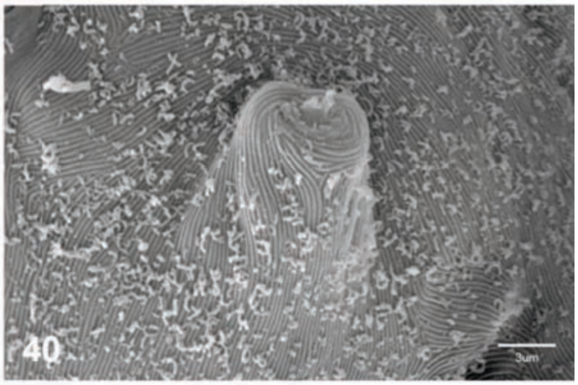
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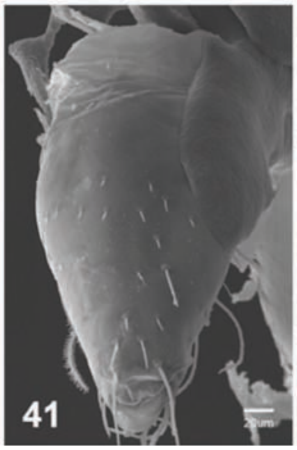
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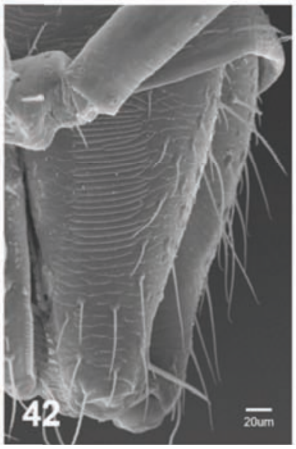
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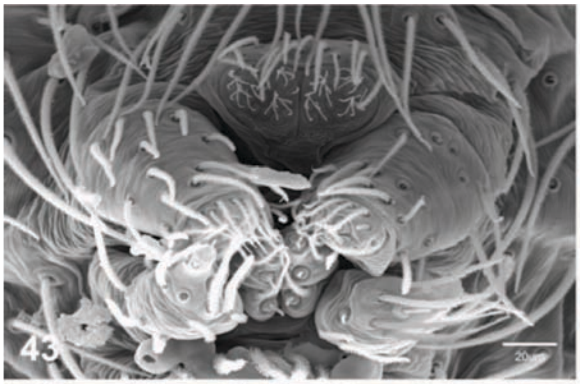
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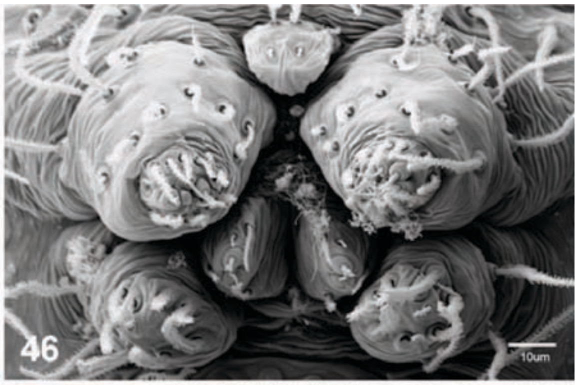
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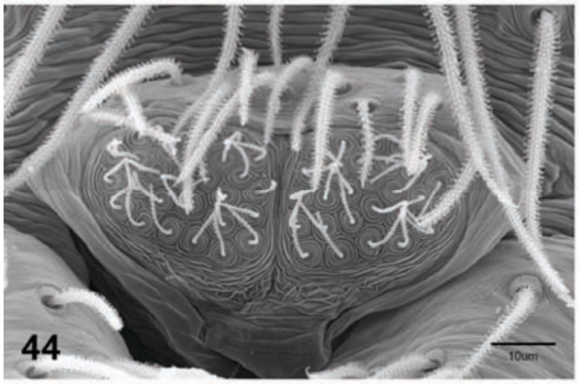
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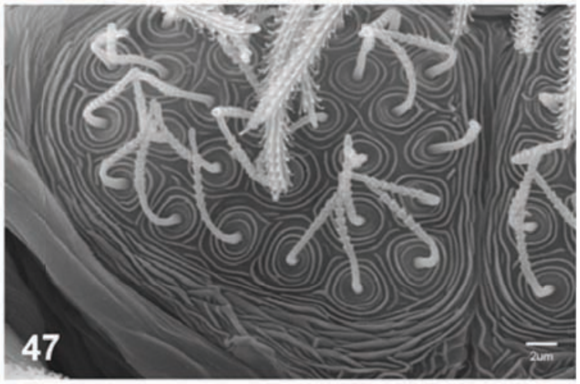
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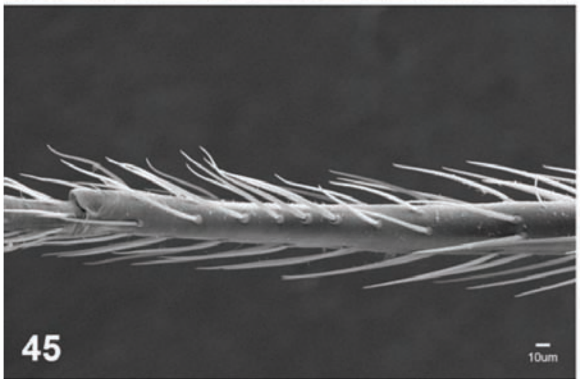
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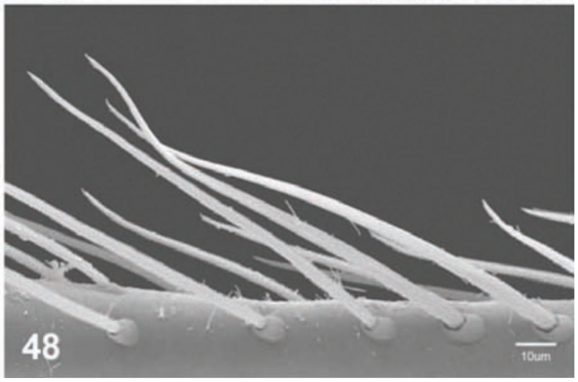
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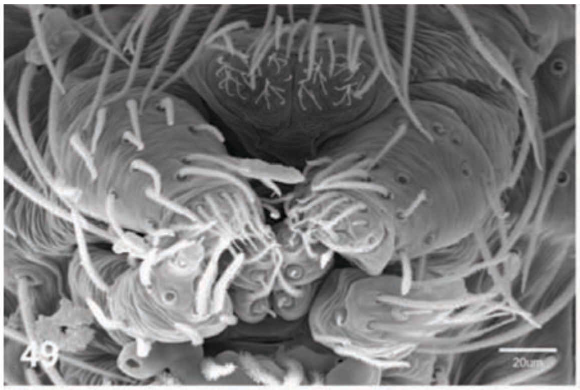
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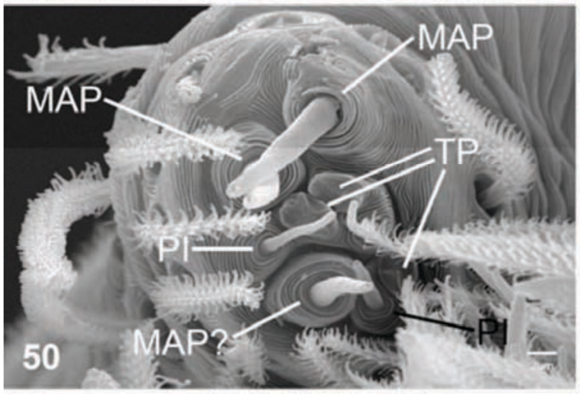
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MAP
TP
PI
MAP?
PI
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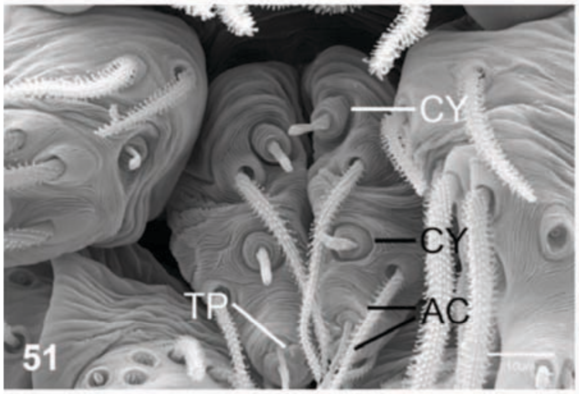
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CY
TP
AC
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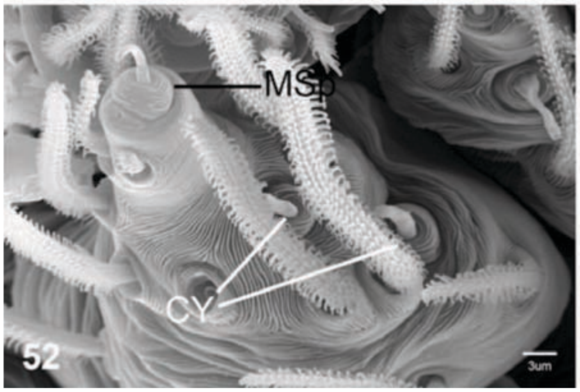
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CY
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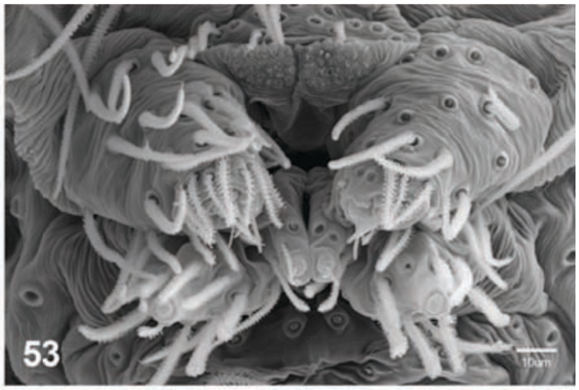
3um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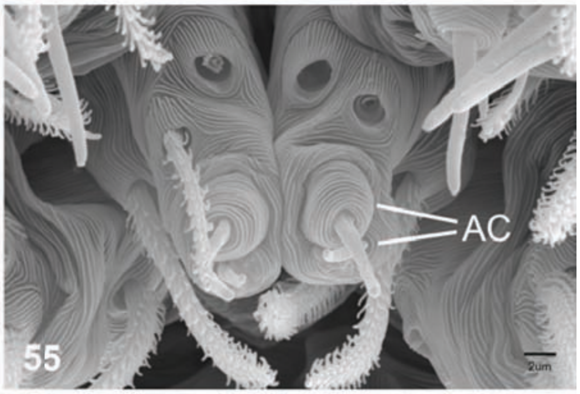
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NuMSp?
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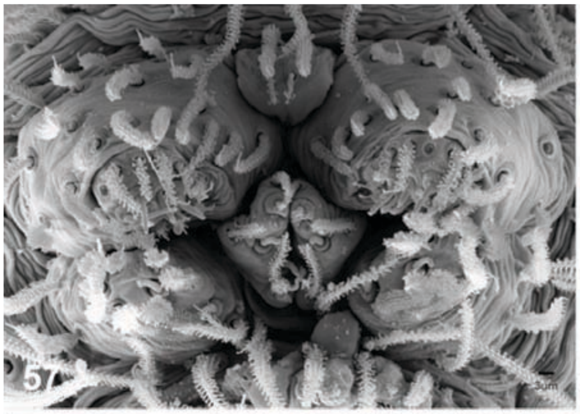
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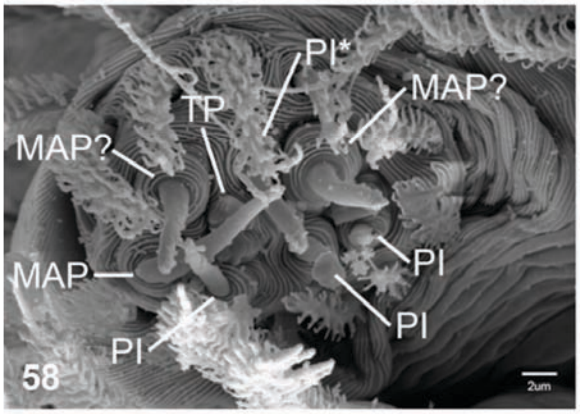
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TP
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PI
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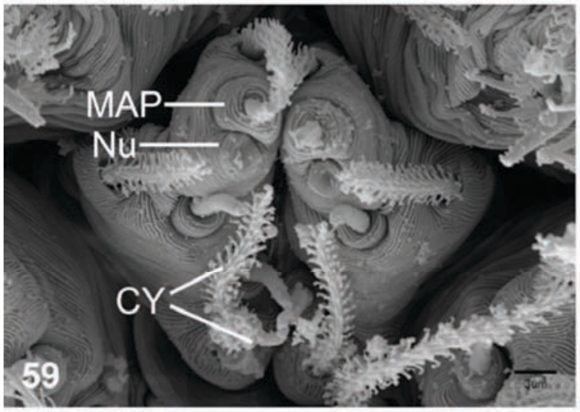
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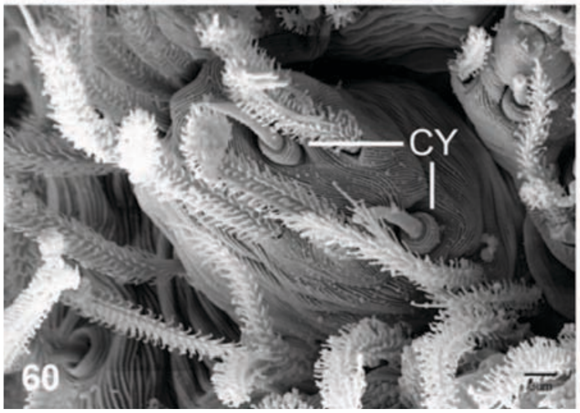
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61
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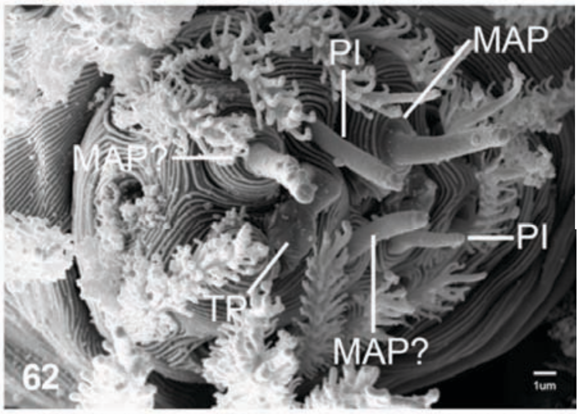
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MAP?
PI
TP
MAP?
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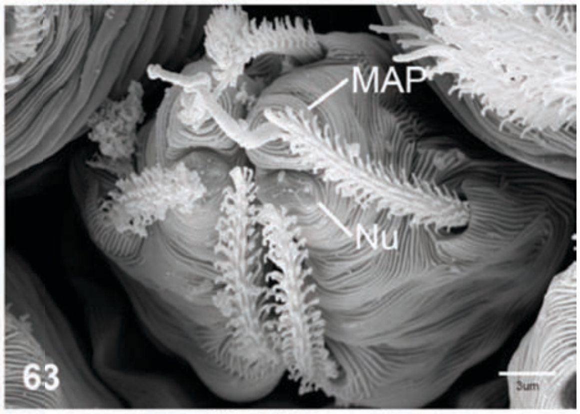
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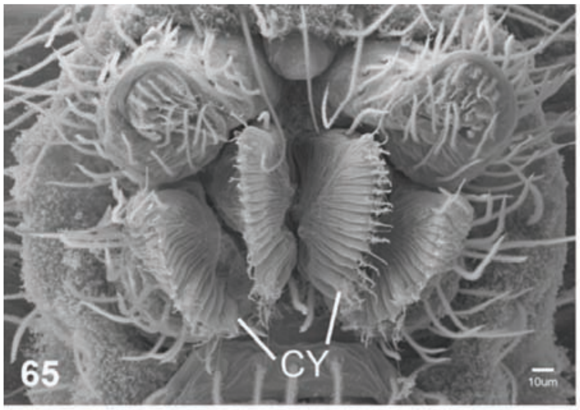
MAP
Nu
3um


64
3um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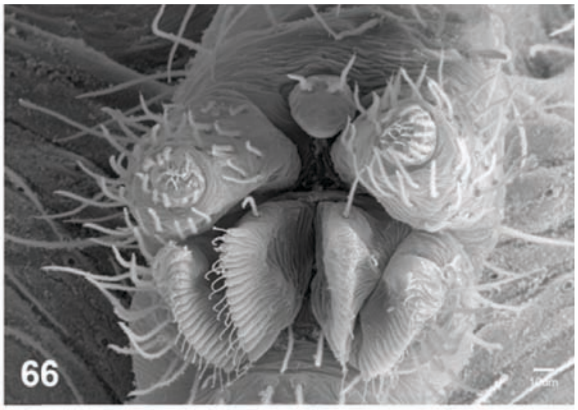
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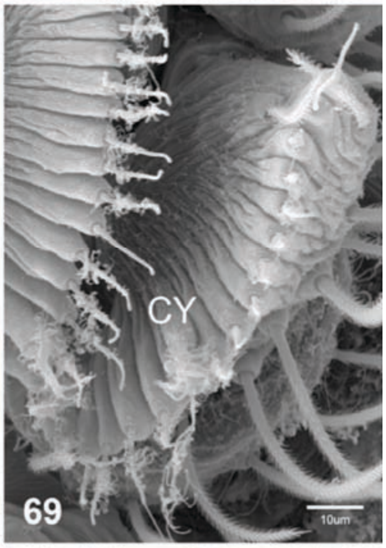
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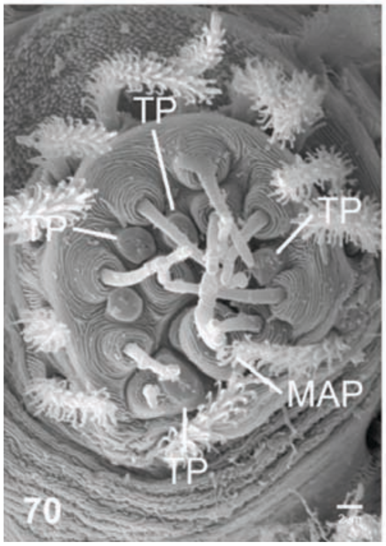
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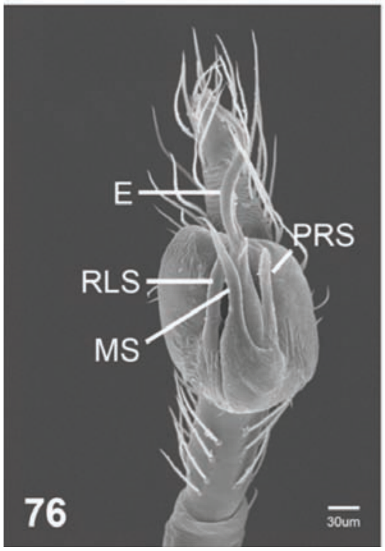
71


72


E
73
30um


74
30um


75
10um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PRS
RLS
MS
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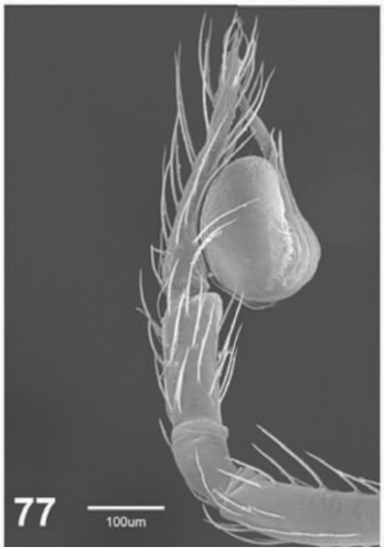
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78
30um


79
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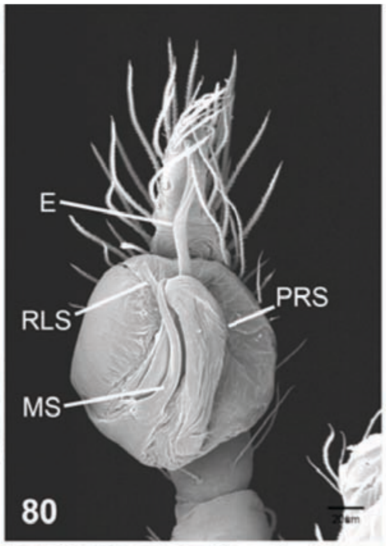
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82
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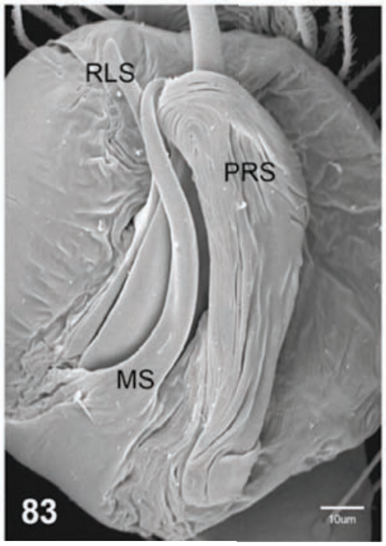
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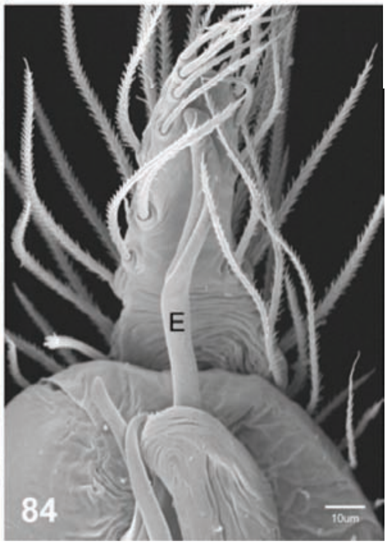
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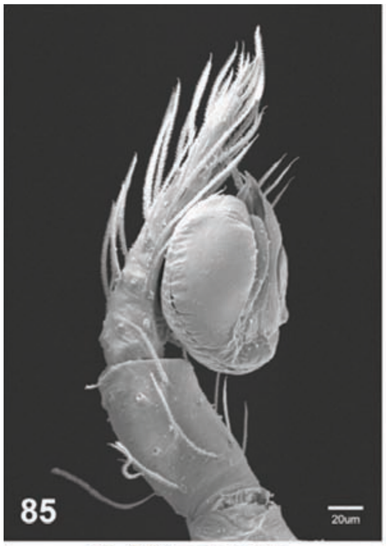
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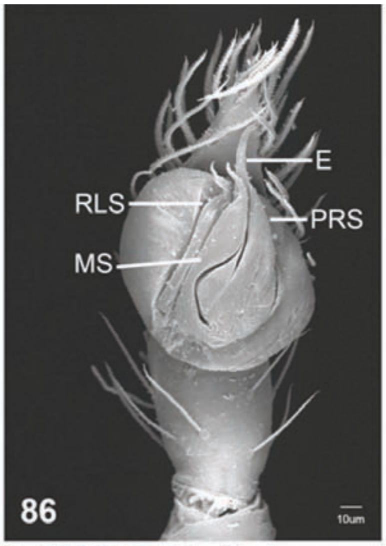
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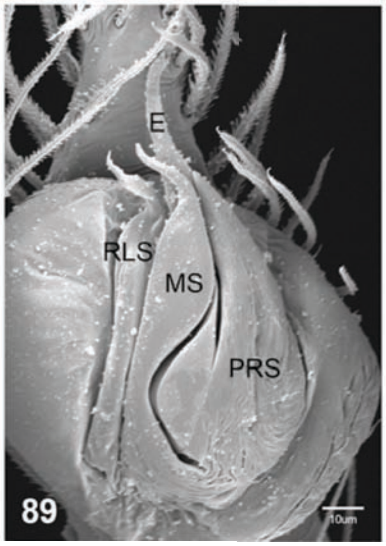
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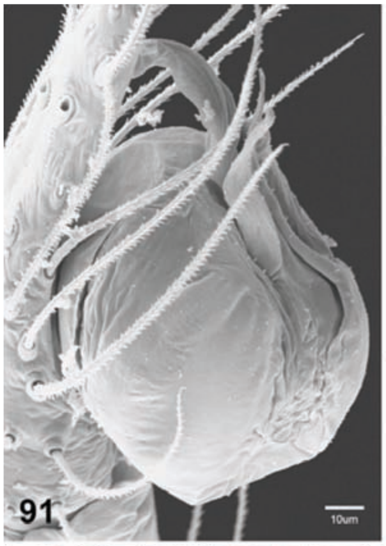
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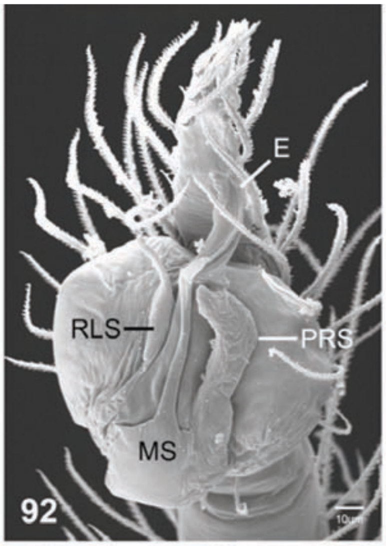
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PRS
MS
92
10um


93
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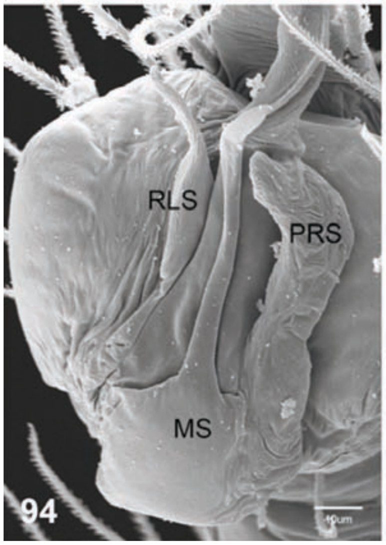
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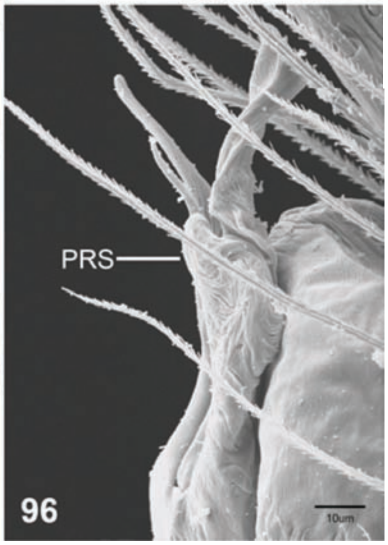
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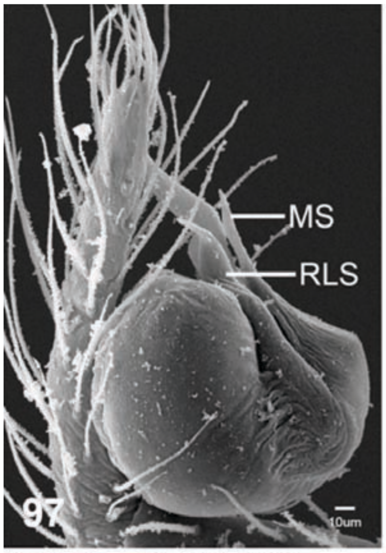
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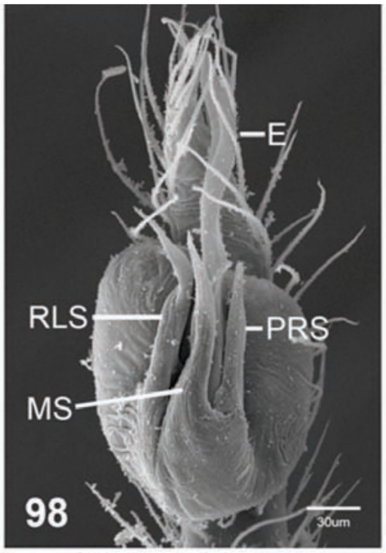
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PRS
MS
98
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PRS
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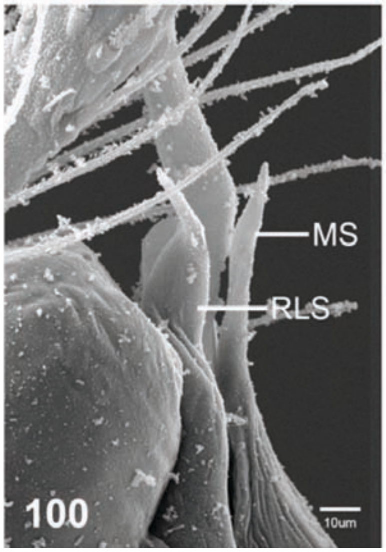
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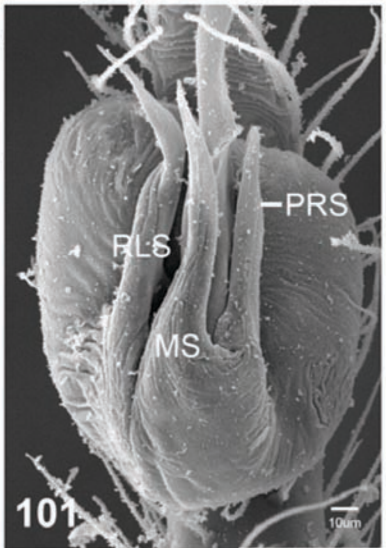
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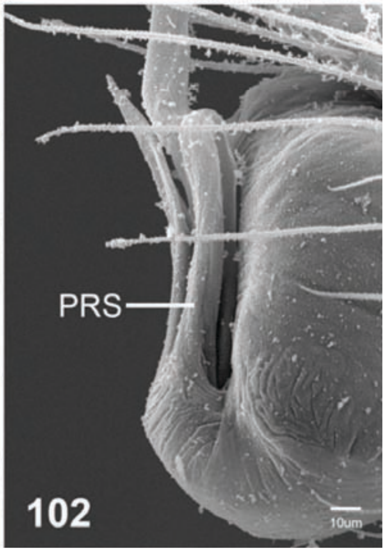
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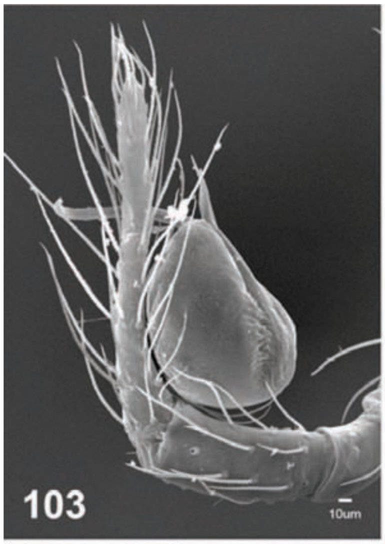
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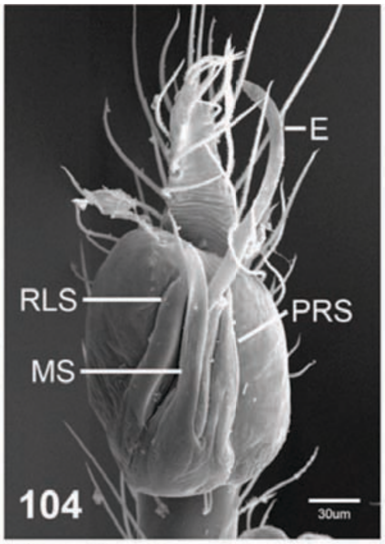
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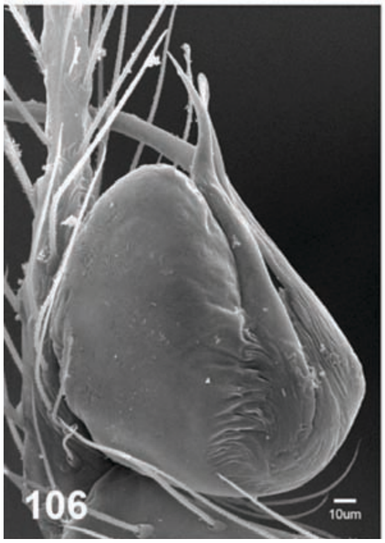
RLS
PRS
MS
104
30um


105
20um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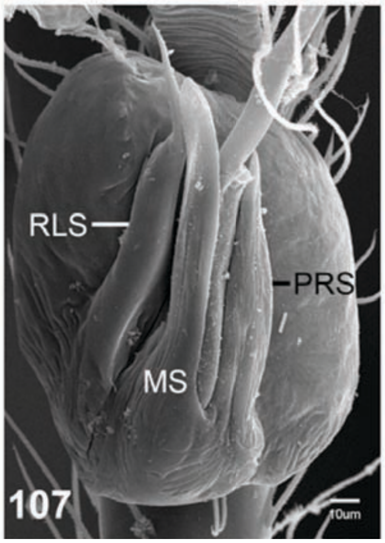
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PRS
MS
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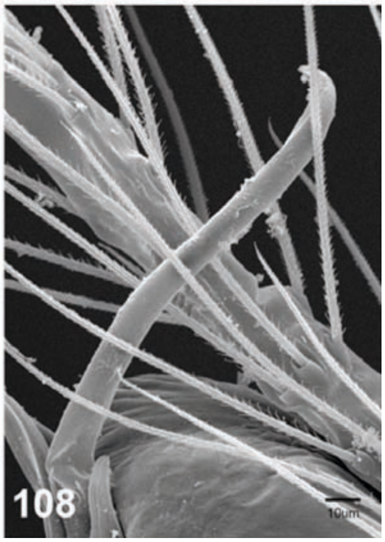
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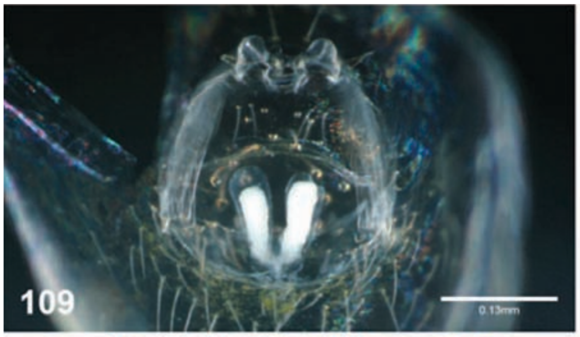
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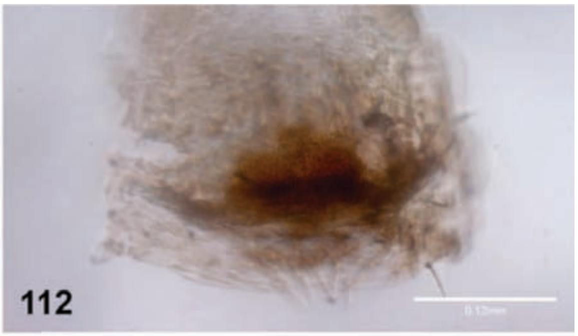
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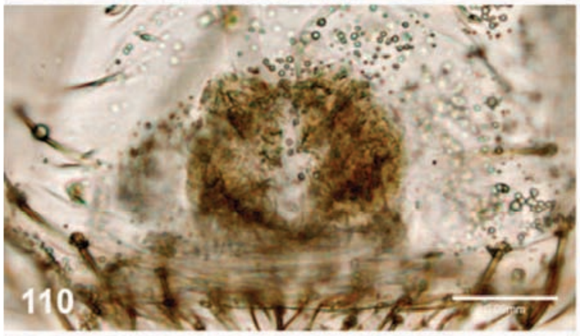
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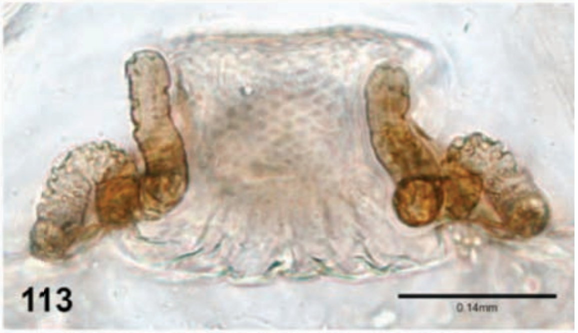
113
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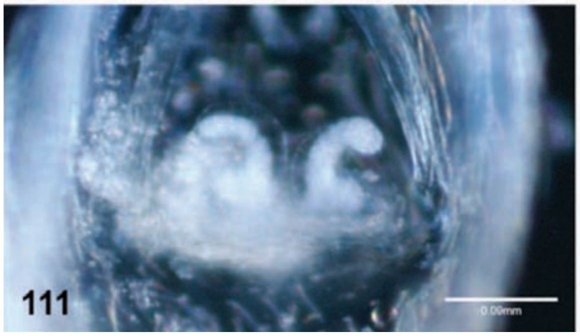
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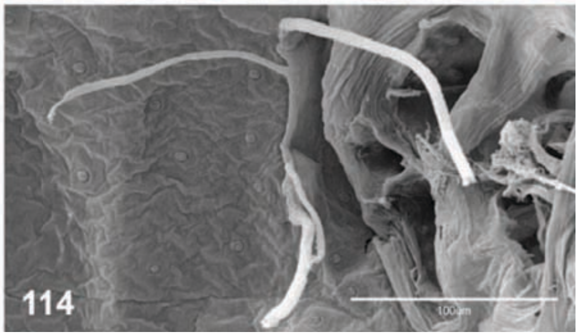
114
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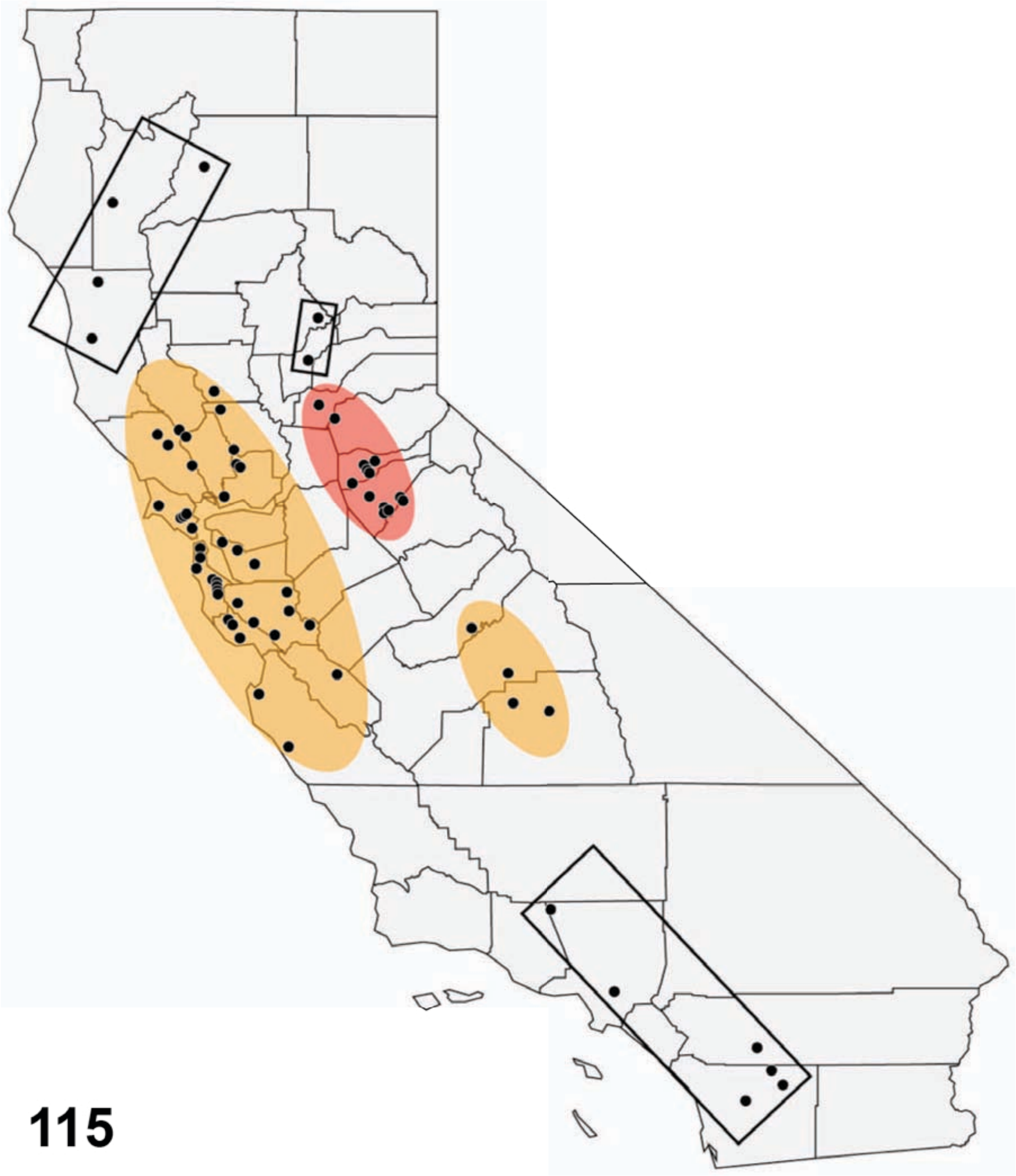
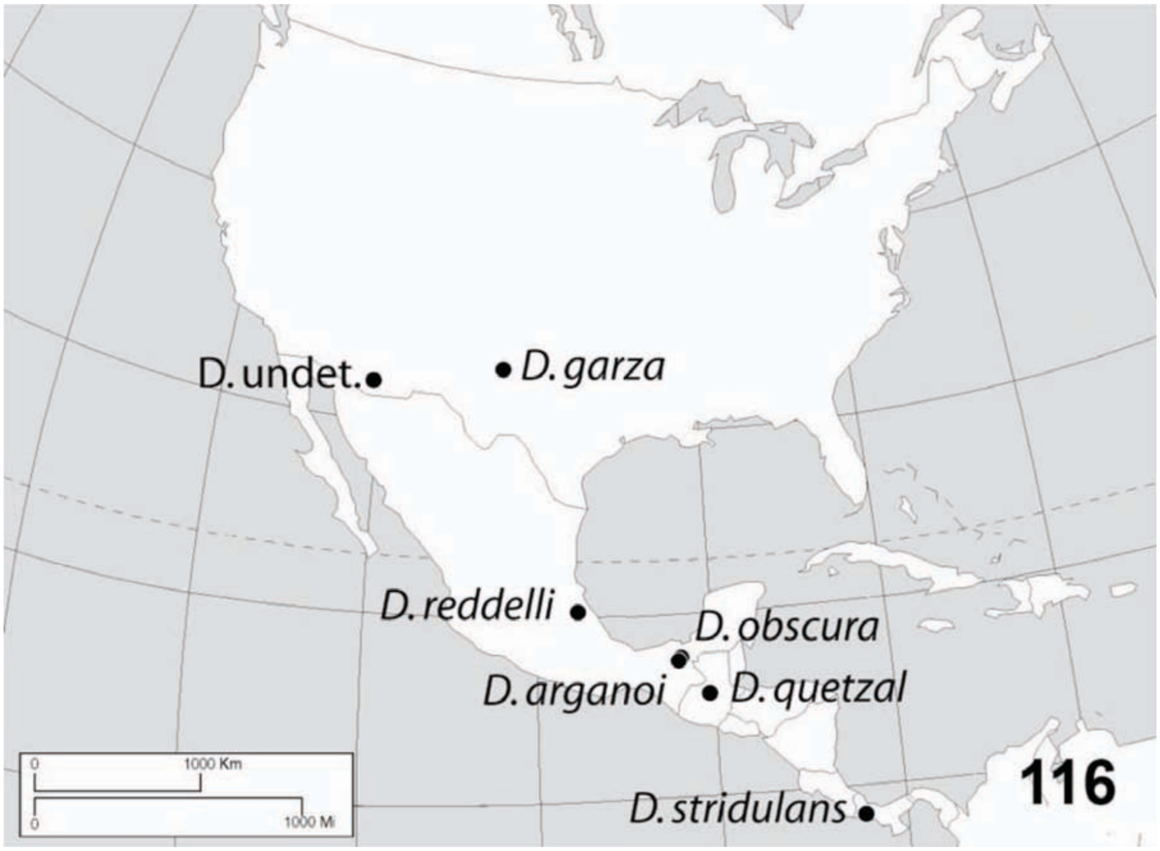


115


D. undet.
D. garza
D. reddelli
D. obscura
D. arganoi
D. quetzal
D. stridulans
0
1000 Km
0
1000 Mi

116

Chapter 2:

Systematics and Evolution of the Spider Genus *Neoleptoneta* Brignoli, 1972 (Araneae: Leptonetidae) with a Discussion of the Morphology and Relationships For the North American Leptonetidae

Abstract

A phylogenetic analysis of the spider genus *Neoleptoneta* Brignoli, 1972 is presented based on molecular sequence variation from three genes (mitochondrial cytochrome oxidase I and nuclear histone 3, and28s rDNA) and including exemplars for all North American leptonetid genera. Analysis of concatenated data and independent genes using Bayesian, maximum likelihood, and parsimony methods fails to recover *Neoleptoneta* as monophyletic. Four clades are discovered within *Neoleptoneta*, each of which has distinct morphology. *Neoleptoneta* is relimited to include seven species restricted to Central Mexico and three new genera are described: 1) *Chisosea* **gen. nov.** from Southwestern Texas and Nuevo Leon, Mexico, 2) *Ozarkia* **gen. nov.** from Arizona and New Mexico Northeast to Arkansas, Alabama, and Georgia, and 3) *Tayshaneta* **gen. nov.** from Texas South to Coahuila, Mexico. The genera *Archoleptoneta*, *Appaleptoneta*, and *Calileptoneta* are monophyletic and a sister group relationship is supported between *Appaleptoneta* and *Calileptoneta*. Morphological data based on a broad survey of leptonetid genera using scanning electron and compound light microscopy is traced on the molecular phylogeny. Several characters of the male and female genitalia corroborate relationships supported by the molecular phylogeny and synapomorphies are proposed for each new genus.

Comparison of the morphology of *Leptoneta sandra* Gertsch, 1974 and *Leptoneta brunnea* Gertsch, 1974 with *Leptoneta convexa* Simon, 1872 shows considerable differences in the structure of the male and female genitalia. The species *Leptoneta brunnea* Gertsch, 1974 is transferred to *Neoleptoneta* based on the details of the male genitalia giving the new combination *Neoleptoneta brunnea* (Gertsch, 1974) **comb. nov.** The morphology of *L. sandra* is compared with the Japanese species *Falcileptoneta striata* (Oi, 1952). A generic grouping of *L. sandra* with either *Leptoneta* or *Falcileptoneta* is rejected and thus a new genus *Montanineta* **gen. nov.** is proposed, giving the new combination *Montanineta sandra* (Gertsch, 1974), **comb. nov.**

Ancestral state reconstruction of ecology indicates that troglobites have evolved at least nine times independently within the North American Leptonetidae and that most species are descended from troglophilic ancestors. Character mapping further shows that two species, *N. capilla* and *N. myopica*, are polymorphic and include both troglophilic and troglobitic morphotypes. Patterns of variation within *N. capilla* and *T. myopica* are illustrated and their implications for species delimitation are discussed.

Key Words: Haplogynae, Leptonetidae, Caves, Troglobites, Phylogenetics

Introduction

Leptonetids are small haplogyne spiders that build sheet webs in cool, moist habitats including leaf litter, rotting logs, and caves (Figs. 1A- D). Up to now six genera have been recognized in North America, the most diverse of which is *Neoleptoneta* Brignoli, 1972 with 31 species described from the Southern United States and Central Mexico (Table 2; Platnick, 2010). *Neoleptoneta* is remarkable in that it includes the largest number of cave specialists, or troglobites, with 80% of described species known only from caves. While few species are completely eyeless, most *Neoleptoneta* share some degree of adaptation to subterranean life including eye reduction, pigment loss, and appendage elongation. Their restricted distributions and specialized biology have made them conservation priorities and two Texas species, *N. microps* and *N. myopica*, are federally endangered (US Fish & Wildlife, 2010).

The systematics of the North American Leptonetidae has a controversial history, largely centered around debate over the taxonomic validity of *Neoleptoneta*. Although leptonetid spiders had been known in Europe since Simon (1872), the first North American species was not described until Banks (1904). Fage (1913) and Brignoli (1967, 1969) were among the first arachnologists to carefully study the European fauna by producing detailed illustrations of genitalic characters using compound light microscopy. In these studies several European leptonetid genera were characterized in detail, including *Leptoneta* Simon, 1872. Despite being aware of the European studies, Gertsch (1971) described six species from Mexico as congeneric with the European genus *Leptoneta* Simon, 1872. Brignoli (1972) repeatedly chastised the taxonomic decisions of Gertsch (1971) and described his new genus *Neoleptoneta* to include the Mexican species. Gertsch (1974) later revised the North American fauna and added several new species from the Appalachians, California, and the Southwest which he once again placed into the genus *Leptoneta*. Furthermore, Gertsch (1974) synonomized both *Neoleptoneta* and the European genus *Paraleptoneta* Fage, 1913 which he never examined in detail. Brignoli (1974, 1977) strongly protested both decisions and argued that the North American species belonged to four or five different genera. The debate remained unsettled until Platnick (1986) discovered a suite of characters on the patellar and tibial leg glands; resurrecting *Neoleptoneta* and describing two additional genera, *Appaleptoneta* from the Appalachians and *Calileptoneta* from California (Fig. 1C).

Despite the historical taxonomic attention, relationships among the North American genera have never been quantitatively analyzed and generic limits are untested. The taxonomy of most genera is poorly resolved and the evolutionary history, particularly of the cave- adapted species, is unexplored. Recent revisionary work has emphasized the importance of scanning electron and compound microscopy in leptonetid systematics by discovering a wealth of new characters on the genitalia and spinning organs (Ledford, 2004; Ledford & Griswold, 2010). Several characters, such as the cribellum in *Archoleptoneta*, not only serve to elucidate relationships among the Leptonetidae but are also likely to impact the higher classification of spiders. Given their taxonomic history, biogeography, and association with caves relationships within *Neoleptoneta* are likely to contribute not only to an understanding of the systematics of the North American fauna but also to their evolution.

In this study, the first quantitative assessment of leptonetid phylogeny is presented based on molecular sequence variation in three genes (mitochondrial cytochorome oxidase I and nuclear histone 3 and 28s rDNA). Bayesian hypothesis testing (Brown and Lemmon, 2007) is used to evaluate the monophyly of *Neoleptoneta,* and ancestral state reconstruction (Schluter et al., 1997; Pagel, 1999) is used to explore hypotheses of cave evolution. Four new genera are described, supported by molecular phylogenetic results and a comprehensive morphological survey using scanning electron and compound light microscopy. Morphological characters are traced on the molecular phylogeny and synapomorphies for each genus are proposed. A dichotomous key is provided for the North American genera along with detailed images for each genus. This study is viewed as the first step towards the taxonomic revision of the North American leptonetid fauna and as a scaffold for understanding the evolution and relationships for the Leptonetidae.

Materials and Methods

Morphology

Prior to examination with a Leo 1450VP Scanning Electron Microscope, all structures were cleaned with a fine brush or ultrasonicator and critical point dried. Best results were obtained by gradually dehydrating the specimen in increasing concentrations of ethanol for 24- 48 hours prior to critical point drying. Dried specimens were then mounted on pin mount SEM stubs (Ted Pella Inc., Redding, USA) on copper- backed tape. Specimens were sputter coated for 120 seconds using a Denton Vacuum Sputter Coater. Large structures were photographed using a Nikon DMX1200 camera attached to a Leica MZ 16 stereomicroscope. Images were then montaged using Helicon Focus v. 4.2.1 (http://www/heliconsoft.com).

Vulvae were carefully excised and placed in a pancreatin solution for 24- 48 hours to digest extraneous tissue (Alvarez-Padilla and Hormiga, 2008) then placed in water and manually cleaned. Best results were obtained by removing the cuticle from the dorsal surface of the abdomen and digesting the entire structure. If the vulva remained unclear, it was stained with Chlorazol Black and reexamined. Images of each species were prepared using a Nikon DMX1200 camera attached to a Leica DM 4000 compound microscope. Genitalia were placed in Hoyer's solution and examined in well slides or temporary mounts following the procedure described by Coddington (1983).

In order to more accurately identify structures on the male palp, representatives from each North American genus were examined in an expanded state. The right palp was removed, boiled for 2- 5 minutes in lactic acid solution, and placed in water where expansion occurred. Both unexpanded and expanded views of the palp were then compared in order to assess the final position of structures.

Descriptions of genera follow the format of Ledford & Griswold (2010) and all measurements are in millimeters. A summary of abbreviations for morphological structures is provided in Table 1. Detailed images of all structures will be made available on Morphbank (www.morphbank.net).

Taxon Sampling

Among the challenges faced by Gertsch (1974) was the limited number of specimens, especially adult males, which impeded his assessment of morphological variation and made species diagnosis ambiguous. Recent collections have more than quadrupled the number of available specimens, adding several new records and discovering most of the unknown sexes. In order to prioritize collection sites, a database combining records for described *Neoleptoneta* species and all collections since Gertsch (1974) was developed. Collection sites were selected that maximized sampling throughout the known range of *Neoleptoneta* with priority given to type localities. Outgroup selection was based on the most recent phylogenies of haplogyne spiders (Platnick et al., 1991; Ramirez, 2000) and specimen availability. Between 1- 10 individuals were collected from each site, placed directly into 95% ethanol, and then transferred to storage at -20 ºC. Each specimen was assigned a unique voucher number and is accessioned in a database maintained at the California Academy of Sciences (CASC).

Voucher specimens for the study are deposited at the California Academy of Sciences (CASC), the Texas Memorial Museum (TMM), the Museum of Texas Tech University (TTU), and the Essig Museum, University of California, Berkeley (UCB). Due to the sensitive nature of cave locations and in the spirit of respecting the rights of property owners while encouraging them to support future research, precise locality information will not be provided. Unless otherwise noted, cave locations are limited to within 2 kilometers. Specimens used in this study along with their voucher codes are listed in Table 3 and a map showing the study area is provided in Fig 2.

Molecular Protocols

Whole genomic DNA was extracted from 2- 4 legs using DNEasy kits (Qiagen, Inc.) following the manufacturer's protocol with the exception of tissue grinding. In order to maximize DNA yield, tissue grinding proceeded in three steps: 1) a custom fit pestle was prepared from a 500ul unfiltered pipette tip, 2) grinding was initiated with 100ul of ATL buffer until no visible tissue remained, and 3) the pestle was rinsed with the remaining 100ul of ATL buffer per the manufacturer's protocol. Between 2- 4 legs were used for each extraction. DNA extractions were then stored at -20ºC. Remaining genomic DNA is stored at the California Academy of Sciences Center for Comparative Genomics at -80ºC.

Three gene fragments were amplified in 25ul reactions: cytochrome oxidase I (~800bp), histone 3 (~330bp), and 28s rDNA (~1000bp). Primers and conditions for each locus are listed in Table 4. Reactions were initially attempted with the following: 2.5 ul 10X AmpliTaq buffer (Applied Biosystems Inc., Foster City, USA), 0.42 ul of 10 mM dNTP, 2.4 ul of 25 mM $MgCl_2$, 1um each of forward and reverse primer 10 uM primers, 1 ul of BSA, 0.1 ul AmpliTaq DNA polymerase (Applied Biosystems Inc., Foster City, USA), 1- 4 ul DNA template, and water to 25 ul. Both temperature and $MgCl_2$ gradients were used to optimize PCR conditions and resolve amplification problems. Failsafe PCR kits (Epicentre Biotechnologies, Madison, USA) were also used to resolve amplification issues for histone 3 and 28s following the manufacturer's protocols. PCR products were purified using Exonuclease I (Exo I) and Shrimp Alkaline Phosphatase (SAP). A mixture consisting of 69 ul of water, 10 ul 10X buffer, 20 ul SAP, and 1 ul Exo I was prepared, diluted 4: 1, and 2.5 ul was added to each 25 ul reaction. The mixture was then incubated at 37ºC for 30 minutes and 80 ºC for another 15 minutes.

Purified PCR product was combined with 1 ul each of 1mM forward and reverse primer and submitted to the U. C. Berkeley DNA Sequencing Facility (Berkeley, USA) for sequencing. Each product was sequenced in both the forward and reverse directions on an ABI 3130XL DNA Analyzer (Applied Biosystems Inc., Foster City, USA).

Sequences were assembled from bi- directional reads using Sequencher v. 4.8 (GeneCodes Co., Ann Arbor, USA). Each sequence was then checked for contamination using an NCBI BLAST search (http://ncbi.nlm.nih.gov/BLAST).

Sequence Alignment

Sequence alignment for the protein coding genes mithochondrial COI and nuclear histone 3 was performed using CLUSTAL X v. 2.0 (Larkin et al., 2007) and manually adjusted in MacClade v.4.08 (Maddison & Maddison, 2000). Sequences were then translated into amino acids using MacClade v.4.08 and further refined by checking for stop codons. 28s rDNA alignments were produced using CLUSTAL X v. 2.0 and Muscle v. 3.8 (Edgar, 2004) then visually evaluated in MacClade v. 4.08. Additional 28s rDNA alignments were produced using modified gap opening and extension costs in CLUSTAL X v. 2.0 (gap opening/ gap extension 24/6) in order to force a more compressed (i.e. less “gappy”) alignment.

Model Selection and Partitioning Strategies

Models of nucleotide evolution were selected for each gene using the Akaike Information Criterion (Akaike, 1973) as implemented in MrModeltest v. 2.2 (Nylander, 2004). 28s rDNA was treated as a single partition and analyzed for each alignment. Partitioning strategies for COI and histone 3 were evaluated using Bayes Factors (Brown & Lemmon, 2007) by subtracting the harmonic mean of the -log likelihood for fully partitioned, partially partitioned, and unpartitioned analyses where: $BF_{1,0}$ =(HarmonicMean – log Likelihood H_1)– (Harmonic Mean – log Likelihood H_0). Acceptance or rejection of each strategy was based on the cutoffs: BF>=10 (strong evidence against the competing hypothesis), 10<BF>-10 (ambiguous, select least complex strategy), and BF <=-10 (strong evidence for the competing hypothesis).

Molecular Phylogeny

Maximum likelihood analysis was performed using the Randomized Accelerated Maximum Likelihood algorithm in RAxML v. 7.0.4 (Stamatakis, 2006). Partitioned analyses in RAxML were limited to the general time- reversible model with gamma distributed among site rate variation (GTR + Γ). 1000 non- parameteric bootstrap replicates were conducted for each search, using the rapid bootstrap algorithm as employed in the program. Both independent gene trees and concatenated data sets were analyzed, with COI and histone 3 fully partitioned by codon.

Bayesian analysis was performed using MrBayes v. 3.1.2 (Huelsenbeck & Ronquist, 2001) on the CIPRES portal v. 3.0 (Cyberinfrastructure for Phylogenetic Research; http://www.phylo.org). Analysis proceeded using 4 independent runs until the standard deviation of split frequencies fell below 0.01. Stationarity was evaluated by examining the stability of posterior probabilities for nodes of each MCMC run using the Cumulative and Compare plots in “Are We There Yet?” (http://ceb.csit.fsu.edu/awty; Nylander et al., 2008). The distributions of each parameter for all runs were also visually inspected in Tracer v.1.5 to insure that they were well-sampled and effective sample sizes (ESS) were above 200. The first 25% of trees were discarded from the posterior distributions of each analysis after examination using the Cumulative plot in AWTY.

Parsimony analyses were performed in PAUP* (Swofford, 2003) using 1000 iterations of heuristic search, with random taxon addition and tree bisection- reconnection (TBR). Nonparametric bootstrap support values were calculated using 1000 replicate searches with random taxon addition.

Aligned data matrices and trees will be made available online at TreeBASE (http://www.treebase.org/).

Hypothesis Testing

Bayes Factors were used to test the monophyly of *Neoleptoneta* by using the 'constraint' command in MrBayes v. 3.1.2 (Huelsenbeck & Ronquist, 2001). This command a priori assigned a posterior probability of 1.0 to all topologies that specified a monophyletic *Neoleptoneta*. Bayes Factors were then calculated by subtracting the harmonic mean of the -log likelihood of the posterior distribution of trees for the unconstrained analysis from that of the constrained analysis post burn-in. Bayes Factor values were evaluated using standard cutoffs.

Character Evolution

Morphological characters were evaluated on the Bayesian concatenated phylogeny using the 'Trace Character History' function in Mesquite v. 2.73 (Maddison and Maddison, 2010). For ancestral state reconstruction, a likelihood based model was used with character evolution modeled by the Markov-*k* 1 parameter model.

Definitions for the degrees of cave adaptation (troglophile/ troglobite) vary widely and are often subjective due to incomplete knowledge of life history. Little is known about the life history of *Neoleptoneta* although their habitat specialization makes them unlikely candidates for active dispersal. Eye and pigment reduction is variable for many species, even within the same population, and not a reliable indicator of ecology independent of other characters. For the purposes of this study, a *troglobite* is defined as species for which there are no surface records and possess a combination of morphological adaptations to subterranean life. *Troglophiles* are identified here by having both cave and surface records or species known only from caves but with one type of morphological adaptation (generally eye reduction). *Epigean* species are classified as those known only from surface records and lacking any obvious subterranean adaptation.

Results

Morphology

Multiple exemplars for each North American leptonetine genus, including all described *Neoleptoneta* species, were photographed using scanning electron and compound microscopy. Holotypes for *Neoleptoneta* species were examined and used to confirm the identity of specimens represented in molecular and morphological analyses. Over 1,500 images were produced based on a set of standardized views and assembled into comparative plates. Careful attention was directed at characters proposed or implied as synapomorphies for each genus and to troglomorphic features in order to characterize the range of variation. Characters were then traced on the Bayesian concatenated phylogeny using the APE 2.6 phylogenetics package in R (Paradis et al., 2004). A list of characters traced and their associated states is provided in Table 9.

Somatic Morphology

Synapomorphies for the Leptonetinae include a unique ocular arrangement, with the PME displaced posteriad of the AEG, a ventroapical preening comb on metatarsus III, and female genitalia with a central atrium and lateral spermathecae (Figs. 24, 113 in Ledford and Griswold, 2010). All species examined in this study share the metatarsal preening comb (Figs. 12- 13 in Ledford, 2004) and the general conformation of female genitalia (Figs. 31- 32). While it was not possible to evaluate the ocular arrangement for blind species, faint eyespots usually remain that match the leptonetine ocular distribution. The triangular patellar plates (Figs. 21- 40 in Platnick, 1986) of *Neoleptoneta* were confirmed for each species examined and no variation was observed. The abdomen lacked distinctive patterning, coloration, and setation. Spinneret morphology is similar to that of *Leptoneta infuscata* Simon, 1872 (Figs. 65- 72 in Ledford and Griswold, 2010) and *Calileptoneta helferi* (Gertsch, 1974) (Figs. 24- 31 in Ledford, 2004) with the exception of bearing fewer aciniform gland spigots (6- 10) on the PMS and PLS.

Male Genitalia

Examination of male genitalia using SEM revealed considerable variation in the morphological details of the palp, including: 1) the shape of the retrolateral tibial spine, 2) the shape of the tarsus, 3) the number, shape, and orientation of accessory sclerites, and 4) the structure of the tarsal organ. Each of these features is discussed below, represented by the following species: *N. alabama* (Gertsch, 1974), *N. capilla* (Gertsch, 1971), *N. coeca* (Chamberlin and Ivie, 1942), and *N. isolata* (Gertsch, 1971).

The retrolateral tibial spine (RTS) proposed as a synapomorphy by Brignoli (1972) and Platnick (1986) was confirmed in each species, however, several structural differences were observed in its shape, position, and orientation. In the type species for the genus, *N. capilla,* the RTS is situated on an extended base and lacks any specialized accessory setae (RTS, Fig. 16D). The spine is smooth and sinuous forming an apical hook distally. In contrast, the RTS of *N. isolata, N. alabama*, and *N. coeca* are on short bases and share fluted sculpturing along the length of the spine (Figs. 14 D, 15 D, 17 D). The shape and setation of the RTS in these species is variable, however, they are typically straight to recurved and not sinuous as in *N. capilla*. Several associated setae are found at the base of the RTS for all species excluding *N. capilla*, the most distinctive of which is *N. alabama* which has two groups of four flattened setae adjacent to the RTS (Fig. 15 D). In *N. isolata* and *N. coeca*, these setae are unmodified and densely clustered around the base of the RTS.

In contrast to most leptonetine genera, including *Appaleptoneta* (Fig. 20) and *Calileptoneta* (Figs. 21- 22), the palpal bulb of most *Neoleptoneta* species bears few accessory sclerites. In *N. capilla*, the ventral sclerite (VS) is elongate with a sharp curve at its base (Fig. 16B, E). Upon expansion, the VS unfolds and projects anteriorly, with the bulb rotating up to 90º (Fig. 29). The embolus (E) is thin and extends the length of the VS, with a vase- like opening at its terminus (Fig. 16E).

In *N. alabama*, two types of accessory sclerites are present; the ventral sclerite (VS, Fig. 15B, E) is filliform and forms a brush near the base of the embolus, the retrolateral sclerite (RS, Figs. 15A, B, E) is rectangular and may serve to support the embolus during expansion. The embolus is oval and has a distinctive lobe posteriorly (E, Figs. 15E). Although the VS and RS do not dramatically unfold during expansion as in *N.*

capilla, the bulb rotates up to 90° on a basal hematodocha which partially divides the tarsus (Fig. 28). In *N. isolata* the apical sclerite is reduced to a single spine at the base of the embolus (VS, Fig. 14B, E). The embolus is triangular and has a sharp, spine- like extension anteriorly (Fig. 14E). Expansion is similar to that of *N. alabama* where the bulb rotates an a basal hematodocha, but the VS projects anteriorly. *N. coeca* lacks the ventroapical sclerite entirely (Fig. 17B, E) and only has a spoon-shaped embolus apically. Palpal expansion for the related species *N. myopica* (Gertsch, 1974) resulted in no significant differences from *N. isolata* (Fig. 27).

Both Brignoli (1972) and Gertsch (1974) noted that the shape of the palpal tarsus among the North American species is variable and used it as a diagnostic feature. The tarsus of most leptonetines is characterized by a middorsal division or constriction, which makes the tarsus appear divided or pseudosegmented (Fig. 14- 22F). The apical portion of the tarsus may also be divided longitudinally and in some genera (*Appaleptoneta, Calileptoneta*, *Leptoneta*) bears a retroapical seta (RS, Figs. 20A, 21E, F, 22A, 23D). The palpal tarsus of *N. capilla* is retrolaterally constricted middorsally, but lacks an apical division and any associated setae (Fig. 16F). In contrast, *N. isolata* has the apical portion of the palpal tarsus divided (Fig. 14F), similar to the genera *Appaleptoneta* (Fig. 20F) and *Calileptoneta* (Figs. 21F), but lacks a retroapical seta. Both *N. alabama* and *N. coeca* lack the apical division of the tarsus which instead tapers anteriorly (Figs. 15F, 17F). In *N. alabama* the anterior portion of the tarsus is very short and quadrate, occupying less than half the width of the entire segment and may separate during the expansion process (Fig. 28).

Ledford and Griswold (2010) were the first to observe structural differences in the tarsal organs between leptonetid subfamilies and further suggested their utility in understanding relationships among leptonetines. Within the North American genera, the tarsal organ is of three types: 1) two or three, small receptors on a very low mound (Figs. 24E- H), 2) three receptors on a slightly elevated mound (Fig. 24C, D), and 3) three receptors on a highly elevated mound (Figs. 24A, B; 25A- F). In *N. capilla*, the tarsal organ is elevated and bears three receptors, one of which is elongate (Figs. 23A, B). An elevated tarsal organ also occurs in the genera *Appaleptoneta*, *Calileptoneta*, and *Leptoneta* (Figs. 24- 25) although each genus differs in its position and microstructural details. In *N. isolata* and *N. coeca* the tarsal organ appears flattened and enclosed in a slightly recessed, circular base (Figs. 24E- H).

Female Genitalia

Although the female genitalia within most leptonetid genera are known to be highly conserved (Cokedolpher, 2004; Ledford, 2004; Ledford and Griswold, 2010), considerable variation exists at deeper phylogenetic levels. The vulvae for most North American leptonetine genera are characterized by having a broadly oval to triangular atrium, covered in fine pores, and with a pair of laterally situated, twisted spermathecae. Each spermatheca is connected to the atrium ventrolaterally via a short, sclerotized tube. The spermathecae are also covered in fine pores and under compound microscopy appear to be composed of an inner and outer membrane.

Several of the vulvae illustrated by Gertsch (1974) are confusing, often appearing inverted, and are inconsistent among closely related species. Specimens dissected by Gertsch are also often badly damaged and the genitalia for several species, including holotypes (*N. furtiva*), are missing. Post examination of the holotypes for each species, it is clear that the viewing angles illustrated by Gertsch (1974) are not always consistent which makes structures appear dramatically different. In order to correct for these issues, each vulva was carefully excised, digested, and positioned using modified "Coddington mounts" (Coddington, 1983). Due to varying amounts of sclerotization on the spermathecal stalk, and undetermined factors related to preparation technique, the spermathecae of some female specimens were observed to shift position during examination. This was especially problematic with species in the Central Texas clade which have narrow and weakly sclerotized spermathecal stalks. All images are of the dorsal view unless otherwise noted.

In *N. capilla*, the atrium is triangular and the spermathecae are loosely coiled apically with slightly enlarged heads (Fig. 31C). Both *N. coeca* (Fig. 31D) and *N. isolata* (Fig. 31A) lack the coiled spermathecae of *N. capilla*, at most bearing a single rotation leading from the ventrolateral surface of the atrium. The spermathecal heads of *N. coeca* are swollen, occupying twice the width of the spermathecal stalk, and project posteriorly (SH, Fig. 31D). In contrast, the spermathecal stalks and heads of *N. isolata* are elongate and narrow, bearing a single u-shaped ventral curve (SS, SH, Fig. 31A). In *N. alabama*, the vulva is oval with a pair of lateral spermathecae that are distinctly sinuous and bear swollen heads (SS, SH Fig. 31B).

DNA Amplification and Sequencing

The genes selected for this study were based on availability, appropriate levels of divergence, and amplification success. Multiple attempts were made to develop additional loci that have proven useful in spider systematics (Miller et al., 2010), but amplification either failed completely or was unreliable. Similar issues have been reported by specialists working on the genus *Leptoneta* in Europe (C. Ribera, pers. comm.). Due to high levels of genetic divergence among genera multiple primers and conditions were often necessary for successful amplification. Histone 3 was especially problematic and often failed to amplify or resulted in ambiguous sequence reads. Low quality sequences were reamplified, sequenced, and checked for contamination using an NCBI BLAST search. If reads remained ambiguous, the data were removed from the matrix.

Sequence Alignment

Alignment of the protein coding genes mitochondrial CO1 and nuclear histone 3 was straightforward and required only minor manual adjustment of end regions. Post translation in MacClade v. 4.08 (Maddison and Maddison, 2000), exemplars for *Appaleptoneta* and Mexican *Neoleptoneta* were discovered to have stop codons in histone 3. These individuals were reamplified with identical results and removed from the data matrix. Representatives of *Neoleptoneta arkansa* (Gertsch, 1974) had stop codons for COI and were also removed from the data matrix. The high level of sequence length variation among leptonetid genera prevented unambiguous alignment for some regions of 28s rDNA, so multiple alignment strategies were used. Alignments produced using CLUSTAL X v.2.0 (Larkin et al., 2007) maximized homology of conserved regions and resulted in an aligned data matrix 498 base pairs shorter than Muscle. Subsequent analysis of both alignments revealed few topological differences, however branch lengths using the Muscle alignment were considerably longer. Alignment using default gap opening/ gap extension costs in CLUSTAL X v.2.0 (Larkin et al., 2007) resulted in an alignment of 1034 base pairs. Adjustment of gap opening/ extension costs to force a more compressed alignment (25/5) resulted in an alignment of 1026 base pairs. Analysis of both alignments resulted in no topological differences and default parameters were used for all concatenated analyses.

Model Selection and Partitioning Strategies

A summary of evolutionary models selected by the Akaike Information Criterion (Akaike, 1973) in MrModeltest v. 2.2 (Nylander, 2004) is presented in Table 4. Bayes Factor analysis of COI and histone 3 partitioning strategies revealed a strong preference for full partitions in each case (Table 6).

Molecular Phylogeny

Summary results, statistics, and conditions for each analysis are presented in Table 6. Bayesian analysis of independent genes (Figs. 7- 9) achieved convergence within 20,000,000 generations (sdsf<0.01). Bayesian analysis of the three gene concatenated data (Fig. 4) was more difficult, and only partially converged (sdsf= 0.05) despite optimization of MCMC, alternative modeling strategies, and large numbers of generations (50,000,000). Given the high proportion of missing data for histone 3 (30%), a second analysis was performed including only COI and 28s rDNA data. This analysis achieved convergence within 20,000,000 generations and shows only minor topological differences with the three- gene tree. MCMC performance was optimized using data from preliminary runs by adjusting default chain temperatures from t= 0.20 to t= 0.15 in order to increase chain swap acceptance rates to between 20- 60%. Nodes with a posterior probability of 95% and greater are considered supported and all remaining nodes are collapsed. Results of maximum likelihood analysis for concatenated data are presented in Figure 5. Parsimony analysis of concatenated data resulted in 41 equally parsimonious trees of 8006 steps, the strict consensus of which is presented in Figure 6. Nodes for maximum likelihood and parsimony analyses with bootstrap support values of 75% and greater are considered supported and all remaining nodes are collapsed.

While there are topological differences among the resulting trees, most discrepancies are limited to the resolution of deep nodes where support values vary by gene and optimality criterion. Six fundamental results are apparent across analyses: 1) *Neoleptoneta* monophyly is not supported, 2) four clades are recovered within *Neoleptoneta*, 3) the North American genera *Archoleptoneta* and *Appaleptoneta* are monophyletic, 4) the European species *Leptoneta infuscata* is sister to the remaining leptonetines, 5) branch lengths for the Central Texas clade are much shorter than the remaining leptonetid genera, and 6) the subfamily Leptonetinae is monophyletic.

Results from concatenated analyses are largely congruent and no conflict among relationships is observed. Topological differences relate to the resolution of *Calileptoneta* and its affinities to *Appaleptoneta* and Mexican *Neoleptoneta* (Clade C, Figs. 4- 7). Bayesian analysis supports *Calileptoneta* monophyly (Node 3, Fig. 4) and a sister group relationship with *Appaleptoneta* (Node 4, Fig. 4). Mexican *Neoleptoneta* are also supported as sister to the *Appaleptoneta* + *Calileptoneta* clade, rendering *Neoleptoneta* paraphyletic (Node 5, Fig. 4). In parsimony analyses, a sister group relationship between

Appaleptoneta and *Calileptoneta* is also recovered (Node 4, Fig. 6), however, two species of *Calileptoneta* fall out of the genus (Node 5, Fig. 6) and the Mexican *Neoleptoneta* are not supported as sister to *Appaleptoneta* + *Calileptoneta* (Fig. 6C). Maximum likelihood results for *Appaleptoneta* and *Calileptoneta* and are identical to the parsimony analysis with the exception that they are not supported as sister groups (Nodes 2 and 3, Fig. 5). Remaining analytical differences are limited to the resolution of two *Neoleptoneta* species from Coahuila, Mexico, which Bayesian analysis recovers as sister to the Central Texas *Neoleptoneta* (Clade D, Fig. 4) but are unresolved in maximum likelihood and parsimony analyses.

Gene trees for COI, histone 3, and 28s rDNA are also largely congruent and show few instances of conflict. With the exception of histone 3, *Neoleptoneta* monophyly is not supported and each gene recovers four independent *Neoleptoneta* clades (Clades A- D, Figs.7- 9). Two results in the COI gene tree (Fig. 7) contrast with concatenated analyses: 1) *Leptoneta infuscata* is recovered as sister to *N. chisosea* (Clade A, Fig. 7), and 2) relationships are more resolved within the Central Texas clade (Clade D, Fig. 7), particularly for the species *N. bullis, N. coeca,* and *N. devia*. Despite limited sampling due to sequencing problems, histone 3 recovers the same four clades within *Neoleptoneta*, however, relationships between *Appaleptoneta* and *Calileptoneta* are not resolved (Fig. 8). While no incongruencies are detected on the 28s rDNA gene tree, relationships within the Central Texas clade are far less resolved and significant branch length differences are observed among genera (Fig. 9). Of particular interest are the differences in branch lengths between the Central Texas clade (Clade D, Fig. 9) and the North American genera, including the remaining *Neoleptoneta* species.

Hypothesis Testing

While analysis fails to support a monophyletic *Neoleptoneta*, few of the resulting trees conclusively reject the possibility of its monophyly. Bayes Factors were used to test the hypothesis of a monophyletic *Neoleptoneta* by comparing results from the concatenated analysis with one in which monophyly was enforced (Table 7). Bayes Factor results are inconclusive (BF= 1.35) and reflect a need for use of more slowly evolving genes to help resolve deep relationships in the tree.

Character Evolution

Likelihood based ancestral state reconstruction of ecology (epigean, troglophile, troglobite) reveals that the troglobitic condition has evolved independently at least nine times, including five times within the Central Texas clade (Fig. 38). In most cases, ancestral nodes have a high probability of troglophily, including clades with species known only from epigean habitats. Ancestral nodes are reconstructed as troglobites only in cases where individuals from different caves were used to represent a single species (Nodes 1- 2, Fig. 38).

In three cases, described species are shown to be composed of both troglobitic and troglophilic populations (Nodes A- C, Fig. 38). In *N. capilla* (Clade A, Fig. 38; Fig. 40), specimens from Cueva de La Mina, Harrison's Sinkhole, and the surface of Cueva de La Capilla have large, well- developed eyes and dark pigmentation (Figs. 40A, B). In contrast, conspecific specimens from Cueva de La Capilla are completely blind, depigmented, and with disproportionally long appendages (Fig. 40C). *N. myopica* (Clade

C, Fig. 38; Figs. 39A- C) and *N. paraconcinna* (Clade B, Fig. 38; Figs. 40D- F) share a similar pattern of variation with epigean and troglobitic populations.

Discussion

Relationships for the North American Leptonetidae

Although relationships among leptonetids had not been quantitatively assessed until this study several morphological characters support the division of the family into two subfamilies, the Archoleptonetinae and Leptonetinae (Ledford and Griswold, 2010). *Archoleptoneta* and the Archoleptonetinae were described by Gertsch (1974) to include species that shared the pleisiomorphic eye arrangement for the family and characteristics of the male genitalia. Although originally based only on pleisiomorphies, Platnick (1986) corroborated the Archoleptonetinae by discovering a unique patellar gland morphology and recent revisionary work (Ledford & Griswold, 2010) has proposed additional synapomorphies relating to the spinning organs and genitalia. Despite repeated efforts to collect individuals of *Darkoneta*, exemplars for this study are limited to two cribellate species, *Archoleptoneta schusteri* Gertsch, 1974 and *A. gertschi* Ledford & Griswold, 2010. Results from all analyses except histone 3 recover *Archoleptoneta* (Node 1, Figs.4-7, 9), and although limited outgroup sampling prevents a comprehensive test of the Archoleptonetinae or Leptonetidae, the Leptonetinae are well- supported (Clade E, Figs. 4-7, 9)

Although Gertsch' s (1971, 1974) arguments that the North American fauna was congeneric with European *Leptoneta* was rejected by other workers (Brignoli, 1972, 1977; Platnick, 1986), neither hypothesis has been quantitatively tested. Our analyses include the European species *Leptoneta infuscata* Simon, 1876 (Figs. 18- 22, 24, 27- 28, 40, 65- 75 in Ledford and Griswold, 2010) which shares nearly identical morphology to *L. convexa* Simon, 1872 the type species for the genus (Fig. 22A- F). All analyses except COI recover *L. infuscata* as sister to a monophyletic North American clade (Clade F, Figs. 4-6, 9). While this relationship does not falsify Gertsch's (1974) hypothesis outright several well- supported clades, each with distinctive morphology, are nested within the North American fauna. Furthermore, extensive examination of European leptonetids using SEM (Ledford et al., in prep) clearly indicates that several characters, particularly on the male genitalia, serve to unite members of European *Leptoneta* to the exclusion of any North American genus. We view the combination of molecular and morphological data in this study as strong evidence for multiple North American genera, corroborating the hypotheses of Brignoli (1972, 1977) and Platnick (1986).

Appaleptoneta was described by Platnick (1986) to include species that share a transversely constricted male palpal tarsus (Fig. 20A, F) and rounded patellar glands with parallel ridges (Figs. 47- 54 in Platnick, 1986). Our study includes four *Appaleptoneta* species sampled from throughout their known range: *A. barrowsi* (Gertsch, 1974) (Figs. 19A- F), *A. fiskei* (Gertsch, 1974), *A. credula* (Gertsch, 1974), and an undescribed species from Lawrence County, Indiana. Interestingly, neither *A. barrowsi*, *A. fiskei,* or *A. credula* was described from males and the only character that supports their placement in *Appaleptoneta* is the shape of the patellar and tibial glands. Recent work in Southeastern caves, particularly in Alabama and Georgia, has recovered the males for each of these species and examination using SEM corroborates their placement in the genus.

Phylogenetic analysis further corroborates *Appaleptoneta* monophyly (Node 2, Figs. 4- 7, 9) although relationships within the genus are poorly resolved.

A sister group relationship with *Calileptoneta* is also supported by several analyses (Node 4, Figs. 4, 6, 7, 9). Biogeographic connection between the Appalachian and Californian spider fauna is not without precedent, especially for relatively ancient taxa (Coyle, 1971; Hedin, 2001), and suggests that distribution patterns for these groups may have been shaped by related processes such as climatic change during cycles of Pleistocene glaciation. Preliminary morphological data for *Appaleptoneta* indicates that the genus is in need of revision and several species remain undescribed.

Calileptoneta includes nine species restricted to California and Oregon and can be divided into two species groups based on morphological differences (Figs. 21- 22; Ledford, 2004). The Northern group is characterized by having an unusual proximal extension on the male palpal bulb (Fig. 21A- C) and is represented in this study by four species: *C. californica* (Banks, 1904) (Fig. 20A- F), *C. helferi* (Gertsch, 1974), *C. noyoana* (Gertsch, 1974), and an undescribed species from El Dorado County, California. The Southern group is represented by three species: *C. oasa* (Fig. 22; Gertsch, 1974), *C. ubicki* (Ledford, 2004), and an undescribed species from Tulare County, California. Brignoli (1977) was the first to suggest that the Northern group belonged in its own genus, and Ledford (2004) further suggested that the dramatic morphological differences between them could show that the genus is paraphyletic. While concatenated Bayesian (Node 3, Fig. 4) and COI (Node 3, Fig. 7) analyses recover *Calileptoneta*, remaining analyses exclude the Southern species group (Figs. 5- 6). However, the Northern group of *Calileptoneta* is well- supported by each analysis and is clearly united by the unusual extension on the male palp.

Of particular interest within the molecular data is dramatic 28s rDNA length variation in *Calileptoneta*, of up to 100 base pairs. Although gene paralogy can not be conclusively dismissed, it is also possible that either rate acceleration or insufficient outgroup sampling is the source of the discrepancy. Three species remain undescribed in California, including the Tulare County representatives in this study and a molecular study directed at biogeographic relationships is in progress (Ledford et al., in prep).

Monophyly of Neoleptoneta

While Brignoli (1972) did not expressly indicate synapomorphies for *Neoleptoneta* in his descriptions, he did argue that several features on the male palp, including the retrolateral tibial spine (RTS), embolus shape, and the shape of the tarsus were unique to the genus (p.135). Platnick (1986) identified both the RTS and the triangular patellar plates as diagnostic features in his study, but did not explore genitalic characters in detail. Given that most structures on the male palp require specialized microscopy to observe, it is not surprising to find new details that impact leptonetid classification. The retrolateral tibial spine, for example, is clearly a more complex and informative structure than previously realized.

Although only one of the analyses presented in this paper (Figs. 4) refutes the possibility of *Neoleptoneta* monophyly, four clades are supported across all analyses each of which is characterized by unique morphology. Five characters in particular serve to unite members within each clade (Table 9) and were traced on the Bayesian concatenated phylogeny in order to evaluate their distributions. (Figs. 33- 37). The retrolateral tibial spine (Fig. 33) has clear phylogenetic value, uniting the members of each clade within *Neoleptoneta*, although it is absent in the genera *Appaleptoneta* and *Calileptoneta*. Furthermore, given its absence in *Archoleptoneta* and *Leptoneta* it may serve as a character that unites the North American Leptonetidae. The shape of the palpal tarsus (Fig. 34) shows a similar distribution, although there is homoplasy within the Central Texas clade, as *N. valverdae* shares the apically divided tarsus with *N. chisosea* and *N. pecki*. Interestingly, *L. infuscata* and several other leptonetine outgroups share the apically divided state but also have a unique retroapical seta (Figs. 20- 22F, 23D) which is lost in all *Neoleptoneta*. The shape of the embolus (Fig. 35) is the primary diagnostic character for separating *Neoleptoneta* species but also shows clear phylogenetic value. In most leptonetine genera, including *Appaleptoneta* and *Calileptoneta*, the embolus is apically situated and vase- like, typically bearing fine sculptural details along its edge (Figs. 20- 21E). Although some *Neoleptoneta* show similar details (Figs. 35C, D) in most species the embolus is smooth and relatively simple (Figs. 35B, D). The overall shape of the embolus is informative for each clade within *Neoleptoneta* as are the variety of accessory sclerites, many of which dramatically expand during mating. The male tarsal organ (Fig. 36) is subtle in structural details and has a more complex phylogenetic distribution. While incomplete resolution deeper in the tree makes optimization ambiguous, the presence of an elevated tarsal organ in *L. infuscata* (Fig. 26A, B) suggests that several clades have the tarsal organ reduced. Within *Neoleptoneta*, the elevated tarsal organ of *N. capilla* contrasts sharply with the remaining clades although *Appaleptoneta* and *Calileptoneta* share similar morphology.

Although several studies have commented on the similarity of female genitalia within leptonetid genera (Cokendolpher and Reddell, 2001; Cokendolpher, 2004; Ledford, 2004), advancement in preparation techniques and microscopy has shown them to be highly informative at deeper levels. Within *Neoleptoneta*, four distinct morphologies are apparent and strongly corroborate phylogenetic results (Fig. 37). In most leptonetine genera, including *L. infuscata*, *Appaleptoneta*, and *Calileptoneta*, the spermathecae are tightly twisted (Figs. 30C- 31) although the number of twists and their orientation are variable. In *Neoleptoneta*, except for the clade including *N. capilla*, the spermathecae are relatively less twisted (Fig. 31D) or sinuous (Figs. 31A, B). Given the morphological diversity found among leptonetine genera, several additional characters are likely to be discovered.

Neoleptoneta is relimited to include 7 species from Central to Southern Mexico (Fig. 3C), united by having males with an elongate ventral sclerite and embolus (VS, E Fig. 16) and having females with twisted apical spermathecae bearing small heads (Figs. 31C, 37C). Three additional genera are described: 1) *Chisosea,* **gen. nov.** includes 4 species from Northern Mexico to West Texas (Fig. 3A), united by males with a triangular embolus bearing an apical spur (E, Fig. 14E), an apically divided palpal tarsus (Fig. 14F), and females with narrow, u- shaped spermathecal stalks bearing elongate heads (SS, SH, Figs. 31A, 37A); 2) *Ozarkia,* **gen. nov.** includes 9 species from the Southern U.S. (Fig. 3B) united by having males with a retrolateral tibial spine bearing two groups of four flattened setae (RTS, Fig. 15D), a rectangular retrolaterl sclerite (RS, Fig. 15B, E), and a filiform ventral sclerite (VS, Fig. 15B, E), and females with sinuous spermathecae (Fig. 30B); 3) *Tayshaneta,* **gen. nov.** includes 11 species from Central Texas south to Coahuila, Mexico (Figs. 3D) diagnosed by males with an elongate, recurved retrolateral spine on the palpal tibia (RTS, Fig. 17D) and females with spermathecae bearing large heads (Fig. 37D).

Placement of Leptoneta sandra Gertsch, 1974 and *Leptoneta brunnea* Gertsch, 1974

Although Platnick (1986) was able to place most North American species using patellar and tibial gland morphology, *L. sandra* from West Virginia and *L. brunnea* from Mexico were maintained in *Leptoneta* as *incertae sedis.* Examination of *L. sandra* (Fig. 19A- C, G) and *L. brunnea* (Fig. 18A- F) shows several morphological differences with *L. convexa* (Fig. 23A- F), *L. infuscata*, or any other described Old World *Leptoneta* species. However, *L. brunnea* does share several characters with Mexican *Neoleptoneta* including the elongate ventral sclerite (Fig. 18B, E) and embolus shape (Fig. 18D). While the retrolateral tibial spine found in most *Neoleptoneta* species is absent, preliminary examination of additional specimens from Central Mexico indicates that this morphology is shared across several undescribed species which may eventually be placed into a separate genus. In the absence of more detailed work on the Mexican fauna, *L. brunnea* is transferred to *Neoleptoneta* based on the elongate ventral sclerite and embolus shape giving the new combination *Neoleptoneta brunnea* (Gertsch, 1974).

In contrast to *N. brunnea*, the genitalic morphology of *L. sandra* was not observed in any other North American leptonetid species (Figs. 19A- C, H). Brignoli (1977) was the first to suggest the possibility of affinities between the North American and Asian faunas, but provided few supporting morphological details. Comparison of *L. sandra* with the Japanese species *Falcipletoneta striata* (Oi, 1952) (Fig. 19D- F, H) reveals striking similarities in the shape and position of the accessory sclerites and embolus. In both species, the ventral sclerite lacks spines or associated apophyses and tapers distally (VS, Fig. 19B, E), however, in *L. sandra* there is an enlarged swelling near the base (Fig. 19H). In both species, the prolateral sclerite is a single filliform process that flattens distally (PS, Fig. 19 G, H). However, the shape of the retrolateral tibial spine is markedly different between species, with *L. sandra* bearing two spines which taper sharply (RTS, Fig. 19A) and *F. striata* having a single enlarged spine on an extended base (RTS, Fig. 19D). Females also show striking differences with *L. sandra* bearing enlarged, circular spermathecae on short stalks (Fig. 32D) and *F. striata* with sinuous spermathecae and a sclerotized basal extension on the atrium (Fig. 32E).

Although the possibility of a connection between the North American and Asian leptonetid faunas is an intriguing hypothesis, relationships for Asian genera are poorly understood and comparative material is difficult to access. The similarities in palpal morphology between *L. sandra* and *F. striata* certainly suggests that there may be characters that support a relationship, but in the absence of additional material this is impossible to comprehensively assess. As pointed out by Brignoli (1977), however, *L. sandra* is clearly not congeneric with *Leptoneta* lacking both the tarsus shape and the shape, position, and number of accessory sclerites. Despite the obvious phylogenetic problems with monotypic genera, the absence of characters uniting *L. sandra* with European *Leptoneta* and any other known North American species, argues that it should be placed into a separate genus. *Montainineta* **gen. nov.** is thus proposed, giving the new combination *Montanineta sandra* (Gertsch, 1974) **comb. nov**.

Cave Evolution

Although leptonetids are among the spider groups that are most frequently associated with caves (Brignoli, 1972; Gertsch, 1971, 1974), relatively few species are completely eyeless (Brignoli, 1977). However, most species show at least some degree of adaptation to subterranean life, even in epigean habitats, where they typically live in cave-like microenvironments. While the life history for leptonetids is unknown, the combination of their habitat preferences and morphology suggests that they are all somewhat troglophilic and thus "pre- adapted" or exapted to live in caves. Ancestral state reconstruction of ecology (Fig. 38) supports this hypothesis as ancestral nodes are largely reconstructed as being troglophiles, even where clades include a high proportion of epigean species. Remarkably, the phylogeny shows that troglobites have evolved nine times independently (Fig. 38), and although not represented in the molecular analysis, each North American leptonetid genus includes at least one troglobitic species.

Among the most interesting aspects of *Neoleptoneta* morphology is the variation in troglomorphic characteristics, particularly in the degree of eye and pigment reduction. Intraspecific polymorphism was first suggested by Gertsch (1974) in his description of *N. capilla* which he reported as having both depigmented, blind (Cueva de La Capilla) and pigmented, eyed (Cueva de La Mina) morphotypes. Gertsch (1974) furthermore stated that the pigmented, eyed characteristics were "maintained in the genes" of the Cueva de La Mina individuals and not yet lost as in the population from Cueva de La Capilla (Gertsch, 1974: 179). Recent inventories at both sites were successful in obtaining a long series of specimens, including new records from both cave and surface locations. Examination of this collection confirms the presence of two morphotypes as described by Gertsch (1974), both of which also show nearly identical genitalic morphology. Molecular phylogenetic analysis (Fig. 40) recovers *N. capilla* as monophyletic, however, the pigmented, eyed morphotypes are well- supported as a clade sister to the population from Cueva de la Capilla. Interestingly, individuals collected near the entrance of Cueva de La Capilla belong to the pigmented, eyed morphotype and were not collected inside the cave despite a thorough search. Two possibilities are thus presented: 1) taxonomic error; with the pigmented, eyed populations remaining to be assigned, or 2) morphological polymorphism within species due to a lack of diagnostic features on the genitalia.

Although genitalic characters have formed the foundation for much of spider taxonomy (refs), several recent studies highlight the need for a more integrative approach (Paquin and Hedin, 2004, Paquin et al., 2008). Cave fauna in particular is plagued by taxonomic problems resulting from evolutionary convergence (Wiens et al., 2003) and sampling issues. Sampling is perhaps the most significant problem to taxonomic resolution as the scientists who collect in caves rarely do so on the surface. Given this bias and the general troglophily of leptonetids it is not at all surprising to find that most species are known only from caves. While it appears certain that the individuals currently included in *N. capilla* belong to two different species, additional sampling may blur species limits especially if intermediate morphologies are discovered. Recent inventories in Central Texas, for example, have discovered populations of *N. myopica* and *N. paraconcinna* that show a range of troglomorphic morphology from darkly pigmented, large- eyed individuals to lightly pigmented, reduced- eyed forms, and depigmented, blind individuals (Fig. 39). In this case, the pattern of variation is far more complex as several intergradient morphologies are observed and in some cases multiple morphotypes occur within the same cave. While taxonomic error similar to that in *N. capilla* is certainly involved, the complexity of morphological variation necessitates the integration of molecular, morphological, and ecological data combined with dense geographic sampling.

Key to the Genera of North American Leptonetidae

Many of the diagnostic features presented in this key require specialized microscopy techniques and examination of internal characters. Scanning electron microscopy may be required to identify key characters. The genera *Appaleptoneta* and *Calileptoneta* are difficult to separate in the absence of the male sex. See the Materials and Methods section for an explanation of techniques useful in specimen preparation and visualizing characters.

1. Eyes contiguous, rarely absent; male palp tarsus cylindrical, with pyriform embolus; cribellate or ecribellate, PMS and PLS cylindrical (Figs. 25, 32, 49, 57, 76- 78 in Ledford and Griswold, 2010) … 2 (Archoleptonetinae)

Eyes with PME posteriorly displaced or eyes absent; male palpal tarsus with dorsal transverse groove or distinctly sinuous; ecribellate, PMS and PLS comb- like with a linear row of aciniform gland spigots (Figs. 27, 65- 72 in Ledford and Griswold, 2010)… 3 (Leptonetinae)

2. Eyes contiguous; cribellum and calamistrum present; embolus sinuous and tapering distally; males lacking stridulatory files on the carapace and abdomen (Figs. 49- 56, 97- 102, 103- 110 in Ledford and Griswold, 2010) … *Archoleptoneta* Gertsch, 1974
Div. Two species, *A. schusteri* Gertsch, 1974 and *A. gertschi* Ledford and Griswold, 2010.
Dist. California

Eyes contiguous or absent; ecribellate; males with or without stridulatory files on the carapace and abdomen (Figs. 11- 17, 57- 64, 79- 84, 111) … *Darkoneta* Ledford and Griswold, 2010
Div. Six species, *D. arganoi* (Brignoli, 1974), *D. garza* (Gertsch, 1974), *D. obscura* (Gertsch, 1974), *D. quetzal* Ledford and Griswold, 2010, *D. reddelli* Ledford and Griswold, 2010, *D. stridulans* (Platnick, 1994)
Dist. Arizona, Guatemala, Mexico, Panama, and Texas

3. Male palpal tibia with retrolateral tibial spine (RTS; Figs. 14- 17D, 33) on a prominent base, rarely absent; male palpal tarsus lacking retroapical seta, with weak transverse groove or retrolateral bend; spermathecae loosely coiled or sinuous, atrium variable (Figs. 31A- D)… 4

Male palpal tibia lacking RTS; or at most represented by a pair of straight, modified setae (Fig. 19A); male palpal tarsus with strong transverse dorsal groove (Fig. 20- 21F); palpal bulb bearing numerous, highly modified accessory sclerites (Figs. 20- 22E); spermathecae tightly coiled or circular, atrium triangular (Figs. 32A- D) … 7

4. Male palpal tarsus with strong retrolateral bend middorsally (Fig. 16F); RTS on elevated base, sinuous, smooth, and lacking accessory setae (Fig. 16D); apical sclerite elongate, straight to curved at its base (Fig. 16E); spermathecae apically situated and loosely coiled (Fig. 37C) …*Neoleptoneta* Brignoli, 1972
Div. Seven species, *N. bonita* (Gertsch, 1974), *N. brunnea* (Gertsch, 1974), **comb. nov.**, *N. capilla* (Gertsch, 1971), *N. delicata* (Gertsch, 1974), *N. limpida* (Gertsch, 1974), *N. rainesi* (Gertsch, 1971), and *N. reclusa* (Gertsch, 1971).
Dist. Central Mexico (Fig. 3C)

Male palpal tarsus apically divided (Fig. 14F) or tapering (Figs. 15F, 17F); RTS on a low base, with serrate sculpture, and numerous accessory setae (Figs. 14- 15D, 17D); spermathecae loosely coiled to sinuous (Figs. 31A- B, D)… 5

5. Male palpal tarsus with strong longitudinal apical division (Fig. 14F); RTS straight with an apical hook (Fig. 14D); embolus triangular with a single spine- like extension apically (Fig. 14B, E); ventral sclerite reduced, spine- like; spermathecal stalks u- shaped, with elongate heads (Fig. 31A) … *Chisosea* **gen. nov.**
Div. Four species, *C. chisosea* (Gertsch, 1974), *C. isolata* (Gertsch, 1971), *C. modica* (Gertsch, 1974), and *C. pecki* (Gertsch, 1971).
Dist. Nuevo Leon, Mexico north to southwestern Texas (Fig. 3D).

Male palpal tarsus not divided, tapering to quadrate apically (Figs. 15F, 17F); spermathecae with enlarged heads or distinctly sinuous (Figs. 31B, D) … 6

6. Male palpal tarsus tapering apically (Fig. 17F); RTS recurved, bearing numerous setae at its base (Fig. 17D); embolus oval to subquadrate (Fig. 17C); ventral sclerite absent; spermathecae with few twists and bearing large heads (Fig. 31D) … *Tayshaneta* **gen. nov.**
Div. Eleven species, *T. anopica* (Gertsch, 1974), *T. bullis* (Cokendolpher, 2004), *T. coeca* (Chamberlin & Ivie, 1942), *T. concinna* (Gertsch, 1974), *T. devia* (Gertsch, 1974), *T. furtiva* (Gertsch, 1974), *T. microps* (Gertsch, 1974), *T. myopica* (Gertsch, 1974), *T. paraconcinna* (Cokendolpher & Reddell, 2001), *T. uvaldea* (Gertsch, 1974), *T. valverdae* (Gertsch, 1974).
Dist. Texas (Fig. 3A).

Male palpal tarsus quadrate apically (Fig. 15F); RTS straight to recurved, with two distinctive groups of modified setae at its base (Fig. 15D); ventral sclerite filliform (Figs. 15B, E); spermathecae distinctly sinuous (Fig. 31B)… *Ozarkia* **gen. nov.**
Div. Nine species, *O. alabama* (Gertsch, 1974), *O. apachea* (Gertsch, 1974), *O. archeri* (Gertsch, 1974), *O. arkansa* (Gertsch, 1974), *O. blanda* (Gertsch, 1974), *O. georgia* (Gertsch, 1974), *O. ivei* (Gertsch, 1974), *O. novaegalleciae* (Brignoli, 1979), and *O. serena* (Gertsch, 1974).
Dist. Alabama, Arkansas, Arizona, Georgia, and New Mexico (Fig. 3B).

7. Male palpal tibia with a pair of clustered spines retrolaterally (Fig. 19A); ventral sclerite straight with a basal knob (fig. 19H), ventral sclerite single and elongate; spermathecae on short, straight stalks bearing circular heads (Fig. 32D) … *Montanineta*, **gen. nov.**
Div. Monotypic, *Montanineta sandra* (Gertsch, 1974) **comb. nov.**
Dist. Virginia, West Virginia

Male palpal tibia lacking spines or with loose cluster of setae (Figs. 20- 22D); spermathecae tightly coiled, bearing numerous twists, atrium triangular, with or without apical division, to subquadrate (Figs. 32A- C) … 8

8. Palpal bulb with elongate ventral extension (Figs. 21A- C) and elongate retrolateral lobe (RL, Fig. 21E); ventral sclerite forked (Fig. 21B); atrium triangular, lacking apical division (Figs. 106- 118 in Ledford, 2004) … *Calileptoneta* Platnick, 1986, in part
Div. Nine species, seven of which key here *C. briggsi* Ledford, 2004, *C. californica* (Banks, 1904), *C. cokendolpheri* Ledford, 2004, *C. helferi* (Gertsch, 1974), *C. noyoana* (Gertsch, 1974), *C. sylva* Chamberlin and Ivie, 1942, *C. wapiti* (Gertsch, 1974).
Dist. California, Oregon

Palpal bulb lacking ventral extension (Figs. 20A- C, 22A- C), retrolateral lobe and accessory sclerites variable… 9

9. Male chelicerae with retrodistal processes (Fig. 3 in Ledford, 2004); palpal bulb with elongate retrolateral lobe (RL, 22A); atrium with distinct apical division (Figs. 32B, C) … *Calileptoneta* Platnick, 1986
Div. Nine species, two of which key here, *C. oasa* (Gertsch, 1974, *C. ubicki*, Ledford, 2004.

10. Male chelicerae lacking retrodistal processes; palpal bulb variable, but bearing numerous accessory sclerites (Figs. 20A- F); atrium triangular (Fig. 32A)… *Appaleptoneta* Platnick, 1986
Div. Seven species, *A. barrowsi* (Gertsch, 1974), *A. coma* (Barrows, 1940), *A. credula* (Gertsch, 1974), *A. fiskei* (Gertsch, 1974), *A. gertschi* (Barrows, 1940), *A. jonesi* (Gertsch, 1974), *A. silvicultrix* (Crosby and Bishop, 1925)
Dist. Appalachian Mountains, Kentucky, South Carolina, Alabama

Taxonomy

Leptonetidae Simon, 1872

Banks, 1904; Crosby and Bishop, 1925; Barrows, 1940; Chamberlin and Ivie, 1942; Brignoli, 1972, 1974, 1977, 1979; Gertsch, 1971, 1974; Platnick, 1986, 1994; Cokendolpher and Reddell, 2001; Cokendolpher, 2004; Ledford, 2004; Ledford and Griswold, 2010.

Type species. *Leptoneta convexa* Simon, 1872.

Diagnosis. Leptonetids can be separated from all other spider families, except Telemidae and Ochyroceratidae, by having the following combination of characters: six eyes, usually with the PME displaced posteriad of the AEG, rarely with eyes contiguous; PLS and PMS comb- like, with a linear row of aciniform gland spigots; patellar and tibial glands present. Separated from Telemidae and Ochyroceratidae by having the chelicerae free, the abdomen lacking a dorsoapical sclerotized ridge, and by having a ventroapical preening comb on metatarsus III. Members of the Archoleptonetinae are further separated by having sinuous patellar and tibial glands, a male palp with a cylindrical tarsus and thread- like embolus, cylindrical PLS, and females with a pair of elongate spermathecae.
Synapomorphies. Characters for the Leptonetidae include an unusual iridescence, especially on the legs and carapace (Figs. 1A- D), autospasy at the patella-tibia joint, the presence of tartipores on the ALS (Figs. 50, 58, 62, 70 in Ledford and Griswold, 2010), male palpi with a fused tegulum and subtegulum but with an expandable basal haematodocha (Figs. 27- 30), and a respiratory system consisting of a pair of short median branches with long laterals that open to a single spiracle anteriad of the ALS (Fig. 114 in Ledford and Griswold, 2010).
Composition. 21 genera, 213 species.
Distribution. Widely distributed in the Holarctic, including China, Mediterranean Europe, Japan, Korea, and North and Central America.

***Chisosea*, new genus**

Leptoneta isolata Gertsch, 1971: 50; Gertsch, 1974: 180.
Neoleptoneta isolata (Gertsch, 1974), Brignoli, 1972: 137.
(Figs. 10A- F, 14A- F, 24E, F, 27A- D, 31A, 33A, 34A, 35A, 36A, 37A)

Type species. *Leptoneta isolata* Gertsch, 1971 here designated.
Etymology. The name for this genus is derived from the Chisos Mountains in Big Bend National Park in Southwestern Texas, type locality of *Chisosea chisosea* (Gertsch, 1974).
Diagnosis. *Chisosea* can be separated from all other leptonetids by having females with elongate spermathecal heads on narrow, u- shaped stalks (Fig. 31A) and males with a divided palpal tarsus (Fig. 14F) and a triangular embolus bearing an apical spur (Fig. 14B, E).
Synapomorphies. *Chisosea* species are united by the unique conformation of the female genitalia, with narrow u- shaped spermathecal stalks bearing elongate heads (Fig. 37A) and by the triangular embolus of males bearing an apical spur (Fig. 35A).
Description. Total length 1.40- 2.30. Carapace depigmented to pale brown, sparsely setose, length 1.0- 1.25x width (Figs. 10A, D). Eyes present, reduced, or absent with the PME displaced posteriad of the AEG, elevated to flattened in lateral profile (Figs. 10C, F); chelicerae with lateral stridulatory file. Sternum oval; abdomen pale yellow to brown, lacking distinctive pattern males with 6 epiandrous spigots. Colulus triangular, ALS cylindrical, PMS and PLS comb- like, with a linear row of 6- 10 aciniform gland spigots. Legs elongate and thin, femur I 1.2- 2.45x carapace length; formula I, IV, II, III, covered in fine setae and with few scattered spines; patellar and tibial glands triangular with single, large pores; metatarsus III with ventroapical preening comb. Male palpal tarsus divided apically, with a middorsal division (Fig. 14F, 34A); tibia with a straight retrolateral spine with a distinctive apical bend (Figs. 14D, 33A); RTS on a weakly

elevated base surrounded by elongate setae (Fig. 14D); palpal bulb oval, longer than wide, with an apically situated triangular embolus bearing a basal tooth (E, Figs. 14B, E); prolateral lobe oval; ventral sclerite present, consisting of a single spine (VS, Figs. 14B, E); tarsal organ circular, shallow, and with a pair of receptors (Figs. 24E- F). Female genitalia consisting of a triangular atrium with a pair of lateral spermathecae bearing elongate, circular heads on twisted stalks with a distinctive u- shaped bend (Figs. 31A, 37A).

Composition. Four species, *C. chisosea* (Gertsch, 1974), *C. isolata* (Gertsch, 1971), *C. modica* (Gertsch, 1974), and *C. pecki* (Gertsch, 1971).

Distribution. Nuevo Leon, Mexico north to southwestern Texas (Fig. 3D).

***Ozarkia*, new genus**

Leptoneta alabama Gertsch, 1974: 160.
Neoleptoneta alabama (Gertsch, 1974), Brignoli, 1977: 216.
(Figs. 1A, 11A- F, 15A- F, 24C- D, 28A- D, 31B, 33B, 34B, 35B, 36B, 37B)

Type species. *Leptoneta alabama* Gertsch, 1974 here designated.

Etymology. This genus is named to commemorate the Ozark Mountains.

Diagnosis. *Ozarkia* are separated from other all leptonetids by the sinuous spermathecal stalks of females (Fig. 31B), the short retrolataeral spine on the male palpal tibia bearing a horizontal row of four flattened setae (Fig. 15D), and the filliform ventral sclerite on the male palpal bulb (Fig. 15B, E).

Synapomorphies. Species of *Ozarkia* are united by the unique conformation of the female genitalia with sinuous spermathecal stalks (Fig. 37B), by the spination on the male palpal tibia with two groups of flattened setae (Fig. 33B), and the presence of a filliform ventral sclerite (Fig. 15B, E).

Description. Total length 1.0- 2.10. Carapace pale brown to red- orange (Figs. 1A, 11A, D), sparsely setose, length 1.10- 1.28x width. Eyes present, reduced, or absent with the PME displaced posteriad of the AEG, elevated to flattened in lateral profile (Fig. 11C, F)); chelicerae with lateral stridulatory file. Sternum triangular (Fig. 11B, E); abdomen pale brown, lacking distinctive pattern. Colulus triangular, ALS cylindrical, PMS and PLS comb- like, with a linear row of 6- 10 aciniform gland spigots. Legs elongate and thin, femur I 1.28- 2.17x carapace length; formula I, IV, II, III, covered in fine setae and with few scattered spines; patellar and tibial glands triangular with single, large pores; metatarsus III with ventroapical preening comb. Male palpal tarsus quadrate apically, with a middorsal division (Figs. 15F); tibia with a short, straight retrolateral spine on a low base with two groups of flattened setae (Fig. 15D); palpal bulb oval, longer than wide, with an apically situated embolus (E, Figs. 15C, E) bearing a rounded lobe; prolateral lobe oval (PL, Fig. 15C); ventral sclerite consisting of an apical brush of filiform appendages (VS, Figs. 15B, E); retrolateral sclerite rectangular (Fig. 15A, E). Female genitalia consisting of an oval atrium with a pair of lateral, sinuous spermathecae bearing circular heads (Figs. 31B, 37B).

Composition. Nine species, *O. alabama* (Gertsch, 1974), *O. apachea* (Gertsch, 1974), *O. archeri* (Gertsch, 1974), *O. arkansa* (Gertsch, 1974), *O. blanda* (Gertsch, 1974), *O. georgia* (Gertsch, 1974), *O. ivei* (Gertsch, 1974), *O. novaegalleciae* (Brignoli, 1979), and *O. serena* (Gertsch, 1974).

Distribution. Alabama, Arkansas, Arizona, Georgia, and New Mexico (Fig. 3B).

Neoleptoneta Brignoli, 1972

Leptoneta capilla Gertsch, 1971: 52; Gertsch, 1974: 179.
Neoleptoneta capilla (Gertsch, 1974), Brignoli, 1972: 135; Brignoli, 1977; Platnick, 1986; Cokendolpher and Reddell, 2001; Cokendolpher, 2004.

(Figs. 1B, 12A- F, 16A- F, 18A- F, 24A- B, 29A- D, 31C, 33C, 34C, 35C, 36C, 37C, 40A- C).

Type species. *Leptoneta capilla* Gertsch, 1971.
Diagnosis. *Neoleptoneta* species are separated from all other leptonetids by having males with a retrolaterally curved palpal tarsus (Fig. 16D), an elongate ventral sclerite and embolus (VS, E Fig. 16), and having females with apically twisted spermathecae bearing small heads (Figs. 31C).
Synapomorphies. Species of *Neoleptoneta* are united by the apically twisted spermathecae of females (Fig. 37C) and the elongate apical sclerite and embolus of males (Figs. 16B, E, 35C).
Description. Total length 1.4- 2.05. Carapace depigmented to pale brown, sparsely setose, length 1.0- 1.3x width. Eyes present, reduced, or absent (Figs. 12A, D) with the PME displaced posteriad of the AEG, elevated to flattened in lateral profile; chelicerae with lateral stridulatory file. Sternum oval with few scattered setae (Fig. 12B, E); abdomen pale brown, lacking distinctive pattern (Figs. 12A, D). Colulus triangular, ALS cylindrical, PMS and PLS comb- like, with a linear row of 6- 10 aciniform gland spigots. Legs elongate and thin, femur I 0.95- 1.58x carapace length; formula I, IV, II, III, covered in fine setae and with few scattered spines; patellar and tibial glands triangular with single, large pores; metatarsus III with ventroapical preening comb. Male palpal tarsus tapering apically, with a distinctive middorsal bend (Figs. 16F); tibia with a single elongate retrolateral spine on an elevated base (Fig. 16D); palpal bulb oval, longer than wide, with scale- like sculpturing laterally (Fig. 16C) , and apically situated elongate embolus (E, Figs. 16B, E) with a distinctive bend at its base; prolateral lobe triangular (PL, Fig. 16C); tarsal organ circular, elevated, and with a pair of receptors (Figs. 24A- B, 36C). Female genitalia consisting of a triangular atrium with a pair of lateral, apically twisted spermathecae bearing circular heads (Figs. 31C, 37C).
Composition. Seven species, *N. bonita* (Gertsch, 1974), *N. brunnea* (Gertsch, 1974), *N. capilla* (Gertsch, 1971), *N. delicata* (Gertsch, 1974), *N. limpida* (Gertsch, 1974), *N. rainesi* (Gertsch, 1971), and *N. reclusa* (Gertsch, 1971).
Distribution. Central to Southern Mexico (Fig. 3C).

Tayshaneta, new genus

Leptoneta Simon, 1872; Chamberlin and Ivie, 1942; Gertsch, 1974.
Neoleptoneta Brignoli, 1972; Brignoli, 1977; Platnick, 1986; Cokendolpher and Reddell, 2001; Cokendolpher, 2004.
(Figs. 1D, 13A- F, 17A- F, 24G- H, 31D, 33D, 34D, 35D, 36D, 37D, 39A- F)

Type species. *Leptoneta coeca* Chamberlin & Ivie, 1942, here designated.

Etymology. This genus is named in honor of the Caddo Indians who are native to Eastern Texas. The Caddo word *Taysha* means "friends, allies" and was used as a greeting among allied tribes in Texas. The word was later mispronounced by the Spanish as *Tejas* and is the origin of the name for the state of Texas.

Diagnosis. *Tayshaneta* is separated from all other leptonetids by having males with an elongate, recurved retrolateral spine on the palpal tibia (Fig. 17D) and females with short spermathecal stalks bearing large heads (Fig. 31D). Further separated from *Chisosea* **gen. nov.** by lacking the u- shaped bend on the spermathecal stalks (Fig. 31A) and lacking the apical spur on the embolus (Fig. 14E).

Synapomorphies. Species of *Tayshaneta* are united by the unique conformation of the female genitalia, with short spermathecal stalks bearing large heads (Fig. 37D) and the recurved retrolateral spine on the male palpal tibia (Fig. 33D).

Description. Total length 1.0- 1.98. Carapace depigmented to orange- brown, sparsely setose, length 0.88- 1.8x width. Eyes present, reduced, or absent with the PME displaced posteriad of the AEG (Fig. 13A, D), elevated to flattened in lateral profile (Fig. 13C, F); chelicerae with lateral stridulatory file. Sternum triangular to subquadrate (Fig. 13B, E); abdomen pale yellow to dark brown, lacking distinctive pattern. Colulus triangular, ALS cylindrical, PMS and PLS comb- like, with a linear row of 6- 10 aciniform gland spigots. Legs elongate and thin, femur I 1.0- 2.26x carapace length; formula I, IV, II, III, covered in fine setae and with few scattered spines; patellar and tibial glands triangular with single, large pores; metatarsus III with ventroapical preening comb. Male palpal tarsus tapering apically, with a middorsal division (Figs. 17F); tibia with a single recurved retrolateral spine on an elevated base surrounded by elongate setae and 2- 4 paddle-shaped setae (Fig. 17D); palpal bulb oval, longer than wide, with an apically situated embolus (E, Figs. 17C, E) and an oval prolateral lobe; ventral sclerite present or absent, consisting of a single spine; tarsal organ circular, shallow, and with a pair of receptors (Figs. 24G- H, 36D). Female genitalia consisting of a single oval to triangular atrium with a pair of lateral spermathecae bearing large, circular heads (Figs. 31D, 37D).

Composition. Eleven species, *T. anopica* (Gertsch, 1974), *T. bullis* (Cokendolpher, 2004), *T. coeca* (Chamberlin & Ivie, 1942), *T. concinna* (Gertsch, 1974), *T. devia* (Gertsch, 1974), *T. furtiva* (Gertsch, 1974), *T. microps* (Gertsch, 1974), *T. myopica* (Gertsch, 1974), *T. paraconcinna* (Cokendolpher & Reddell, 2001), *T. uvaldea* (Gertsch, 1974), *T. valverdae* (Gertsch, 1974).

Distribution. Central Texas (Fig. 3A).

***Montanineta*, new genus**

Leptoneta sandra Gertsch, 1974: 153; Platnick, 1986.
(Figs. 19A-C, H, 26C-D, 32D)

Type species. *Leptoneta sandra* Gertsch, 1974, here designated.

Etymology. This genus is derived from the state motto of West Virginia "Montani Semper Liberi" meaning mountaineers always free.

Diagnosis. *L. sandra* is separated from other leptonetids by having females with circular spermathecae on short, untwisted stalks (Fig. 32D). Males are diagnosed from other leptonetid genera, except *Falcileptoneta*, by the conformation of the palpal bulb with a single ventral sclerite (VS, Fig. 19H) and a filiform prolateral sclerite (PS, Fig. 19H).

Separated from *Falcileptoneta* by the paired retrolateral spines on the palpal tibia (Fig. 19A) and the basal lobe on the ventral sclerite (Fig. 19H).

Description. Total length 1.8- 2.0. Carapace orange- brown, darker along margins, sparsely setose, length 1.10- 1.17x width. Eyes present with the PME displaced posteriad of the AEG, enclosed by dark patterning, and elevated in lateral profile. Sternum oval, with few scattered setae; abdomen pale brown, lacking distinctive pattern. Colulus triangular, ALS cylindrical, PMS and PLS comb- like, with a linear row of aciniform gland spigots. Legs elongate and thin, femur I 1.82- 2.0x carapace length; formula I, IV, II, III, covered in fine setae and with few scattered spines; patellar and tibial glands oval, pores indistinct (Figs. 3- 4 in Platnick, 1986). Male palpal tarsus tapering apically, with a middorsal division; tibia with a pair of retrolateral spines on an elevated base surrounded by several scattered setae (RTS, Fig. 19A); palpal bulb oval, as long as wide, with an apically situated oval embolus (E, Figs. 19B) with fine sculpture along its margins; prolateral lobe oval (PL, Fig. 19C); ventral sclerite elongate, with a distinctive basal swelling (Fig. 19H);

tarsal organ circular, shallow, and with a pair of receptors.

Female genitalia consisting of a trapezoidal atrium with a pair of lateral spermathecae bearing large, circular heads (Figs. 32D).

Composition. Monotypic, *Montanineta sandra* (Gertsch, 1974) **comb. nov.**

Distribution. Virginia, West Virginia.

Acknowledgements

This study would not have been possible without the encouragement and support of several people and institutions. I thank my advisors, Charles Griswold, Rosemary Gillespie, George Roderick, Marshal Hedin, and Brent Mishler for their constant guidance and support. Pierre Paquin was instrumental to the project, providing specimens, fieldwork assistance, encouragement, and various lessons in Quebecois. James Cokedolpher and James Reddell provided regular guidance and specimens through the Museum of Texas Tech University and the Texas Memorial Museum.

I thank the members of the Evolab at U.C. Berkeley, Griswold lab, California Academy of Sciences, Hedin lab, San Diego State University, and the Susan Masta lab, Portland State University. Norm Platnick, Darrell Ubick, Jeremy Miller, Josh Campbell, and James Cokendolpher provided helpful comments and discussion about leptonetid spiders. Jean Krejca and Mike Slay provided photos of leptonetids, cave coordinates, and helpful discussions about cave biology. Anthea Carmichael, Sarah Crews, and Sean Schoville provided invaluable assistance in the lab. Jeremy Brown and the Bodega Phylogenetics Workshop provided instruction on phylogenetic methods. Giovanni Maki provided help with the figures. Pierre Paquin, Mark Sanders, Josh Campell, Kathleen O' Connor, James Reddell, and Peter Sprouse provided specimens and help in the field. Oscar Franke, Jean Louis Lacaille- Musquiz, Martin Archambault, and Pierre Provost were instrumental to fieldwork for Mexbebitte 2008 at the Rancho de El Cielo in Tamaulipas, Mexico. Peter Sprouse was especially helpful with providing numerous coordinates to caves in Mexico. The amazing Jim "Crash" Kennedy and Kerr Wardlaw facilitated access to Fawcett's Cave at the Devil's River State Natural Area in Val Verde County, Texas.

Permits and cave access were kindly facilitated through Cyndee Watson, U.S. Fish and Wildlife, David Riskind, Texas Parks and Wildlife, Kimble White, SWCA Environmental Consultants, and Kathleen O'Connor, Zara Environmental. I am especially grateful to all of my fellow cavers and friends in the Texas caving community for putting up with my constant questions about cave locations, history, and requests for access and/ or specimens.

Anthea Carmichael provided me with a home away from home and constant canine companionship. Lastly, I thank my wife and each member of the Ubick and Lindstrom families without whom none of this would have been possible.

This study was supported by a National Science Foundation Doctoral Dissertation Improvement Grant (DDIG-0909872), the Exline- Frizzell fund at the California Academy of Sciences, the Walker Fund at U.C. Berkeley, the National Speleological Society (NSS general research grant), and the University of California.

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Table 1: List of morphological abbreviations used in the text and figures.

Abbreviation	Structure
At	Atrium
BH	Basal Hematodocha
E	Embolus
PL	Prolateral Lobe
Rs	Retrolateral Tarsal Seta
RS	Retrolateral Sclerite
RTS	Retrolateral Tibial Spine
SH	Spermathecal Head
SS	Spermathecal Stalk
Ts	Palpal Tarsus
VS	Ventral Sclerite

Table 2: List of described *Neoleptoneta* species, distribution, known sexes, and ecology. Species marked with an '*' are represented in the molecular analysis.

Species, author	Sexes	Ecology
Neoleptoneta alabama (Gertsch, 1974)*	Male, Female	Troglophile
Neoleptoneta anopica (Gertsch, 1974)*	Female	Troglobite
Neoleptoneta apachea (Gertsch, 1974)	Male	Epigean
Neoleptoneta archeri (Gertsch, 1974)	Male	Epigean
Neoleptoneta arkansa (Gertsch, 1974)*	Female	Troglobite
Neoleptoneta blanda (Gertsch, 1974)	Female	Troglophile
Neoleptoneta bonita (Gertsch, 1974)	Male	Troglophile
Neoleptoneta bullis Cokendolpher, 2004*	Male, Female	Troglophile
Neoleptoneta caliginosa Brignoli, 1977	Female	Troglophile
Neoleptoneta capilla (Gertsch, 1971)*	Male, Female	Troglophile
Neoleptoneta chisosea (Gertsch, 1974)*	Female	Epigean
Neoleptoneta coeca (Chamberlin & Ivie, 1942)*	Male, Female	Troglophile
Neoleptoneta concinna (Gertsch, 1974)*	Male, Female	Troglophile
Neoleptoneta delicata (Gertsch, 1971)	Male, Female	Troglophile
Neoleptoneta devia (Gertsch, 1974)*	Female	Troglophile
Neoleptoneta furtiva (Gertsch, 1974)	Female	Epigean
Neoleptoneta georgia (Gertsch, 1974)*	Female	Troglobite
Neoleptoneta isolata (Gertsch, 1971)	Male, Female	Troglobite
Neoleptoneta iviei (Gertsch, 1974)	Female	Epigean
Neoleptoneta limpida (Gertsch, 1974)	Female	Troglophile
Neoleptoneta microps (Gertsch, 1974) *	Female	Troglobite
Neoleptoneta modica (Gertsch, 1974)*	Male	Epigean
Neoleptoneta myopica (Gertsch, 1974) *	Male, Female	Troglobite
Neoleptoneta novaegalleciae Brignoli, 1979	Male	Troglophile
Neoleptoneta paraconcinna Cokendolpher and Reddell, 2001*	Male, Female	Troglophile
Neoleptoneta pecki (Gertsch, 1971)	Male,	Troglobite

	Female	
Neoleptoneta rainesi (Gertsch, 1971)*	Male, Female	Troglophile
Neoleptoneta reclusa (Gertsch, 1974)	Male, Female	Troglobite
Neoleptoneta serena (Gertsch, 1974)	Female	Troglophile
Neoleptoneta uvaldea (Gertsch, 1974)	Female	Troglophile
Neoleptoneta valverdae (Gertsch, 1974)*	Male, Female	Troglophile

Table 3:
List of specimens used in the study, localities, deposition, and voucher codes.

Voucher Code/ GenBank Acc.	Genus	Species, author	Country	State	County	Locality	Lat. Long.
Lep 1 F5/	*Appaleptoneta*	*barrowsi* (Gertsch, 1974)	USA	Alabama	Blount	Bangor Cave	33.98N, 86.73W
Lep 9 C8/	*Appaleptoneta*	*credula* (Gertsch, 1974)	USA	Alabama	Lauderdale	Bat Cave	34.90N, 87.59W
Lep 1 F7/	*Appaleptoneta*	undet.	USA	Indiana	Lawrence	Smith Falley Cave	38.75N, 86.59W
Lep 2 B8/	*Archoleptoneta*	*gertschi* Ledford & Griswold, 2010	USA	California	Amador	Volcano, at surface of Humming Bird Cave	38.44N, 120.63W
Lep 4 B7/	*Archoleptoneta*	*schusteri* (Gertsch, 1974)	USA	California	Marin	Mt Burdell 0.85mi W. Hwy 101 off San Marin Drive & Simmons Lane	38.12N, 122.57W
Lep 3 A1/	*Archoleptoneta*	*schusteri* (Gertsch, 1974)	USA	California	San Diego	Hwy 78, ~1.2mi. NE Descanso Junction, NW side of Guatay Mtn.	32.51N, 116.35
Lep 3 B5/	*Calileptoneta*	*californica* (Banks, 1894)	USA	California	Contra Costa	Mt. Diablo State Park	37.85N, 121.91W
Lep 4 A9/	*Calileptoneta*	undet.	USA	California	El Dorado	HWY 50 at Riverton, Southside of South fork of American River	38.77N, 120.44W
Lep 4 A5/	*Calileptoneta*	undet.	USA	California	Kern	Packsaddle Cave, 1.4mi E. Fairview	35.93N, 118.46W
Lep 2 A6/	*Calileptoneta*	*noyoana* (Gertsch, 1974)	USA	California	Mendocino	Camp Dunlap	39.34N, 123.56W
Lep 3 A3/	*Calileptoneta*	*ubicki* Ledford, 2004	USA	California	Monterey	Arroyo Seco Campground, SW of Lakes	36.23N, 121.48W
Lep 2 H8/	*Calileptoneta*	*sylva* (Chamberlin & Ivie, 1942)	USA	California	Siskiyou	Gazelle- Callahan Road, 8.3 mi. W. of Gazelle	41.45N, 122.63W
Lep 4 C4/	*Chisosea*	*chisosea* (Gertsch, 1974)	USA	Texas	Brewster	Big Bend National Park, nr. parking lot of Casa gravier trail	29.27N, 103.28W
Lep 5 A5/	*Neoleptoneta*	*capilla* (Gertsch, 1971)	Mexico	Tamaulipas	Tamaulipas	Cueva de la Capilla	23.10N, 99.24W
Lep 5 B9/	*Neoleptoneta*	*capilla* (Gertsch, 1971)	Mexico	Tamaulipas	Tamaulipas	Cueva de la Mina	23.10N, 99.21W

Lep 5 D2/	*Neoleptoneta*	*capilla* (Gertsch, 1971)	Mexico	Tamaulipas	Tamaulipas	Harrison Sinkhole	23.10N, 99.19W
Lep 5 D8/	*Neoleptoneta*	*capilla* (Gertsch, 1971)	Mexico	Tamaulipas	Tamaulipas	At surface of Cueva de la Capilla	23.10N, 99.24W
Lep 5 E1/	*Neoleptoneta*	undet.	Mexico	Tamaulipas	Tamaulipas	Cueva de Ojo de Agua	23.03N, 99.12W
Lep 5 E2/	*Neoleptoneta*	undet.	Mexico	Tamaulipas	Tamaulipas	Gruta de Quintero	22.64N, 99.04W
Lep 5 G7/	*Neoleptoneta*	*rainesi* (Gertsch, 1971)	Mexico	Tamaulipas	Tamaulipas	Cueva de El Pachon	22.60N, 99.04W
zara-5044/	*Chisosea*	*modica* (Gertsch, 1974)	Mexico	Nuevo Leon	Nuevo Leon	Cueva Martiniano	25.30N, 100.20W
unam3/	*Neoleptoneta*	undet.	Mexico	Coahuila	Coahuila	Cueva de La Falla	27.81N, 101.59W
unam4/	*Neoleptoneta*	undet.	Mexico	Coahuila	Coahuila	Cueva Cerezo	27.81N, 101.57W
Lep 7 A9/	*Ozarkia*	*alabama*	USA	Alabama	Calhoun	Lady Cave	33.73N, 85.81W
Lep 9 C7/	*Ozarkia*	*alabama* (Gertsch, 1974)	USA	Alabama	DeKalb	Cemetery Cave no.444	34.42N, 85.81W
Lep 9 A9/	*Ozarkia*	*serena* (Gertsch, 1974)	USA	Alabama	Lauderdale	Collier Cave	34.74N, 87.80W
Lep 9 F1/	*Ozarkia*	*arkansa* (Gertsch, 1974)	USA	Arkansas	Stone	Blanchard Springs Cave, The Titans	36.01N, 92.22W
Lep 4 F7/	*Ozarkia*	*georgia* (Gertsch, 1974)	USA	Georgia	Dade	Byer's Cave	38.87N, 85.50W
Lep 8 A7/	*Ozarkia*	*georgia* (Gertsch, 1974)	USA	Georgia	Dade	Kilpatrick Cave	34.74N, 85.54W
Lep 8 B8/	*Ozarkia*	*fiskei* (Gertsch, 1974)	USA	Georgia	Walker	Pettijohn's Cave	34.66N, 85.36W
Lep 3 I6/	*Tayshaneta*	undet.	USA	Texas	Bell	Witt’s Cave	30.89N, 97.68W
p1_peep_in_the_deep/	*Tayshaneta*	*paraconcinna* (Cokendolpher & Reddell, 2001)	USA	Texas	Bell	Peep in the Deep Cave, Fort Hood	31.20N, 97.51W
Lep 1 H3/	*Tayshaneta*	*bullis* (Cokendolpher, 2004)	USA	Texas	Bexar	UTSA area, Hill's and Dale's Pit	29.59N, 98.63W

Lep 7 G6/	*Tayshaneta*	sp. nov.	USA	Texas	Bexar	Lithic Ridge Cave, Government Canyon State Natural Area	29.56N, 98.74W
Lep 9 E8/	*Tayshaneta*	sp. nov.	USA	Texas	Bexar	At surface of Madla's Cave	29.60N, 98.69W
zara-5551/	*Tayshaneta*	sp. nov.	USA	Texas	Bexar	Cave 1604-F019	29.47N, 98.70W
Lep 1 A9/	*Tayshaneta*	sp. nov.	USA	Texas	Bexar	Madla's Cave	29.60N, 98.69W
Lep 1 C2/	*Tayshaneta*	*microps* (Gertsch, 1974)	USA	Texas	Bexar	Goverment Canyon Bat Cave	29.56N, 98.76W
Lep 1 E2/	*Tayshaneta*	sp. nov.	USA	Texas	Bexar	Caracol Creek Coon Cave	29.45N, 98.71W
Lep 1 H9/	*Tayshaneta*	*bullis* (Cokendolpher, 2004)	USA	Texas	Bexar	Camp Bullis, Up the Creek Cave	29.63N, 98.55W
Lep 1 H4/	*Tayshaneta*	*paraconcinna* (Cokendolpher & Reddell, 2001)	USA	Texas	Blanco	Pedernales State Park	30.30N, 98.26W
Lep 1 G4/	*Tayshaneta*	undet.	USA	Texas	Comal	Guadalupe river	29.81N, 98.17W
Lep 7 D7/	*Tayshaneta*	sp. nov.	USA	Texas	Hays	Grapevine Cave	30.04N, 98.21W
Lep 8 C7/	*Tayshaneta*	undet.	USA	Texas	Hays	Pulpit Cave	29.88N, 98.02W
Lep 8 E8/	*Tayshaneta*	undet.	USA	Texas	Hays	Hackberry Cave	30.01N, 97.94W
Lep 8 G4/	*Tayshaneta*	undet.	USA	Texas	Hays	McCarty Cave	29.85N, 97.99W
Lep 1 B3/	*Tayshaneta*	coeca	USA	Texas	Hays	Root Beard Cave	29.97N, 97.98W
Lep 1 E6/	*Tayshaneta*	sp. nov.	USA	Texas	Hays	Cathy's Cave	29.90N, 98.08W
Lep 1 H7/	*Tayshaneta*	undet.	USA	Texas	Kerr	Road 1338, West of Kerrville	30.08N, 99.16W
9038787/	*Tayshaneta*	sp. nov.	USA	Texas	Medina	Medina Dam Cave	29.54N, 98.93W
Lep 3 H3/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Travis	Tooth Cave, BCP	30.40N, 97.85W

Lep 3 I7/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Travis	Root Cave, BCP	30.40N, 97.85W
Lep 4 D1/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Travis	Geode Cave, BCP	30.39N, 97.86W
Lep 4 F8/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Travis	Jester Estate's Cave	30.39N, 97.79W
Lep 4 i2/	*Tayshaneta*	*devia* (Gertsch, 1974)	USA	Texas	Travis	At the surface of Tooth Cave, BCP	30.40N, 97.85W
Lep 6 F2/	*Tayshaneta*	*paraconcinna* (Cokendolpher & Reddell, 2001)	USA	Texas	Travis	Pedernales River and Highway 71	30.38N, 98.08W
Lep 7 E8/	*Tayshaneta*	sp. nov.	USA	Texas	Travis	District Park Cave	30.21N, 97.85W
Lep 7 F5/	*Tayshaneta*	*concinna* (Gertsch, 1974)	USA	Texas	Travis	Stark's North Mine	30.38N, 97.67W
Lep 8 D3/	*Tayshaneta*	*devia* (Gertsch, 1974)	USA	Texas	Travis	Brewpot Sink	30.41N, 97.85W
Lep 8 D5/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Travis	Tight Pit, BCP	
Lep 8 E1/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Travis	Cortaña Cave	30.38N, 97.85W
Lep 1 A1/	*Tayshaneta*	sp. nov.	USA	Texas	Travis	Slaughter Creek Cave	30.19N, 97.87W
Lep 1 A2/	*Tayshaneta*	*concinna* (Gertsch, 1974)	USA	Texas	Travis	County Line Bat Cave	30.14N, 97.88W
Lep 1 A6/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Travis	Gallifer Cave, BCP	30.40N, 97.85W
Lep 1 A7/	*Tayshaneta*	*devia* (Gertsch, 1974)	USA	Texas	Travis	McDonald Cave	30.43N, 97.86W
Lep 1 A8/	*Tayshaneta*	*concinna* (Gertsch, 1974)	USA	Texas	Travis	Seibert Sink	30.25N, 97.82W
Lep 1 C3/	*Tayshaneta*	sp. nov.	USA	Texas	Travis	Whirlpool Cave	30.21N, 97.84W
Lep 1 G1/	*Tayshaneta*	*concinna* (Gertsch, 1974)	USA	Texas	Travis	Lost Gold Cave	30.26N, 97.81W
Lep 6 A9/	*Tayshaneta*	sp. nov.	USA	Texas	Val Verde	Fawcett's Cave, Devil's River State Natural Area	29.90N, 100.91W
Lep 7 i1/	*Tayshaneta*	*paraconcinna* (Cokendolpher	USA	Texas	Williamson	Twin Springs Cave (=Whitney West	30.69N,

		& Reddell, 2001)				Cave)	97.78W
Lep 3 D3/	*Tayshaneta*	*paraconcinna* (Cokendolpher & Reddell, 2001)	USA	Texas	Williamson	On Campus Cave	30.61N, 97.69W
Lep 3 G5/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Williamson	Goat Cave	30.49N, 97.71W
Lep 3 G7/	*Tayshaneta*	undet.	USA	Texas	Williamson	Prairie's Flats Cave	30.74N, 97.73W
Lep 4 D3/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Williamson	Steiner Telephone Pole Cave	30.39N, 97.86W
Lep 4 D9/	*Tayshaneta*	*paraconcinna* (Cokendolpher & Reddell, 2001)	USA	Texas	Williamson	Three Miles Cave	30.63N, 97.73W
Lep 4 H9/	*Tayshaneta*	*anopica* (Gertsch, 1974)	USA	Texas	Williamson	Corn Cobb's Cave	30.75N, 97.73W
Lep 9 G9/	*Tayshaneta*	undet.	USA	Texas	Williamson	Flat Rock Cave	30.63N, 97.72W
Lep 1 C4/	*Tayshaneta*	*myopica* (Gertsch, 1974)	USA	Texas	Williamson	McNeil Bat Cave	30.45N, 97.72W
Lep 1 G2/	*Tayshaneta*	*anopica* (Gertsch, 1974)	USA	Texas	Williamson	Cobb's Cave	30.78N, 97.73W
Lep 3 A5/	*Usofila*	*pacifica* (Banks, 1894)	USA	Oregon	Clatsop	Ecola State Park, N. of Ecola Point, N. of Cannon Beach	45.92N, 123.97W
Lep 3 A4/	*Usofila*	*pacifica* (Banks, 1894)	USA	Oregon	Columbia	5.4 mi. Southwest of Clatskanie on HWY 47	46.06N, 123.26W
Lep 2 F3/	*Usofila*	*pacifica* (Banks, 1894)	USA	Oregon	Lane	McKenzie Ridge, Willamette National Forest	44.18N, 122.11W

Table 4:
Primer sequences, source, and annealing temperatures. Optimized annealing temperatures in bold.

Gene	Forward	Sequence	Reference	Reverse	Sequence	Reference	Annealing Temperature
COI	1718	5- GGA GGA TTT GGA AAT TGA TTA GTT CC- 3	Simon et al. (1994)	2568	5- GCT ACA ACA TAA TAA GTA TCA TG- 3	Simon et al. (1994)	44- 50, **48ºC**
COI	1751	5 -GAG CTC CTG ATA TAG CTT TTC C- 3	Simon et al. (1994)	2568	5- GCT ACA ACA TAA TAA GTA TCA TG- 3	Simon et al. (1994)	44- 50, **48ºC**
COI	PMT1	5- GGT CAA CAA ATC ATA AAG ATA TTG G- 3	Folmer et al. (1994)	2568	5- GCT ACA ACA TAA TAA GTA TCA TG- 3	Simon et al. (1994)	44- 50, **45ºC**
COI	1490-ONO	5- CW ACA AAY CAT ARR GAT ATT GG- 3	Simon et al. (1994)	2568	5- GCT ACA ACA TAA TAA GTA TCA TG- 3	Simon et al. (1994)	44- 50, **45ºC**
COI	2309	5- TTT ATG CTA TAG TTG GAA TTG G- 3	Simon et al. (1994)	2776	5- GGA TAA TCA GAA TAN CGN CGA GG- 3	Simon et al. (1994)	44- 50, **48ºC**
28srDNA	ZX1	5- ACC CGC TGA ATT TAA GCA TAT- 3	Mallatt and Sullivan (1998)	ZR2	5- CCG AAG TTT CCC TCA GGA TAG C- 3	Mallatt and Sullivan (1998)	50- 60, **55ºC**
28srDNA	28sOCS	5- CGT GAA ACT GCT CAG AGG- 3	Miller et al. (2010)	28sC	5- GGC GAA AGA CTA ATC GAA CC- 3	Miller et al. (2010)	50- 60, **55ºC**
Histone 3	H3af	5- ATG GCT CGT ACC AAG CAG ACV GC- 3	Colgan et al. (1998)	H3ar	5- ATA TCC TTR GGC ATR ATR GTG AC- 3	Colgan et al. (1998)	48- 55, **50ºC**
Histone 3	H3nf	5- ATG GCT CGT ACC AAG CAG AC- 3	Colgan et al. (1998)	H3nr	5- ATR TCC TTG GGC ATG ATT GTT AC- 3	Colgan et al. (1998)	48- 55, **50ºC**

Table 5:
Evolutionary models used for Bayesian analysis as selected by the Akaike Information Criterion in MrModeltest v. 2.2 (Nylander, 2004).

Partition	**Model**	**AIC Score**
COI position 1	GTR +I +G	4442.53
COI position 2	GTR +I +G	2740.73
COI position 3	GTR +G	20142.94
H3 position 1	GTR +G	4406.61
H3 position 2	JC +I +G	459.97
H3 position 3	GTR +I	811.03
28s rDNA	GTR +I +G	40623.77

Table 6:
Summary tree statistics and conditions for each analysis.

Analysis	**Optimality Criterion, Software**	**Conditions**	**Statistics**
Concatenated	Parsimony, PAUP* v.4b10	1000 iterations, heuristic search with TBR	41 trees, 8006 steps
COI (full partitions)	Likelihood, RAxML v.7.0.4	1000 non- parametric bootstrap replicates	-lnL 16062.90
Histone 3 (full partitions)			-lnL 2910.70
28s rDNA			-lnL 20318.74
Three- gene concatenated			-lnL 34742.79
Two- gene concatenated (COI, 28s)			-lnL 34550.09
COI (full partitions)	Bayesian, Mr. Bayes v.3.1.2	20,000,000 generations, burnin= 25%	sdsf 0.003
COI (1st & 2nd, 3rd positions)			sdsf 0.003
COI (unpartitioned)			sdsf 0.003
Histone 3 (full partitions)			sdsf 0.004
Histone 3 (1st & 2nd, 3rd positions)			sdsf 0.01
Histone 3 (unpartitioned)			sdsf 0.03
28s rDNA			sdsf 0.008
Three- gene concatenated		50,000,000 gen, burnin= 25%	sdsf 0.05
Two- gene concatenated (COI, 28s)		20,000,000 gen, burnin= 25%	sdsf 0.01

Table 7:
Results of Bayes Factor hypothesis testing for partitioning strategies (Brown & Lemmon, 2007).

Partitions	-lnL Harmonic Mean (post burnin)	Bayes Factor	Support for Rejection
COI- 3 partitions (1st, 2nd, and 3rd codon positions)	-13993.97	--	--
COI- 2 partitions (1st&2nd, 3rd codon positions)	-14040.81	46.84	Very Strong
COI- 0 partitions (1st&2nd&3rd codon positions)	-14525.37	531.4	Very Strong
Histone 3- 3 partitions (1st, 2nd, and 3rd codon positions)	-3111.80	--	--
Histone 3- 2 partitions (1st&2nd, 3rd codon positions)	-3350.68	238.8	Very Strong
Histone 3- 0 partitions (1st&2nd&3rd codon positions)	-3370.91	259.1	Very Strong

Table 8:
Results of Bayes Factor hypothesis testing (three gene concatenated analyses; (Brown & Lemmon, 2007).

Constraint	-lnL Harmonic Mean (post burnin of 25%)	Bayes Factor	Support for Rejection
No constraint	-34698.11	--	--
Neoleptoneta monophyletic; includes all included species listed from Platnick (2010).	-34699.46	1.35	Weak

Table 9:
Morphological characters and states used for character mapping.

1) **Retrolateral tibial spine:**
(0) absent; (1) low base, hooked apically; (2) low base, two groups of flattened setae; (3) high base, sinuous; (4) low base, recurved.

2) **Palp tarsus shape:**
(0) entire, elongate; (1) entire, tapering apically; (2) entire, sinuous; (3) divided, with retroapical seta; (4) divided, retroapical seta absent; (5) entire, quadrate apically.

3) **Embolus shape:**
(0) pyriform; (1) suboval; (2) oval with apical knob; (3) triangular with apical spur; (4) suboval, elongate; (5) suboval, folded, with sculptured edges.

4) **Tarsal organ:**
(0) hooded, with elongate receptors; (1) low, two or three receptors; (2) slightly elevated, two or three receptors; (3) elevated, three receptors.

5) **Female genitalia**
(0) single spermatheca; (1) paired spermathecae, no atrium; (2) tightly coiled spermathecae; (3) elongate heads, u- shaped stalks; (4) apically coiled; (5) sinuous; (6) enlarged heads, loosely coiled.

Explanation of Figures

Figure 1: Images of living Leptonetidae.
A. *Ozarkia arakansas* (Gertsch, 1974) female, Blanchard Springs Caverns, Arkansas (M. Slay); B. *Neoleptoneta brunnea* (Gertsch, 1974) male, Sotano de Cilantro, Mexico (J. Krejca); C. *Calileptoneta helferi* (Getsch, 1974) male, Angelo Reserve, California; D. *Tayshaneta valverdae* (Gertsch, 1974) male and female in web, Fawcett's Cave, Texas.

Figure 2: Map of the study area.
A. Inset showing the Edward's Plateau and Balcones Escarpment, Texas. Note that much of leptonetid diversity is associated with caves along the Balcones Escarpment. B. Arrow to El Cielo Biosphere Reserve, type locality for *Neoleptoneta capilla* (Gertsch, 1974).

Figure 3: Distribution map for "*Neoleptoneta*". Highlighted areas are color coded to correspond to clades recovered by phylogenetic analyses.
A. *Tayshaneta* **gen. nov.**; B. *Ozarkia* **gen. nov.**; C. *Neoleptoneta* Brignoli, 1972; D. *Chisosea* **gen nov.**

Figure 4: Three gene concatenated Bayesian phylogeny. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.
A. *Chisosea* **gen. nov.**; B. *Ozarkia* **gen. nov.**; C. *Neoleptoneta* Brignoli, 1972; D. *Tayshaneta* **gen. nov.**; E. Leptonetinae; F. North American Leptonetinae.

Figure 5: Three gene concatenated maximum likelihood phylogeny. Black nodes correspond to a posterior probability of 75% and greater.
A. *Chisosea* **gen. nov.**; B. *Ozarkia* **gen. nov.**; C. *Neoleptoneta* Brignoli, 1972; D. *Tayshaneta* **gen. nov.**; E. Leptonetinae; F. North American Leptonetinae.

Figure 6: Three gene concatenated parsimony phylogeny. Black nodes correspond to a posterior probability of 75% and greater.
A. *Chisosea* **gen. nov.**; B. *Ozarkia* **gen. nov.**; C. *Neoleptoneta* Brignoli, 1972; D. *Tayshaneta* **gen. nov.**; E. Leptonetinae; F. North American Leptonetinae.

Figure 7: Bayesian gene tree, cytochrome oxidase I (COI). Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.
A. *Chisosea* **gen. nov.**; B. *Ozarkia* **gen. nov.**; C. *Neoleptoneta* Brignoli, 1972; D. *Tayshaneta* **gen. nov.**; E. Leptonetinae; F. North American Leptonetinae.

Figure 8: Bayesian gene tree, histone 3 (H3). Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.
A. *Chisosea* **gen. nov.**; B. *Ozarkia* **gen. nov.**; C. *Neoleptoneta* Brignoli, 1972; D. *Tayshaneta* **gen. nov.**; E. Leptonetinae; F. North American Leptonetinae.

Figure 9: Bayesian gene tree, 28s rDNA (28s). Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.

A. *Chisosea* **gen. nov.**; B. *Ozarkia* **gen. nov.**; C. *Neoleptoneta* Brignoli, 1972; D. *Tayshaneta* **gen. nov.**; E. Leptonetinae; F. North American Leptonetinae.

Figure 10: *Chisosea isolata* (Gertsch, 1971), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH), habitus.
A. *C. isolata* male, dorsal; B. *C. isolata* male, ventral; C. *C. isolata* male, lateral; D. *C. isolata* female, dorsal; E. *C. isolata* female, ventral; F. *C. isolata* female, lateral.

Figure 11: *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun County, Alabama (CASC), habitus.
A. *O. alabama* male, dorsal; B. *O. alabama* male, ventral; C. *O. alabama* male, lateral; D. *O. alabama* female, dorsal; E. *O. alabama* female, ventral; F. *O. alabama* female, lateral.

Figure 12: *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC), habitus.
A. *N. capilla* male, dorsal; B. *N. capilla* male, ventral; C. *N. capilla* male, lateral; D. *N. capilla* female, dorsal; E. *N. capilla* female, ventral; F. *N. capilla* female, lateral.

Figure 13: *Tayshaneta coeca* (Chamberlin and Ivie, 1942), **comb. nov.**, Brehmmer Cave, Comal County (AMNH), Texas, habitus.
A. *T. coeca* holotype male, dorsal; B. *T. coeca* holotype male, ventral; C. *T. coeca* holotype male, lateral; D. *T. coeca* female, dorsal; E. *T. coeca* female, ventral; F. *T. coeca* female, lateral.

Figure 14: *Chisosea isolata* (Gertsch, 1974), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH), male right palp.
A. Retrolateral; B. Ventral; C; Prolateral; D. Retrolateral tibial spine; E. Ventroapical; F. Tarsus, dorsal.

Figure 15: *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun County, Alabama (CASC), male right palp.
A. Retrolateral; B. Ventral; C; Prolateral; D. Retrolateral tibial spine; E. Ventroapical; F. Tarsus, dorsal.

Figure 16: *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC), male right palp.
A. Retrolateral; B. Ventral; C; Prolateral; D. Retrolateral tibial spine; E. Ventroapical; F. Tarsus, dorsal.

Figure 17: *Tayshaneta coeca* (Chamberlin and Ivie, 1942), Brehmmer Cave, Comal County (AMNH), Texas, male right palp.
A. Retrolateral; B. Ventral; C; Prolateral; D. Retrolateral tibial spine; E. Ventroapical; F. Tarsus, dorsal.

Figure 18: *Neoleptoneta brunnea* (Gertsch, 1974), Sotano de Cilantro, San Louis Potosi (UNAM), male right palp.
A. Retrolateral; B. Ventral; C; Prolateral; D. Retrolateral tibial spine; E. Ventroapical; F. Tarsus, dorsal.

Figure 19: Comparison of *Montanineta sandra*, comb. nov. and *Falcileptoneta striata* (Oi, 1952), male right palp.
A. *Montanineta sandra*, comb. nov. retrolateral tibial spine; B. *Montanineta sandra*, comb. nov. ventral; C; *Montanineta sandra*, comb. nov. prolateral; D. *F. striata,* retrolateral tibial spine; E. *F. striata,* ventral; F. *F. striata*, prolateral; G. *F. striata,* ventroapical; H. *Montanineta sandra*, comb. nov. ventroapical.

Figure 20: *Appaleptoneta barrowsi* (Gertsch, 1974), Bangor Cave, Blount County, Alabama (CASC), male right palp.
A. Retrolateral; B. Ventral; C; Prolateral; D. Tibia and tarsus, retrolateral; E. Ventroapical; F. Tarsus, dorsal.

Figure 21: *Calileptoneta helferi* (Gertsch, 1974), Angelo Reserve, Mendocino County, California (CASC), male right palp.
A. Retrolateral; B. Ventral; C; Prolateral; D. Tibia and tarsus, retrolateral; E. Ventroapical; F. Tarsus, dorsal.

Figure 22: *Calileptoneta oasa* (Gertsch, 1974), Andreas Canyon, Riverside County, California (AMNH), male right palp.
A. Retrolateral; B. Ventral; C; Prolateral; D. Tibia and tarsus, retrolateral; E. Ventroapical; F. Tarsus, dorsal.

Figure 23: *Leptoneta convexa* (Simon, 1872), Grotte de Lique, Ariège, France (CASC), male right palp
A. Retrolateral; B. Ventral; C; Prolateral; D. Tibia and tarsus, retrolateral; E. Ventroapical; F. Tarsus, dorsal.

Figure 24: Comparative images of male tarsal organs, showing position on the tarsus and microstructure.
A. *Neoleptoneta capilla* (Gertsch, 1971), right tarsus, dorsal; B. *N. capilla*, tarsal organ; C. *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, right tarsus, dorsal; D. *O. alabama*, tarsal organ; E. *Chisosea isolata* (Gertsch, 1971), **comb. nov.**, right tarsus, dorsal; F. *C. isolata*, tarsal organ; G. *Tayshaneta coeca* (Gertsch, 1974), **comb. nov.**, right tarsus, dorsal; H. *T. coeca*, tarsal organ.

Figure 25: Comparative images of male tarsal organs, showing position on the tarsus and microstructure.
A. *Calileptoneta oasa* (Gertsch, 1974), right tarsus, dorsal; B. *C. oasa*, tarsal organ; C. *Appaleptoneta barrowsi* (Gertsch, 1974), right tarsus, dorsal; D. *A. barrowsi*, tarsal organ; E. *Calileptoneta helferi* (Gertsch, 1974), right tarsus, dorsal; F. *C. helferi*, tarsal organ.

Figure 26: Comparative images of male tarsal organs, showing position on the tarsus and microstructure.
A. *Leptoneta infuscata* (Simon, 1872), right tarsus, dorsal; B. *L. infucata*, tarsal organ; C. *Montanineta sandra* (Gertsch, 1974), right tarsus, dorsal; D. *Montanineta sandra*, tarsal organ.

Figure 27: *Chisosea isolata* (Gertsch, 1974), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH), expanded male right palp.
A. Retrolateral, unexpanded; B. Prolateral, unexpanded; C. Retrolateral, expanded; D. Prolateral, expanded.

Figure 28: *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun County, Alabama (CASC), male right palp.
A. Retrolateral, unexpanded; B. Prolateral, unexpanded; C. Retrolateral, expanded; D. Prolateral, expanded.

Figure 29: *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC), male right palp.
A. Retrolateral, unexpanded; B. Prolateral, unexpanded; C. Retrolateral, expanded; D. Prolateral, expanded.

Figure 30: *Tayshaneta myopica* (Gertsch, 1974), **comb. nov.**, Geode Cave, Travis County, Texas (CASC), male right palp.
A. Retrolateral, unexpanded; B. Prolateral, unexpanded; C. Retrolateral, expanded; D. Prolateral, expanded.

Figure 31: Comparative views of female vulvae, dorsal.
A. *Chisosea isolata* (Gertsch, 1974), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH); B. *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun County, Alabama (CASC); C. *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC); D. *Tayshaneta myopica* (Gertsch, 1974), **comb. nov.**, Geode Cave, Travis County, Texas (CASC).

Figure 32: Comparative views of female vulvae, dorsal.
A. *Appaleptoneta barrowsi* (Gertsch, 1974), Bangor Cave, Blount County, Alabama (CASC); B. *Calileptoneta oasa* (Gertsch, 1974), Andreas Canyon, Riverside County, California (AMNH); C. *Calileptoneta oasa* (Gertsch, 1974), Andreas Canyon, Riverside County, California (AMNH), left spermatheca showing sclerotized connection to atrium; D. *Montanineta sandra*, comb. nov.; E. *Falcileptoneta striata* (Oi, 1952); F. *Leptoneta infuscata* (Simon, 1872), Cova de l'avenc, Spain (CASC).

Figure 33: Ultrametric Bayesian concatenated phylogeny showing the optimization of the male retrolateral tibial spine (RTS). Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.
A. *Chisosea isolata* (Gertsch, 1974), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH); B. *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun

County, Alabama (CASC); C. *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC); D. *Tayshaneta coeca* (Chamberlin and Ivie, 1942), **comb. nov.**, Brehmmer Cave, Comal County, Texas (AMNH).

Figure 34: Ultrametric Bayesian concatenated phylogeny showing the optimization of the male palpal tarsus shape. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.
A. *Chisosea isolata* (Gertsch, 1974), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH); B. *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun County, Alabama (CASC); C. *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC); D. *Tayshaneta coeca* (Chamberlin and Ivie, 1942), **comb. nov.**, Brehmmer Cave, Comal County, Texas (AMNH).

Figure 35: Ultrametric Bayesian concatenated phylogeny showing the optimization of the embolus. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.
A. *Chisosea isolata* (Gertsch, 1974), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH); B. *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun County, Alabama (CASC); C. *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC); D. *Tayshaneta coeca* (Chamberlin and Ivie, 1942), **comb. nov.**, Brehmmer Cave, Comal County, Texas (AMNH).

Figure 36: Ultrametric Bayesian concatenated phylogeny showing the optimization of the male tarsal organ. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.
A. *Chisosea isolata* (Gertsch, 1974), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH); B. *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun County, Alabama (CASC); C. *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC); D. *Tayshaneta coeca* (Chamberlin and Ivie, 1942), **comb. nov.**, Brehmmer Cave, Comal County, Texas (AMNH).

Figure 37: Ultrametric Bayesian concatenated phylogeny showing the optimization of the female vulva. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.
A. *Chisosea isolata* (Gertsch, 1974), **comb. nov.**, Gruta de Garcia, Nuevo Leon, Mexico (AMNH); B. *Ozarkia alabama* (Gertsch, 1974), **comb. nov.**, Lady Cave, Calhoun County, Alabama (CASC); C. *Neoleptoneta capilla* (Gertsch, 1971), Cueva de La Capilla, Tamaulipas, Mexico (CASC); D. *Tayshaneta coeca* (Chamberlin and Ivie, 1942), **comb. nov.**, Brehmmer Cave, Comal County, Texas (AMNH).

Figure 38: Ancestral stare reconstruction of ecology type (epigean, troglophile, troglobite) on Bayesian concatenated phylogeny.

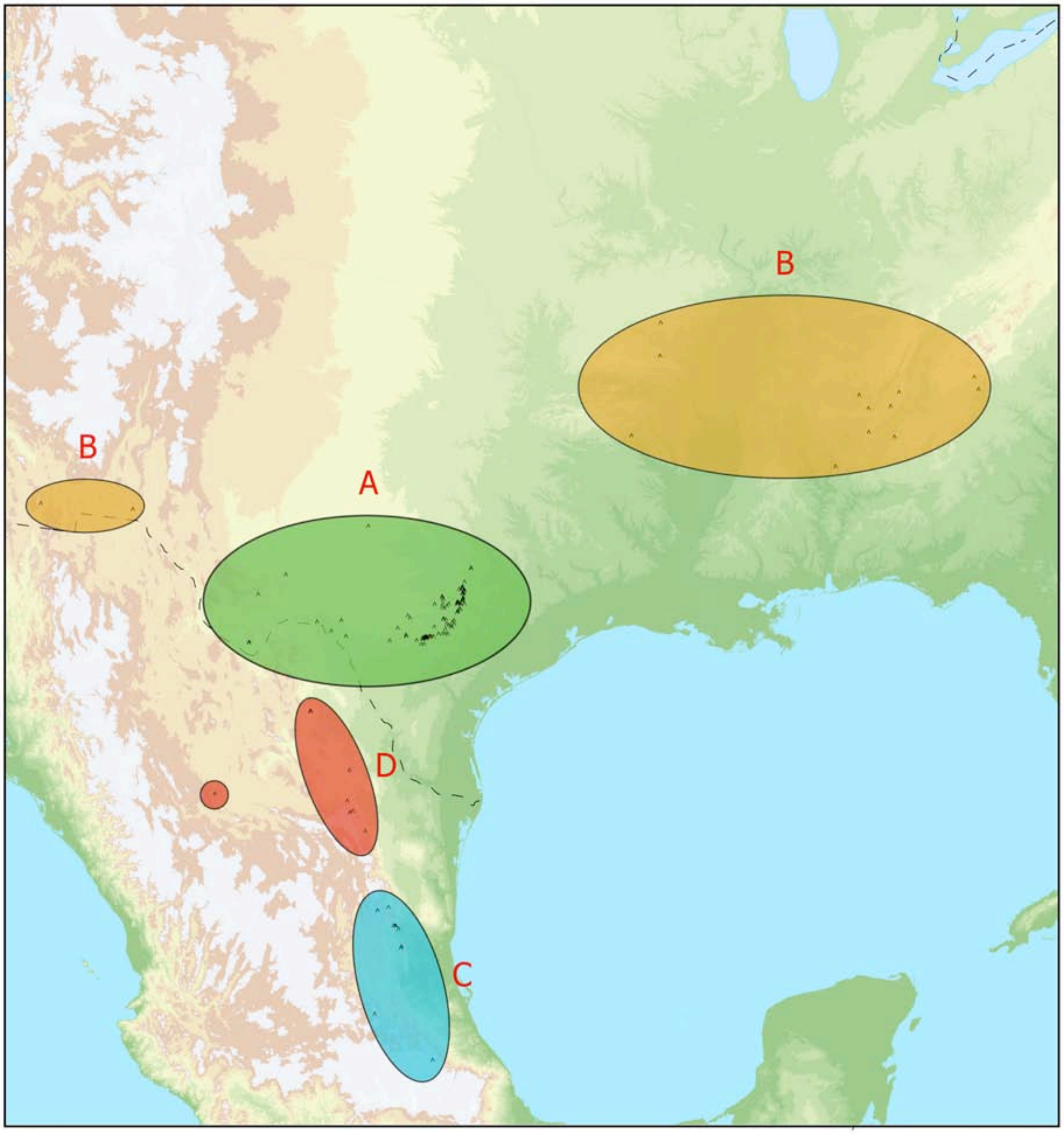
Figure 39: Phylogeny, morphology, and distribution of *Tayshaneta myopica* (Gertsch, 1974), **comb. nov.** and *T. paraconcinna* (Cokendolpher and Reddell, 2001), **comb. nov.** in Central Texas. Note the variation in somatic morphology between populations within each species.

A. *T. myopica*, Jester Estates Cave, Travis County, Texas (sample 4f8); B. *T. myopica*, Steiner Telephone Pole Cave, Travis County, Texas (sample 4d3); C. *T. myopica*, Tooth Cave, Travis County, Texas; D. *T. paraconcinna*, Three Mile Bat Cave, Williamson County, Texas (sample 4d9); E. *T. paraconcinna*, Pedernales State Park, Blanco County, Texas (sample 1h4); F. *T. paraconcinna*, Peep in the Deep Cave, Bell County, Texas (sample p1).

Figure 40: Phylogeny, morphology, and distribution of *Neoleptoneta capilla* (Gertsch, 1971)
A. *N. capilla*, Harrison's Sinkhole, Tamaulipas, Mexico (sample 5d2); B. *N. capilla*, Cueva de La Mina, Tamaulipas, Mexico (sample 5b9); C. *N. capilla*, Cueva de La Capilla, Tamaulipas, Mexico (sample 5a5).


A
B
C
D


Edwards Plateau
Balcones Escarpment
0 10 20 30 40 50 Miles
0 20 40 60 80 Kilometers
El Cielo
Tamaulipas
0 100 200 300 400 500 Miles
0 200 400 600 800 Kilometers


B
B
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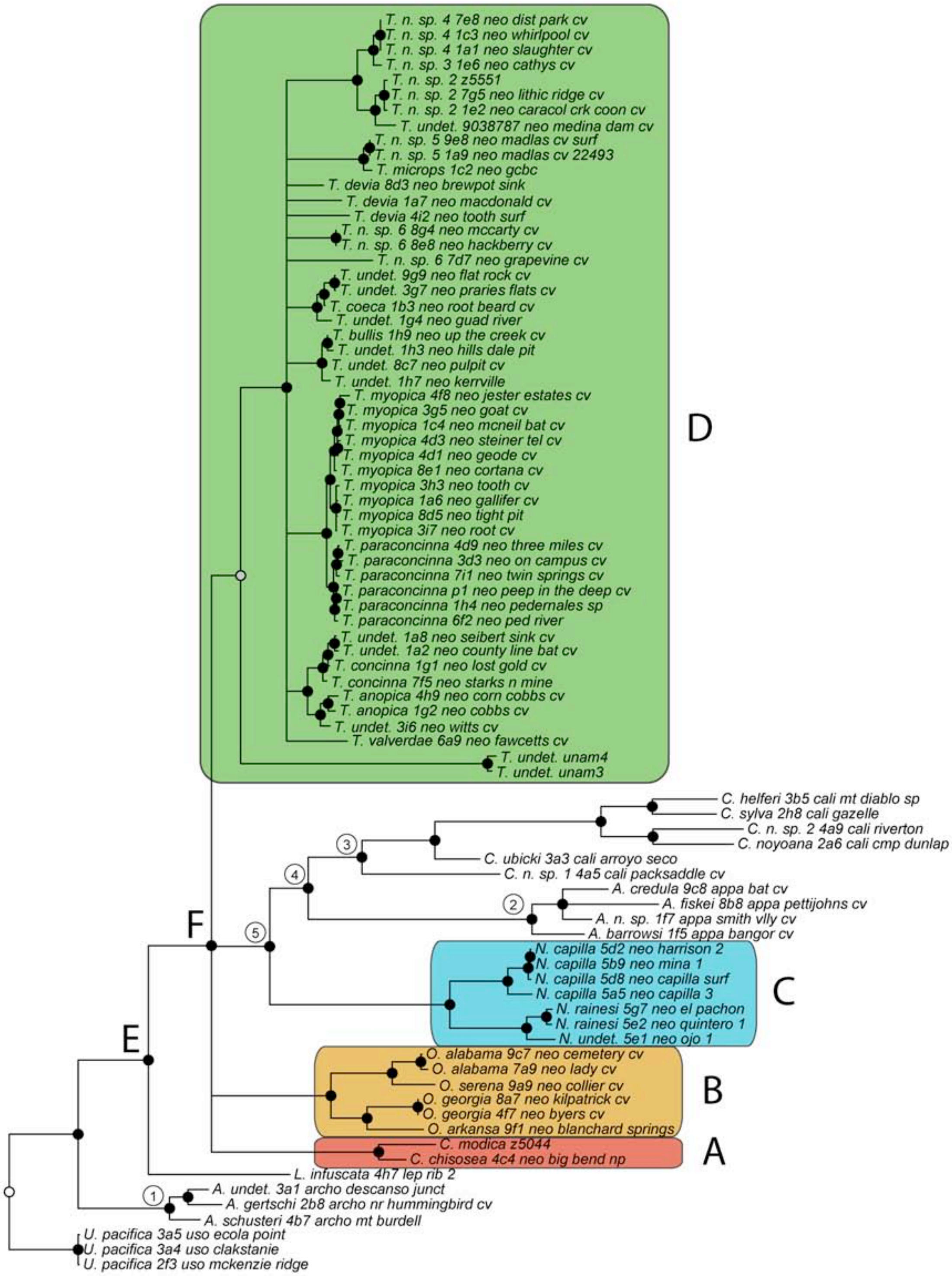
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T. devia 4i2 neo tooth surf
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T. n. sp. 6 8e8 neo hackberry cv
T. n. sp. 6 7d7 neo grapevine cv
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T. undet. 3g7 neo praries flats cv
T. coeca 1b3 neo root beard cv
T. undet. 1g4 neo guad river
T. bullis 1h9 neo up the creek cv
T. undet. 1h3 neo hills dale pit
T. undet. 8c7 neo pulpit cv
T. undet. 1h7 neo kerrville
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T. myopica 1c4 neo mcneil bat cv
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T. myopica 8e1 neo cortana cv
T. myopica 3h3 neo tooth cv
T. myopica 1a6 neo gallifer cv
T. myopica 8d5 neo tight pit
T. myopica 3i7 neo root cv
T. paraconcinna 4d9 neo three miles cv
T. paraconcinna 3d3 neo on campus cv
T. paraconcinna 7i1 neo twin springs cv
T. paraconcinna p1 neo peep in the deep cv
T. paraconcinna 1h4 neo pedernales sp
T. paraconcinna 6f2 neo ped river
T. undet. 1a8 neo seibert sink cv
T. undet. 1a2 neo county line bat cv
T. concinna 1g1 neo lost gold cv
T. concinna 7f5 neo starks n mine
T. anopica 4h9 neo corn cobbs cv
T. anopica 1g2 neo cobbs cv
T. undet. 3i6 neo witts cv
T. valverdae 6a9 neo fawcetts cv
T. undet. unam4
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D
C. helferi 3b5 cali mt diablo sp
C. sylva 2h8 cali gazelle
C. n. sp. 2 4a9 cali riverton
C. noyoana 2a6 cali cmp dunlap
3
C. ubicki 3a3 cali arroyo seco
C. n. sp. 1 4a5 cali packsaddle cv
4
A. credula 9c8 appa bat cv
A. fiskei 8b8 appa pettijohns cv
2
A. n. sp. 1f7 appa smith vlly cv
A. barrowsi 1f5 appa bangor cv
F
5
N. capilla 5d2 neo harrison 2
N. capilla 5b9 neo mina 1
N. capilla 5d8 neo capilla surf
N. capilla 5a5 neo capilla 3
C
N. rainesi 5g7 neo el pachon
N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
E
O. alabama 9c7 neo cemetery cv
O. alabama 7a9 neo lady cv
O. serena 9a9 neo collier cv
B
O. georgia 8a7 neo kilpatrick cv
O. georgia 4f7 neo byers cv
O. arkansa 9f1 neo blanchard springs
C. modica z5044
A
C. chisosea 4c4 neo big bend np
L. infuscata 4h7 lep rib 2
A. undet. 3a1 archo descanso junct
1
A. gertschi 2b8 archo nr hummingbird cv
A. schusteri 4b7 archo mt burdell
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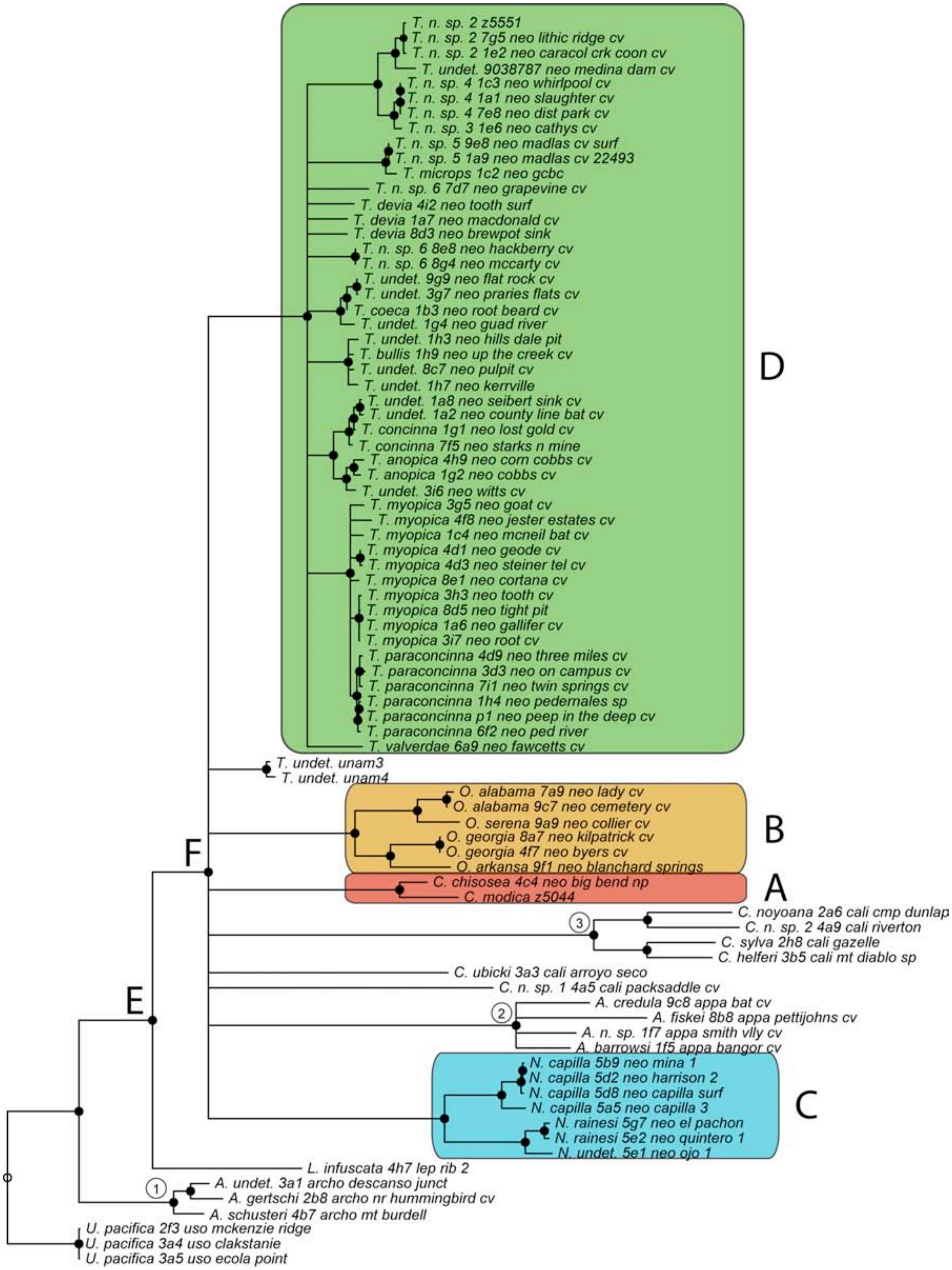
U. pacifica 3a4 uso clakstanie
U. pacifica 2f3 uso mckenzie ridge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T. undet. 1h7 neo kerrville
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T. anopica 1g2 neo cobbs cv
T. undet. 3i6 neo witts cv
T. myopica 3g5 neo goat cv
T. myopica 4f8 neo jester estates cv
T. myopica 1c4 neo mcneil bat cv
T. myopica 4d1 neo geode cv
T. myopica 4d3 neo steiner tel cv
T. myopica 8e1 neo cortana cv
T. myopica 3h3 neo tooth cv
T. myopica 8d5 neo tight pit
T. myopica 1a6 neo gallifer cv
T. myopica 3i7 neo root cv
T. paraconcinna 4d9 neo three miles cv
T. paraconcinna 3d3 neo on campus cv
T. paraconcinna 7i1 neo twin springs cv
T. paraconcinna 1h4 neo pedernales sp
T. paraconcinna p1 neo peep in the deep cv
T. paraconcinna 6f2 neo ped river
T. valverdae 6a9 neo fawcetts cv
D
T. undet. unam3
T. undet. unam4
O. alabama 7a9 neo lady cv
O. alabama 9c7 neo cemetery cv
O. serena 9a9 neo collier cv
O. georgia 8a7 neo kilpatrick cv
O. georgia 4f7 neo byers cv
O. arkansa 9f1 neo blanchard springs
B
F
C. chisosea 4c4 neo big bend np
C. modica z5044
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C. noyoana 2a6 cali cmp dunlap
C. n. sp. 2 4a9 cali riverton
C. sylva 2h8 cali gazelle
C. helferi 3b5 cali mt diablo sp
C. ubicki 3a3 cali arroyo seco
C. n. sp. 1 4a5 cali packsaddle cv
E
②
A. credula 9c8 appa bat cv
A. fiskei 8b8 appa pettijohns cv
A. n. sp. 1f7 appa smith vlly cv
A. barrowsi 1f5 appa bangor cv
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N. capilla 5d2 neo harrison 2
N. capilla 5d8 neo capilla surf
N. capilla 5a5 neo capilla 3
N. rainesi 5g7 neo el pachon
N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
C
L. infuscata 4h7 lep rib 2
①
A. undet. 3a1 archo descanso junct
A. gertschi 2b8 archo nr hummingbird cv
A. schusteri 4b7 archo mt burdell
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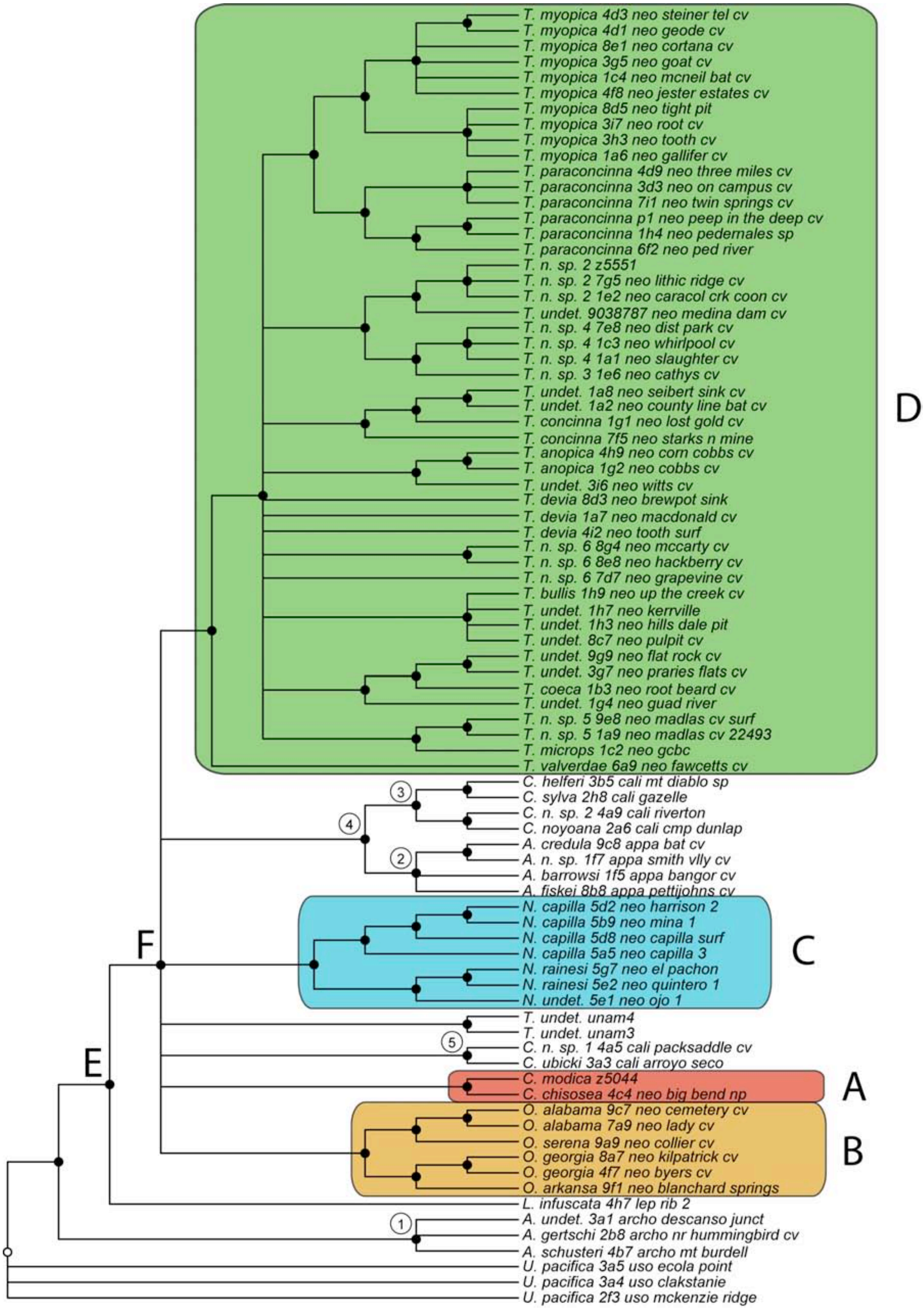
U. pacifica 3a5 uso ecola point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T. n. sp. 4 1c3 neo whirlpool cv
T. n. sp. 4 1a1 neo slaughter cv
T. n. sp. 3 1e6 neo cathys cv
T. undet. 1a8 neo seibert sink cv
T. undet. 1a2 neo county line bat cv
D
T. concinna 1g1 neo lost gold cv
T. concinna 7f5 neo starks n mine
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T. devia 8d3 neo brewpot sink
T. devia 1a7 neo macdonald cv
T. devia 4i2 neo tooth surf
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T. undet. 1h7 neo kerrville
T. undet. 1h3 neo hills dale pit
T. undet. 8c7 neo pulpit cv
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T. undet. 1g4 neo guad river
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T. n. sp. 5 1a9 neo madlas cv 22493
T. microps 1c2 neo gcbc
T. valverdae 6a9 neo fawcetts cv
C. helferi 3b5 cali mt diablo sp
③
C. sylva 2h8 cali gazelle
C. n. sp. 2 4a9 cali riverton
④
C. noyoana 2a6 cali cmp dunlap
A. credula 9c8 appa bat cv
②
A. n. sp. 1f7 appa smith vlly cv
A. barrowsi 1f5 appa bangor cv
A. fiskei 8b8 appa pettijohns cv
N. capilla 5d2 neo harrison 2
N. capilla 5b9 neo mina 1
F
N. capilla 5d8 neo capilla surf
N. capilla 5a5 neo capilla 3
C
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N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
T. undet. unam4
T. undet. unam3
⑤
C. n. sp. 1 4a5 cali packsaddle cv
E
C. ubicki 3a3 cali arroyo seco
C. modica z5044
A
C. chisosea 4c4 neo big bend np
O. alabama 9c7 neo cemetery cv
O. alabama 7a9 neo lady cv
O. serena 9a9 neo collier cv
B
O. georgia 8a7 neo kilpatrick cv
O. georgia 4f7 neo byers cv
O. arkansa 9f1 neo blanchard springs
L. infuscata 4h7 lep rib 2
①
A. undet. 3a1 archo descanso junct
A. gertschi 2b8 archo nr hummingbird cv
A. schusteri 4b7 archo mt burdell
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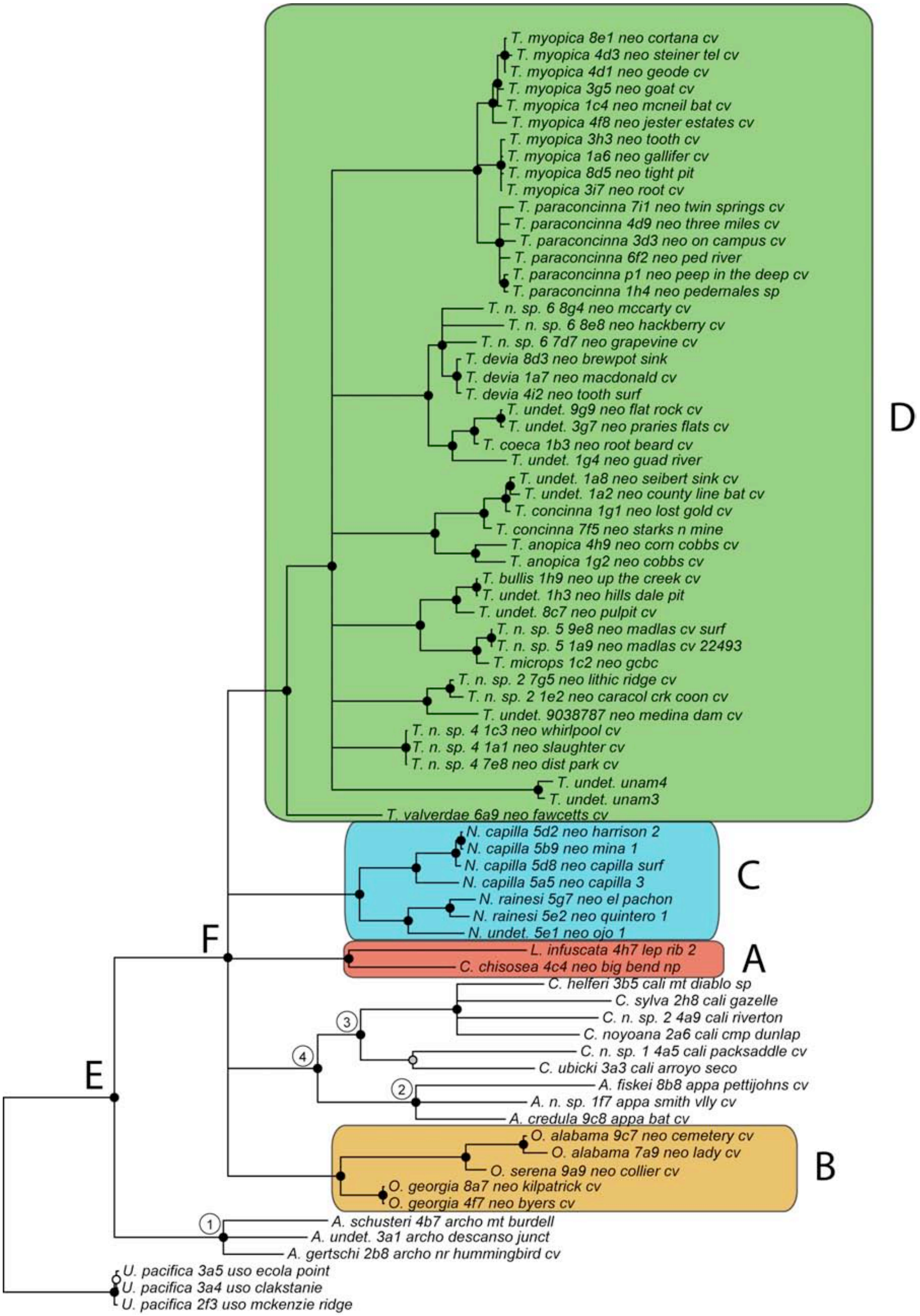

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T. myopica 1a6 neo gallifer cv
T. myopica 8d5 neo tight pit
T. myopica 3i7 neo root cv
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T. paraconcinna 4d9 neo three miles cv
T. paraconcinna 3d3 neo on campus cv
T. paraconcinna 6f2 neo ped river
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T. concinna 7f5 neo starks n mine
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T. anopica 1g2 neo cobbs cv
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T. undet. 1h3 neo hills dale pit
T. undet. 8c7 neo pulpit cv
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T. valverdae 6a9 neo fawcetts cv
D
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N. capilla 5b9 neo mina 1
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N. rainesi 5g7 neo el pachon
N. rainesi 5e2 neo quintero 1
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C. sylva 2h8 cali gazelle
C. n. sp. 2 4a9 cali riverton
C. noyoana 2a6 cali cmp dunlap
C. n. sp. 1 4a5 cali packsaddle cv
C. ubicki 3a3 cali arroyo seco
③
④
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A. n. sp. 1f7 appa smith vlly cv
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O. serena 9a9 neo collier cv
O. georgia 8a7 neo kilpatrick cv
O. georgia 4f7 neo byers cv
B
①
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U. pacifica 3a4 uso clakstanie
U. pacifica 2f3 uso mckenzie ridge


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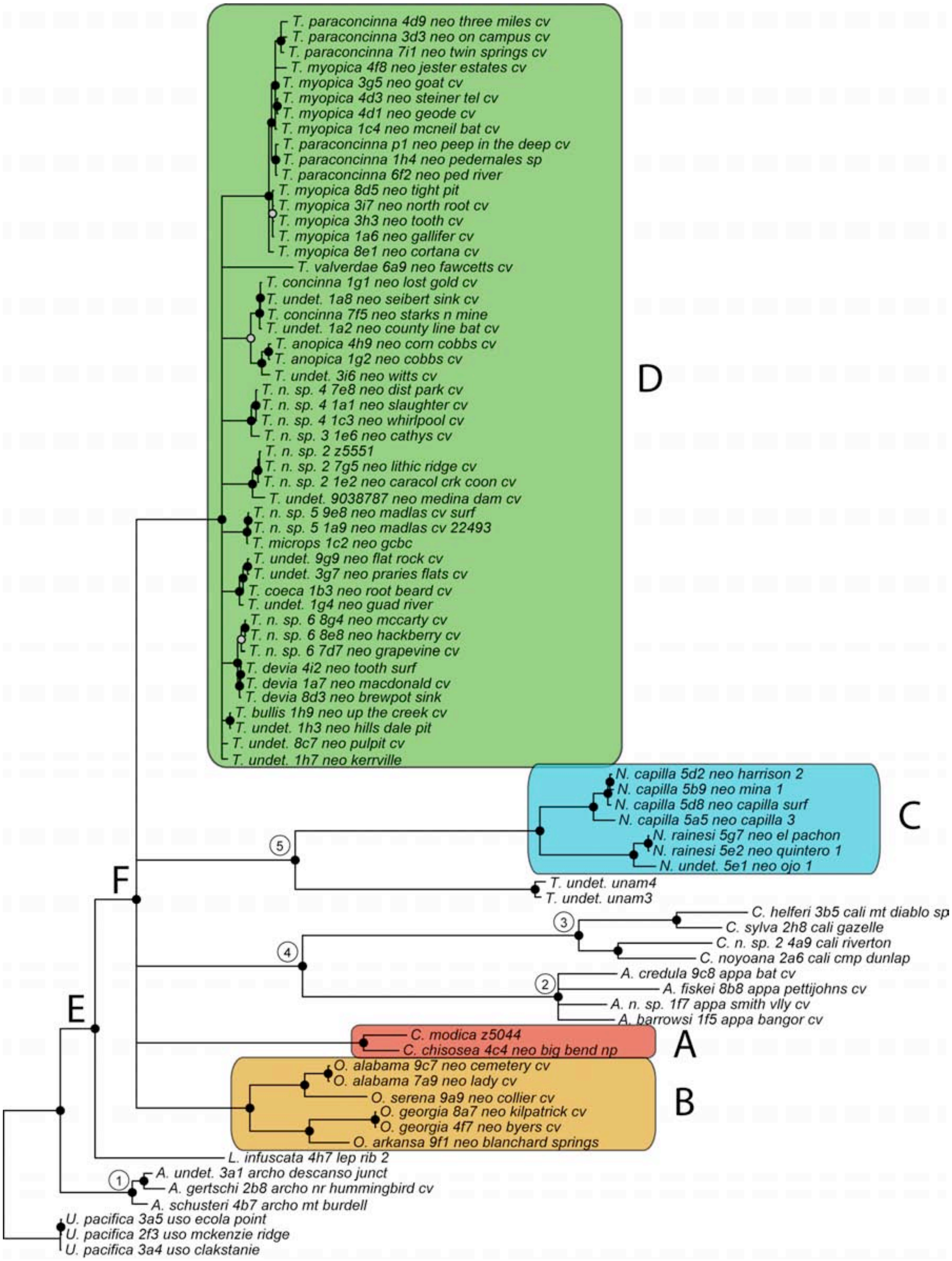
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O. georgia 4f7 neo byers cv
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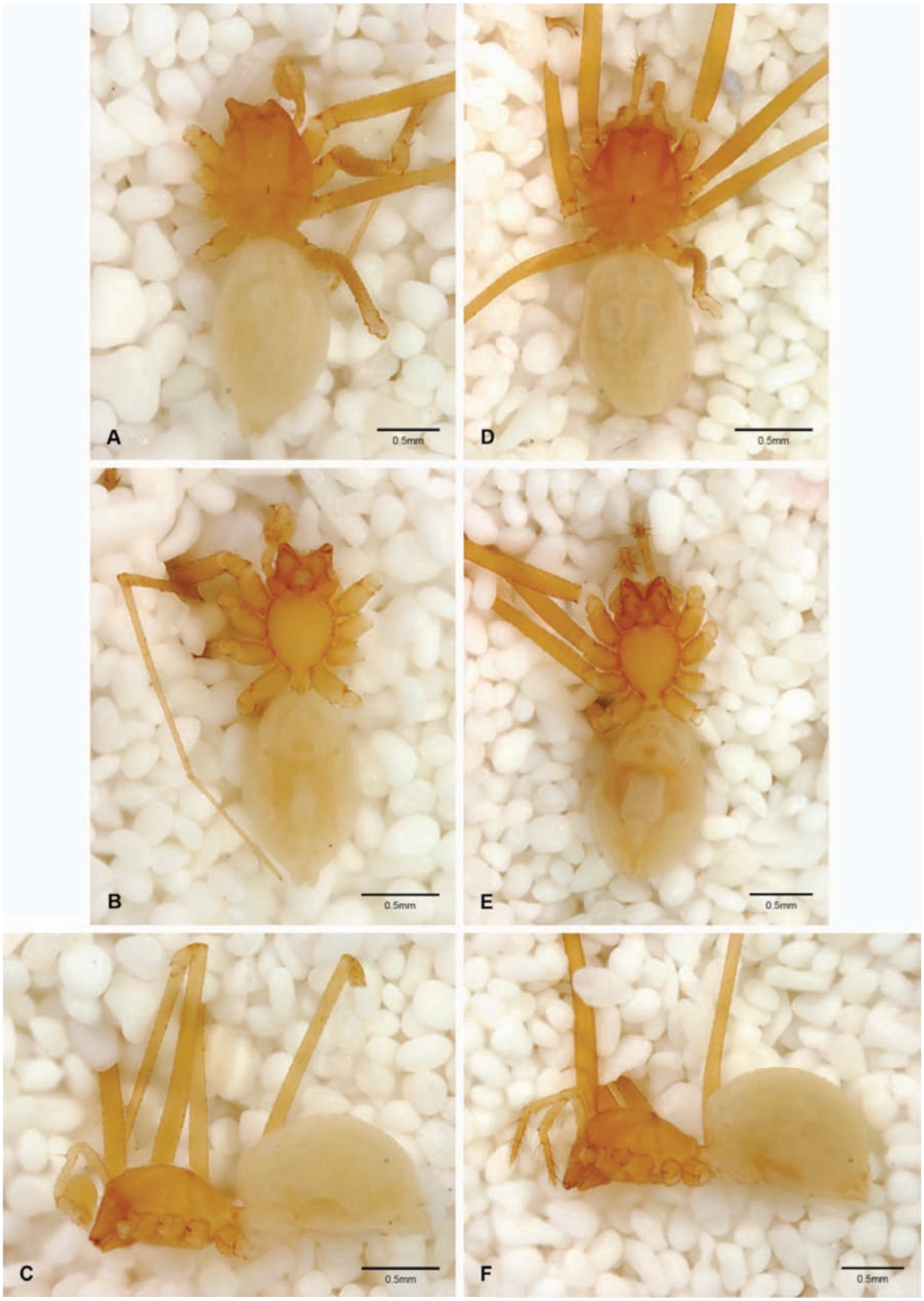
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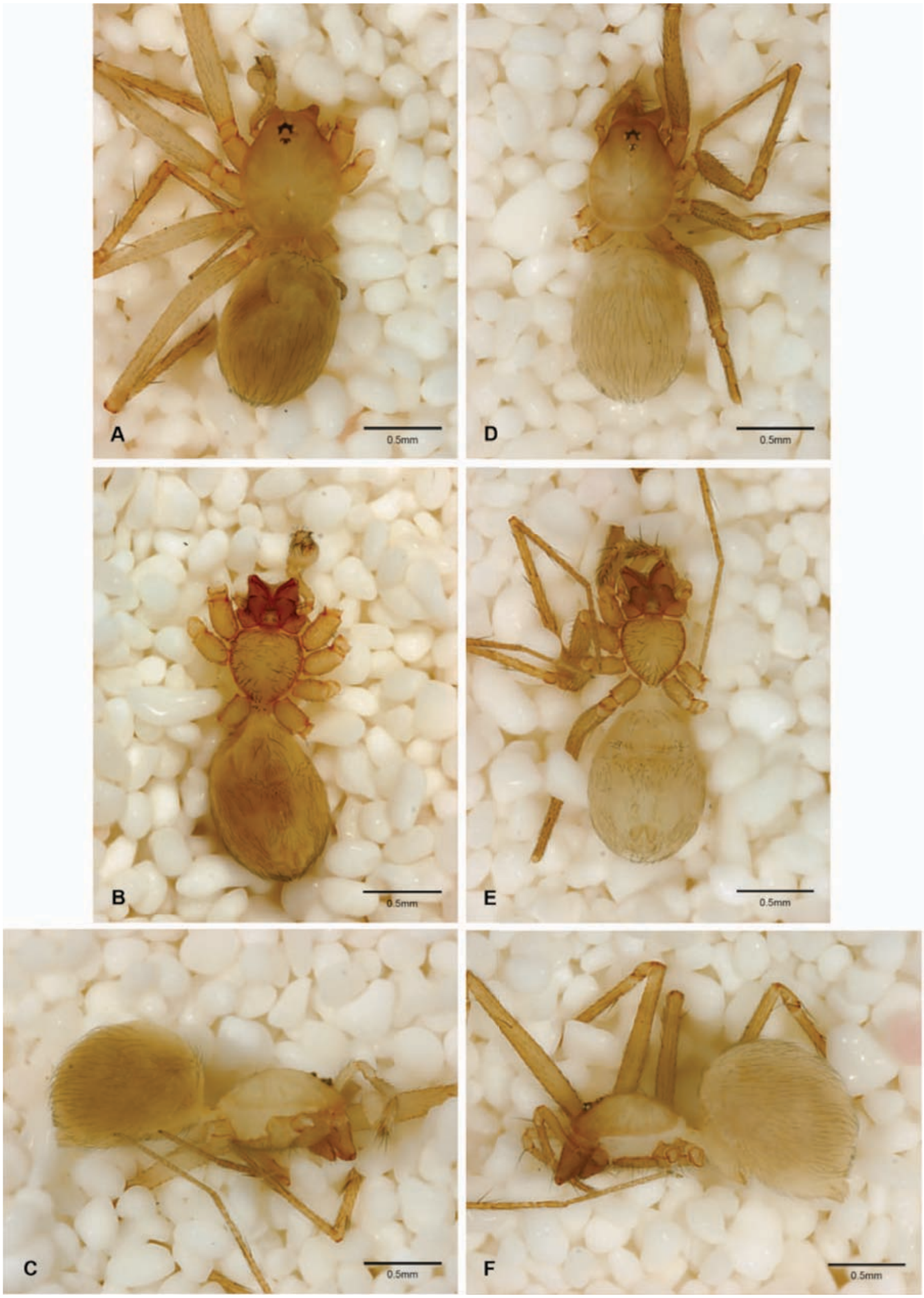
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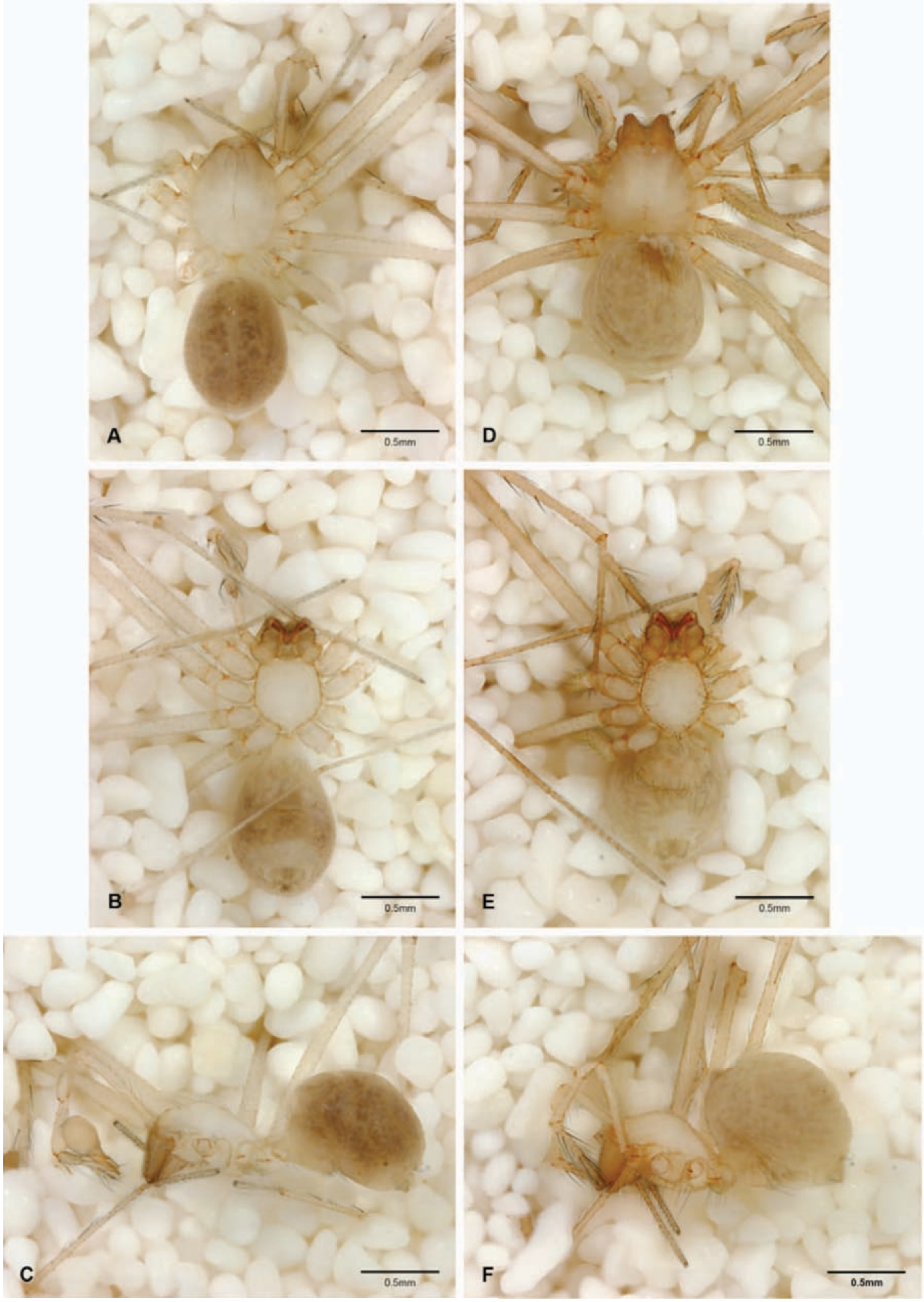
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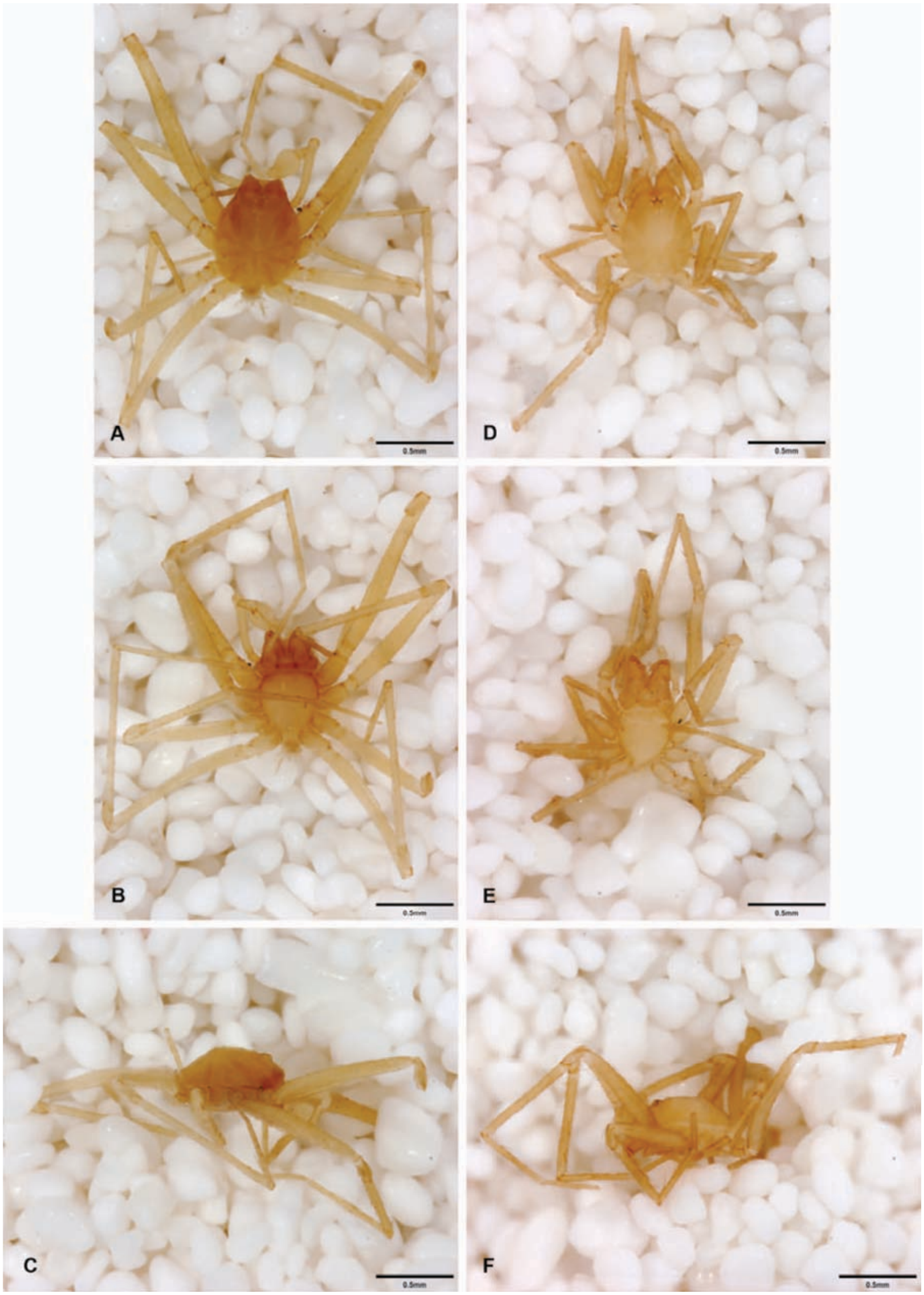
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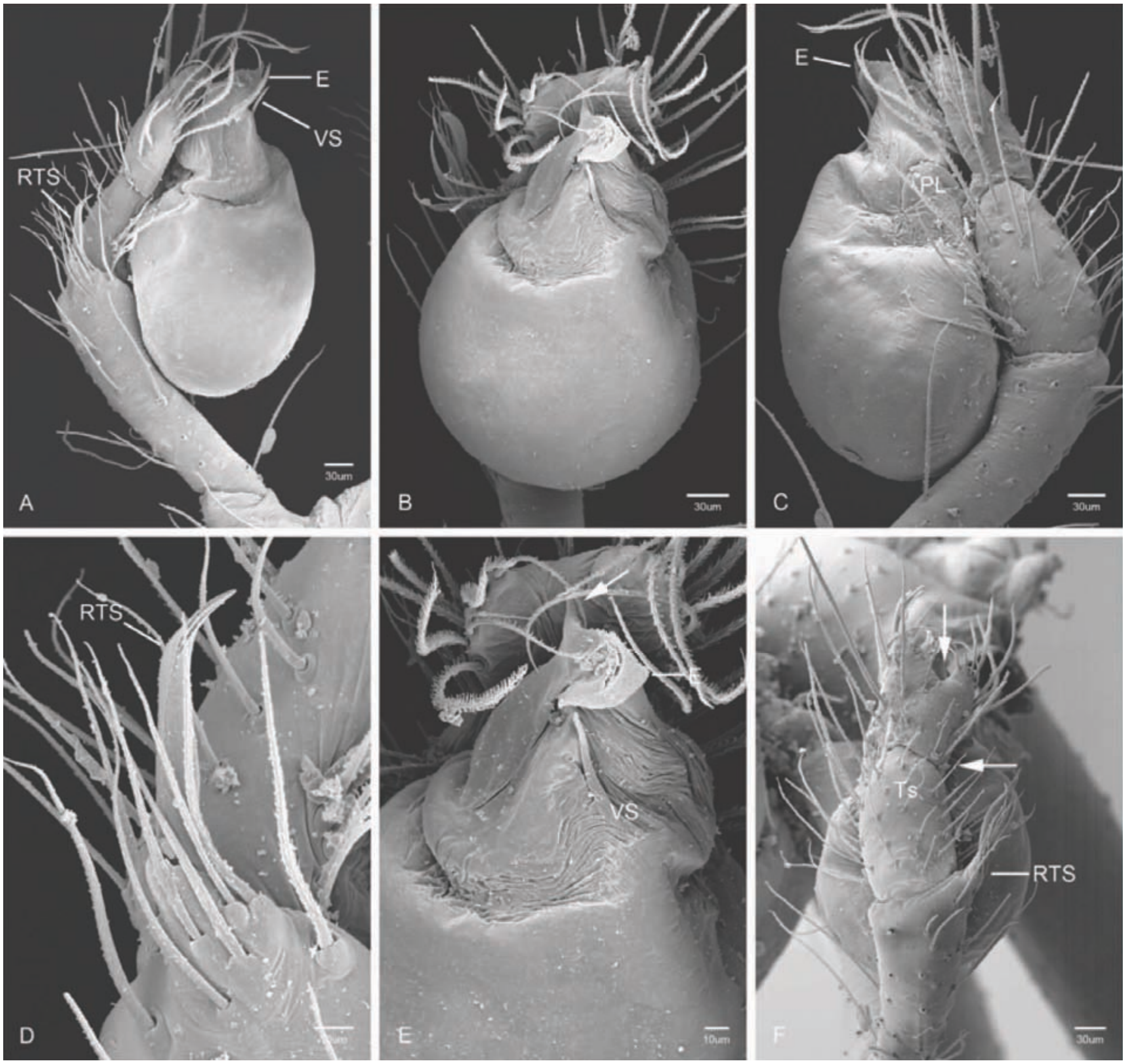
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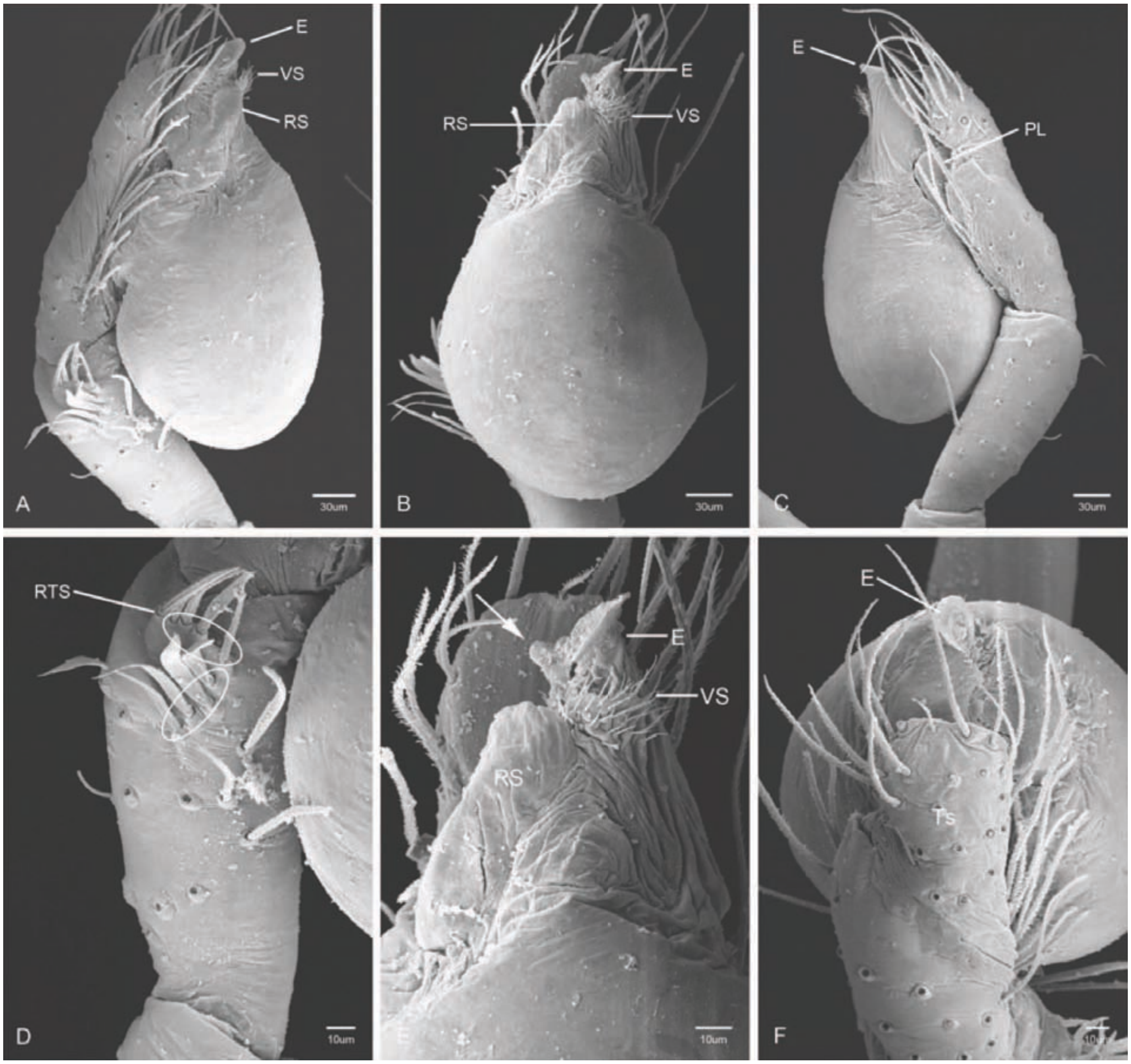
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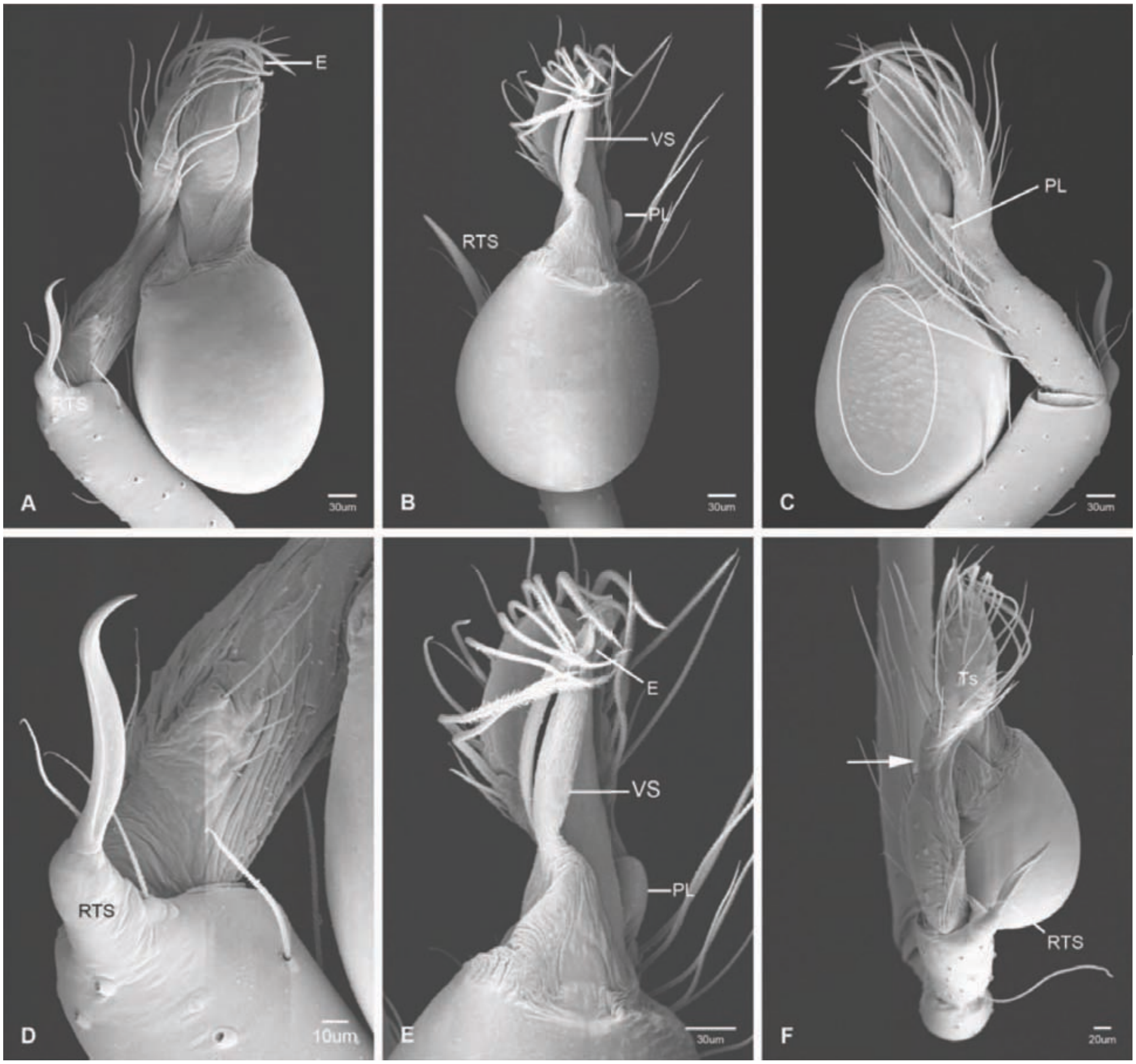
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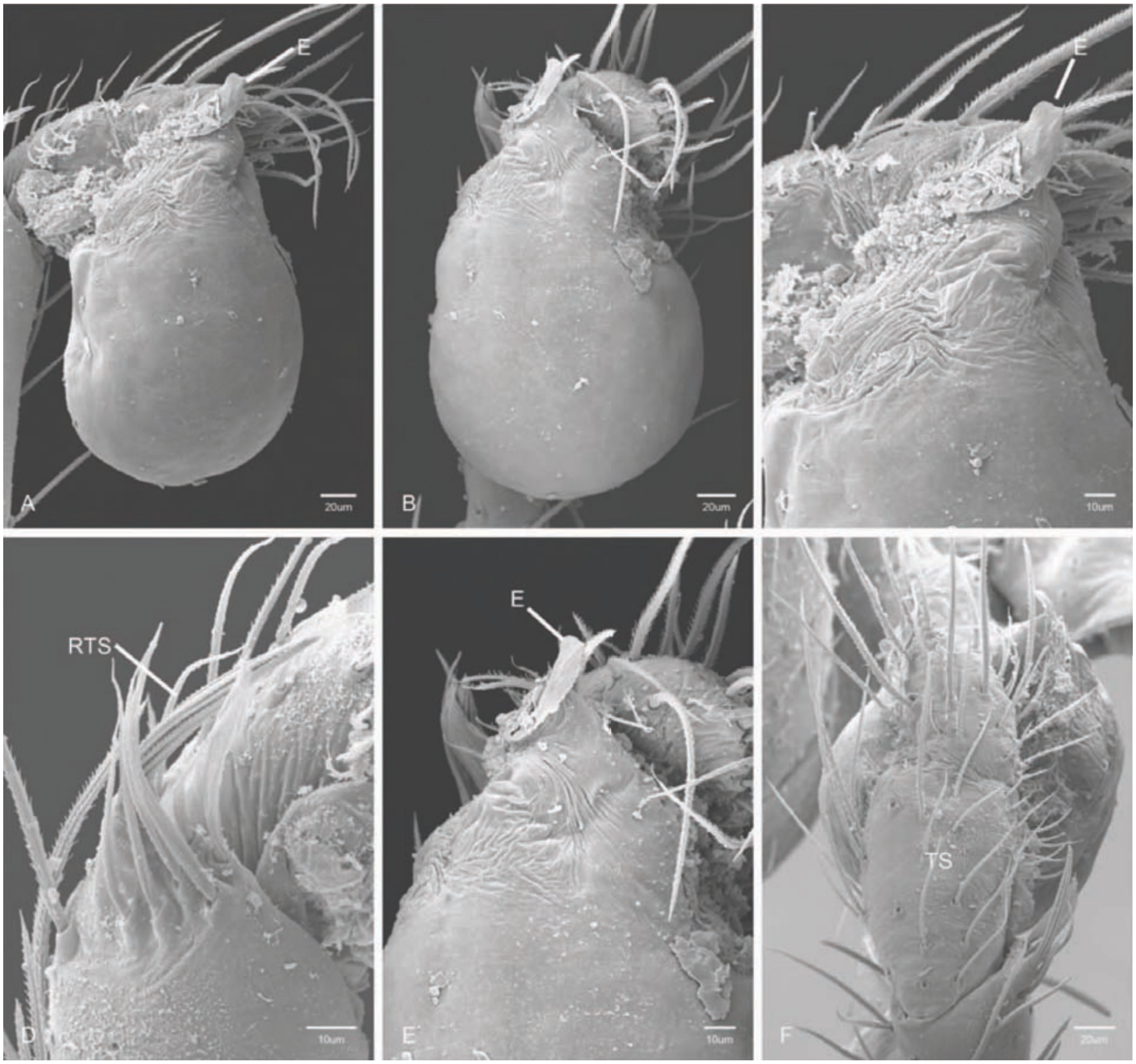
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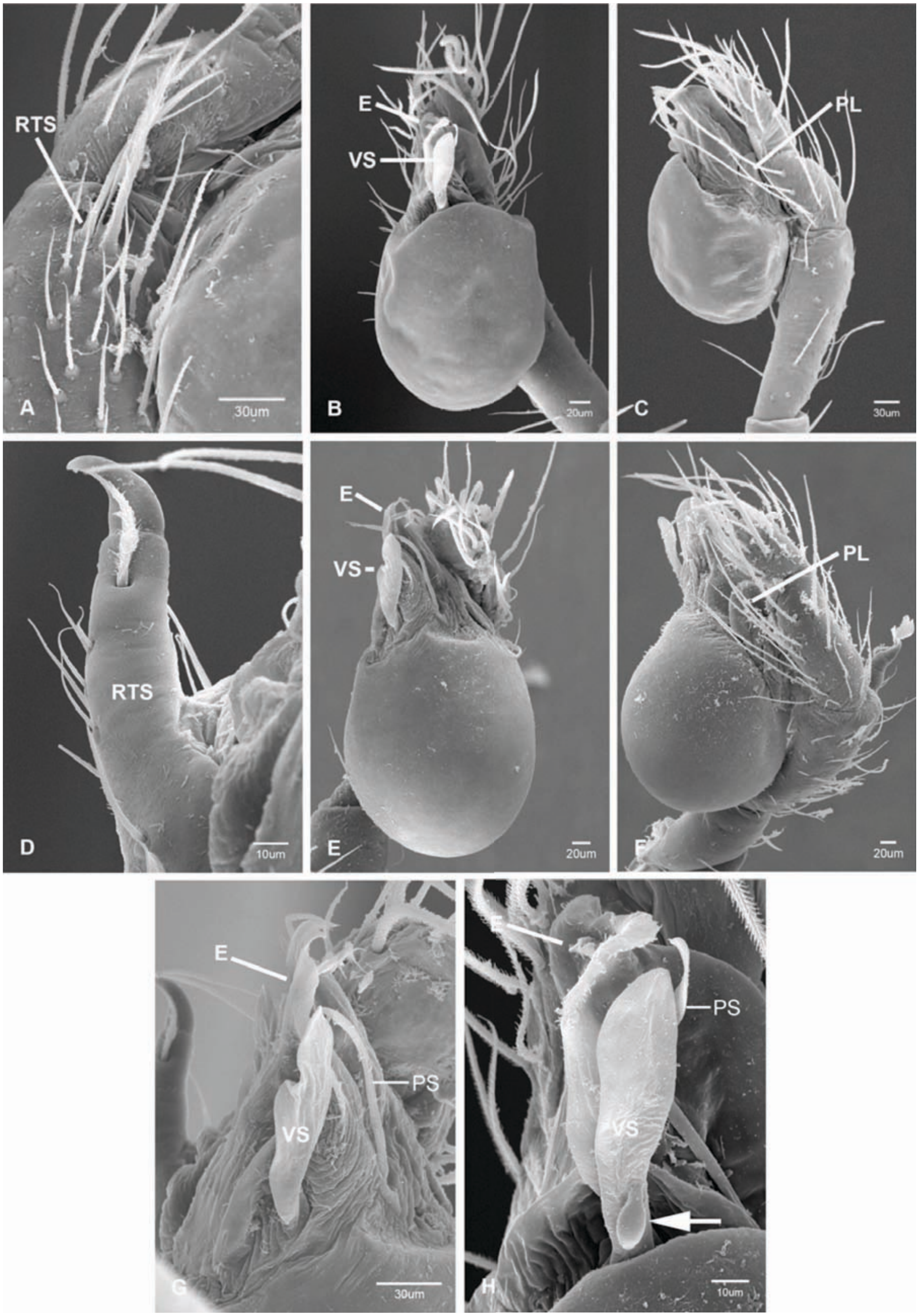
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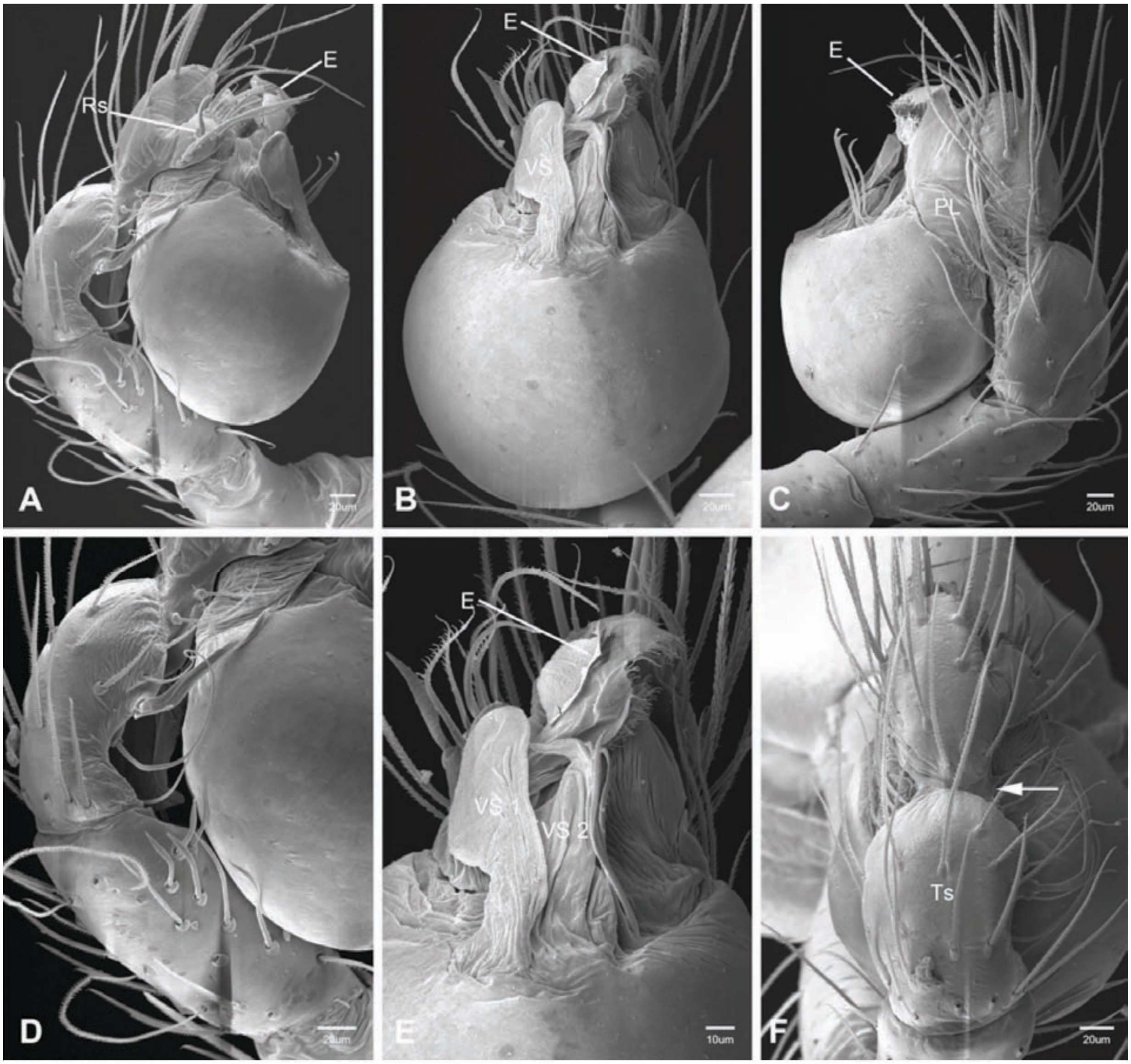
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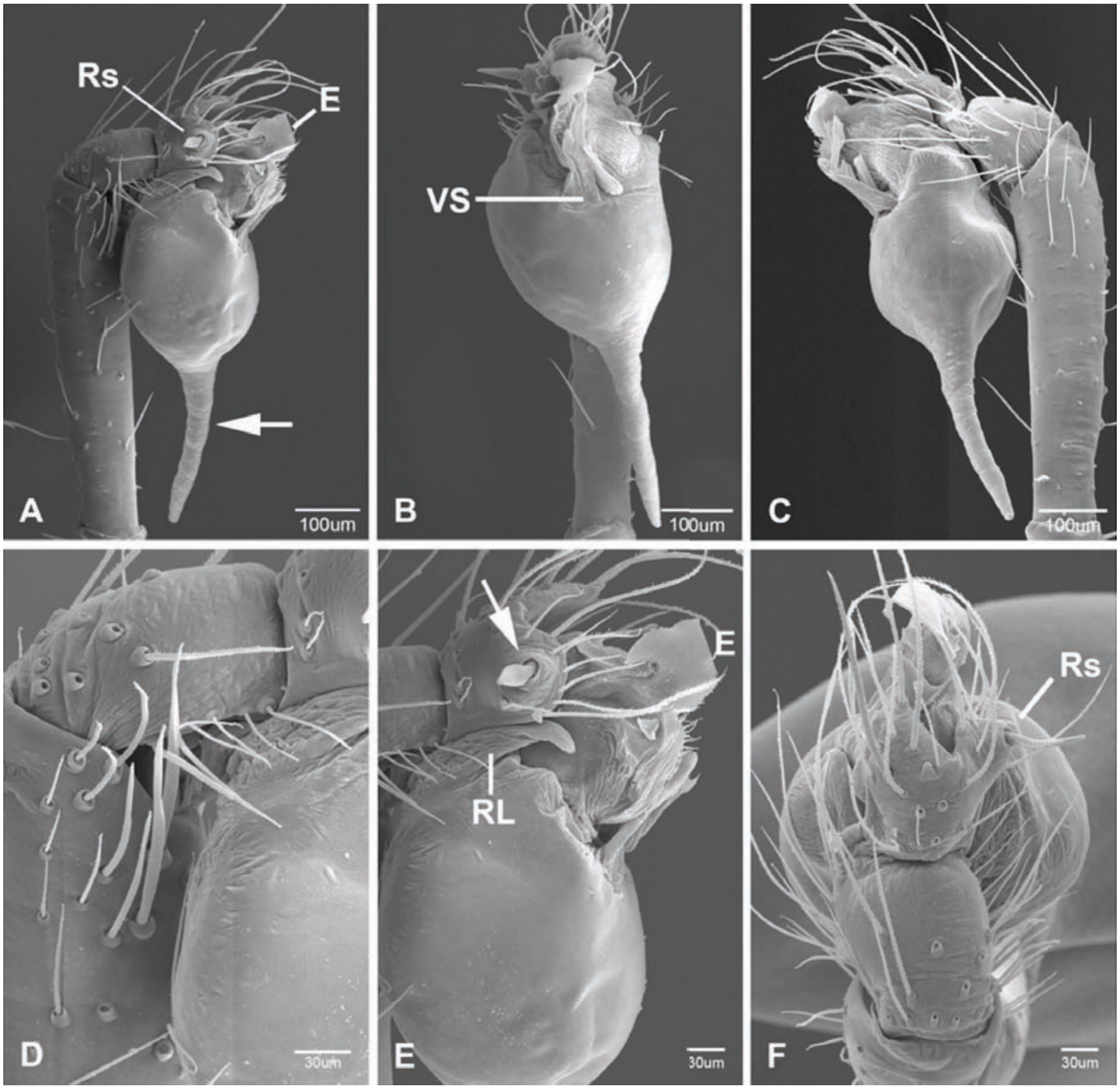
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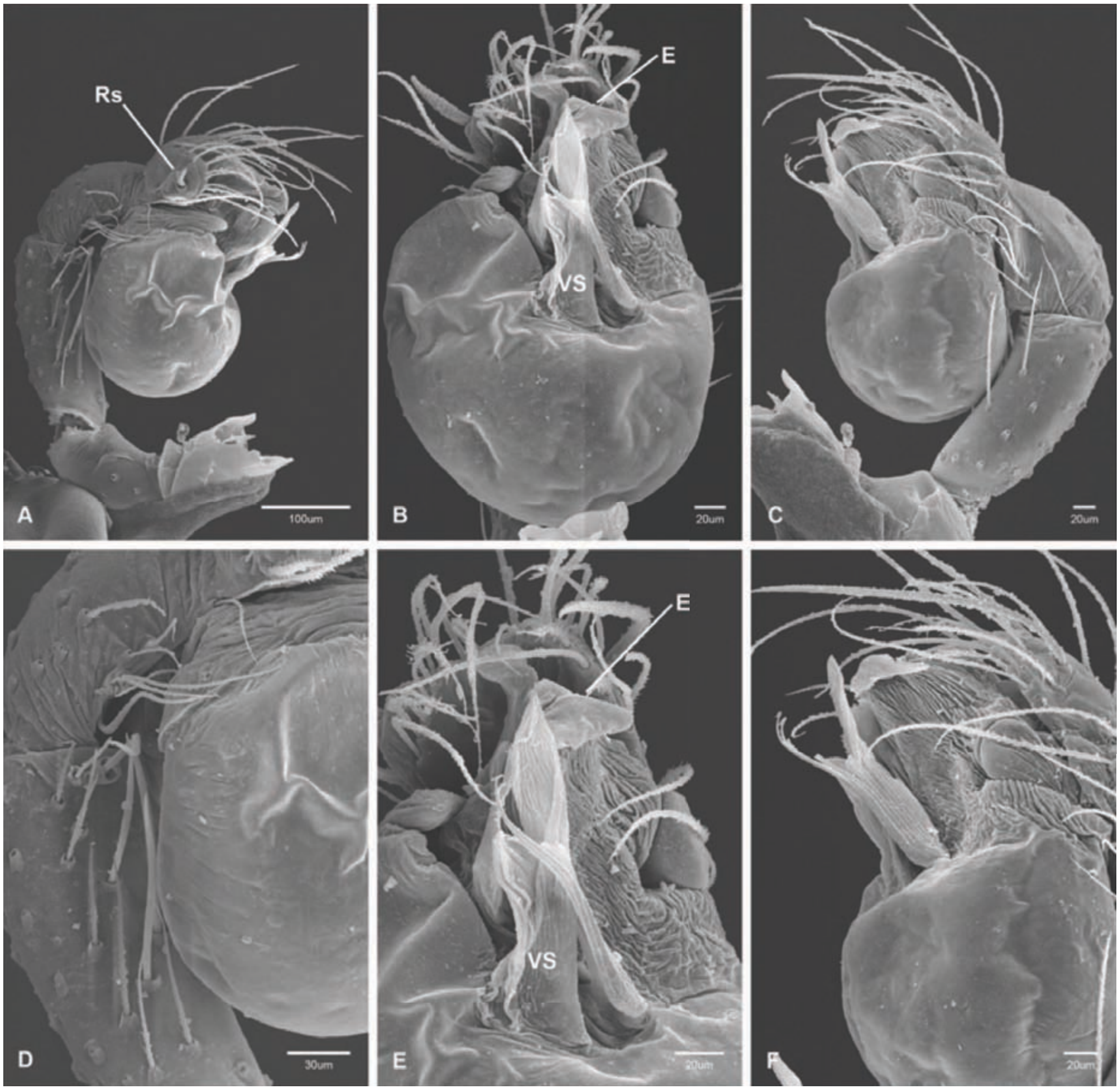
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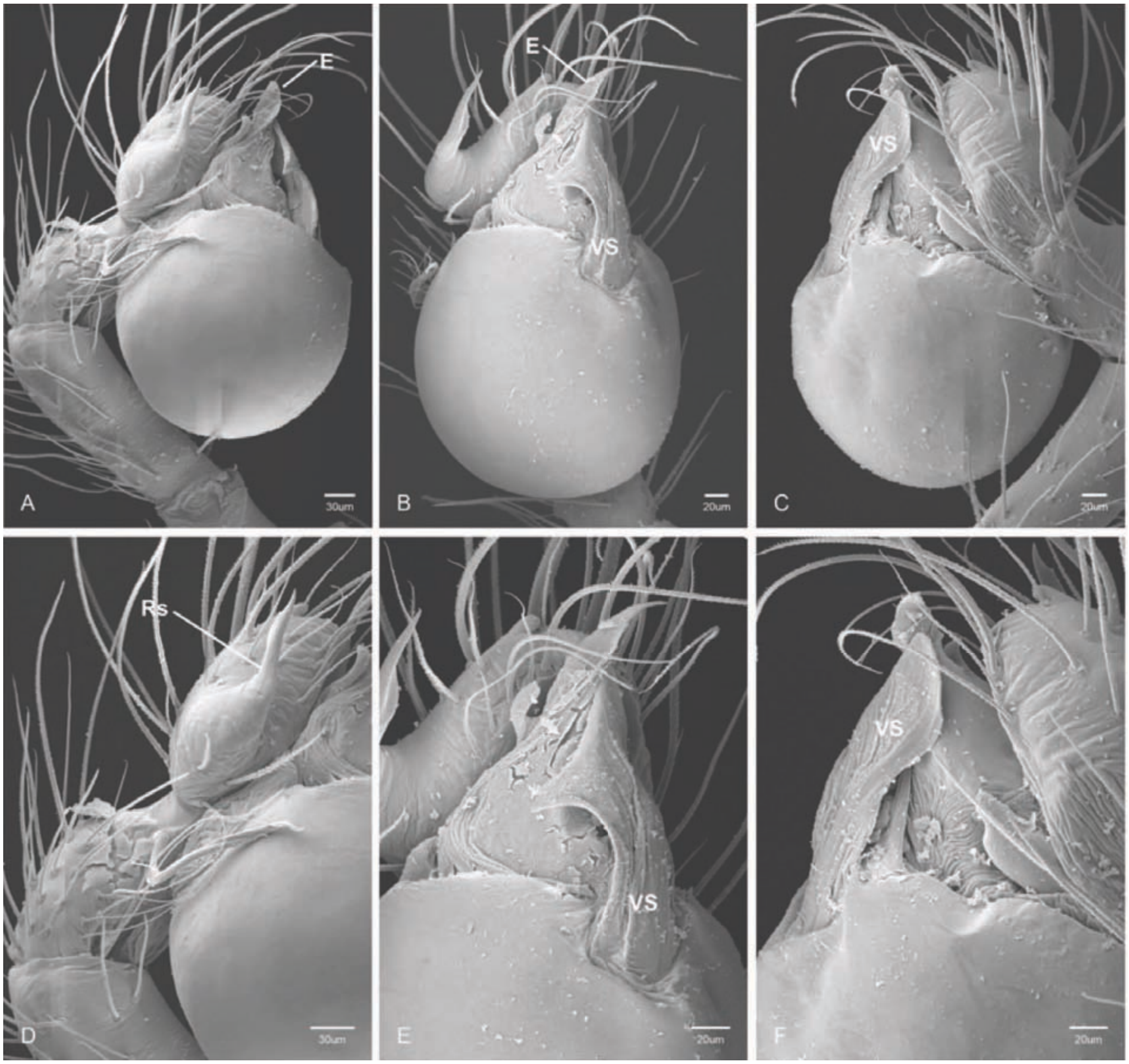
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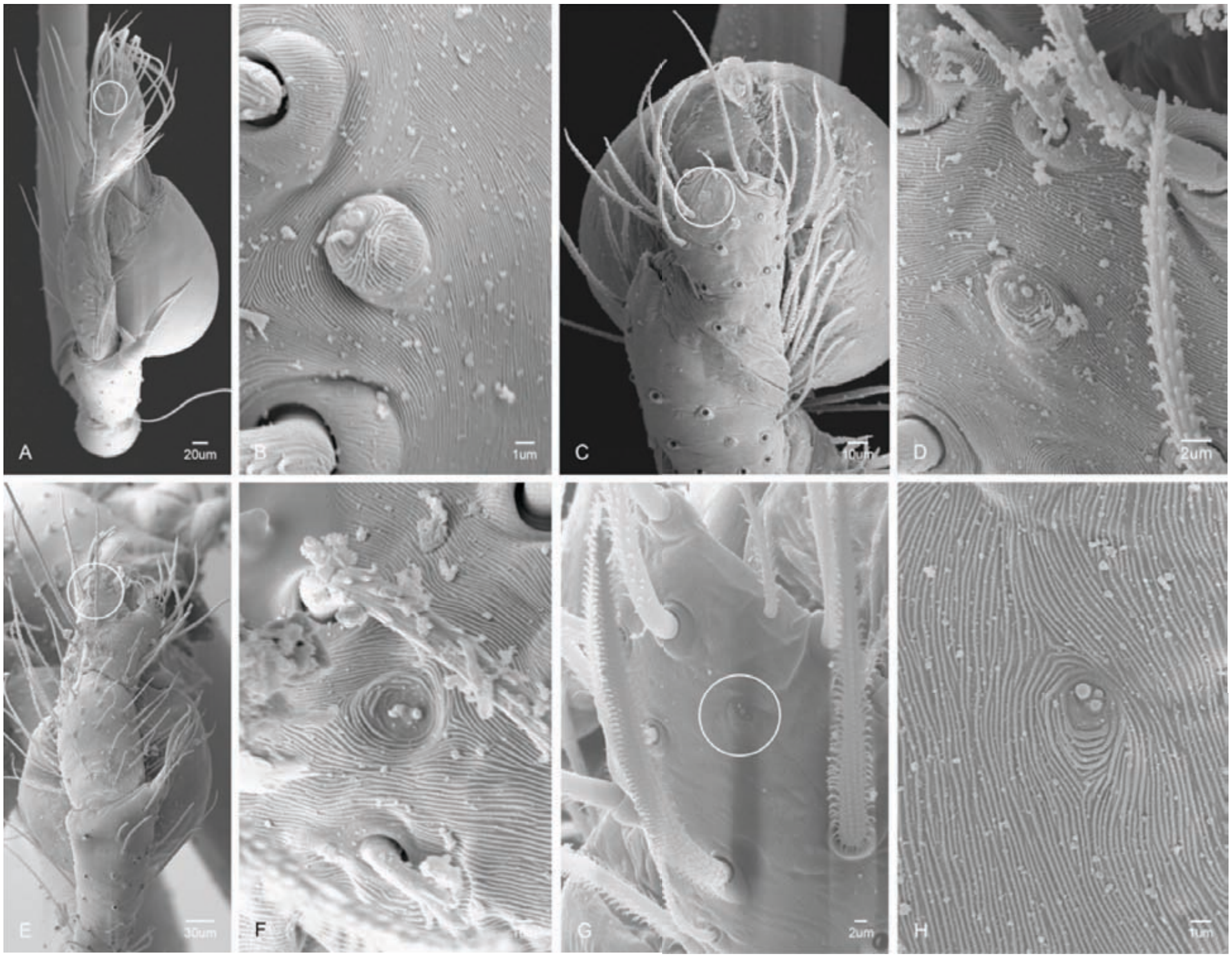
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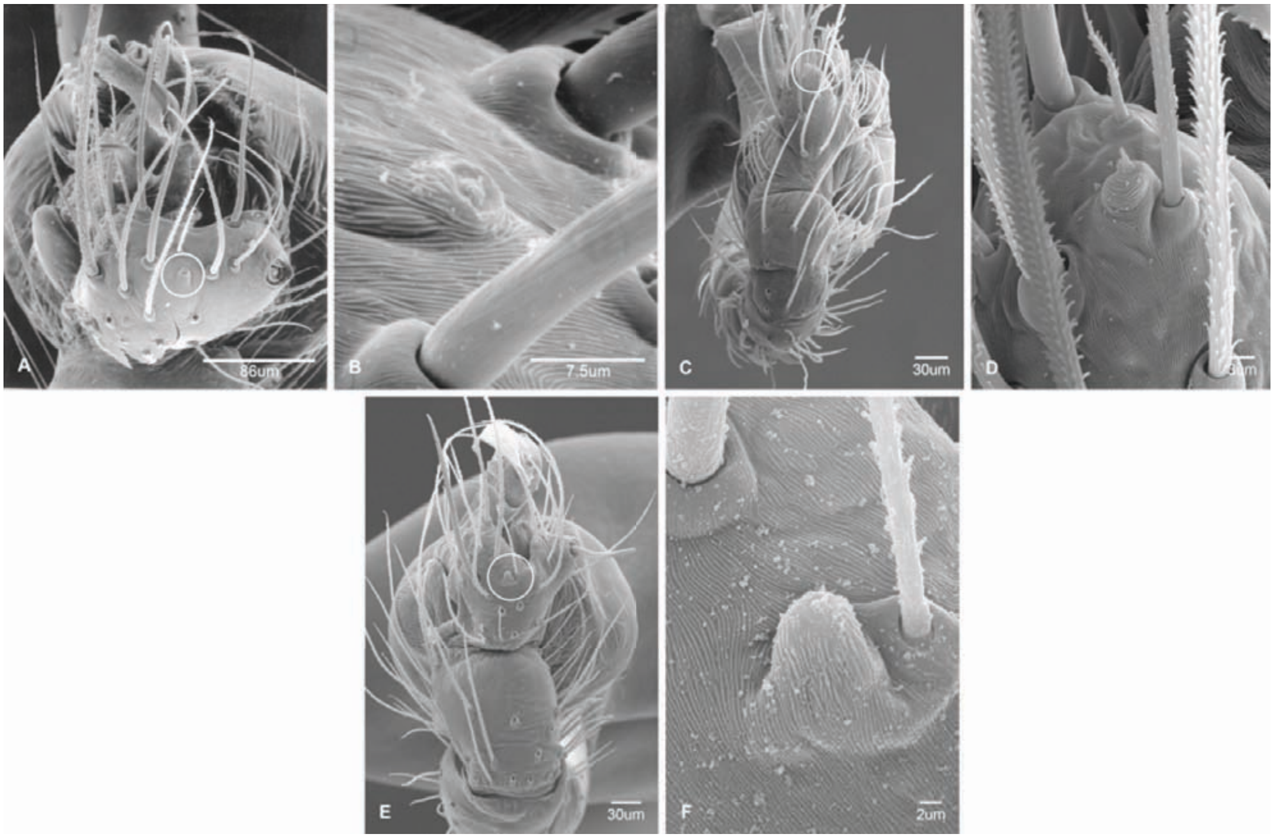
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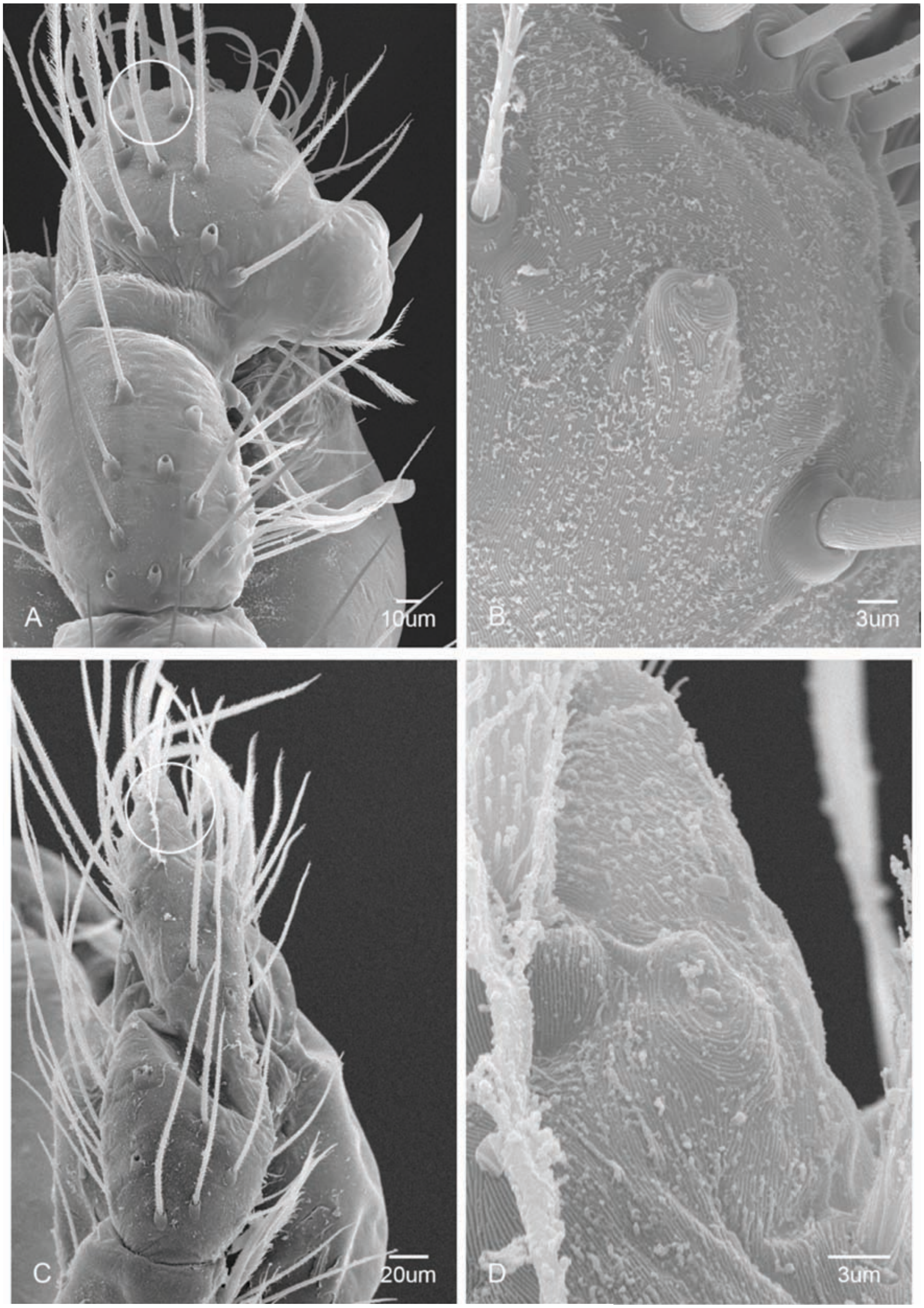
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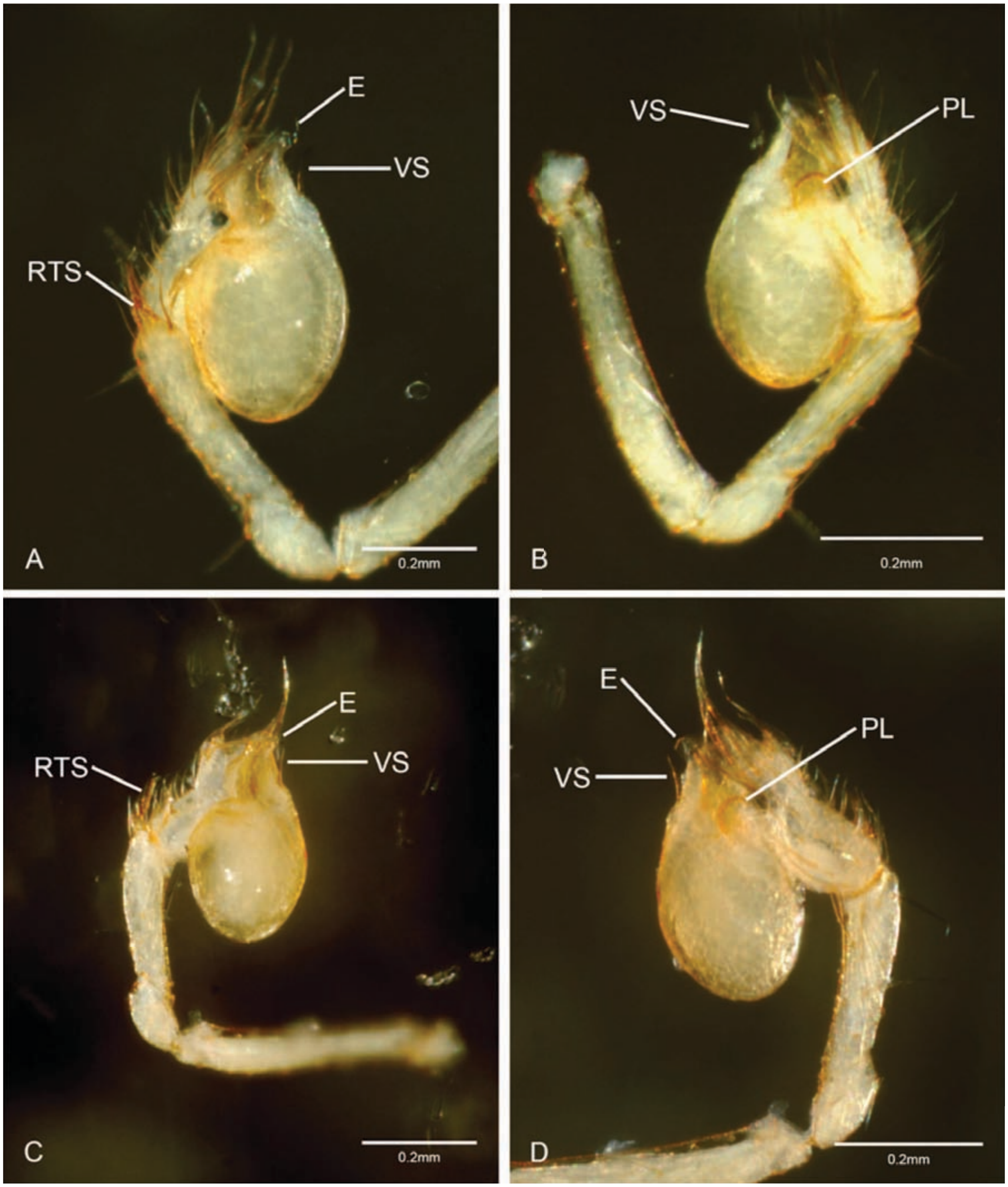
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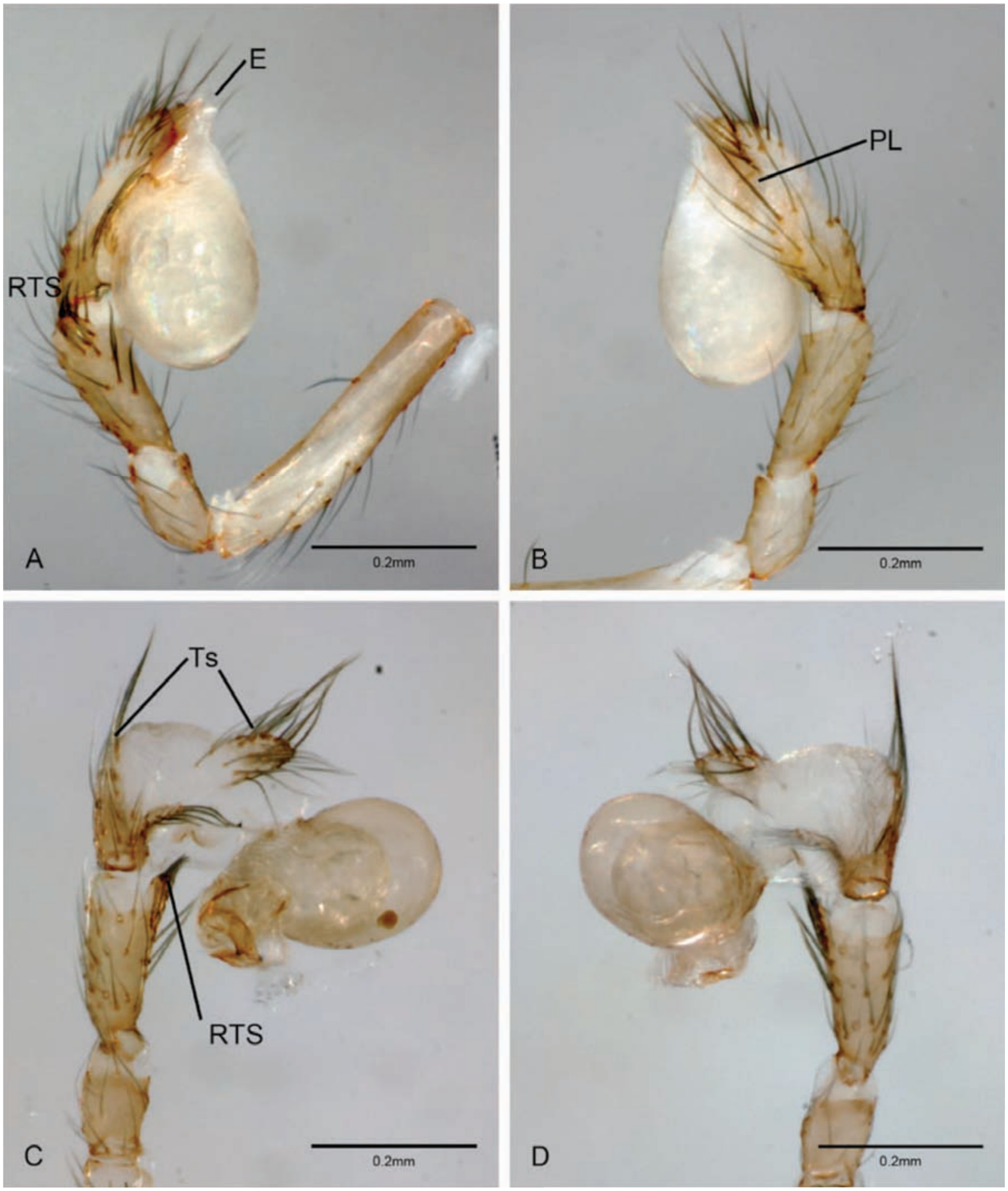
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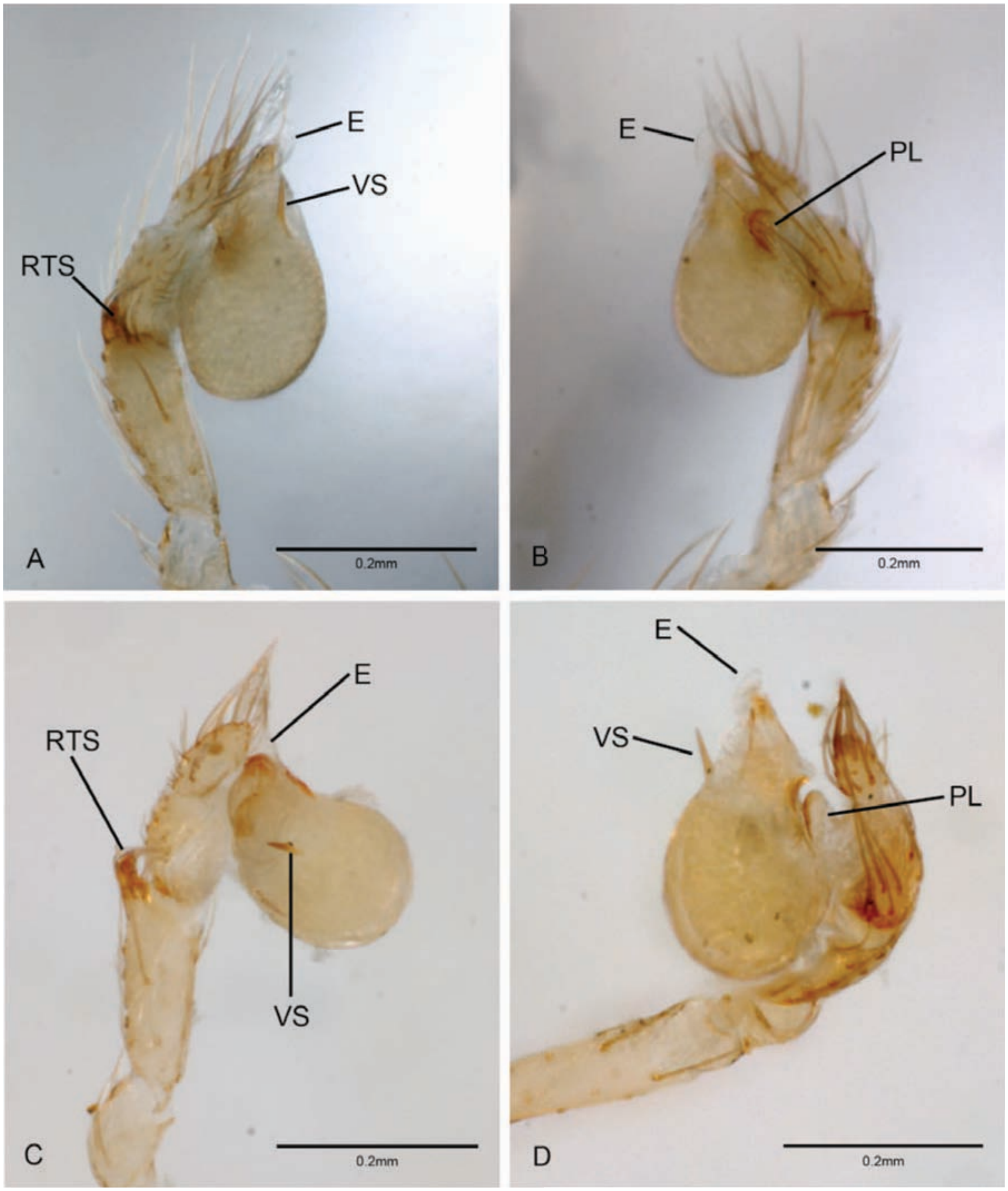
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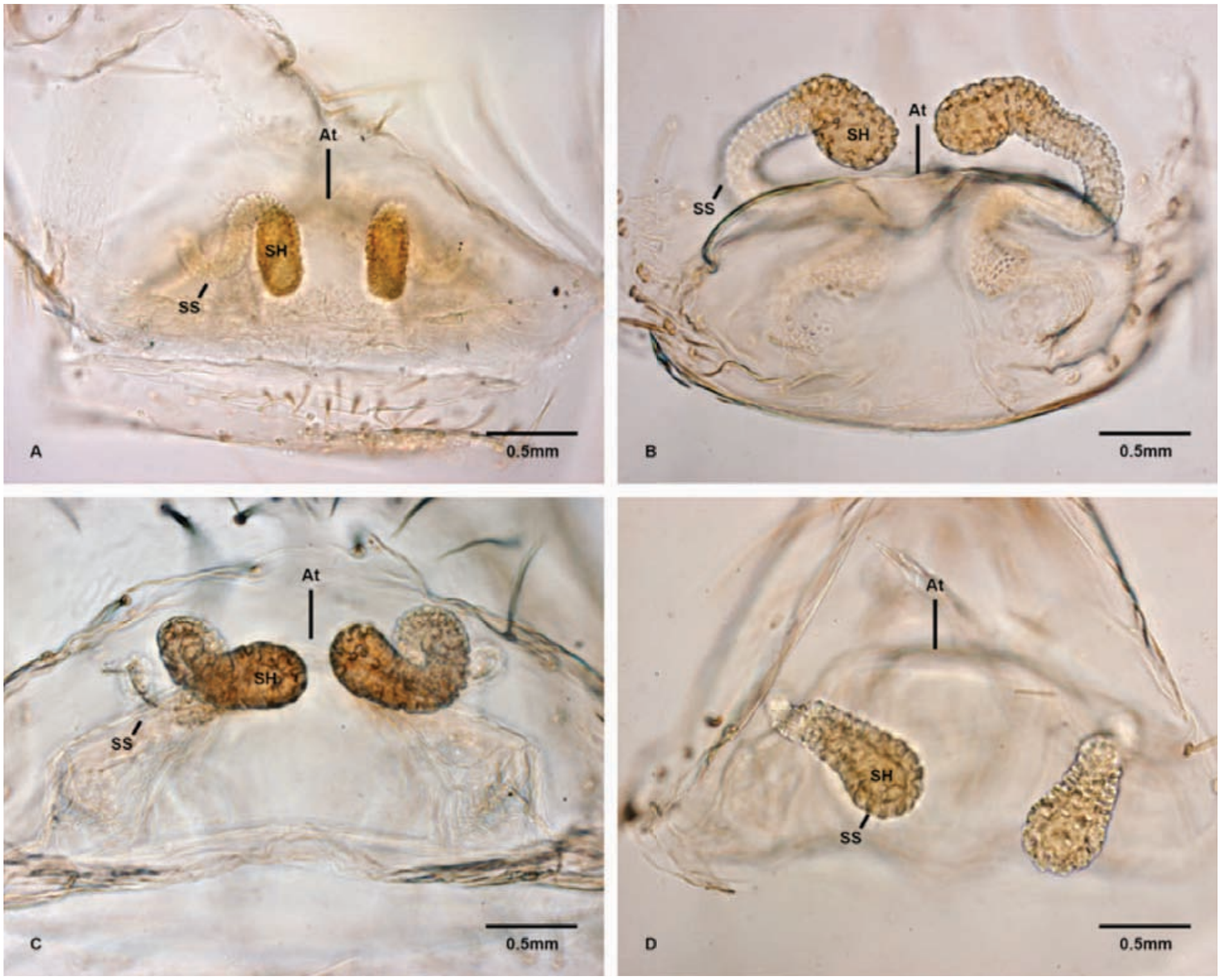
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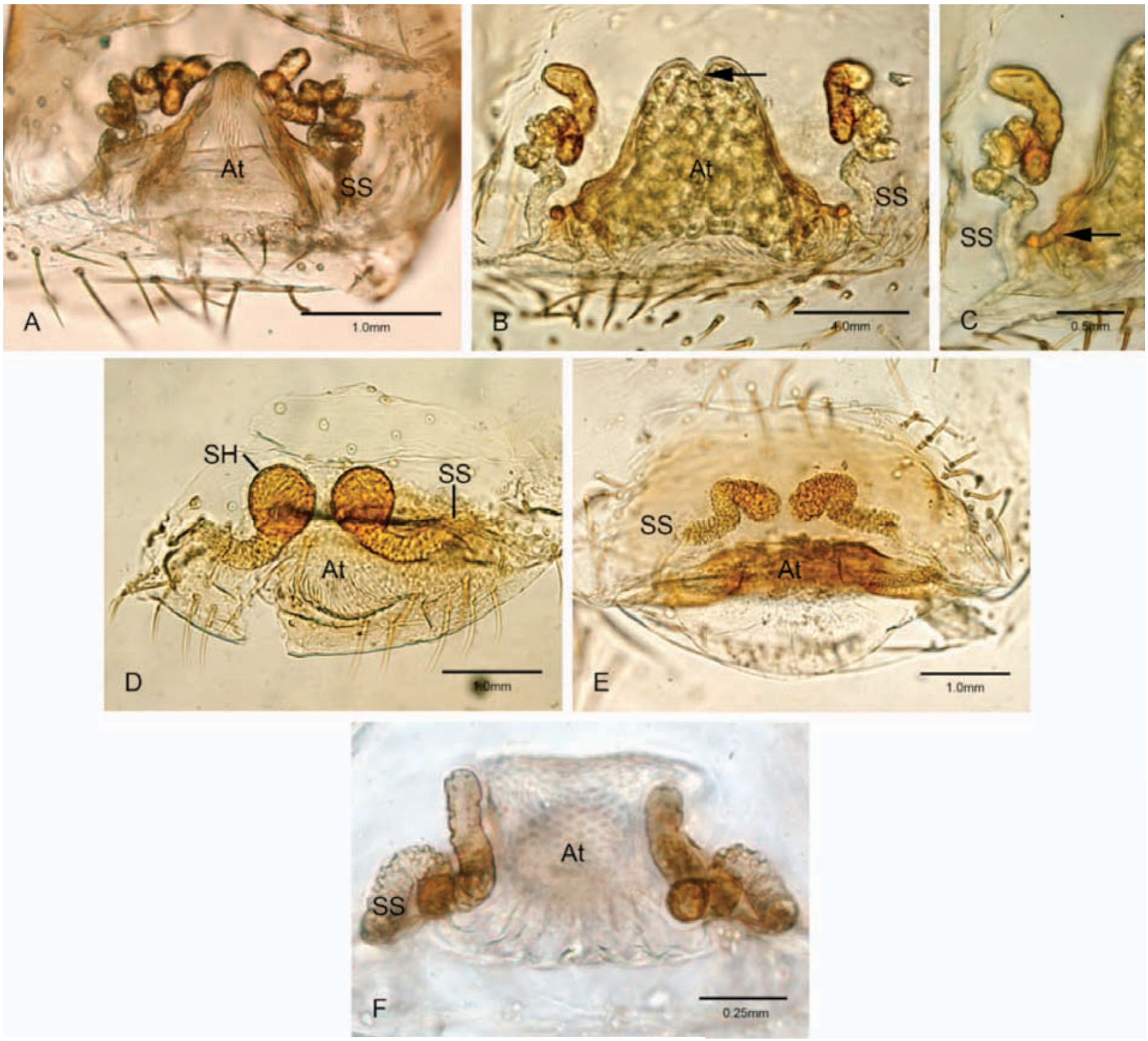
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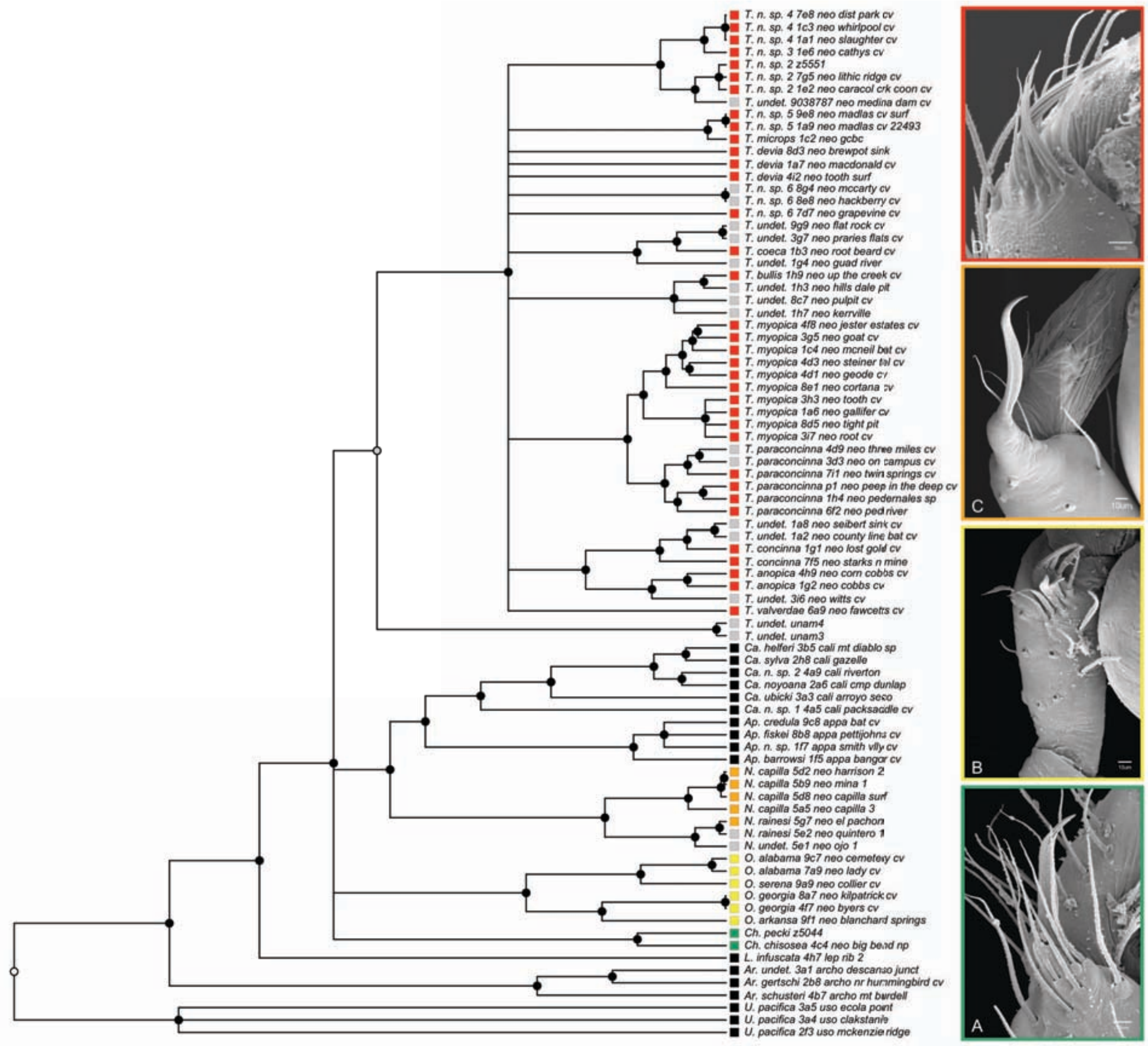
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T. paraconcinna 1h4 neo pedernales sp
T. paraconcinna 6f2 neo ped river
T. undet. 1a8 neo seibert sink cv
T. undet. 1a2 neo county line bat cv
T. concinna 1g1 neo lost gold cv
T. concinna 7f5 neo starks n mine
T. anopica 4h9 neo corn cobbs cv
T. anopica 1g2 neo cobbs cv
T. undet. 3i6 neo witts cv
T. valverdae 6a9 neo fawcetts cv
T. undet. unam4
T. undet. unam3
Ca. helferi 3b5 cali mt diablo sp
Ca. sylva 2h8 cali gazelle
Ca. n. sp. 2 4a9 cali riverton
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Ca. ubicki 3a3 cali arroyo seco
Ca. n. sp. 1 4a5 cali packsaddle cv
Ap. credula 9c8 appa bat cv
Ap. fiskei 8b8 appa pettijohns cv
Ap. n. sp. 1f7 appa smith vlly cv
Ap. barrowsi 1f5 appa bangor cv
N. capilla 5d2 neo harrison 2
N. capilla 5b9 neo mina 1
N. capilla 5d8 neo capilla surf
N. capilla 5a5 neo capilla 3
N. rainesi 5g7 neo el pachon
N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
O. alabama 9c7 neo cemetery cv
O. alabama 7a9 neo lady cv
O. serena 9a9 neo collier cv
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O. georgia 4f7 neo byers cv
O. arkansa 9f1 neo blanchard springs
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Ch. chisosea 4c4 neo big bend np
L. infuscata 4h7 lep rib 2
Ar. undet. 3a1 archo descanso junct
Ar. gertschi 2b8 archo nr hummingbird cv
Ar. schusteri 4b7 archo mt bardell
U. pacifica 3a5 uso ecola point
U. pacifica 3a4 uso clakstanie
U. pacifica 2f3 uso mckenzie ridge
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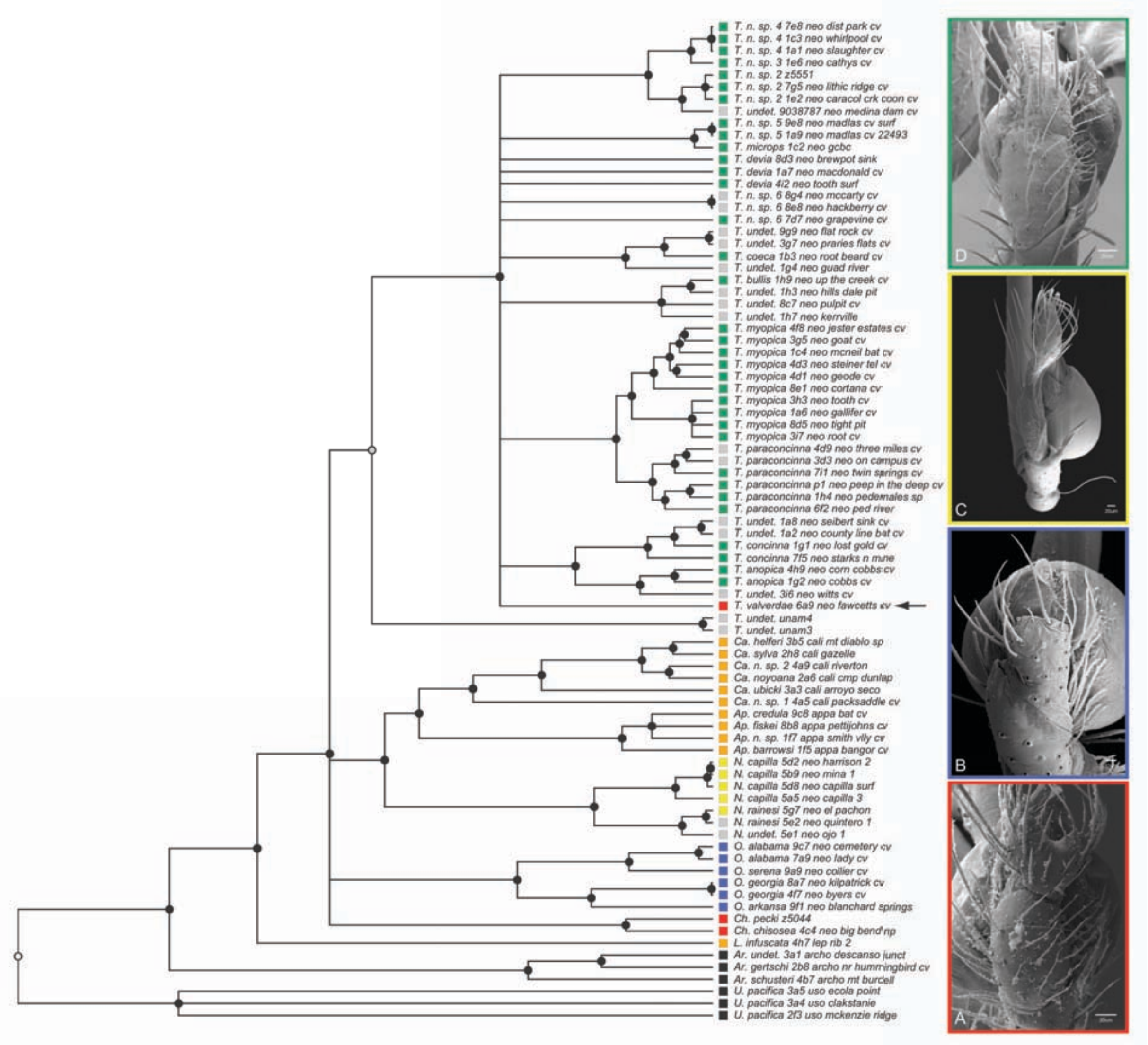
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T. myopica 3h3 neo tooth cv
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T. concinna 7f5 neo starks n mine
T. anopica 4h9 neo corn cobbs cv
T. anopica 1g2 neo cobbs cv
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N. capilla 5a5 neo capilla 3
N. rainesi 5g7 neo el pachon
N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
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O. georgia 4f7 neo byers cv
O. arkansa 9f1 neo blanchard springs
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Ch. chisosea 4c4 neo big bend np
L. infuscata 4h7 lep rib 2
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Ar. gertschi 2b8 archo nr hummingbird cv
Ar. schusteri 4b7 archo mt burcell
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U. pacifica 2f3 uso mckenzie ridge
D
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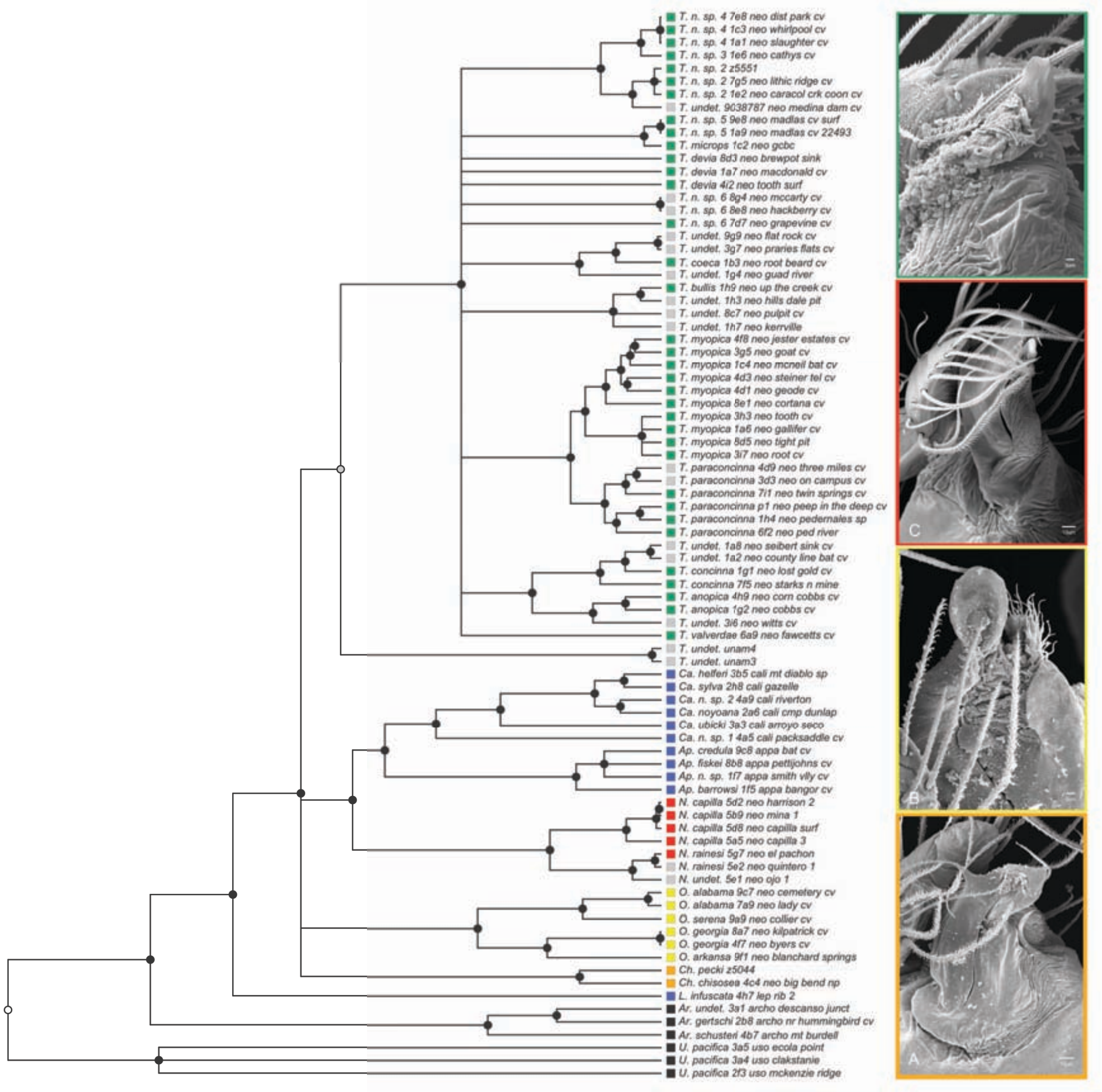
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T. n. sp. 2 1e2 neo caracol crk coon cv
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T. n. sp. 5 1a9 neo madlas cv 22493
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T. devia 4i2 neo tooth surf
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T. n. sp. 6 7d7 neo grapevine cv
T. undet. 9g9 neo flat rock cv
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T. coeca 1b3 neo root beard cv
T. undet. 1g4 neo guad river
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T. undet. 8c7 neo pulpit cv
T. undet. 1h7 neo kerrville
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T. myopica 1c4 neo mcneil bat cv
T. myopica 4d3 neo steiner tel cv
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T. valverdae 6a9 neo fawcetts cv
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N. capilla 5a5 neo capilla 3
N. rainesi 5g7 neo el pachon
N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
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Ch. chisosea 4c4 neo big bend np
L. infuscata 4h7 lep rib 2
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Ar. gertschi 2b8 archo nr hummingbird cv
Ar. schusteri 4b7 archo mt burdell
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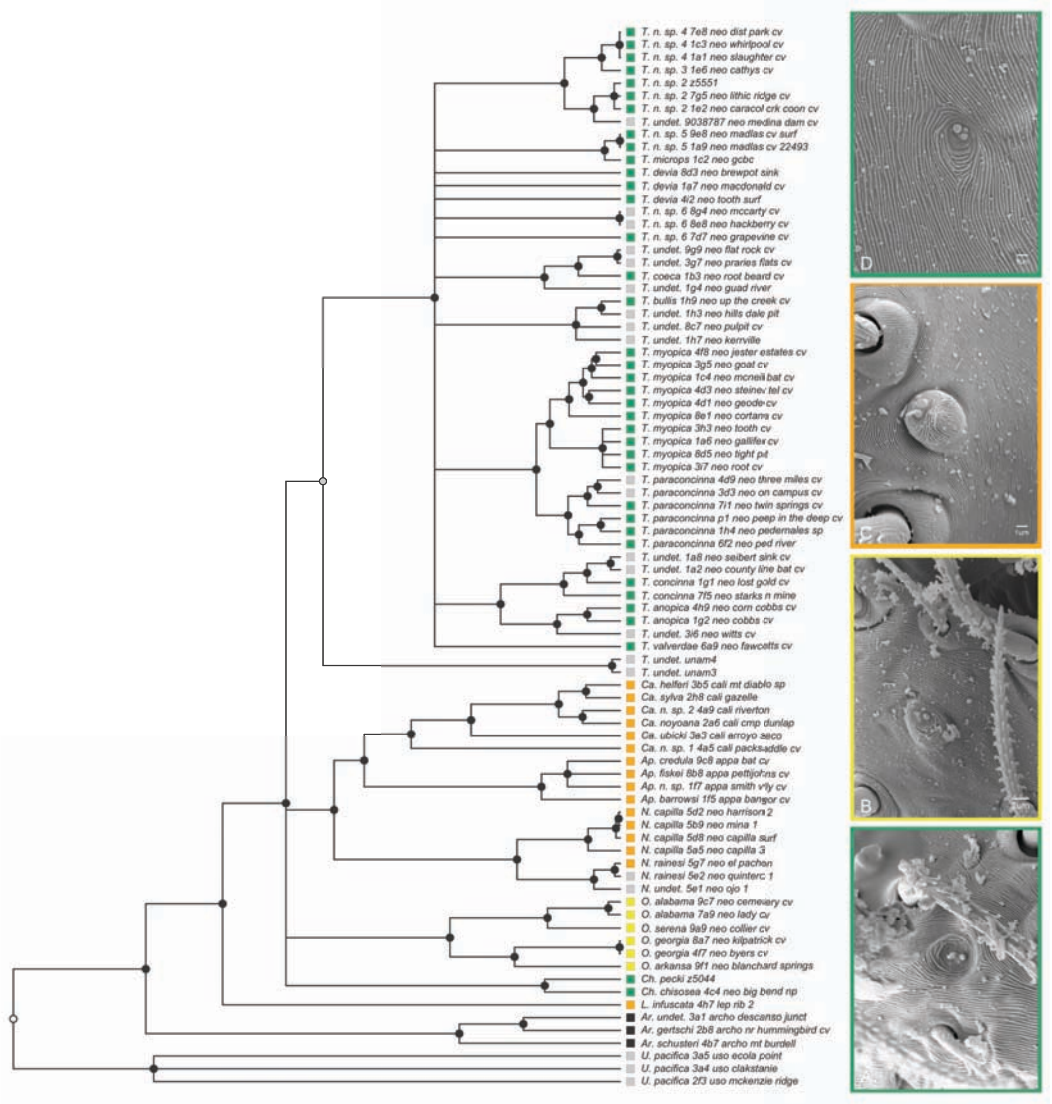
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T. n. sp. 2 1e2 neo caracol crk coon cv
T. undet. 9038787 neo medina dam cv
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T. concinna 7f5 neo starks n mine
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T. valverdae 6a9 neo fawcetts cv
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O. serena 9a9 neo collier cv
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Ch. pecki z5044
Ch. chisosea 4c4 neo big bend np
L. infuscata 4h7 lep rib 2
Ar. undet. 3a1 archo descanso junct
Ar. gertschi 2b8 archo nr hummingbird cv
Ar. schusteri 4b7 archo mt burdell
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D
C
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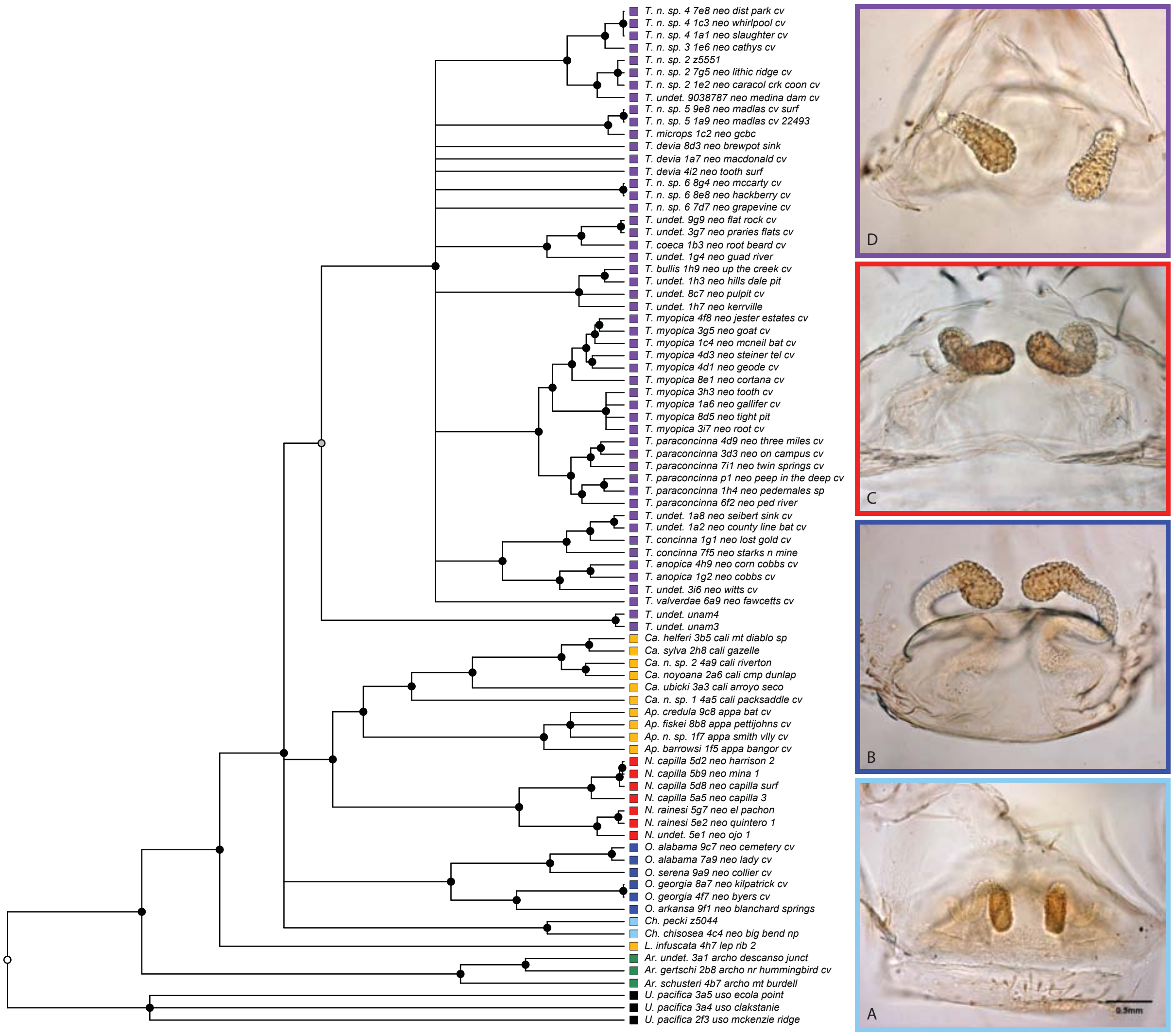
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T. coeca 1b3 neo root beard cv
T. undet. 1g4 neo guad river
T. bullis 1h9 neo up the creek cv
T. undet. 1h3 neo hills dale pit
T. undet. 8c7 neo pulpit cv
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T. myopica 3g5 neo goat cv
T. myopica 1c4 neo mcneil bat cv
T. myopica 4d3 neo steiner tel cv
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T. myopica 8e1 neo cortana cv
T. myopica 3h3 neo tooth cv
T. myopica 1a6 neo gallifer cv
T. myopica 8d5 neo tight pit
T. myopica 3i7 neo root cv
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T. paraconcinna 3d3 neo on campus cv
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T. concinna 7f5 neo starks n mine
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T. undet. unam4
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Ca. helferi 3b5 cali mt diablo sp
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Ap. fiskei 8b8 appa pettijohns cv
Ap. n. sp. 1f7 appa smith vlly cv
Ap. barrowsi 1f5 appa bangor cv
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N. capilla 5b9 neo mina 1
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N. capilla 5a5 neo capilla 3
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N. undet. 5e1 neo ojo 1
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Ch. pecki z5044
Ch. chisosea 4c4 neo big bend np
L. infuscata 4h7 lep rib 2
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Ar. gertschi 2b8 archo nr hummingbird cv
Ar. schusteri 4b7 archo mt burdell
U. pacifica 3a5 uso ecola point
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U. pacifica 2f3 uso mckenzie ridge
D
C
B
A
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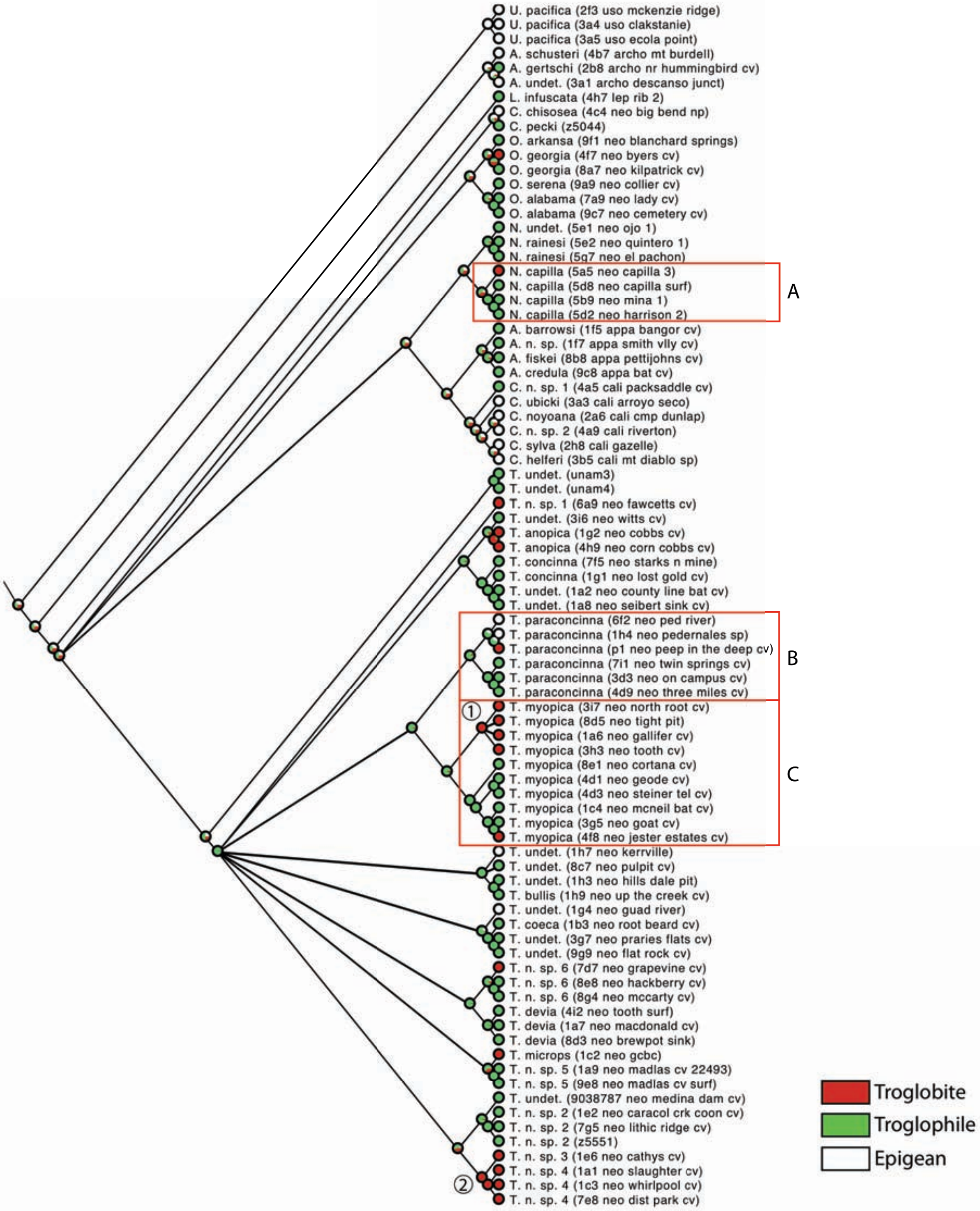
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A
A. barrowsi (1f5 appa bangor cv)
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C. ubicki (3a3 cali arroyo seco)
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C. sylva (2h8 cali gazelle)
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T. undet. (3i6 neo witts cv)
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T. anopica (4h9 neo corn cobbs cv)
T. concinna (7f5 neo starks n mine)
T. concinna (1g1 neo lost gold cv)
T. undet. (1a2 neo county line bat cv)
T. undet. (1a8 neo seibert sink cv)
T. paraconcinna (6f2 neo ped river)
T. paraconcinna (1h4 neo pedernales sp)
T. paraconcinna (p1 neo peep in the deep cv)
T. paraconcinna (7i1 neo twin springs cv)
T. paraconcinna (3d3 neo on campus cv)
T. paraconcinna (4d9 neo three miles cv)
B
①
T. myopica (3i7 neo north root cv)
T. myopica (8d5 neo tight pit)
T. myopica (1a6 neo gallifer cv)
T. myopica (3h3 neo tooth cv)
T. myopica (8e1 neo cortana cv)
T. myopica (4d1 neo geode cv)
T. myopica (4d3 neo steiner tel cv)
T. myopica (1c4 neo mcneil bat cv)
T. myopica (3g5 neo goat cv)
T. myopica (4f8 neo jester estates cv)
C
T. undet. (1h7 neo kerrville)
T. undet. (8c7 neo pulpit cv)
T. undet. (1h3 neo hills dale pit)
T. bullis (1h9 neo up the creek cv)
T. undet. (1g4 neo guad river)
T. coeca (1b3 neo root beard cv)
T. undet. (3g7 neo praries flats cv)
T. undet. (9g9 neo flat rock cv)
T. n. sp. 6 (7d7 neo grapevine cv)
T. n. sp. 6 (8e8 neo hackberry cv)
T. n. sp. 6 (8g4 neo mccarty cv)
T. devia (4i2 neo tooth surf)
T. devia (1a7 neo macdonald cv)
T. devia (8d3 neo brewpot sink)
T. microps (1c2 neo gcbc)
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T. n. sp. 2 (z5551)
T. n. sp. 3 (1e6 neo cathys cv)
T. n. sp. 4 (1a1 neo slaughter cv)
②
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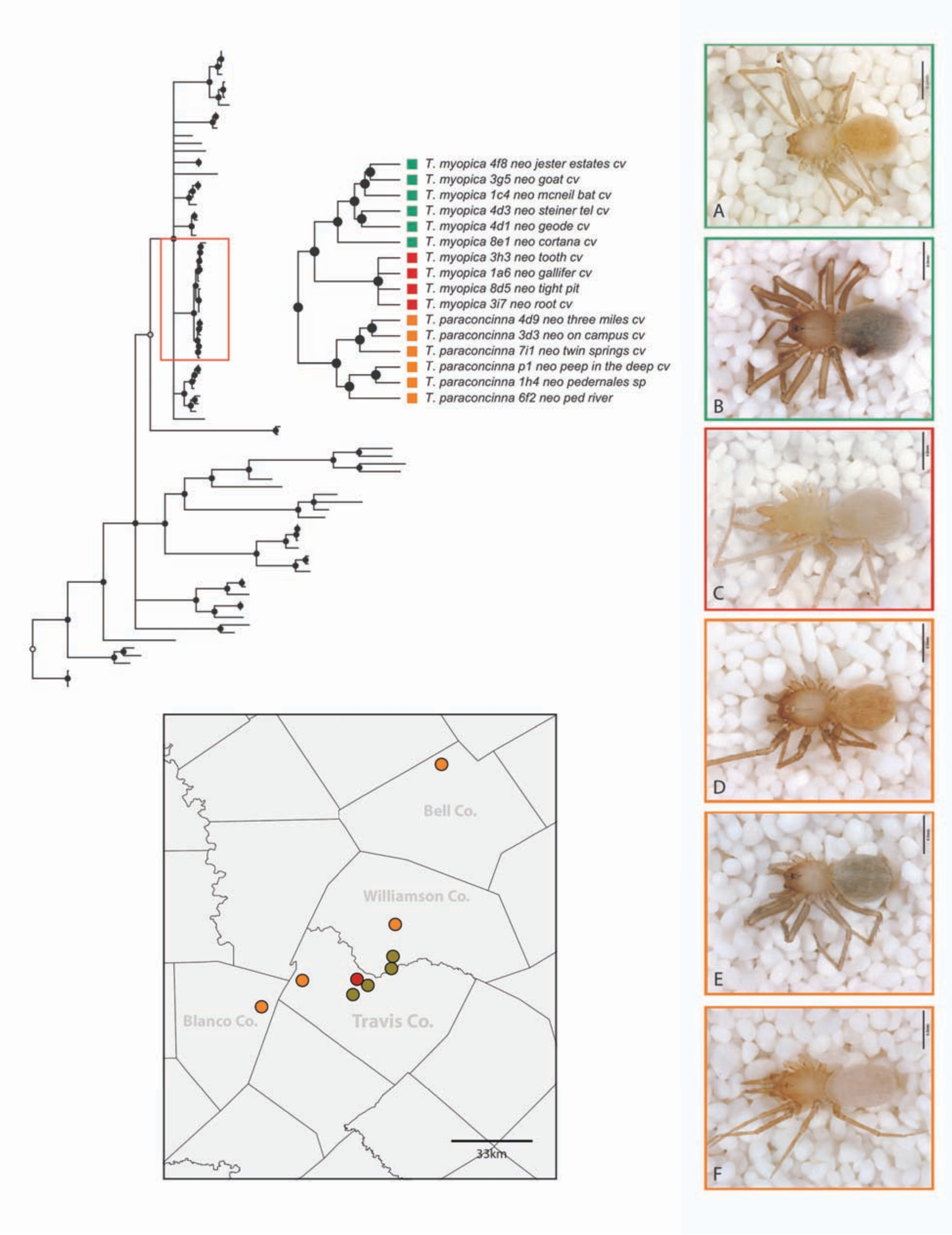
🟩 Troglophile
☐ Epigean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🟥 T. myopica 8d5 neo tight pit
🟥 T. myopica 3i7 neo root cv
🟧 T. paraconcinna 4d9 neo three miles cv
🟧 T. paraconcinna 3d3 neo on campus cv
🟧 T. paraconcinna 7i1 neo twin springs cv
🟧 T. paraconcinna p1 neo peep in the deep cv
🟧 T. paraconcinna 1h4 neo pedernales sp
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Williamson Co.
Blanco Co.
Travis Co.
33km
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B
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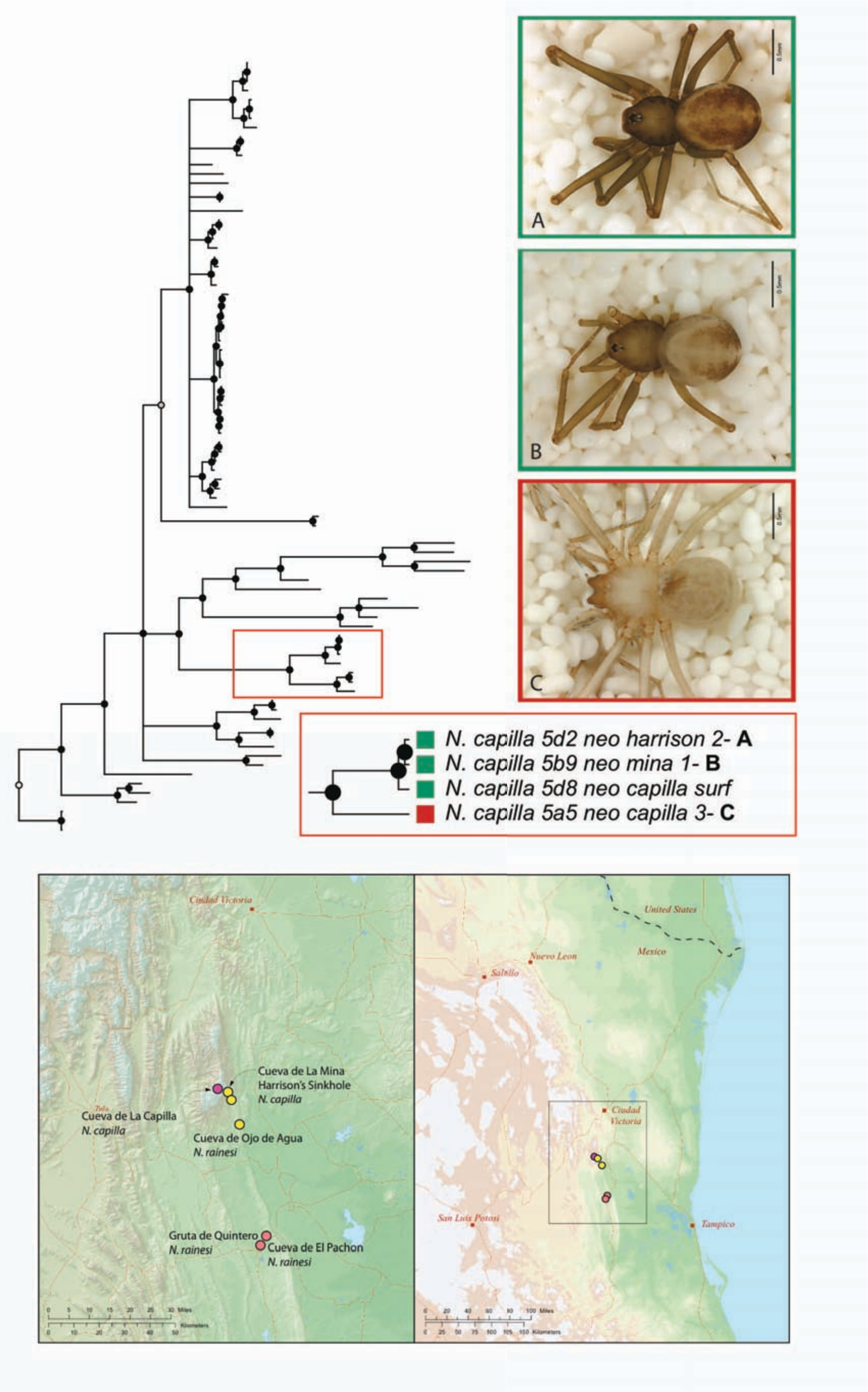
F


A
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0.5mm
🟩 N. capilla 5d2 neo harrison 2- A
🟩 N. capilla 5b9 neo mina 1- B
🟩 N. capilla 5d8 neo capilla surf
🟥 N. capilla 5a5 neo capilla 3- C
Ciudad Victoria
Cueva de La Mina
Harrison's Sinkhole
N. capilla
Tula
Cueva de La Capilla
N. capilla
Cueva de Ojo de Agua
N. rainesi
Gruta de Quintero
N. rainesi
Cueva de El Pachon
N. rainesi
0 5 10 15 20 25 30 Miles
0 10 20 30 40 50 Kilometers
United States
Mexico
Nuevo Leon
Saltillo
Ciudad Victoria
San Luis Potosi
Tampico
0 20 40 60 80 100 Miles
0 25 50 75 100 125 150 Kilometers

Chapter 3:
Systematics, Conservation, and Morphology of the Spider Genus *Tayshaneta* (Araneae, Leptonetidae) in Central Texas Caves

Abstract

The spider genus *Tayshaneta* is revised based on results from a three gene phylogenetic analysis (Ledford et al., in prep) and a comprehensive morphological survey using scanning electron (SEM) and compound light microscopy. The morphology and relationships within *Tayshaneta* are discussed, and five species groups are supported by phylogenetic analyses: the *anopica* group, the *coeca* group, the *myopica* group, the *microps* group, and the *sandersi* group. Branch lengths within *Tayshaneta* contrast sharply with the remaining North American genera and are viewed as evidence for a relatively recent radiation of species. Variation in troglomorphic morphology is discussed and compared to patterns found in other Texas cave invertebrates. Several species previously known as single cave endemics have wider ranges than expected, suggesting that some caves are not isolated habitats but instead form part of interconnected karst networks. Distribution maps are compared with karst faunal regions (KFR's) in Central Texas and the implications for the conservation and recovery of *Tayshaneta* species are discussed. Ten new species are described: *T. archambaulti* **sp. nov.**, *T. emeraldae* **sp. nov.**, *T. fawcetti* **sp. nov.**, *T. grubbsi* **sp. nov.**, *T. madla* **sp. nov.**, *T. oconnori* **sp. nov.**, *T. sandersi* **sp. nov.**, *T. sprousei* **sp. nov.**, *T. vidrio* **sp. nov.**, and *T. whitei* **sp. nov.** The males for three species, *T. anopica* (Gertsch, 1974), *T. devia* (Gertsch, 1974), and *T. microps* (Gertsch, 1974) are described for the first time. *T. furtiva* (Gertsch, 1974) and *T. uvaldea* (Gertsch, 1974) are declared *nomen dubia* as the female holotypes are not diagnoseable and efforts to locate specimens at the type localities were unsuccessful. All *Tayshaneta* species are thoroughly illustrated, diagnosed, and keyed. Distribution maps are also provided highlighting areas of taxonomic ambiguity in need of additional sampling.

Key Words: Spiders, Haplogynae, Leptonetidae, *Neoleptoneta,* Caves, Endangered Species, Troglobites, Edwards Aquifer, Karst Faunal Regions, Phylogenetics.

Introduction

Tayshaneta are small spiders that belong to the family Leptonetidae, a group recognized for its association with caves and similar cryptic habitats (Ledford et al., 2004). *Tayshaneta* are widely distributed in caves of the Edward's Plateau (Fig. 3), an extensive limestone region in Central Texas that drains into the Edward's Aquifer and serves as the primary source of water for over 2 million people. The region is famous for its endemism and includes a high proportion of endangered and threatened species, many of which are subterranean specialists and known only from single springs or caves (Culver et al., 2003). Two *Tayshaneta* species are federally listed as endangered in Central Texas, *T. microps* (Gertsch, 1974) and *T. myopica* (Gertsch, 1974), and most others are of conservation concern (Bender et al., 2005; U. S. Fish and Wildlife, 1998, 2010). However, management and recovery efforts are limited by existing taxonomy which is poorly resolved and leaves the identity and distribution of *Tayshaneta* species ambiguous.

Gertsch (1974) described the majority of the North American Leptonetidae and considered twelve species as part of a closely related Texas fauna. Although he originally described these species as congeneric with European *Leptoneta*, several authors (Brignoli, 1977, 1979; Platnick, 1986) refuted this hypothesis and transferred the Texas fauna to the genus *Neoleptoneta* Brignoli, 1972. Two species were later added by Cokendolpher and Reddell (2001) and Cokendolpher (2004), who also provided details on their general biology. Recent phylogenetic work has shown that *Neoleptoneta* is paraphyletic and three additional genera, *Chisosea*, *Ozarkia*, and *Tayshaneta*, were described (Ledford et al., in prep). *Tayshaneta* presently includes eleven species restricted to Texas caves with close relatives in the Southeast, Southern Texas, and Northern Mexico (Ledford et al., in prep).

While Gertsch's (1974) study was the first to comprehensively treat the North American fauna, the taxonomic challenges of leptonetids frustrated him (D. Ubick, pers. comm.). Most species are represented by few specimens which in addition to being relatively small (1- 2mm) are also delicate and easily damaged during examination. Furthermore, the characters used to separate species are exceptionally fine and not often visible using conventional microscopy. European specialists, including Brignoli (1972, 1974), Fage (1913), and Machado (1941, 1945) relied heavily on compound light microscopy to produce detailed illustrations which Gertsch was reluctant to use. Consequently, most species remain poorly diagnosed and positive identification is only possible with topotypic material. Morphological homogeneity within female specimens is also problematic (Ledford, 2004; Ledford and Griswold, 2010) and although microscopy and preparation techniques have improved, leptonetid taxonomy remains dependent upon the details of male genitalia. Diagnostic features for *Tayshaneta* in particular are subtle and often require examination using scanning electron microscopy.

Recent studies on *Cicurina* spiders in Texas caves (Paquin and Hedin, 2004; Paquin et al., 2008) have addressed similar problems by using molecular phylogenetic methods and fine scale geographic sampling to help resolve species limits. Although based on a single genetic locus, Paquin and Hedin (2004) clearly demonstrate that the integration of molecular data is a valuable aid to overcoming the difficulties of working with cave fauna, especially when specimens are rare or present diagnostic challenges. Studies of cave invertebrates are also underscored by conservation concerns, especially in

Central Texas, where taxonomic identity can have profound socioeconomic impact. As emphasized by Paquin et al. (2008), the interaction between taxonomists, conservation biologists, and development interests can be volatile and highlights the need for robust, integrative taxonomy based on multiple lines of evidence.

Several geological areas are recognized on the Edward's Plateau, however most of the subterranean diversity is known from caves along the heavily faulted Balcones Escarpment (Fig. 3). The faulting serves to isolate regions of limestone and is likely correlated with the diversification patterns of cave invertebrates (White et al., 2009). Conservation biologists have used this fragmented geology to develop a conservation strategy based on "karst faunal regions" (KFR's), hypothesized as biologically discrete areas of cave habitat that are used to manage species recovery (U. S. Fish and Wildlife, 1994; Veni, 1992, 1994). Three KFR's (Figs. 61- 62) are currently recognized in Bexar, Travis, and Williamson counties each of which includes large numbers of caves and encompasses the distributions of multiple endangered invertebrates. However, KFR boundaries are limited by existing taxonomy which in most cases does not accurately reflect species distributions (White and Carothers, 2001). Furthermore, KFR's have never been assessed using phylogenetic data which will likely provide finer scale resolution of species distributions and facilitate the delineation of conservation boundaries.

This study revises the taxonomy of *Tayshaneta* based on the phylogenetic results of Ledford et al. (in prep) and data collected from a morphological survey using scanning electron and compound light microscopy. Ten new species are described, along with three previously unknown sexes, and all remaining species are imaged, diagnosed, and keyed. The morphology and relationships within *Tayshaneta* are discussed and five species groups are identified. Distribution maps are provided along with an evaluation of KFR's based on revised species distributions. The primary objective of this study is to produce a functional taxonomy for *Tayshaneta* that will facilitate conservation and management efforts and contribute to an understanding of the Texas cave fauna.

Materials and Methods

Taxon Sampling

A resurgence of interest in Texas cave biology, driven largely by conservation efforts, has produced a wealth of new *Tayshaneta* specimens more than doubling records since Gertsch (1974). In order to prioritize collection sites, a database combining records for described species and all recent collections was developed. Collection sites were then selected to maximize sampling throughout known ranges with priority given to type localities. Outgroup selection was based on the most recent phylogenies of haplogyne spiders (Platnick et al., 1991; Ramirez, 2000) and specimen availability. Between 1- 10 individuals were collected from each site, placed directly into 95% ethanol, and then transferred to storage at -20ºC. Each specimen was assigned a unique voucher number and is accessioned in a database maintained at the California Academy of Sciences (CASC).

Voucher specimens for the study are deposited at the California Academy of Sciences (CASC), the Texas Memorial Museum (TMM), the Museum of Texas Tech University (TTU), and the Essig Museum, University of California, Berkeley (UCB). Due to the sensitive nature of cave locations and in the spirit of respecting the rights of property owners and encouraging future research, precise locality information is not provided. Unless otherwise noted, all cave locations are limited to within 2 kilometers. Specimens used in this study along with their voucher codes are listed in Ledford et al. (in prep) and a map highlighting the study area is provided in Fig 3.

Distribution maps were produced using Arc GIS 10.0 (Environmental Systems Research Institute, CA). Karst faunal region boundaries were derived from shape files provided by Zara Environmental (K. O'Connor) through the U.S. Fish and Wildlife Service.

Morphology

Prior to examination with a Leo 1450VP Scanning Electron Microscope, all structures were cleaned with a fine brush or ultrasonicator and critical point dried. Best results were obtained by gradually dehydrating the specimen in increasing concentrations of ethanol for 24- 48 hours prior to critical point drying. Dried specimens were then mounted on pin mount SEM stubs (Ted Pella Inc., Redding, USA) on copper- backed tape. Specimens were sputter coated for 120 seconds using a Denton Vacuum Sputter Coater. Large structures were photographed using a Nikon DMX1200 camera attached to a Leica MZ 16 stereomicroscope. Images were then montaged using Helicon Focus v. 4.2.1 (http://www/heliconsoft.com). For male specimens, the right palp was scanned and the left was maintained with the specimen post examination using compound light microscopy.

Vulvae were carefully excised and placed in a pancreatin solution for 24- 48 hours to digest extraneous tissue (Alvarez- Padilla and Hormiga, 2008) then placed in water and manually cleaned. Best results were obtained by removing the cuticle from the dorsal surface of the abdomen and digesting the entire structure. If the vulva remained unclear, it was stained with Chlorazol Black and reexamined. Images of each species were prepared using a Nikon DMX1200 camera attached to a Leica DM 4000 compound microscope. Genitalia were placed in Hoyer's solution and examined in well slides or temporary mounts following the procedure described by Coddington (1983).

Descriptions follow the format of Ledford & Griswold (2010) and Ledford (2004). Descriptions of previously unknown sexes were based upon individuals collected at the type locality. All measurements are in millimeters and quantify the structure at its widest or longest point. A summary of anatomical abbreviations used in the descriptions and keys is provided in Table 1. Individual images of all structures will be made available at the time of publication in Morphbank (www.morphbank.net) and species pages will be available in the Encyclopedia of Life (http://www.eol.org).

Phylogeny

Detailed protocols for the extraction, amplification, and sequencing of DNA are reported in Ledford et al. (in prep). Three gene fragments were selected based on availability, prior use in systematics studies, and amplification success. Mitochondrial cytochrome oxidase I (~800bp), nuclear histone 3 (~330bp), and 28s rDNA (~1000bp) were amplified following Ledford et al. (in prep), and the primers and conditions used are reported in Table 3. Phylogenetic methods also follow Ledford et al. (in prep), and both independent genes and concatenated data were analyzed under a variety of optimality criteria and conditions (Table 2). Sequence alignment was performed using CLUSTAL X v. 2.0 (Larkin et al., 2007) and additional 28s rDNA alignments were produced using

Muscle v. 3.8 (Edgar, 2004). Models of nucleotide evolution were selected using the Akaike Information Criterion (Akaike, 1973) as implemented in MrModeltest v. 2.2 (Nylander, 2004). Partitioning strategies for COI and histone 3 were evaluated using Bayes Factors (Brown & Lemmon, 2007) for fully partitioned, partially partitioned, and unpartitioned analyses.

Bayesian analysis was performed using MrBayes v. 3.1.2 (Huelsenbeck & Ronquist, 2001) using 4 independent runs until the standard deviation of split frequencies fell below 0.01. Stationarity was evaluated by examining the stability of posterior probabilities for nodes of each MCMC run using the Cumulative and Compare plots in Are We There Yet? (http://ceb.csit.fsu.edu/awty; Nylander et al., 2008) and the first 25% of trees were discarded from the posterior distributions of each analysis. Maximum likelihood analysis was performed using 1000 bootstrap replicates in RAxML v. 7.0.4 (Stamatakis, 2006) and parsimony analyses were performed in PAUP* (Swofford, 2003) using 1000 iterations of heuristic search, with random taxon addition and tree bisection-reconnection (TBR). Nonparametric bootstrap support values were calculated using 1000 replicate searches with random taxon addition.

Aligned data matrices and trees will be made available online in TreeBASE (http://www.treebase.org/).

Results

Morphology

Exemplars for each *Tayshaneta* species, including undescribed species discovered during the course of this study, were photographed using automontage, compound, and scanning electron microscopy. Holotype specimens for each species were examined in order to confirm the identity of exemplars used in analyses. Images provided in this study are either taken directly from the holotype or from specimens collected at the type locality. Over 3,000 images were produced based on a set of standardized views and assembled into comparative plates. Careful attention was directed at diagnostic characters provided in Gertsch (1974) and to somatic features in order to assess variation in troglomorphic morphology.

Synapomorphies for *Tayshaneta* include a unique conformation of the female genitalia, with short spermathecal stalks bearing large heads (SH, Figs. 52- 54) and the recurved to straight retrolateral spine on the male palpal tibia (RTS, Figs. 32A- F). Body color ranges from pale brown- yellow to depigmented with faint dark patterns surrounding the eyes and ocular area. The legs are covered in fine setae and bear few scattered spines. A ventroapical preening comb on metatarsus III was observed in each species examined (Fig. 12- 13 in Ledford, 2004). Patellar and tibial gland morphology was similar to that described by Platnick (1986) with triangular patellar plates bearing single small pores (Figs. 30- 31, 33, 38, 40, 46 in Platnick, 1986). The abdomen lacks distinctive patterning, is sparsely setose, and pale yellow to white in color. Spinning organs follow the descriptions of *Leptoneta infuscata* Simon, 1872 (Ledford and Griswold, 2010) and *Calileptoneta* (Ledford, 2004) with the exception of bearing fewer aciniform gland spigots (6- 10) on the PMS and PLS (Figs. 11A- C).

In contrast to other leptonetine genera, the palpal morphology of *Tayshaneta* is relatively conserved and the bulb bears few spines, specialized setae, or accessory sclerites. The shape of the palpal tarsus is of two basic types; divided, as in *T. fawcetti* **sp.**

nov. (Fig. 31D) and tapering, as in *T. coeca*, *T. microps*, and *T. myopica* (Figs. 31A- C). The depth of the division ranges from deeply divided as in *T. fawcetti* **sp. nov.** and *T. vidrio* **sp. nov.** (Figs. 31D- E) to weakly divided or swollen as in *T. madla* **sp. nov.** (Fig. 31F) An exposed tarsal organ is present dorsoapically and consists of a shallow circular base with a pair of round receptors (Figs. 24G- H in Ledford et al., in prep). The embolus is weakly sclerotized, transparent, and connected via a short tube to a large reservoir in the bulb (Figs. 30A- D in Ledford et al., in prep). The sculpture along the margins of the embolus ranges from smooth as in *T. coeca* and *T. myopica* (Figs. 36D, 44D) to bearing tooth- like extensions and folds as in *T. anopica* (Fig. 33D). The embolus is typically curved or folded around the ventroapical portion of the bulb and bears a single, circular opening (Fig. 44F).

The ventral sclerite (VS) is a single, spine- like projection that extends approximately half the length of the embolus. The position and length of the VS ranges from elongate and mesal as in *T. fawcetti* **sp. nov.** (VS, Fig. 40E), to retroventral as in *T. myopica* (VS, Fig. 44B), and short as in *T. sprousei* **sp. nov.** (VS, Fig. 48E) The VS is absent in several species, including *T. coeca* (Fig. 36E), and despite repeated efforts to determine whether this structure was related to expansion no VS was observed. The retrolateral sclerite (RS) is of two types, a shallow, pocket- like invagination as in *T. fawcetti* **sp. nov.** (RS, Fig. 40E- F) or a distinctly separated, oval sclerite as in *T. whitei* **sp. nov.** (RS, Figs. 51D- E).

The retrolateral tibial spine (RTS) is recurved to straight and ranges from short, occupying less than half the length of the palpal tarsus (RTS, Figs. 31A- B, D, 32A- B, 36F), to elongate in which the spine extends greater than half the length of the palpal tarsus (RTS, Figs. 31C, F, 32C, F). The RTS is situated on a shallow to pronounced base and is moveable, possibly serving as a positioning structure during mating. A fine, comb-like sculpturing extends along the entire length of the RTS in most species, but may also be smooth near the base as in *T. fawcetti* **sp. nov.** (Fig. 32D) and *T. devia* (Fig. 32B). Between three and four flattened setae are located near the base of the RTS (Figs. 32A- F) along with several unmodified setae surrounding the base.

Careful examination of female genitalia using compound microscopy revealed relatively little variation among species, and in most cases female specimens appear nearly identical in structural details (Figs. 52- 54). The preparation of female genitalia was problematic as the weakly sclerotized spermathecal stalks do not remain in a fixed position and slight differences in orientation can dramatically alter the structure's appearance. Even with careful preparation techniques the vulva is difficult to precisely position for comparison among individuals. The atrium is suboval to triangular and covered in fine pores. The spermathecal stalks are twisted and connect to the atrium basally via short sclerotized tubes. The spermathecal heads are swollen, circular (Figs. 52A, C- F, 53A- B, D- F, 54A- C, E) to elongate (Figs. 53C, 54D), and covered in fine pores.

Phylogeny

Results of phylogenetic analyses follow Ledford et al. (in prep) and summary statistics for each analysis are presented in Table 2. Phylograms for concatenated analyses (Bayesian, maximum likelihood, parsimony) are presented in Figures 4- 6 and independent gene trees are in Figures 7- 9. Nodes with a posterior probability of 95% and greater are considered supported and all remaining nodes are collapsed. Nodes for maximum likelihood and parsimony analyses with bootstrap support values of 75% and greater are considered supported and all remaining nodes are collapsed.

Tree topologies are identical to Ledford et al. (in prep) and few instances of conflict are observed. *Tayshaneta* monophyly is corroborated by all analyses although its relationship to other North American leptonetid genera is ambiguous (Figs. 4- 9). Eight described species are represented in the analyses, including *T. anopica* (Gertsch, 1974), *T. bullis* (Cokendolpher, 2004), *T. coeca* (Chamberlin and Ivie, 1942), *T. concinna* (Gertsch, 1974), *T. devia* (Gertsch, 1974), *T. microps* (Gertsch, 1974), *T. myopica* (Gertsch, 1974), and *T. paraconcinna* (Cokendolpher and Reddell, 2001). Five undescribed species are also represented, *T. fawcetti* **sp. nov.** (Figs. 19, 40), *T. madla* **sp. nov.** (Figs. 21, 42), *T. oconnori* **sp. nov.** (Figs. 24, 45), T. *sandersi* **sp. nov.** (Figs. 26, 47), and *T. whitei* **sp. nov.** (Figs. 30, 51), each of which has diagnostic morphology.

Four clades recovered by analyses are identified as species groups in the discussion: 1) the *anopica* group, consisting of *T. anopica* + *T. concinna* (Node A), 2) the *myopica* group, consisting of *T. myopica* + *T. paraconcinna* (Node B), 3) the *microps* group, consisting of *T. microps* + *T. madla* (Node C), and 4) the *sandersi* group, consisting of *T. sandersi* **sp. nov.** + *T. whitei* sp. nov (Node D). Although conflict among trees is limited, the resolution among three species (*T. bullis, T. coeca, T. devia*) in concatenated analysis differs with results from independent analysis of COI and 28s rDNA. In both gene trees, *T. devia* is supported (Node E, Fig. 7) and in the COI tree a sister group relationship is recovered with *T. coeca* (Node F, Fig. 7). Furthermore, the COI tree supports *T. bullis* as sister to the *microps* species group (Node G, Fig. 7). However, *T. devia* is not supported by concatenated analyses and relationships among *T. coeca* and *T. bullis* are unresolved.

Discussion

Among the most interesting result of the phylogenetic analyses is the contrast in branch lengths between *Tayshaneta* and the remaining North American genera (Figs. 4- 6). Although sampling and rate variation among genes (Figs. 7- 9) are known to affect branch lengths, the close relationships, morphological similarity, and narrow geographic distributions of *Tayshaneta* suggest that it is a relatively recent radiation of species. Similar radiations are known for *Cicurina* spiders (Paquin and Dupérré, 2009; Paquin and Hedin, 2004) and *Texella* harvestmen (Ubick and Briggs, 1992, 2004) both of which show similar biogeographic patterns and affinity for caves. Recent work has shown that the diversification patterns of *Cicurina* is correlated with the complex faulting in the region (White et al., 2009) and may serve as a general model to explain the diversity of the Texas cave fauna. On-going work has been directed at synthesizing the distributions for multiple cave invertebrates in order to develop a comprehensive understanding of the Texas fauna (Reddell et al., in prep).

Although most *Tayshaneta* species have relatively conserved genitalic morphology, intraspecific variation in somatic features related to cave life (troglomorphism) is extreme and often includes a range of eye and pigment reduction. In *T. myopica*, for example, multiple morphotypes are often found within a narrow geographic distribution and range from darkly pigmented, large- eyed individuals (Figs. 55E- F) to lightly pigmented, reduced- eyed forms (Fig. 55A- C), to complete eye and pigment loss (Fig. 55D). While these differences likely indicate varying degrees of local adaptation to caves, the intergradient morphologies observed suggest that some species may have an adaptive cline from surface to cave- adapted morphotypes. Similar patterns of troglomorphic variation have been reported in *Texella* harvestmen that show multiple degrees of troglomorphic morphology between closely related species (Ubick and Briggs, 1992, 2004). In *T. reddelli* and *T. reyesi* for example, species limits are often indistinct as specimens show a gradual reduction in eyes, pigment, and tubercles on the carapace. One intriguing hypothesis is that populations are actively colonizing caves and becoming increasingly more troglomorphic, similar to the adaptive shift model proposed for Hawaiian isopods (Rivera et al., 2002).

Biogeographic relationships within *Tayshaneta* reflect the fragmented geology of region as distributions are allopatric and few cases of sympatry are known. However, distributions for most species remain poorly characterized and reflect incomplete sampling, especially of surface localities, which are rarely inventoried as part of cave surveys. Species distributions in Bexar and Travis counties are particularly complex, and several undetermined records (Fig. 61) likely represent range extensions or additional species, the identification of which will help resolve areas of taxonomic ambiguity. The most significant area of biogeographic ambiguity are caves and surface habitats in Comal and Hays Counties both of which remain poorly inventoried and are essential to resolving species limits, especially between *T. coeca* (Chamberlin and Ivie, 1942) and *T. devia* (Gertsch, 1974).

The majority of species described by Gertsch (1974) were known from single localities and was used as the primary justification for the endangered status of *T. microps* (Gertsch, 1974) and *T. myopica* (Gertsch, 1974) (U. S. Fish and Wildlife, 1994, 2000). Recent sampling efforts, combined with the molecular and morphological data presented in this study, have shown that most species are more broadly distributed than expected but still of limited distribution. Furthermore, molecular data suggest that most troglobitic species are actively using subterranean microfissures and voids as corridors for dispersal between caves. The most striking examples are for the species *T. anopica* (Gertsch, 1974), *T. myopica* (Gertsch, 1974), and *T. sandersi* **sp. nov.** each of which have populations in different caves that share identical haplotypes for the loci surveyed in this study. While these connections are not surprising given the geology of the area, they set a precedent for interpreting the distribution of other *Tayshaneta* species and are likely to effect conservation and management decisions.

Karst Faunal Regions

Karst faunal regions (KFR's) were originally developed as tools to aid the recovery of endangered karst invertebrates by identifying geologically independent regions that had a relatively high proportion of endemic species (Veni, 1992, 1994). Although an evolutionary model was not explicitly proposed, the inherent reasoning is that the present distribution of the karst invertebrate fauna can be explained by the fragmented geology of the region (White and Carothers, 2001). Although recent work has shown that phylogenetic divergence within *Cicurina* spiders is likely correlated with faulting, the distributions of most invertebrate groups are poorly understood which precludes a synthesis of biogeographic patterns in the area. Furthermore, the endemicity index used to help define KFR's is necessarily constrained by existing taxonomy, most of which is inadequately resolved or erroneous (Paquin and Dupérré, 2009).

While the distribution of *Tayshaneta* is broader than anticipated, it is nevertheless highly restricted, especially when compared to other endangered invertebrate groups. *Cicurina* and *Texella,* for example, have highly active hunting lifestyles and are known to occur in far more caves. In contrast, *Tayshaneta* are far more sedentary, spending most of their lives in webs with the exception of males that may leave the web upon maturity. Not surprisingly, the distribution of most *Tayshaneta* species closely corresponds to established KFR's. In Bexar County, *T. microps* is restricted to the Government Canyon KFR (Fig. 63) and despite extensive sampling no additional populations have been discovered. *T. madla* **sp. nov.** and *T. whitei* sp nov., however, occur in multiple KFR's and although are not currently listed as endangered show that KFR's are not biologically exclusive as presently defined. *T. myopica* (Fig. 62) shows a similar pattern in Travis County, where most populations are known from the Jollyville KFR as well as in the McNeil/ Round Rock KFR.

Following the arguments of White and Carothers (2001), the presentation of this data is not designed to be a critique of the KFR strategy but rather highlights that the geological complexity and phylogenetic histories of invertebrates in the region make the delineation of boundaries a daunting task. From a conservation perspective, the use of KFR's have been successful at acquiring new cave habitat and establishing karst preserves, both of which are essential to the long- term protection of the karst invertebrate fauna. As recovery plans, local initiatives, and monitoring continue to develop in the region taxonomic studies that integrate all available data will be essential to the successful implementation of the KFR conservation strategy.

Taxonomy

Key to species of *Tayshaneta*

The key presented here relies heavily on fine details of the male and female genitalia, some features of which are not visible using conventional light microscopy or without special preparation techniques. Scanning electron and compound light microscopy is essential for positive identification and the females of most species are not diagnosable in the absence of associated males.

1. Palpal tarsus tapering apically, rarely with weak division (Figs. 31A- C); embolus rounded to rectangular, retrolateral sclerite absent; females with round spermathecal heads (Figs. 52A- F, 53A, D- F, 54A- C, E) … 2
Note. The division of the palpal tarsus in some species is very weak and often appears entire except under high magnification (Fig. 31F).

Palpal tarsus with strong apical division (Figs. 31D- F); ventral sclerite present, retrolateral sclerite pocket- like; females usually with elongate spermathecal heads (Figs. 53B- C; 54D) … 15

2. Bulb bearing a prominent ventral sclerite (VS, Figs. 33, 37, 44- 48); embolus rounded to sculptured along margin, with or without a large basal tooth or fold (Figs. 33, 37, 45, 47) … 3

Bulb lacking a ventral sclerite (Figs. 34- 36, 38, 42- 43, 51); embolus rounded to distinctly sculptured along margin, with or without a small basal tooth (Figs. 42- 43, 51) … 9

3. Ventral sclerite elongate (VS, Figs. 44E, 46E) to greatly reduced (VS, Fig. 48E); embolus rounded and spoon- shaped (E, Figs. 44D, 46D) to suboval (E, Fig. 48D), lacking sculpture along margin … 4

Ventral sclerite elongate; embolus shape irregular, with sculpture, bifurcation, or large basal tooth along margin (E, Figs. 33 D, 37D, 45D, 47D) … 6

4. Ventral sclerite short, occupying less than width of the embolus (VS, Figs. 48B, D- F); retrolateral tibial spine elongate, straight to slightly curved, at least 0.50x tarsus length; embolus suboval, flush with apical portion of bulb (E, Fig. 48D- F) … *T. sprousei* **sp. nov.**
Dist. Known from two caves on Camp Bullis, Bexar County, Texas (Fig. 59).
Note. Females for this species are unknown.

Ventral sclerite elongate, occupying at least 0.50x length of apical portion of bulb (VS, Figs. 44E, 46E); retrolateral tibial spine recurved, short, occupying much less than 0.50x length palpal tarsus (RTS, Figs. 32A, 44A, 46A); embolus spoon shaped, apically extended beyond bulb (E, Figs. 44E, 46E) … 5

5. Base of embolus sharply curved, projecting ventrally (Fig. 44D); embolus u- shaped and folded over apical portion of bulb (E, Fig. 44E); retrolateral tibial spine weakly recurved, on elevated base (RTS, Fig. 31A, 32A); eyes and pigmentation variable, but usually greatly reduced (Figs. 23A- F); large, thin spiders, length femur I 1.5- 2.0x carapace length … *T. myopica* (Gertsch, 1974)
Dist. Caves of Travis and Williamson counties, Texas (Fig. 57).
Notes. *T. myopica* and *T. paraconcinna* are difficult to separate and require close inspection of subtle genitalic characters, preferably using scanning electron microscopy. In several cases, particularly in Williamson County, these species are only reliably diagnosed using a combination of genitalic morphology and molecular data.

Embolus weakly curved at base, projecting anteriorly, often with an apical cleft (E, Fig. 46D); ventral sclerite sharply recurved, pick- like, on short base (RTS, Fig. 46A); eyes and pigmentation variable, but usually darkly pigmented with well- developed eyes (Figs. 25A- F); short, robust spiders, length femur I 1.2- 1.5x carapace length … *T. paraconcinna* (Cokendolpher and Reddell, 2001)
Dist. Broadly distributed in caves and surface habitats from Bell County South through Williamson, Travis, and Blanco Counties (Fig 57).

6. Depigmented, blind spiders (faint eyespots may be present under high magnification), length femur I at least 1.90x carapace length; retrolateral tibial spine short to elongate; embolus narrowly or broadly bifurcate, with or without large basal tooth … 7

Pigmented, large- eyed spiders with dark patterns surrounding the ocular area; retrolateral tibial spine short, occupying less than 0.5x length of palpal tarsus; embolus broad, with prominent basal tooth … *T. concinna* (Gertsch, 1974)
Dist. Caves and surface habitats in Travis County, Texas (Fig. 56).

7. Embolus bifurcate, with sharp lobes (E, Figs. 33D, 47D); ventral sclerite positioned retrolaterally, base indistinct; retrolateral tibial spine short to elongate … 8

Embolus bifurcate, with rounded lobes (E, Fig. 45D); ventral sclerite positioned mesally, on distinct base (VS, Fig. 45E); retrolateral tibial spine short, occupying less than 0.5x length tarsus … *T. oconnori* **sp. nov.**
Dist. Known from two caves in Southern Hays County, Texas (Fig. 58).

8. Embolus broad, with distinct basal tooth (E, Fig. 33D); ventral sclerite straight; retrolateral tibial spine elongate, occupying at least 0.50x length of palpal tarsus … *T. anopica* (Gertsch, 1974)
Dist. Known from two caves in Northern Williamson County, Texas (Fig. 56).

Embolus narrow, bifurcate (E, Fig. 47D); ventral sclerite prolaterally curved (VS, Fig. 47E); retrolateral tibial spine short, occupying less than 0.5x length of palpal tarsus … *T. sandersi* **sp. nov.**
Dist. Known from three caves in the Onion Creek watershed of Barton Springs, Travis County, Texas (Fig. 56).

9. Embolus oval to rectangular, lacking basal tooth, and with minimal sculpture along margins (E, Figs. 34- 36, 38); retrolateral tibial spine short to elongate, recurved or straight … 10

Embolus oval to rectangular, with prominent basal tooth (E, Figs. 42, 43, 51); retrolateral tibial spine elongate, occupying at least 0.50x length of the palpal tarsus … 13

10. Embolus oval or tapering apically (E, Figs. 34D, 38D), flush or extended beyond apical portion of bulb (Figs. 34B, 38B); retrolateral tibial spine short, occupying less than 0.50x length of palpal tarsus … 11

Embolus rectangular to gently curved along its base, flush with apical portion of bulb; retrolateral tibial spine short to elongate … 12

11. Eyes reduced, lacking pigmentation near ocular area (Figs. 13A- F); femur I 1.35-1.75x carapace length; embolus rectangular to oval, not tapering apically (E, Fig. 34D), retrolateral tibial spine sculptured along its entire length (RTS, Fig. 34A) … *T. archambaulti* **sp. nov.**
Dist. Known from two caves in Southern Hays County, Texas (Fig. 58).

Eyes large and darkly pigmented near ocular area (Figs. 17A- E); femur I 1.0- 1.3x carapace length; embolus tapering apically, extending beyond apical portion of bulb (E, Fig. 38D); retrolateral tibial spine stout, distinctly lacking sculpture along its base (RTS, Figs. 31B, 32B) … *T. devia* (Gertsch, 1974)
Dist. Known from caves and surface habitats in Southern Williamson through Travis Counties, Texas (Fig. 56).

12. Embolus rectangular, folded apically (E, Figs. 35D- F); retrolateral tibial spine elongate, occupying at least 0.50x length of the palpal tarsus (RTS, Fig. 35A) … *T. bullis* (Cokendolpher, 2004).
Dist. Known from two caves on Camp Bullis, Bexar County, Texas (Fig. 59).

Embolus rectangular and gently curved along its base (E, Fig. 36D); retrolateral tibial spine short, occupying less than 0.50x length of palpal tarsus (RTS, Fig. 36F) … *T. coeca* (Chamberlin and Ivie, 1942).
Dist. Known from caves and surface habitats in Hays through Comal Counties, Texas (Fig. 58).

13. Eyes and pigmentation variable, greatly reduced in one species (Figs. 22A- F, 30A- F); palpal tarsus tapering apically (Figs. 31A- C); femur I 1.3- 1.9x carapace length; embolus with small basal tooth, rounded to quadrate apically (E, Figs. 43D, 51E) … 14

Eyes large and darkly pigmented near ocular area (Figs. 21A- C); palpal tarsus weakly divided apically (TS, Fig. 31F); femur I 1.3- 1.7x carapace length; embolus with large basal tooth, rounded at apex (E, Fig. 42D)… *T. madla* **sp. nov.**
Dist. Known from caves and surface habitats in Bexar County, Texas (Fig. 59).

14. Eyes and pigment greatly reduced, only faint eyespots present (Figs. 10A- B, 22A- F); embolus distinctly rounded at apex (E, Fig. 43D) … *T. microps* (Gertsch, 1974)
Dist. Known only from Government Canyon Bat Cave, Bexar County, Texas (Fig. 58).

Eyes and pigment normal, with dark marking surrounding ocular area (Figs. 30A- F); retrolateral sclerite present, distinctly separated from bulb (RS, Figs. 51D- E); embolus quadrate, curved apically (E, Fig. 51D) … *T. whitei* **sp. nov.**
Dist. Known from caves in Bexar and Medina Counties, Texas (Fig. 59).

15. Embolus with distinctive basal tooth, shape rectangular to bifurcate (E, Figs. 40F, 49D) … 16

Embolus smooth along margins, shape oval to subquadrate, with weakly developed basal swelling or absent (E, Figs. 39D, 41D, 50D)… 18

16. Eyes and pigment greatly reduced (Figs. 19A- F), femur I 1.60- 1.83x carapace length; embolus rectangular, with distinctive basal tooth (E, Fig. 40F); retrolateral tibial spine short, smooth at base (RTS, Figs. 40A, D); female genitalia with elongate spermathecal heads (SH, Fig. 53C) … *T. fawcetti* **sp. nov.**

Dist. Known only from Fawcett's Cave in the Devil's River State Natural Area, Val Verde County, Texas (Fig. 60).

17. Eyes and pigment variable (Figs. 28A- F), femur I 1.40- 1.50x carapace length; embolus with large basal tooth and distinctive fold (E, Fig. 49D); retrolateral tibial spine elongate, sculptured along its length (RTS, Fig. 49A); female genitalia with circular spermathecal heads (SH, Fig. 54C) … *T. valverdae* (Gertsch, 1974).
Notes. Known from caves and surface habitats in Bandera, Uvalde, and Val Verde Counties, Texas (Fig. 60).

18. Embolus oval, with or without apical fold (E, Figs. 41D, 50D); ventral sclerite reduced or bifurcate apically (VS, Figs. 41E, 50D- F)… 19

Embolus rectangular, tapering apically, with weak basal swelling (E, Fig. 39D); ventral sclerite stout (VS, Fig. 39E); females with large, circular spermathecal heads (SH, Fig. 53B) … *T. emeraldae* **sp. nov.**
Dist. Known only from Emerald Sink, in Western Val Verde County, Texas (Fig. 60).

19. Eyes and pigment reduced (Figs. 29A- C), femur I 1.57- 1.84x carapace length; ventral sclerite with distinctive division apically (VS, Figs. 50D- F); embolus elongate, oval, and without apical fold (E, Fig. 50D); female genitalia with elongate spermathecal heads (SH, Fig. 54D) … *T. vidrio* **sp. nov.**
Dist. Known only from 400ft. Cave, Brewster County, Texas (Fig. 60).

Ventral sclerite reduced (VS, Fig. 41E); embolus oval with distinctive apical fold (E, Fig. 41D) … *T. grubbsi* **sp. nov.**
Dist. Known only from Litterbarrel Cave, Val Verde County, Texas (Fig. 60).

Tayshaneta Ledford et al., in prep

Leptoneta Simon, 1872; Chamberlin and Ivie, 1942; Gertsch, 1974.
Neoleptoneta Brignoli, 1972; Brignoli, 1977; Platnick, 1986; Cokendolpher and Reddell, 2001; Cokendolpher, 2004; Ledford et al., in prep.

Type species. *Leptoneta coeca* Chamberlin and Ivie, 1942.
Nomen dubia. *Leptoneta furtiva* (Gertsch, 1974) is described based on a single female specimen from Blackwell, Nolan County, Texas. The holotype is in poor condition, missing most of its appendages and genitalia. Efforts to recollect the species at the type locality have proven unsuccessful and the lack of diagnostic features prevents its diagnosis from any other *Tayshaneta* species. *Leptoneta uvaldea* (Gertsch, 1974) was described from Story Cave, Uvalde County, Texas based on a single female specimen. While the holotype is in good condition, the genitalia are damaged and it cannot be separated from any other *Tayshaneta* species. Furthermore, the type locality, Story Cave, is widely recognized as a lost cave somewhere on the Marneldo Ranch (A. Gluesenkamp, pers. comm.). Given their lack of diagnostic features, both species are declared *nomen dubia* until additional specimens near the type localities can be obtained.

Diagnosis. *Tayshaneta* is separated from all other leptonetids by having males with a recurved to straight retrolateral spine on the palpal tibia (Figs. 32A- F) and females with short spermathecal stalks bearing large circular to oval heads (Figs. 52- 54).
Synapomorphies. Species of *Tayshaneta* are united by the unique conformation of the female genitalia, with short spermathecal stalks bearing large heads (Figs. 52- 54) and the recurved to straight retrolateral spine on the male palpal tibia (Figs. 32A- F).
Description. Total length 1.0- 1.98. Carapace depigmented to orange- brown; oval and covered by fine, irregular sculpturing which refracts light producing a distinctive iridescence (Figs. 10A, C), sparsely setose, length 0.88- 1.8x width. Eyes present, reduced, or absent with the PME displaced posteriad of the AEG (Fig. 10B), elevated to flattened in lateral profile (Fig. 10E); chelicerae free and with lateral stridulatory file (Fig. 10E). Sternum triangular to subquadrate (Fig. 10D); abdomen pale yellow to dark brown, lacking distinctive pattern. Colulus triangular, ALS cylindrical, PMS and PLS comb- like, with a linear row of 6- 10 aciniform gland spigots (Figs. 11A- C). Legs elongate and thin, femur I 1.0- 2.26x carapace length; formula I, IV, II, III, covered in fine setae and with few scattered spines; patellar and tibial glands triangular with single, large pores; metatarsus III with ventroapical preening comb. Male palpal tarsus divided or tapering apically, with a middorsal division (Figs. 31A- F); tibia with a single recurved to straight retrolateral spine on an elevated base surrounded by elongate setae and 2- 4 paddle- shaped setae (Figs. 32A- F); palpal bulb oval, longer than wide, with an apically situated embolus (E, Figs. 33- 51) and an oval prolateral lobe (PL, Figs. 33- 51); ventral sclerite present (VS, Figs. 33, 37, 39- 41, 44- 50) or absent (Figs. 34- 36, 38, 42- 43, 51), consisting of a single spine; retrolateral sclerite present or absent, curved and weakly invaginated to oval (RS, Figs. 39- 41, 49- 50) or distinctly separated from the bulb (RS, Fig. 51); tarsal organ circular, shallow, and with a pair of receptors. Female genitalia (Figs. 52- 54) consisting of a single oval to triangular atrium with a pair of lateral spermathecae bearing large, circular (Figs. 52A, C- F; 53A- B, D- F; 54A- C, E) to elongate heads (Figs. 53C, 54D) that are covered in fine pores.
Composition. Nineteen species, ten of which are described in this paper:
T. anopica (Gertsch, 1974), *T. archambaulti* **sp. nov.**, *T. bullis* (Cokendolpher, 2004), *T. coeca* (Chamberlin and Ivie, 1942), *T. concinna* (Gertsch, 1974), *T. devia* (Gertsch, 1974), *T. emeraldae* **sp. nov.**, *T. fawcetti* **sp. nov.**, *T. grubbsi* **sp. nov.**, *T. madla* **sp. nov.**, *T. microps* (Gertsch, 1974), *T. myopica* (Gertsch, 1974), *T. oconnori* **sp. nov.**, *T. paraconcinna* (Cokendolpher and Reddell, 2001), *T. sandersi*, **sp. nov.**, *T. sprousei* **sp. nov.**, *T. valverdae* (Gertsch, 1974), *T. vidrio* **sp. nov.**, *T. whitei* **sp. nov.**
Distribution. Central to West Texas (Figs. 3, 56- 61).

***Tayshaneta anopica* (Gertsch, 1974)**

Leptoneta anopica Gertsch, 1974: 172.
Neoleptoneta anopica (Gertsch, 1974): Brignoli, 1977: 216; Platnick, 1986: 6; Platnick, 2010.
(Figs. 1A, 2D, 12A- F, 33A- F, 52A- B, 56)

Type data. Female holotype from Cobb Cave, 15 miles N. Georgetown, Williamson County, Texas, 31-Mar-1963, J. Reddell, D. McKenzie, 30.78N, 97.73W, (AMNH, examined).

Notes. Cobb Cave is also known as Cobb's Caverns and is located on the Cobb Ranch in Northern Williamson County (Figs. 1A, 55). The general area of Cobb's Spring has a long history of occupation by Indians who likely discovered the cave thousands of years ago (K. White, pers. comm.). The cave was first reported by the National Speleological Society in 1948 (NSS, 1948) and briefly operated as a commercial cave from 1962 to 1969.

Other Material Examined. USA: Texas: **Williamson County:** Cobb's Caverns, 15mi. N. Georgetown, 30-March-2004, M. Warton, 30.78N, 97.73W, 1MM, (TTU); Cobb's Caverns, 15mi. N. Georgetown, 12-October-2004, K. White, 30.78N, 97.73W, 1FF, (TMM); Cobb's Caverns, 15mi. N. Georgetown, 24-November-2004, P. Paquin, 30.78N, 97.73W, 1FF, (TMM); Cobb's Caverns, 15mi. N. Georgetown, 7-September-2007, P. Paquin, 30.78N, 97.73W, 1MM, (TMM); Cobb's Caverns, 15mi. N. Georgetown, 10-December-2009, P. Paquin, C. Crawford, 30.78N, 97.73W, 3 JJ, (TMM); Corn Cobb's Cave, 17-July-2008, M. Archambault, J. Ledford, P. Paquin, 30.75N, 97.73W, 1FF, (TMM); Corn Cobb's Cave, 15-October-2008, P. Paquin, Parker, Baird, 30.75N, 97.73W, 1FF, (TMM); Corn Cobb's Cave, 31-October-2008, P. Paquin, Crawford, Parker, 30.75N, 97.73W, 1FF, (TMM).

Diagnosis. *T. anopica* may be separated from all *Tayshaneta* species that have a ventral sclerite and an undivided male palpal tarsus, except *T. concinna, T. oconnori*, and T. *sandersi*, by the following combination of characters: pigmentation and eyes entirely absent (Figs. 12A- B); femur I elongate, 1.7- 2.3x carapace length; male retrolateral tibial spine thin, sculptured throughout, length 0.50x tarsus length (Fig. 33A); embolus curved distally and with prominent basal tooth (E, Fig. 33D). Separated from *T. concinna*, *T. oconnori*, and T. *sandersi* by having a straight ventral sclerite (VS, Figs. 33B, E) and by the unique shape of the embolus (E, Fig. 33D).

Description. Complete description of female in Gertsch (1974: 172). Habitus of female in Figs. 12D- F, genitalia as in Fig. 52A, and images of eggsac in Figs. 2D, 52B.

Male (Cobb's Caverns). Body length 1.38, carapace 0.62 long, 0.45 wide, length 1.36x width. Carapace depigmented to light brown, eyes absent, sparsely setose (Figs. 12A- C). Legs elongate and thin, femur I 2.0x carapace length, covered in fine setae. Palpal tarsus entire, tapering apically; retrolateral tibial spine straight, on shallow base, sculptured throughout, length 0.50x tarsus length (RTS, Fig. 33A). Bulb suboval, length 1.84x width; embolus circular, with prominent basal tooth (E, Fig. 33D), length 1.17x width. Abdomen pale to yellow- brown, without pattern, 0.76 long, 0.54 wide, covered in fine setae.

Variation (*n* = 2). Total length 1.25- 1.38; carapace length 1.19- 1.36 x carapace width; length femur I 2.0- 2.2 x carapace width.

Distribution. Known only from two caves in Williamson County, Texas (Figs. 1A, 56). Cobb's Caverns is the largest known cave in the area, however, several smaller karst features occur on the property including Corn Cobb's Cave (K. White, pers. comm.). The records of *T. anopica* from Corn Cobb's Cave suggest that it may be more broadly distributed in the Cobb's Spring region.

Natural History. An eggsac for this species was found with a female specimen from Corn Cobb's cave (Figs. 2D, 52B). The eggsac was found hanging by a single thread covered with small pebbles and contained two eggs.

Tayshaneta archambaulti, new species

(Figs. 13A- F, 34A- F, 52C, 58)

Type data. Male holotype from Grapevine Cave, 7 miles West Wimberly, Hays County, Texas, 18-Nov-2009, J. Ledford, K. O'Connor, 30.04N, 98.22W, (CASC).
Etymology. This species is named in honor of Martin Archambault, fellow caver and friend who helped collect many leptonetids in Texas and Mexico.
Other Material Examined. USA: Hays County: Burnett Ranch Cave, 7mi. W. of Wimberly, 1982, A. Grubbs, 30.02N, 98.21W, 1MM, 2FF, 3JJ (AMNH); Grapevine Cave, 7mi. West of Wimberly, 26-May-1989, A. Grubbs, 30.04N, 98.22W, 1MM (AMNH); Grapevine Cave, 7mi. West of Wimberly, 23-April-1995, A. Grubbs, Vreeland, 30.04N, 98.22W, 1MM, 1FF, 5JJ, (TMM); Grapevine Cave, 7mi. West of Wimberly, 18-November-2009, J. Ledford, K. O'Connor, 30.04N, 98.22W, 4MM, 5FF, 7JJ, (TMM).
Diagnosis. *T. archambaulti* can be separated from all *Tayshaneta* species that lack a ventral sclerite, except *T. coeca* and *T. devia*, by the following combination of characters: embolus oval to quadrate, lacking sculpture along its margin (E, Fig. 34D); retrolateral tibial spine short, occupying less than 0.50x the length of the palpal tarsus (RTS, Fig. 34A). Separated from *T. devia* by having a retrolateral tibial spine with sculpture along its entire length and from *T. coeca* by having the embolus curved distally and extending beyond the apical portion of the bulb (E, Fig. 34E).
Description. Male (holotype)**.** Body length 1.35, carapace 0.64 long, 0.56 wide, length 1.13x width. Carapace light brown, eyes reduced, sparsely setose (Figs. 13A- F). Legs elongate and thin, femur I 1.5x carapace length, covered in fine setae with few scattered spines. Palpal tarsus entire, tapering apically; retrolateral tibial spine weakly recurved, on weakly elevated base, sculptured throughout, length 0.32x tarsus length (RTS, Fig. 34A). Bulb suboval, length 1.71x width; embolus oval to quadrate (E, Fig. 34D), length 2.0x width. Abdomen pale to yellow- brown, without pattern, 0.70 long, 0.54 wide, covered in fine setae.
Variation (*n* = 4). Total length 1.34- 1.63; carapace length 0.88- 1.36 x carapace width; length femur I 1.35- 1.65 x carapace width.
Female (paratype). Body length 1.32, carapace 0.63 long, 0.51 wide, length 1.25x width. Pigmentation and setation same as for male (Figs. 13D- F). Legs elongate and thin, femur I 1.34x carapace length, covered in fine setae with few scattered spines. Atrium oval, length 0.51x width, spermathecae with twisted stalks and large, circular heads (Fig. 52C). Abdomen pale to yellow- brown, without pattern, 0.69 long, 0.54 wide, covered in fine setae.
Variation (*n* = 4). Total length 1.32- 1.72; carapace length 1.20- 1.29 × carapace width; length femur I 1.34- 1.75 × carapace width.
Distribution. This species is known only from Burnett Ranch Cave and Grapevine Cave in Southwestern Hays County (Fig. 58).
Natural History. Individuals for this species were collected throughout Grapevine cave, however, most specimens were encountered at the base of the cave's vertical entrance in the twilight area under stones. They were collected in fine sheet webs similar to other *Tayshaneta* species.

Tayshaneta bullis (Cokendolpher, 2004)

Neoleptoneta bullis Cokendolpher, 2004: 65.
(Figs. 14A- F, 35A- F, 52D, 59)

Type data. Male holotype from Up the Creek Cave, Camp Bullis, Bexar County, Texas, 10-September-1998, J. Cokendolpher, J. Reddell, J. Krejca, M. Reyes, 29.63N, 98.55W, (AMNH, examined).
Notes. Two female specimens from Hills and Dale's Pit are tentatively assigned to this species based on the similarity of the female genitalia and by having identical COI and 28s rDNA sequences to specimens collected in Up the Creek Cave.
Other Material Examined. USA: Texas: **Bexar County:** Up the Creek Cave, Camp Bullis, 30-March-1995, J. Cokendolpher, J. Reddell, M. Reyes, J. Krejca 29.63N, 98.55W, 4FF, (TMM); Up the Creek Cave, Camp Bullis, 5-October-1995, J. Cokendolpher, J. Reddell, M. Reyes, J. Krejca, 29.63N, 98.55W, 1MM, 3FF, (TMM); Up the Creek Cave, Camp Bullis, 5-October-1995, J. Cokendolpher, J. Reddell, M. Reyes, J. Krejca, 29.63N, 98.55W, 1MM, 1FF, (CASC); Up the Creek Cave, Camp Bullis, 5-October-1995, J. Cokendolpher, J. Reddell, M. Reyes, J. Krejca, 29.63N, 98.55W, 1MM, 1FF, (TTU); Up the Creek Cave, Camp Bullis, 14-November-1995, J. Cokendolpher, J. Reddell, M. Reyes, J. Krejca, 29.63N, 98.55W, 1MM, (TTU); Up the Creek Cave, Camp Bullis, 10-September-1998, J. Krejca, J. Reddell, M. Reyes, 29.63N, 98.55W, 2MM, 2FF, 2 JJ, (TTU); Up the Creek Cave, Camp Bullis, 4-November-1998, J. Krejca, J. Reddell, M. Reyes, 29.63N, 98.55W, 2MM, 1FF, (TTU); UTSA Area, Hills and Dale's Pit, 28-October-2000, K. White, H. Bechtol, 29.59N, 98.63W, 1FF, (TTU); Up the Creek Cave, Camp Bullis, 16-January-2002, J. Krejca, Engelhard, Schuman, 29.63N, 98.55W, 1MM, 1FF, (TTU); Up the Creek Cave, Camp Bullis, 6-August-2008, P. Sprouse, 29.63N, 98.55W, 1FF, (TMM).
Diagnosis. *T. bullis* can be separated from all other *Tayshaneta* species that lack a ventral sclerite by having an elongate retrolateral tibial spine at least 0.5x the length of the palpal tarsus (RTS, Fig. 35A) and a distinctly quadrate shaped embolus (E, Fig. 35D).
Description. Complete description in Cokendolpher (2004: 65). Habitus of male and female in Figs. 14A- F, scanning electron micrographs of male palp in Figs. 35A- F, and female genitalia in Fig. 52D.
Distribution. Known from two caves in Bexar County, Up the Creek Cave on Camp Bullis and Hills and Dale's Pit (Fig. 59).
Natural History. Cokendolpher (2004) reported on the shape of the eggsac for this species along with details on their general biology. The eggsac was covered in small pebbles or detritus similar to that reported for *T. anopica* (Fig. 2D, 53B). Females were observed to retain sperm for several months and the eggsacs contained few, relatively large eggs.

Tayshaneta coeca (Chamberlin & Ivie, 1942)

Leptoneta coeca Chamberlin and Ivie, 1942: 10; Gertsch, 1974: 170.
Neoleptoneta coeca (Chamberlin and Ivie, 1942): Brignoli, 1977: 216; Platnick, 1986: 7; Cokendolpher, 2004: 64.
(Figs. 15A- F, 36A- F, 52E, 58)

Type data. Male holotype from Heidrich's Cave, New Braunfels, 20-June-1938, Comal County, Texas, 20-June-1938, 29.70N, 98.10W, (AMNH, formerly in the University of Utah collection, examined).

Notes. Heidrich's Cave was the name used by Chamberlin and Ivie (1942) for Brehmmer Cave in the original description of the species (Reddell and Cokendolpher, 2004). Gertsch (1974) considered specimens from Natural Bridge Caverns as conspecific with *T. coeca*, however, no illustrations or diagnostic details were provided. Female specimens from Natural Bridges Caverns show similar somatic morphology and genitalia, but cannot be confidently determined in the absence of associated males. While male specimens are reported in Gertsch (1974) they were not located in collections. Given its proximity to the type locality, and morphological similarity the specimens are tentatively maintained as conspecific. In several cases, specimens of *T. devia* were difficult to separate from *T. coeca* except by the fine details of the retrolateral tibial spine and embolus. Given the geographic disjunction between populations in Comal and Williamson counties, additional sampling is required in these area, especially on the surface, in order to refine species limits.

Other Material Examined. USA: Texas: **Comal County:** Brehmmer Cave (=Heidrich's Cave), 5mi. W. New Braunfels, 19-March-1960, W. Gertsch, W. Ivie, Schrammel, 29.70N, 98.10W, 1MM, 1FF, (AMNH); Coreth Bat Cave, 28-October-1995, J. Reddell, M. Reyes, 1MM, 1FF, 1JJ, (TMM); Coreth Bat Cave, 28-October-1995, J. Reddell, M. Reyes, 1MM, 1FF, (TTU); Guadeloupe River, 19-November-2004, P. Paquin, 29.81N, 98.17W, 3FF, (CASC); Natural Bridge Caverns, 13mi. W. New Braunfels, 23-February-1963, O. Knox, J. Reddell, M. Reyes, 29.70N, 98.10W, 1FF, (TMM); Natural Bridge Caverns, 13mi. W. New Braunfels, 13-July-1963, J. Reddell, 29.70N, 98.10W, 2FF, 3JJ, (TMM); Natural Bridge Caverns, 13mi. W. New Braunfels, 23-September-1989, O. Knox, J. Reddell, M. Reyes, 29.70N, 98.10W, 1FF, (TMM); Natural Bridge Caverns, 13mi. W. New Braunfels, 1-March-1990, O. Knox, J. Reddell, M. Reyes, 29.70N, 98.10W, 1FF, (TTU); 7mi. W. New Braunfels, 27-January-1995, A. Grubbs, 3MM, 2FF, 1JJ (TMM); **Hays County:** Freeman Crawl, 8-August-2009, P. Sprouse, 1JJ, (TMM); Hackberry Cave, 7-May-2009, P. Sprouse, 30.01N, 97.94W, 1MM, 3JJ, (TMM); Hackberry Cave, 13-October-2009, P. Sprouse, 30.01N, 97.94W, 2MM, 2FF, 2JJ, (TMM); McCarty Cave, 14-October-2009, P. Sprouse, 29.85N, 97.99W, 1FF, 1JJ, (TMM); McGlothlin Sink, 26-May-1989, A. Grubbs, J. Reddell, M. Reyes, 29.92N, 97.94W, 1MM, 1FF, 4JJ, (TMM); Root Beard Cave, 14-March-2005, P. Paquin, 29.97N, 97.98W, 2MM, (CASC); Root Beard Cave, 7-June-2009, P. Sprouse, 29.97N, 97.98W, 2MM, 1JJ, (TMM); Wiseman's Sink No. 2, 10mi. W. San Marcos, 22-April-1995, A. Grubbs, 29.97N, 97.98W, 2FF, 4JJ, (TMM); Wiseman's Sink, 28-April-1995, A. Grubbs, 29.97N, 97.98W, 1MM, (TMM); Wiseman's Sink, 30-April-1995, A. Grubbs, 29.97N, 97.98W, 4FF, 1JJ, (TMM).

Diagnosis. *T. coeca* can be separated from other *Tayshaneta* species that lack a ventral sclerite, except *T. archambaulti* and *T. devia*, by having a short retrolateral tibial spine, occupying less than 0.5x the length of the palpal tarsus (RTS, Fig. 36F) and a rectangular embolus that lacks sculpture along its margin (E, Fig. 36D). Separated from *T. devia* by having a retrolateral tibial spine with sculpture along its entire length (RTS, Fig. 36C, F) and from *T. archambaulti* by the distinctive shape of the embolus (E, Fig. 36D).

Description. Complete description in Gertsch (1974: 170- 171). Habitus of male and female in Figs. 15A- F, scanning electron micrographs of male palp in Figs. 36A- F, and female genitalia in Fig. 52E.
Distribution. Caves and surface localities in Hays and Comal Counties (Fig. 58).

Tayshaneta concinna **(Gertsch, 1974)**

Leptoneta concinna Gertsch, 1974: 169.
Neoleptoneta concinna (Gertsch, 1974): Brignoli, 1977: 216; Platnick, 1986: 7;
Cokendolpher and Reddell, 2001: 46.
(Figs. 16A- C, 37A- F, 53F, 56)

Type data. Male holotype from Lost Gold Cave, 13 miles SW of Austin, Travis County, Texas, 27-May-1963, J. Reddell and B. Frank, 30.26N, 97.81W, (AMNH, examined).
Notes. Gertsch (1974) included a single female specimen from Stark's North Mine in Travis County as conspecific with *T. concinna* although it is unclear which characters he based this decision upon. Stark's North Mine is a unique feature in the Austin chalk formation and appears to be largely artificial, probably carved out by local residents. Recent inventories at the site have recovered additional *Tayshaneta* specimens, including adult males, which share the genitalic morphology of *T. concinna* and are recovered as part of the *concinna* clade (Clade A, Fig. 4). Given the highly disturbed nature of the habitat, it is likely that *T. concinna* also occurs on the surface. Although adult males are not available from the populations in Seibert Sink (Travis County) or County Line Bat Cave (Williamson County), molecular analyses support them as close relatives of *T. concinna* and they are tentatively assigned to the species pending the discovery of males.
Other Material Examined. USA: Texas: **Travis County:** Lost Gold Cave, 5mi. W. Austin, 3-March-1985, J. Reddell, M. Reyes, 30.26N, 97.81W, 1FF, (AMNH); Lost Gold Cave, 5mi. W. Austin, 24-November-2004, P. Paquin, 30.26N, 97.81W, 2MM, 2FF, (CASC); Seibert Sink (=Stinkin Sink), 1-January-1998, M. Sanders, 30.25N, 97.82W, 1FF, (TMM); Seibert Sink (=Stinkin Sink), 5-January-1998, M. Sanders, 30.25N, 97.82W, 2FF, (TMM, TTU); Stark's North Mine, 9mi. NNE Austin, 20-August-1963, W. Russell, 30.38N, 97.67W, 1FF, (AMNH); Stark's North Mine, 9mi. NNE Austin, 18-September-2000, J. Jenkins, 30.38N, 97.67W, 1FF, (TMM); Stark's North Mine, 9mi. NNE Austin, 21-November-2009, J. Ledford, P. Paquin, 30.38N, 97.67W, 1MM, 3FF, 1J (CASC).
Diagnosis. *T. concinna* may be separated from all *Tayshaneta* species that have a ventral sclerite, except *T. anopica*, *T.* oconnori, and T. *sandersi*, by the following combination of characters: male palpal tarsus undivided, tapering apically; male retrolateral tibial spine stout, sculptured throughout, length 0.4x tarsus length (RTS, Fig. 37B); embolus curved distally and with basal tooth (E, Fig. 37D). Separated from *T. anopica*, *T. oconnori*, and T. *sandersi* by being darkly pigmented with large eyes (Fig. 16A- C) and by the unique shape of the embolus (E, Fig. 37D).
Description. Complete description in Gertsch (1974: 169- 170). Habitus of male in Figs. 16A- C, scanning electron micrographs of male palp in Figs. 37A- F, and female genitalia in Fig. 52F.
Distribution. Known from three caves in Travis County, Texas (Fig. 54).

Natural History. Individuals collected in Stark's North Mine were found in small sheet webs at the base of chalk walls, rotting wood, and breakdown material.

Tayshaneta devia (Gertsch, 1974)

Leptoneta devia Gertsch, 1974: 171.
Neoleptoneta devia (Gertsch, 1974): Brignoli, 1977: 216; Platnick, 1986: 8.
(Figs. 17A- E, 31B, 38A- F, 53A, 56)

Type data. Female holotype from Shultz Cave, 2mi. E. Volente, Travis County, Texas, 21-August-1963, B. Russell, 30.43N, 97.86W, (AMNH, examined).
Notes. Shultz Cave is commonly referred to as MacDonald Cave and is located approximately 2.5mi. NE of Volente in Travis County. Although the male for this species was not available to Gertsch (1974), recent inventories of caves in this area have produced the first male specimens and added several new records from nearby caves. Of special interest are records from leaf litter near the entrance of Tooth Cave (type locality for *T. myopica*), approximately 2 miles south of MacDonald Cave. Although Gertsch (1974: 171- 172) originally described *T. devia* as a troglobite based on the type specimen's reduced eyes and pigment, the discovery of surface populations suggests that the species is a widespread troglophile although some populations may be locally adapted to caves. One record from Williamson County (Village Idiot Cave) is tentative as diagnostic information on the male palp is partially obscured.
Other Material Examined. USA: Texas: **Travis County:** Brewpot Sink, 19-October-2009, K. O'Connor, 30.41N, 97.85W, 3FF, 1JJ, (TMM); Hammett's Crossing, 14mi. NW Dripping Springs, 29-September-94, A. Grubbs, 30.33N, 98.13W, 1MM, 2FF, (TMM); Highway 71 and Pedernales River, 23mi. W. Austin, 20-September-94, A. Grubbs, 30.38N, 98.08W, 2MM, 6FF, 2JJ, (TMM); MacDonald Cave, 18-April-84, Pate, J. Reddell, M. Reyes, 30.43N, 97.86W, 1FF, (TMM); MacDonald Cave, 29-April-89, W. Elliot, J. Reddell, M. Reyes, 30.43N, 97.86W, 3FF, (AMNH); MacDonald Cave, 7-January-05, P. Paquin, 30.43N, 97.86W, 1FF, (CASC); MacDonald Cave, September-08, P. Paquin, 30.43N, 97.86W, 3MM, 4FF, 4JJ, (CASC); Stovepipe Cave, 25-October-90, J. Reddell, M. Reyes, 30.42N, 97.84W, 1MM, 1FF, (TMM); Stovepipe Cave, 18-September-09, K. O'Connor, 30.42N, 97.84W, 1FF, (TMM); Tooth Cave surface, 21-November-08, P. Paquin, K. O'Connor, 30.40N, 97.85W, 1MM, 3FF, (TMM); 9K-2 Cave (=Moonmilk Cave), Spicewood Springs Road, 11-February-95, Elliot, Sprouse, 30.37N, 97.76W**,** 1MM, 2FF, 1JJ, (TMM); **Williamson County:** Village Idiot Cave, 31-October-94, Warton, 30.73N, 97.83W, 1MM, 1FF, (TMM).
Diagnosis. *T. devia* may be separated from other *Tayshaneta* species that lack a ventral sclerite, except *T. archambaulti* and *T. coeca*, by having a short retrolateral tibial spine, occupying less than 0.5x the length of the palpal tarsus (RTS, Fig. 38A) and an apically tapering subquadrate embolus that lacks sculpture along its margin (E, Fig. 38D). Separated from *T. archambaulti* and *T. coeca* by having a retrolateral tibial spine with a base that lacks distinctive sculpture (RTS, Fig. 31B) and by the unique shape of the embolus (E, Fig. 38D).
Description. Complete description of female in Gertsch (1974: 171- 172). Habitus of male and female in Figs. 17A- E and female genitalia in Fig. 53A.

Male (MacDonald Cave)**.** Body length 1.4, carapace 0.58 long, 0.49 wide, length 1.18x width. Carapace light brown- yellow, sparsely setose; eyes large, ocular area enclosed in a dark pattern. Legs elongate and thin, femur I 1.4x carapace length, covered in fine setae with few scattered spines. Palpal tarsus entire, tapering apically; retrolateral tibial spine on an elevated base, weakly recurved, and smooth at its base, length 0.36x tarsus length. Bulb suboval, length 1.70x width; embolus oval, tapering apically (Fig. 38D), length 1.90x width. Abdomen yellow- brown, without pattern, 0.81 long, 0.61 wide, covered in fine setae.

Variation (*n* = 6). Total length 1.25- 1.40; carapace length 1.20- 1.52 x carapace width; length femur I 1.0- 1.4 x carapace width.

Distribution. Known from caves and surface localities in Travis and Williamson Counties, Texas (Fig. 56).

***Tayshaneta emeraldae*, new species**

(Figs. 18A- F, 39A- F, 53B, 60)

Type data. Male holotype and female paratype from Emerald Sink, Val Verde County, Texas, 3-November-1984, J. Reddell, M. Reyes, 29.84N, 101.55W, (AMNH).

Etymology. The species name is taken in opposition to the type locality.

Diagnosis. *T. emeraldae* **sp. nov.** can be separated from all *Tayshaneta* species, except *T. fawcetti, T. grubbsi*, *T. valverdae*, and *T. vidrio*, by having the following combination of characters: male palpal tarsus divided apically; ventral sclerite short, mesoapically positioned (VS, Fig. 39E); retrolateral sclerite present, pocket- like (RS, Fig. 39D). Separated from *T. fawcetti, T. grubbsi*, *T. valverdae*, and *T. vidrio* by having a distally tapering subquadrate embolus (E, Fig. 39D).

Description. Male (holotype)**.** Body length 1.45, carapace 0.63 long, 0.52 wide, length 1.20x width. Carapace orange- brown, sparsely setose; eyes large, ocular area enclosed in a dark pattern (Figs. 18A- C). Legs elongate and thin, femur I 1.63x carapace length, covered in fine setae and with few scattered spines. Palpal tarsus divided apically; retrolateral tibial spine smooth at its base, length 0.51x tarsus width. Bulb suboval, length 1.66x width; embolus subquadrate, with weak basal swelling (E, Fig. 39D), length 2.0x width. Ventral sclerite stout, situated mesoapically (VS, Fig. 39E); retrolateral sclerite pocket- like, weakly invaginated (RS, Fig. 39D). Abdomen pale yellow, without pattern, 0.81 long, 0.61 wide, covered in fine setae.

Female (paratype). Body length 1.60, carapace 0.63 long, 0.50 wide, length 1.25x width. Pigmentation and setation same as for male (Figs. 18D- F). Legs elongate and thin, femur I 1.4x carapace length, covered in fine setae and with few scattered spines. Atrium trapezoidal, length 0.5x width, spermathecae with twisted stalks and large, circular heads (Fig. 53B). Abdomen pale yellow, without pattern, 0.96 long, 0.65 wide, covered in fine setae.

Distribution. Known only from Emerald Sink, Val Verde County, Texas (Fig. 60).

***Tayshaneta fawcetti*, new species**

Leptoneta valverdae Gertsch, 1974: 174.

(Figs. 2B, 19A- F, 31D, 40A- F, 53C, 60)

Type data. Male holotype from Fawcett's Cave, Devil's River State Natural Area, Val Verde County, Texas, 10-November-2009, J. Ledford, J. Kennedy, M. Sanders, T. Garot, K. Wardlaw, 29.90N, 100.91W, (CASC).

Etymology. This species is named in honor of the Fawcett family, the owners of Fawcett's Cave and the surrounding Fawcett Ranch prior to its transition as a State Natural Area in 1988.

Notes. Specimens from Fawcett's Cave were originally considered by Gertsch (1974) as conspecific with *T. valverdae* based on similarities in somatic morphology and geography. Male specimens from Fawcett's Cave were unknown at the time and Gertsch (1974) could not evaluate their genitalic morphology. Recent work at Fawcett's Cave has recovered a series of male and female specimens which are morphologically distinct from *T. valverdae* and appear to not be closely related to other species groups within *Tayshaneta* (Figs. 4- 7).

Other Material Examined. USA: Texas: **Val Verde County:** Fawcett's Cave, 8mi. W. Loma Alta, 25-March-1961, M. Tandy, 29.90N, 100.91W, 2JJ, (AMNH); Fawcett's Cave, 6mi. N. Del Rio, 10-April-1968, J. Reddell, 29.90N, 100.91W, 1FF, 2JJ, (AMNH); Fawcett's Cave, 6mi. N. Del Rio, 10-November-2009, J. Ledford, J. Kennedy, M. Sanders, T. Garot, K. Wardlaw, 29.90N, 100.91W, 6MM, 12FF, (TMM).

Diagnosis. *T. fawcetti* can be separated from all *Tayshaneta* species, except *T. emeraldae, T. grubbsi*, *T. valverdae*, and *T. vidrio*, by having the following combination of characters: male palpal tarsus divided apically (TS, Fig. 31D); ventral sclerite short, mesoapically positioned (VS, Fig. 40E); retrolateral sclerite present, pocket- like (RS, Fig. 40E, F). Separated from *T. fawcetti, T. grubbsi*, *T. valverdae*, and *T. vidrio* by having a distally tapering subquadrate embolus with a distinct basal tooth (E, Fig. 40C, F).

Description. Male (holotype)**.** Body length 1.56, carapace 0.67 long, 0.58 wide, length 1.15x width. Carapace pale brown, slightly darker surrounding edges, sparsely setose; eyes reduced, ocular area depigmented (Figs. 19A- C). Legs elongate and thin, femur I 1.83x carapace length, covered in fine setae and with few scattered spines. Palpal tarsus divided apically (Fig. 31D); retrolateral tibial spine smooth at its base (RTS, Fig. 40D), length 0.38x tarsus width. Bulb suboval, length 1.8x width; embolus rectangular, with basal tooth (E, Fig. 40F), length 1.25x width. Ventral sclerite stout, situated mesoapically (VS, Fig. 40E), retrolateral sclerite pocket- like, weakly invaginated (RS, Figs. 40E, F). Abdomen pale brown, without pattern, 0.89 long, 0.67 wide, covered in fine setae.

Variation (*n* = 2). Total length 1.50- 1.56; carapace length 1.15- 1.2 x carapace width; length femur I 1.72- 1.83 x carapace width.

Female (paratype). Body length 1.4, carapace 0.60 long, 0.50 wide, length 1.17x width. Pigmentation and setation same as for male, except ocular area with a faint dark pattern enclosing the AER (Figs. 19D- F). Legs elongate and thin, femur I 1.6x carapace length, covered in fine setae and with few scattered spines. Atrium trapezoidal, length 0.73x width, spermathecae with short twisted stalks and elongate heads (Fig. 53C). Abdomen pale brown, without pattern, 0.80 long, 0.58 wide, covered in fine setae.

Variation (*n* = 2). Total length 1.25- 1.40; carapace length 1.20- 1.52 x carapace width; length femur I 1.0- 1.4 x carapace width.

Distribution. Known only from Fawcett's Cave in the Devil's River State Natural Area, Val Verde County, Texas (Fig. 60).

Natural History. Individuals of *T. fawcetti* were photographed during a 2009 expedition to Fawcett's Cave (Fig. 2B) where they were observed to make fine sheet webs similar to other leptonetid spiders. Male and female pairs were often found in the same web and the eggsacs were suspended near the web margins. Most specimens were found at the base of the cave's vertical entrance in twilight under loose rocks and breakdown material.

Tayshaneta grubbsi, new species

(Figs. 20A- C, 32E, 41A- F, 60)

Type data. Male holotype from Litterbarrel Cave, 5mi. SE Comstock, Val Verde County, Texas, 1-September-1974, S. Sweet, M. Reaka, 29.65N, 101.16W, (AMNH).
Etymology. This species is named in honor of Andy Grubbs, a remarkable collector of several new *Tayshaneta* species throughout Texas.
Note. The coloration of this specimen has likely been affected by its preservation conditions.
Diagnosis. *T. grubbsi* can be separated from all *Tayshaneta* species, except *T. emeraldae, T. fawcetti*, *T. valverdae*, and *T. vidrio*, by having the following combination of characters: male palpal tarsus divided apically; ventral sclerite short, mesoapically positioned (VS, Fig. 41E); retrolateral sclerite present, pocket- like (RS, Fig. 40A, E). Separated from *T. emeraldae, T. fawcetti*, *T. valverdae*, and *T. vidrio* by the unique oval shape of the embolus (Fig. 41D) and the very short ventral sclerite (VS, Fig. 41E).
Description. Male (holotype)**.** Body length 1.36, carapace 0.58 long, 0.51 wide, length 1.14x width. Carapace dark orange- brown, sparsely setose; eyes large, ocular area enclosed in a faint dark pattern (Figs. 20A- C). Legs elongate and thin, femur I 1.8x carapace length, covered in fine setae and with few scattered spines. Palpal tarsus divided apically; retrolateral tibial spine smooth at its base, length 0.40x tarsus width (RTS, Fig. 41A). Bulb suboval, length 1.8x width; embolus oval, with apical fold (E, Fig. 41D), length 1.8x width. Ventral sclerite short, situated mesoapically (VS, Fig. 41E); retrolateral sclerite pocket- like, weakly invaginated (RS, Figs. 41A, E). Abdomen pale yellow, without pattern, 0.81 long, 0.61 wide, covered in fine setae.
Distribution. Known only from Litterbarrel Cave, Val Verde County, Texas (Fig. 60).

Tayshaneta madla, new species

(Figs. 21A- C, 31F, 32F, 42A- F, 53D, 59)

Type data. Male holotype from Madla's Cave, Bexar County, Texas, 18-December-2003, K. White, 29.60N, 98.69W, (CASC).
Etymology. This species is named in honor of the Madla family, owners of Madla's Cave and the surrounding property.
Notes. Although the majority of records for this species are from caves, a small series of individuals have been collected from leaf litter near the entrance to Madla's Cave that are genetically identical to specimens within the cave. The somatic morphology of the species (large, darkly pigmented eyes; Figs. 21A- C) coupled with the surface records suggests that it is likely a widespread troglophile.
Other Material Examined. USA: Texas: **Bexar County**: Cave Number 18, 4 miles NE Helotes, 13-January-1995, A. Grubbs, 29.60N, 98.69W, 1MM, 2FF, (TMM); Cave

Number 189, 4 miles NE Helotes, 12-January-1995, A. Grubbs, N. Lake, Wade, 4MM, 6FF, 4J (TTU); Madla's Cave, 18-December-2003, K. White, 29.60N, 98.69W, 1MM, 1FF, (TMM); Madla's Cave, 9-March-2005, P. Paquin, 29.60N, 98.69W, 1MM, 1FF, 1JJ, (CASC); Madla's Drop, 8-June-1993, Loftin, J. Reddell, M. Reyes, G. Veni, 29.62N, 98.71W, 1MM, (TMM); Scorpion Cave, 1-June-1993, Loftin, J. Reddell, 29.58N, 98.68W, 1MM, 6FF, 1JJ (TMM); Young Cave Number 1, 6-September-1993, J. Reddell, M. Reyes, 29.62N, 98.66W, 1MM, (TMM).

Diagnosis. *T. madla* may be separated from all *Tayshaneta* species, except *T. bullis* and *T. microps,* by having males with an elongate retrolateral tibial spine (Figs. 31F, 32F), more than 0.5x length of the palpal tarsus, and lacking a ventral sclerite (Figs. 42B, E). Separated from *T. bullis* and *T. microps* by the unique shape of the embolus with an enlarged basal tooth (E, Fig. 42D, F).

Description. Male (holotype)**.** Body length 1.21, carapace 0.58 long, 0.45 wide, length 1.28x width. Carapace pale brown, slightly darker surrounding edges, sparsely setose. Eyes large, ocular area enclosed in a dark pattern (Figs. 21A- C). Legs short and thin, femur I 1.3x carapace length, covered in fine setae and with few scattered spines. Palpal tarsus tapering to weakly divided apically (TS, Fig. 31F); retrolateral tibial spine elongate, sculptured throughout, length 0.58x tarsus length (RTS, Fig. 32F). Bulb suboval, length 1.84x width; embolus oval, with large basal tooth (E, Fig. 42F), length 1.32x width. Abdomen yellow- white, without pattern, 0.63 long, 0.45 wide, covered in fine setae.

Variation (*n* = 5). Total length 1.14- 1.45; carapace length 1.16- 1.29 x carapace width; length femur I 1.3- 1.71 x carapace width.

Female (paratype). Body length 1.83, carapace 0.74 long, 0.58 wide, length 1.28x width. Pigmentation and setation same as for male. Legs short and thin, femur I 1.5x carapace length, covered in fine setae and with few scattered spines. Atrium trapezoidal, length 0.56x width, spermathecae with twisted stalks and large, circular heads (Fig. 53D). Abdomen yellow- white, without pattern, 1.09 long, 0.78 wide, covered in fine setae.

Variation (*n* = 3). Total length 1.45- 1.83; carapace length 1.21- 1.34 x carapace width; length femur I 1.14- 1.51 x carapace width.

Distribution. Known only from Madla's Cave in Bexar County, Texas (Fig. 59).

***Tayshaneta microps* (Gertsch, 1974)**

Leptoneta microps Gertsch, 1974: 171- 172.
Neoleptoneta microps (Gertsch, 1974): Brignoli, 1977: 216; Platnick, 1986: 8; Reddell, 1988: 34; Cokendolpher, 2004: 64; Reddell and Cokendolpher, 2004: 86; Platnick, 2010;
(Figs. 1B, 10A- B, 22A- F, 31C, 32C, 43A- F, 53E, 59)

Type data. Female holotype from Government Canyon Bat Cave, 5 miles SW Helotes, Bexar County, Texas, 11-August-1965, J. Reddell, J. Fish (AMNH, examined).

Notes. *T. microps* was listed under the Endangered Species Act in 2001 (U. S. Fish and Wildlife, 2010) due to pressure from urbanization in areas surrounding San Antonio, Texas. Two records are currently reported for the species, Government Canyon Bat Cave and Surprise Sink, both of which are in Northern Bexar County. The two specimens from Surprise Sink were examined in detail and while they share reduced eyes similar to *T.*

microps, both specimens are immature cannot be confirmed as this species in the absence of associated males.

Other Material Examined. USA: Texas: **Bexar County**: Government Canyon Bat Cave, 5 miles SW Helotes, 24-April-1993, J. Reddell, M. Reyes, 29.56N, 98.76W, 1FF, (TTU); Government Canyon Bat Cave, 5 miles SW Helotes, 24-May-1993, J. Reddell, M. Reyes, 29.56N, 98.76W, 1FF, (TMM); Government Canyon Bat Cave, 5 miles SW Helotes, 24-May-1998, J. Reddell, M. Reyes, 29.56N, 98.76W, 4FF, (TMM); Government Canyon Bat Cave, 5 miles SW Helotes, 12-March-2005, P. Paquin, 29.56N, 98.76W, 2MM, 2FF, 6JJ, (TMM); Government Canyon Bat Cave, 5 miles SW Helotes, 12-November-2009, J. Ledford, M. Sanders, N. Lake, 29.56N, 98.76W, 1MM, (TMM).

Diagnosis. *T. microps* may be separated from all *Tayshaneta* species, except *T. bullis* and *T. madla*, by having males with an elongate retrolateral tibial spine (RTS, Figs. 31F, 32F), more than 0.5x length of the palpal tarsus and lacking a ventral sclerite (Figs. 42B, E). Separated from *T. bullis* and *T. madla* by the unique shape of the embolus (Fig. 43D).

Description. Complete description of female in Gertsch (1974: 171- 172). Habitus of male and female in Figs. 22A- F, scanning electron micrographs of male genitalia in Figs. 43A- F, and female genitalia in Fig. 53E.

Male. (Government Canyon Bat Cave). Body length 1.27, carapace 0.56 long, 0.47 wide, length 1.19x width. Carapace light brown, sparsely setose; eyes greatly reduced (Figs. 10A- B; 22A- C). Legs elongate and thin, femur I 1.64x carapace length, covered in fine setae with few scattered spines. Palpal tarsus entire, tapering apically (Fig. 31C); retrolateral tibial spine elongate, sculptured throughout, length 0.50x tarsus length (Fig. 31C, 32C). Bulb suboval, length 1.76x width; embolus distally oval, curved, and with basal tooth (E, Fig. 43D), length 2.0x width. Abdomen light brown, without pattern, 0.70 long, 0.50 wide, covered in fine setae.

Variation (*n* = 6). Total length 1.25- 1.40; carapace length 1.20- 1.52 x carapace width; length femur I 1.0- 1.4 x carapace width.

Natural History. One adult male specimen was collected for DNA extraction and scanning electron microscopy in November 2009. Although only a single male was found, immature and female specimens were commonly observed in small sheet webs under breakdown material and at the base of walls on opposite sides of the cave entrance.

Distribution. Known only from Government Canyon Bat Cave, Bexar County, Texas (Fig. 59).

Tayshaneta myopica (Gertsch, 1974)

Leptoneta myopica Gertsch, 1974: 168.
Neoleptoneta myopica (Gertsch, 1974): Brignoli, 1977: 216; Platnick, 1986: 9.
(Figs. 2A, 2C, 23A- F, 31A, 32A, 44A- F, 53F, 55, 57)

Type data. Male holotype from Tooth Cave, Travis County, Texas, 30-March-1965, J. Reddell, 30.40N, 97.85W, (AMNH, examined).

Notes. *T. myopica* was listed under the Endangered Species Act in 1988 (U. S. Fish and Wildlife, 2010) due to its extremely limited distribution in a rapidly urbanizing area outside of Austin, Texas. Recent work has been directed at refining the distribution of the species in order to set recovery goals and several additional localities were discovered during the course of this study (Fig. 56). Of special interest are caves near the type locality which share identical mitochondrial and nuclear DNA haplotypes (Tooth Cave, Root Cave, Gallifer Cave, and Tight Pit) suggesting that individuals migrate between sites.

Other Material Examined. USA: Texas: **Travis County:** Cortaña Cave, 13-September-2006, Shade, Rykwalder, 30.38N, 97.85W, 1FF, (TTU); Cortaña Cave, 25-September-2007, P. Sprouse, K. McDermid, 30.38N, 97.85W, 2FF, (TTU); Cortaña Cave, 3-October-2007, J. Krejca, P. Sprouse, 30.38N, 97.85W, 1JJ, (TTU); Cortaña Cave, 14-October-2009, K. O'Connor, 30.38N, 97.85W, 1MM, 1FF, 1JJ, (TMM); Gallifer Cave, 20-April-1991, J. Reddell, M. Reyes, 30.40N, 97.85W, 1MM, 3JJ, (TMM); Gallifer Cave, 7-January-2005, J. Reddell, M. Reyes, 30.40N, 97.85W, 1MM, 3FF, (TMM); Geode Cave, 11-August-1993, W. Elliot, 30.39N, 97.86W, 1FF, (TMM); Geode Cave, 21-July-1994, W. Elliot, P. Sprouse, 30.39N, 97.86W, 2MM, 7FF, 2JJ, (TMM); Geode Cave, 11-August-1994, W. Elliot, 30.39N, 97.86W, 2MM, 4FF, 1JJ, (TMM); Geode Cave, 13-September-1994, W. Elliot, 30.39N, 97.86W, 1FF, (TMM); Geode Cave, 18-July-2007, K. O'Connor, 30.39N, 97.86W, 1MM, 1FF, 1JJ, (TMM); Geode Cave, 16-October-2007, Myers, 30.39N, 97.86W, 2JJ, (TTU); Geode Cave, 31-October-2007, J. Krejca, 30.39N, 97.86W, 2MM, 4FF, 8JJ, (TTU); Jester Estate's Cave, 14-March-2006, M. Sanders, 30.39N, 97.79W, 1FF, 1JJ, (TMM); Jester Estate's Cave, 18-September-2009, M. Sanders, 30.39N, 97.79W, 1MM, 3FF, 1JJ, (TMM); McNeil Bat Cave, 2-March-1986, J. Reddell, M. Reyes, 30.09N, 97.72W, 1MM, 1FF, (AMNH); McNeil Bat Cave, 11-March-2005, P. Paquin, 30.45N, 97.72W, 1FF, 1JJ, (CASC); New Comanche Trail Cave, 11-January-1989, J. Reddell, M. Reyes, 30.39N, 97.86W, 2FF, (AMNH); New Comanche Trail Cave, 26-January-1989, J. Reddell, M. Reyes, 30.39N, 97.86W, 2MM, 1FF, 2JJ, (AMNH); New Comanche Trail Cave, 16-October-2007, J. Krejca, 30.39N, 97.86W, 1MM, 3FF, (TTU); New Comanche Trail Cave, 23-October-2007, P. Sprouse, 30.39N, 97.86W, 2JJ, (TMM); Root Cave, 1-September-2008, P. Paquin, 30.40N, 97.85W, 1JJ, (TMM); Steiner Telephone Pole Cave, 17-July-2008, J. Ledford, P. Paquin, M. Archambault, 30.39N, 97.86W, 1MM, 3FF, 1JJ, (CASC); Tight Pit, 14-October-2009, K. O'Connor, 1FF, (TMM); Tooth Cave, 25-February-1963, D. McKenzie, J. Reddell, 30.40N, 97.85W, 1MM, 3FF, (AMNH); Tooth Cave, 5-March-1964, J. Reddell, D. McKenzie, T. Phillips, 30.40N, 97.85W, 1FF, (AMNH); Tooth Cave, 9-June-1967, D. McKenzie, J. Reddell, 30.40N, 97.85W, 2MM, 4FF, (AMNH); Tooth Cave, 8-March-1968, J. Reddell, W. Russell, S. Fowler, 30.40N, 97.85W, 1FF, (AMNH); Tooth Cave, 19-July-1970, D. McKenzie, J. Reddell, 30.40N, 97.85W, 4FF, (AMNH); Tooth Cave, 24-May-1992, J. Reddell, 30.40N, 97.85W, 1JJ, (AMNH); Tooth Cave, 1-September-2008, P. Paquin, 30.40N, 97.85W, 2MM, 8FF, 6JJ, (TMM); **Williamson County:** Goat Cave, 1-September-2008, P. Paquin, 30.49N, 97.71W, 1FF, 2JJ, (CASC).

Diagnosis. *T. myopica* may be separated from all other *Tayshaneta* species, except *T. paraconcinna*, by having an elongate ventral sclerite (VS, Fig. 44E) and a broad spoon shaped embolus (E, Fig. 44D). Separated from *T. paraconcinna* by having the embolus sharply projecting ventrally (Fig. 44D) and having a recurved, but not sickle- shaped, retrolateral tibial spine (RTS, Fig. 44A).

Description. Complete description in Gertsch (1974: 169- 170). Habitus of male and female in Figs. 23A- F, scanning electron micrographs of male palp in Figs. 44A- F, and female genitalia in Fig. 53F.

Distribution. Known from caves in Travis and Williamson Counties, Texas (Fig. 57).
Natural History. Individuals in Geode Cave and Tooth Cave were observed suspended beneath sheet webs at the bases of stable rocks and breakdown material (Figs. 2A, 2C). When disturbed, individuals would drop from their webs and fold their legs in a protective posture similar to that reported for *Calileptoneta* (Ledford, 2004).

***Tayshaneta oconnori*, new species**

(Figs. 24A- C, 45A- F, 58)

Type data. Male holotype from Fern Cave, Hays County, Texas, 26-May-1989, A. Grubbs, J. Reddell, M. Reyes, 29.97N, 97.99W, (AMNH).
Etymology. This species is named in honor of Kathleen O' Connor, fellow caver and biologist who helped collect many exciting *Tayshaneta* specimens.
Notes. A single adult male collected from Cathy's Cave, Hays County, Texas shares the genitalic morphology of *T. oconnori* but was damaged during examination and only the right palp remains. The specimen was highly troglobitic (P. Paquin, pers. comm.) and is tentatively assigned to *T. oconnori* until additional specimens can be collected.
Other Material Examined. USA: Texas: **Hays County:** Cathy's Cave, 15-March-2005, P. Paquin, 29.90N, 98.08W, 1MM, (CASC).
Diagnosis. *T. oconnori* may be separated from all *Tayshaneta* species, except *T. anopica* and *T. sandersi*, by having the following combination of characters: pigmentation and eyes entirely absent (Figs. 24A- C); legs extremely long and thin, femur I 1.8- 1.9x carapace length; embolus with a distinctive apical bifurcation (E, Fig. 45D). Separated from *T. anopica* and *T. sandersi* by having the ventral sclerite straight and short, not extending past the base of the embolus (VS, Fig. 45E) and by the unique shape of the embolus (E, Fig. 45D).
Description. Male (holotype). Body length 1.1, carapace 0.52 long, 0.40 wide, length 1.31x width. Carapace depigmented, sparsely setose; eyes absent (Figs. 24A- C). Legs elongate and thin, femur I 1.93x carapace length, covered in fine setae and with few scattered spines. Palpal tarsus entire, tapering apically; retrolateral tibial spine recurved, sculptured throughout, length 0.40x tarsus length. Bulb suboval, length 1.66x width; embolus oval, bifurcate apically (E, Fig. 45D), length 1.2x width. Abdomen depigmented, without pattern, 0.58 long, 0.45 wide, covered in fine setae.
Distribution. Known only from two caves in Hays County, Texas (Fig. 58).

***Tayshaneta paraconcinna* (Cokendolpher and Reddell, 2001)**

Neoleptoneta paraconcinna Cokendolpher and Reddell, 2001: 46; Platnick, 2010.
(Figs. 25A- F, 46A- F, 54A, 57)

Type data. Male holotype from Peep in the Deep Cave, Fort Hood, Bell County, Texas, 8-May-1998, J. Reddell, M. Reyes, 31.20N, 97.51W, (AMNH).
Other Material Examined. USA: Texas: **Bell County:** Camp 6 Cave Number 1, Fort Hood, 5-April-1999, J. Reddell, M. Reyes, 31.20N, 97.51W, 1MM, (TMM); Figure 8 Cave, Fort Hood, 20-April-1998, Graves, J. Reddell, M. Reyes, 31.20N, 97.51W, 1FF, (TMM); Hidden Pit Cave, Fort Hood, 18-August-2003, Perkins, J. Reddell, M. Reyes, 31.20N, 97.51W, 1FF, 3JJ, (TMM); Hidden Pit Cave, Fort Hood, 21-March-2004, J.

Fant, J. Reddell, M. Reyes, 31.20N, 97.51W, 1FF, 3JJ, (TMM); Peep in the Deep Cave, Fort Hood, 8-May-1998, J. Reddell, M. Reyes, 31.20N, 97.51W, 1FF, (TMM); Peep in the Deep Cave, Fort Hood, 21-April-1998, J. Reddell, M. Reyes, 31.20N, 97.51W, 2FF, (TMM); Peep in the Deep Cave, Fort Hood, 3-November-1998, J. Reddell, M. Reyes, 31.20N, 97.51W, 1FF, (TMM); Peep in the Deep Cave, Fort Hood, 8-June-2010, J. Fant, 31.20N, 97.51W, 3FF, 1JJ, (TMM); Talking Crows Cave, Fort Hood, 20-May-1998, Graves, J. Reddell, M. Reyes, 31.20N, 97.51W, 1JJ, (TMM); **Blanco County:** Flat Creek Ranch, 12miles E. Johnson City, 28-May-1995, A. Grubbs, 30.27N, 98.21W, 1MM, 1FF, (TTU); Pedernales State Park, 17-December-2003, P. Paquin, W. Wytrykush, 30.30N, 98.26W, 1MM, 1FF, (CASC); **Burnet County:** Doublehorn Creek and Highway 71, 4.9 miles SE Marble Falls, 20-January-1995, A. Grubbs, 30.49N, 98.23W, 3MM, 5FF, 4JJ, (TMM); Moon Rocks Ranch, 5 miles W. Spicewood, A. Grubbs, Waid, 30.47N, 98.24W, 1MM, (TMM); County Road 404, 5 miles W. Spicewood, site #1, 29-November-1994, A. Grubbs, 30.47N, 98.24W, 1MM, 3FF, (TTU); **Travis County:** Hwy. 71 and Pedernales River, 23mi. W. Austin, 3-October-1994, Grubbs, 30.38N, 98.08W, 1MM, 1FF, (TMM); Hwy. 71 and Pedernales River, 23mi. W. Austin, 17-November-2009, P. Paquin, J. Ledford, 30.38N, 98.08W, 18MM, 14FF, 4JJ, (CASC).

Diagnosis. *T. paraconcinna* may be separated from all other *Tayshaneta* species, except *T. myopica*, by having an elongate ventral sclerite (VS, Fig. 46E) and a broad spoon shaped embolus (E, Fig. 46D). Separated from *T. myopica* by having the embolus projecting anteriorly (E, Fig. 46D) and having a sharply recurved, sickle- shaped, retrolateral tibial spine (RTS, Fig. 46A).

Description. Complete description in Cokendolpher (2001: 46). Habitus of male and female in Figs. 25A- F, scanning electron micrographs of male palp in Figs. 46A- F, and female genitalia in Fig. 54A.

Distribution. Caves of Fort Hood, Bell County, Texas (Fig. 57).

Tayshaneta sandersi, new species

(Figs. 1C, 26A- C, 47A- F, 54B, 56)

Type data. Female holotype from District Park Cave, Travis County, Texas, 19-November-2009, J. Ledford, M. Sanders, 30.21N, 97.85W, (CASC).

Etymology. This species is named in honor of Mark Sanders, fellow caver, biologist, and collector of several *Tayshaneta* species in Texas.

Notes. The only known adult male for *T. sandersi* is from Whirlpool Cave and is missing most of its appendages and the carapace. Individuals from District Park Cave, Slaughter Creek Cave, and Whirlpool Cave are genetically identical suggesting that the species may occur more broadly in the Onion Creek watershed of Barton Springs.

Other Material Examined. USA: Texas: **Travis County:** Slaughter Creek Cave, 6-January-2005, P. Paquin, 30.19N, 97.87W, 1J, (CASC); Whirlpool Cave, 2-March-2005, P. Paquin, 1M, (TMM); District Park Cave, 19-November-2009, J. Ledford, M. Sanders, 30.21N, 97.85W, 1FF, 2J, (TMM).

Diagnosis. *T. sandersi* may be separated from all *Tayshaneta* species, except *T. anopica* and *T. oconnori,* by having the following combination of characters: pigmentation and eyes entirely absent (Figs. 26A- C); legs extremely long and thin, femur I 1.8- 1.9x carapace length; embolus with a distinctive apical bifurcation (E, Fig. 47D). Separated from *T. anopica* and *T. oconnori* by having the ventral sclerite curved prolaterally (VS, Fig. 47E) and by the unique shape of the embolus (E, Fig. 47D).

Description. Male (Whirlpool Cave, genitalia only). Palpal tarsus entire, tapering apically; retrolateral tibial spine recurved, sculptured throughout, length 0.38x tarsus length (Fig. 47A). Bulb suboval, length 1.97x width; embolus suboval, bifurcate apically (E, Fig. 47D), length 1.6x width. Ventral sclerite elongate, curved prolaterally (VS, Fig. 47E).

Female (holotype). Body length 1.2, carapace 0.58 long, 0.41 wide, length 1.39x width. Carapace depigmented, sparsely setose; eyes absent. Legs elongate and thin, femur I 1.90x carapace length, covered in fine setae and with few scattered spines. Atrium suboval, length 0.41x width, spermathecae with twisted stalks and large, circular heads (Fig. 54B). Abdomen depigmented, 0.61 long, 0.49 wide, covered in fine setae.

Natural History. Three individuals were found deep in District Park Cave in fine sheet webs under loose rocks. The single male individual was found wandering among loose rocks in Whirlpool Cave.

Distribution. Known from three caves in Travis County, Texas (Fig. 56).

***Tayshaneta sprousei*, new species**

(Figs. 27A- C, 48A- F, 59)

Type data. Male holotype from Constant Sorrow Cave, Camp Bullis, Bexar County, Texas, 6-March-2001, G. Veni, 29.63N, 98.58W, (AMNH).

Etymology. This species is named in honor of Peter Sprouse, fellow caver, biologist, and collector of several *Tayshaneta* species in Texas caves.

Other Material Examined. USA: Texas: **Bexar County:** Breached Dam Cave, 4-October-1995, J. Reddell, M. Reyes, 1JJ, (TMM); Breached Dam Cave, 1-November-2000, J. Reddell, M. Reyes, 1MM, (TMM).

Diagnosis. *T. sprousei* may be separated from all *Tayshaneta* species by having the following combination of characters: male palpal tarsus undivided, tapering apically (Fig. 48C); retrolateral tibial spine elongate, 0.5x length of palpal tarsus; embolus oval, smooth along margins (E, Fig. 48D); ventral sclerite short, less than the width of the embolus (Fig. 48B, D- F).

Description. Male (holotype). Body length 1.1, carapace 0.47 long, 0.40 wide, length 1.18x width. Carapace pale yellow, sparsely setose; eyes surrounded by faint dark markings (Figs. 27A- C). Legs elongate and thin, femur I 1.19x carapace length, covered in fine setae and with few scattered spines. Palpal tarsus entire, tapering apically (TS, Fig. 48C); retrolateral tibial spine straight, sculptured throughout, length 0.49x tarsus length. Bulb suboval, length 1.52x width; embolus oval, smooth along margins (E, Fig. 48D), length 2.0x width; ventral sclerite short, less than embolus width (VS, Figs. 48B, D- F). Abdomen pale yellow, without pattern, 0.63 long, 0.50 wide, covered in fine setae.

Variation (*n* = 2). Total length 1.10- 1.12; carapace length 1.18- 1.36 x carapace width; length femur I 1.19- 1.2 x carapace width.

Distribution. Known from two caves in Bexar County, Texas (Fig. 59).

***Tayshaneta valverdae* (Gertsch, 1974)**

Leptoneta valverdae Gertsch, 1974: 173.

Neoleptoneta valverdae (Gertsch, 1974): Brignoli, 1977: 216; Platnick, 1986: 10.
(Figs. 28A- F, 49A- F, 54C, 60)

Type data. Male holotype from Oriente Milestone Molasses Bat Cave, 20 miles NE of Del Rio, Val Verde County, Texas, 25-January-1964, J. Reddell, McKenzie, Porter, 29.56N, 100.77W, (CASC).
Other Material Examined. USA: Texas: **Bandera County:** Melanie's Cave, Hill Country State Natural Area, 23-July-2000, J. Reddell, M. Reyes, 29.63N, 99.18W, 1MM, 5FF, 2JJ, (TMM); Harvestman Cave, Hill Country State Natural Area, 24-July-2000, J. Reddell, M. Reyes, 29.63N, 99.18W, 1MM, 2FF, 2JJ, (TMM); Love Creek Ranch, 10.5 miles W. Medina, 6-October-1996, A. Grubbs, 29.79N, 99.42W, 1MM, 1FF, (AMNH); **Uvalde County:** Big Fucking Snake Cave, 8-June-1985, A. Grubbs, AC, RW, 29.43N, 99.65W, 1MM, 1FF, (AMNH); Marneldo Ranch, 18-April-1997, A. Grubbs, 29.50N, 99.61W, 1MM, (TMM); **Val Verde County:** Oriente Milestone Molasses Bat Cave, 20 miles NE of Del Rio, 25-January-1964, 1MM, (AMNH).
Diagnosis. *T. valverdae* may be separated from all other *Tayshaneta* species, except *T. emeraldae, T. fawcetti, T. grubbsi*, and *T. vidrio* by having the male palpal tarsus divided apically (TS, Fig. 31D) and by having a mesoapically positioned ventral sclerite on the palpal bulb (VS, Fig. 49E). Separated from *T. emeraldae, T. fawcetti, T. grubbsi*, and *T. vidrio* by the unique shape of the embolus with a prominent basal tooth (Fig. 49D).
Description. Complete description in Gertsch (1974: 173). Habitus of male and female in Figs. 28A- F, scanning electron micrographs of male palp in Figs. 49A- F, and female genitalia in Fig. 54C.
Distribution. Known from caves and surface localities in Bandera, Uvalde, and Val Verde Counties, Texas (Fig. 60).

***Tayshaneta vidrio*, new species**
(Figs. 29A- C, 31E, 50A- F, 54D, 60)

Type data. Male holotype from 400 Foot Cave, Glass Mountains, Brewster County, Texas, 30.38N, 103.15W, (AMNH).
Etymology. This species name is derived from the Spanish name for the Glass Mountains "Sierra del Vidrio" in West Texas.
Diagnosis. *T. vidrio* may be separated from all other *Tayshaneta* species, except *T. emeraldae, T. fawcetti, T. grubbsi*, and *T. valverdae* by having the male palpal tarsus divided apically (Fig. 31D) and by having a mesoapically positioned ventral sclerite on the palpal bulb (VS, Fig. 50E). Separated from *T. emeraldae, T. fawcetti, T. grubbsi*, and *T. valverdae* by having an oval embolus that is smooth along its margins and a ventral sclerite with a distinct apical division (VS, Fig. 50D- F).
Description. Male (holotype). Body length 1.98, carapace 0.80 long, 0.65 wide, length 1.22x width. Carapace orange- yellow, sparsely setose; eyes reduced, surrounded by faint dark markings (Figs. 29A- C). Legs elongate and thin, femur I 1.84x carapace length, covered in fine setae and with few scattered spines. Palpal tarsus divided apically (Fig. 31E); retrolateral tibial spine straight, sculptured throughout, length 0.51x tarsus length. Bulb suboval, length 1.70x width; embolus oval, curved at its base, smooth along

margins (E, Fig. 50D), length 2.5x width. Abdomen pale yellow, without pattern, 1.18 long, 0.92 wide, covered in fine setae.

Female (paratype). Body length 1.49, carapace 0.63 long, 0.50 wide, length 1.25x width. Pigmentation, setation, and eyes same as for male. Legs elongate and thin, femur I 1.57x carapace length, covered in fine setae and with few scattered spines. Atrium oval, length 1.5x width, spermathecae with twisted stalks and elongate heads (Fig. 54D). Abdomen pale yellow, 0.85 long, 0.70 wide, covered in fine setae.

Variation (*n* = 2). Total length 1.49- 1.81; carapace length 1.10- 1.25 x carapace width; length femur I 1.50- 1.57 x carapace width.

Distribution. Known only from 400 foot Cave, Brewster County, Texas (Fig. 60).

Tayshaneta whitei, new species

(Figs. 1D, 30A- F, 51A- F, 54E, 59)

Type. Male holotype from Lithic Ridge Cave, Government Canyon State Natural Area, Bexar County, Texas, 6-November-2002, Engelhard, J. Krejca, 29.56N, 98.74W, (AMNH).

Etymology. This species is named in honor of Kemble White, fellow caver, geologist, and collector of many *Tayshneta* species in Texas.

Other Material Examined. USA: Texas: **Bexar County:** Caracol Creek Coon Cave, 15-June-1993, Loftin, J. Reddell, M. Reyes, G. Veni, 29.45N, 98.71W, 1JJ, (TMM); Caracol Creek Coon Cave, 10-March-2005, P. Paquin, 29.45N, 98.71W, 1MM, 2FF, 1JJ, dep; Cave site #801, West of Helotes, November-1999, K. White, 1MM, 1FF, 1JJ, (CASC); Lithic Ridge Cave, Government Canyon State Natural Area, 1-October-1994, Palit, Atkinson, 29.56N, 98.74W, 1JJ, (TMM); Lithic Ridge Cave, Government Canyon State Natural Area, 4-June-1995, G. Veni, 29.56N, 98.74W, 1FF, (TMM); Lithic Ridge Cave, Government Canyon State Natural Area, 6-November-2002, Englehard, J. Krejca, 29.56N, 98.74W, 2MM, 2FF, 1JJ, (TMM); Lithic Ridge Cave, Government Canyon State Natural Area, 12-November-2009, J. Ledford, M. Sanders, N. Lake, 29.56N, 98.74W, 2MM, 2FF, 1JJ, (TMM); **Medina County:** Medina Dam Cave, June-2010, K. McDermid, 1JJ, (TMM); Nisbet Cave, 4-March-2001, G. Veni, Waters, 29.53N, 98.91W, 1MM, (TMM).

Diagnosis. *T. whitei* may be separated from all *Tayshaneta* species, except *T. bullis* and *T. microps,* by having a combination of males with an elongate retrolateral tibial spine, more than 0.5x length of the palpal tarsus and lacking a ventral sclerite (Figs. 51B, E). Separated from *T. bullis* and *T. microps* by the unique shape of the embolus (E, Fig. 51D) and the distinctive retrlolateral sclerite (RS, Figs. 51D- E).

Description. Male (holotype). Body length 1.52, carapace 0.61 long, 0.50 wide, length 1.21x width. Carapace brown, sparsely setose; eyes surrounded by dark markings (Figs. 30A- C). Legs elongate and thin, femur I 1.61x carapace length, covered in fine setae and with few scattered spines. Palpal tarsus undivided, tapering apically; retrolateral tibial spine straight, sculptured throughout, length 0.51x tarsus length. Bulb suboval, length 1.71x width; embolus subquadrate, with small basal tooth (E, Fig. 51D- F), length 1.6x width. Abdomen white, without pattern, 0.90 long, 0.67 wide, covered in fine setae.

Variation (*n* = 4). Total length 1.52- 1.70; carapace length 1.16- 1.21 x carapace width; length femur I 1.45- 1.92 x carapace width.

Female (paratype). Body length 1.49, carapace 0.61 long, 0.49 wide, length 1.25x width. Carapace light brown, sparsely setose; eyes surrounded by dark markings (Figs. 30D- F). Legs elongate and thin, femur I 1.58x carapace length, covered in fine setae and with few scattered spines. Atrium oval, length 0.5x width, spermathecae with twisted stalks and large, circular heads (Fig. 54E). Abdomen light brown, 0.90 long, 0.60 wide, covered in fine setae.

Variation (*n* = 3). Total length 1.41- 1.80; carapace length 1.18- 1.28 x carapace width; length femur I 1.33- 1.58 x carapace width.

Natural History. Several individuals of *T. whitei* were collected under loose stones near the bases of walls in Lithic Ridge Cave, Bexar County Texas.

Distribution. Known from caves in Bexar and Medina Counties, Texas (Fig. 59).

Acknowledgements

This study would not have been possible without the encouragement and support of several people and institutions. I thank my advisors, Charles Griswold, Rosemary Gillespie, George Roderick, Marshal Hedin, and Brent Mishler for their guidance and support. Pierre Paquin was instrumental to the project, providing specimens, fieldwork assistance, encouragement, and various lessons in Quebecois. James Cokedolpher and James Reddell provided regular guidance, cave locations, and specimens through the Museum of Texas Tech University and the Texas Memorial Museum.

I thank the members of the Evolab at U.C. Berkeley, Griswold lab, California Academy of Sciences, Hedin lab, San Diego State University, and the Masta lab, Portland State University. Josh Campbell, James Cokendolpher, Jeremy Miller, Norm Platnick, and Darrell Ubick provided several helpful discussions about leptonetid spiders. Jean Krejca, James Reddell, Mark Sanders, and Mike Slay provided photos of leptonetids, cave coordinates, and helpful discussions about cave biology. Rusty Scalf provided technical expertise with distribution maps and ArcGIS. Anthea Carmichael, Sarah Crews, and Sean Schoville provided invaluable assistance in the lab. Giovanni Maki provided help with the figures. Pierre Paquin, Mark Sanders, Josh Campell, Kathleen O' Connor, James Reddell, and Peter Sprouse provided specimens and help in the field. Oscar Franke, Jean Louis Lacaille- Musquiz, Martin Archambault, and Pierre Provost were instrumental to fieldwork for Mexbebitte 2008 at the Rancho de El Cielo in Tamaulipas, Mexico. Peter Sprouse was especially helpful with providing numerous coordinates to caves in Texas and Mexico. The amazing Jim "Crash" Kennedy, Tone Garot, and Kerr Wardlaw facilitated access to Fawcett's Cave at the Devil's River State Natural Area in Val Verde County, Texas.

Permits and cave access were kindly facilitated through Cyndee Watson, U.S. Fish and Wildlife Service, David Riskind, Texas Parks and Wildlife, Kimble White, SWCA Environmental Consultants, and Kathleen O' Connor, Zara Environmental. I am especially grateful to all of my fellow cavers and friends in the Texas caving community for putting up with my constant questions and harassment about cave locations, history, and requests for access and/ or specimens.

This study was supported by a National Science Foundation Doctoral Dissertation Improvement Grant (DDIG-0909872), the Exline- Frizzell fund at the California Academy of Sciences, the Walker Fund at U.C. Berkeley, the National Speleological Society (NSS general research grant) and the University of California.

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Table 1: List of Anatomical Abbreviations used in the text and figures.

Abbreviation	Structure
AER	Anterior Eye Row
AME	Anterior Median Eyes
At	Atrium
E	Embolus
PME	Posterior Median Eyes
RS	Retrolateral Sclerite
RTS	Retrolateral Tibial Sclerite
SH	Spermathecal Head
SS	Spermathecal Stalk
TS	Palpal Tarsus
VS	Ventral Sclerite

Table 2: Summary tree statistics and conditions for each analysis.

Analysis	**Optimality Criterion, Software**	**Conditions**	**Statistics**
Concatenated	Parsimony, PAUP* v.4b10	1000 iterations, heuristic search with TBR	41 trees, 8006 steps
COI (full partitions)	Likelihood, RAxML v.7.0.4	1000 non- parametric bootstrap replicates	-lnL 16062.90
Histone 3 (full partitions)			-lnL 2910.70
28s rDNA			-lnL 20318.74
Three- gene concatenated			-lnL 34742.79
Two- gene concatenated (COI, 28s)			-lnL 34550.09
COI (full partitions)	Bayesian, Mr. Bayes v.3.1.2	20,000,000 generations, burnin= 25%	sdsf 0.003
COI (1st & 2nd, 3rd positions)			sdsf 0.003
COI (unpartitioned)			sdsf 0.003
Histone 3 (full partitions)			sdsf 0.004
Histone 3 (1st & 2nd, 3rd positions)			sdsf 0.01
Histone 3 (unpartitioned)			sdsf 0.03
28s rDNA			sdsf 0.008
Three- gene concatenated		50,000,000 gen, burnin= 25%	sdsf 0.05
Two- gene concatenated (COI, 28s)		20,000,000 gen, burnin= 25%	sdsf 0.01

Table 3:
Primer sequences, source, and annealing temperatures. Optimized annealing temperatures in bold.

Gene	Forward	Sequence	Reference	Reverse	Sequence	Reference	Annealing Temperature
COI	1718	5- GGA GGA TTT GGA AAT TGA TTA GTT CC- 3	Simon et al. (1994)	2568	5- GCT ACA ACA TAA TAA GTA TCA TG- 3	Simon et al. (1994)	44- 50, **48ºC**
COI	1751	5 -GAG CTC CTG ATA TAG CTT TTC C- 3	Simon et al. (1994)	2568	5- GCT ACA ACA TAA TAA GTA TCA TG- 3	Simon et al. (1994)	44- 50, **48ºC**
COI	PMT1	5- GGT CAA CAA ATC ATA AAG ATA TTG G- 3	Folmer et al. (1994)	2568	5- GCT ACA ACA TAA TAA GTA TCA TG- 3	Simon et al. (1994)	44- 50, **45ºC**
COI	1490-ONO	5- CW ACA AAY CAT ARR GAT ATT GG- 3	Simon et al. (1994)	2568	5- GCT ACA ACA TAA TAA GTA TCA TG- 3	Simon et al. (1994)	44- 50, **45ºC**
COI	2309	5- TTT ATG CTA TAG TTG GAA TTG G- 3	Simon et al. (1994)	2776	5- GGA TAA TCA GAA TAN CGN CGA GG- 3	Simon et al. (1994)	44- 50, **48ºC**
28srDNA	ZX1	5- ACC CGC TGA ATT TAA GCA TAT- 3	Mallatt and Sullivan (1998)	ZR2	5- CCG AAG TTT CCC TCA GGA TAG C- 3	Mallatt and Sullivan (1998)	50- 60, **55ºC**
28srDNA	28sOCS	5- CGT GAA ACT GCT CAG AGG- 3	Miller et al. (2010)	28sC	5- GGC GAA AGA CTA ATC GAA CC- 3	Miller et al. (2010)	50- 60, **55ºC**
Histone 3	H3af	5- ATG GCT CGT ACC AAG CAG ACV GC- 3	Colgan et al. (1998)	H3ar	5- ATA TCC TTR GGC ATR ATR GTG AC- 3	Colgan et al. (1998)	48- 55, **50ºC**
Histone 3	H3nf	5- ATG GCT CGT ACC AAG CAG AC- 3	Colgan et al. (1998)	H3nr	5- ATR TCC TTG GGC ATG ATT GTT AC- 3	Colgan et al. (1998)	48- 55, **50ºC**

Explanation of Figures

Figure 1: Images of habitat and cave entrances for *Tayshaneta* species.
A. Cobb's Ranch, near Cobb's Caverns, Williamson County, Texas, type locality for *T. anopica* (Gertsch, 1974) showing karstic terrain; B. Entrance to Government Canyon Bat Cave, Bexar County, Texas, type locality for *T. microps* (Gertsch, 1974); C. General habitat of *T. sandersi* **sp. nov.**, District Park Cave, Travis County, Texas, (M. Sanders); D. Entrance to Lithic Ridge Cave, Bexar County, Texas, type locality for *T. whitei* **sp. nov.**; E. Entrance to Three Miles Bat Cave, Williamson County, Texas.

Figure 2: Live images of *Tayshaneta* species
A. *T. myopica* (Gertsch, 1974), female, Geode Cave, Travis County, Texas; B. *T. fawcetti* **sp. nov.**, male and female in web, Fawcett's Cave, Val Verde County, Texas; C. *T. myopica* (Gertsch, 1974), male, Tooth Cave, Travis County, Texas; D. Eggsac of *T. anopica*, Corn Cobb's Cave, Williamson County, Texas.

Figure 3: Map of the study area, with an inset highlighting the distribution of *Tayshaneta* on the Edward's Plateau.

Figure 4: Three gene concatenated Bayesian phylogeny from Ledford et al. (in prep). Highlighted and enlarged area indicates *Tayshaneta*. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%. *Tayshaneta* highlighted in green and enlarged at right.
A. *anopica* species group; B. *myopica* species group; C. *microps* species group; D. *sandersi* species group.

Figure 5: Three gene concatenated maximum likelihood phylogeny from Ledford et al. (in prep). Highlighted and enlarged area indicates *Tayshaneta*. Black nodes correspond to bootstrap support of 75% and greater. *Tayshaneta* highlighted in green and enlarged at right.
A. *anopica* species group; B. *myopica* species group; C. *microps* species group; D. *sandersi* species group.

Figure 6: Three gene concatenated parsimony phylogeny from Ledford et al. (in prep). Highlighted and enlarged area indicates *Tayshaneta*. Black nodes correspond to bootstrap support of 75% and greater. *Tayshaneta* highlighted in green and enlarged at right.
A. *anopica* species group; B. *myopica* species group; C. *microps* species group; D. *sandersi* species group.

Figure 7: Bayesian gene tree, cytochrome oxidase I (COI) from Ledford et al. (in prep). Highlighted and enlarged area indicates *Tayshaneta*. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%. *Tayshaneta* highlighted in green and enlarged at right.
A. *anopica* species group; B. *myopica* species group; C. *microps* species group; D. *sandersi* species group.

Figure 8: Bayesian gene tree, histone 3 (H3) from Ledford et al. (in prep). Highlighted and enlarged area indicates *Tayshaneta*. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%.%. *Tayshaneta* highlighted in green and enlarged at right.
A. *anopica* species group; B. *myopica* species group; C. *microps* species group; D. *sandersi* species group.

Figure 9: Bayesian gene tree, 28s rDNA (28s) from Ledford et al. (in prep). Highlighted and enlarged area indicates *Tayshaneta*.. Black nodes correspond to a posterior probability of 95% and greater, gray nodes to 75- 94%. *Tayshaneta* highlighted in green and enlarged at right.
A. *anopica* species group; B. *myopica* species group; C. *microps* species group; D. *sandersi* species group.

Figure 10: General morphology of *Tayshaneta* species.
A. *T. microps* (Gertsch, 1974) male, Government Canyon Bat Cave, carapace dorsal view; B. *T. microps* (Gertsch, 1974) male, Government Canyon Bat Cave, ocular area; C. *T. coeca* (Chamberlin and Ivie, 1942) male, New Braunfels, carapace dorsal view; D. *T. myopica* (Gertsch, 1974) male, Pedernales River, sternum; E. *T. myopica* (Gertsch, 1974) male, Pedernales River, carapace lateral view, arrow highlighting stridulatory file.

Figure 11: Spinneret morphology for male *Tayshaneta*
A. *T. myopica* (Gertsch, 1974) male, Pedernales River, arrow to colulus; B. *T. devia* (Gertsch, 1974), MacDonald Cave, spinning field; C. *T. devia* (Gertsch, 1974), MacDonald Cave, epiandrous spigots in circled region.

Figure 12: *Tayshaneta anopica* (Gertsch, 1974), Cobb's Cave, Williamson County, Texas (CASC), habitus.
A. *T. anopica* male, dorsal; B. *T. anopica* male, ventral; C. *T. anopica* male, lateral; D. *T. anopica* female, dorsal; E. *T. anopica* female, ventral; F. *T. anopica* female, lateral.

Figure 13: *Tayshaneta archambaulti* **sp. nov.**, Burnett Ranch Cave, Hays County, Texas (AMNH), habitus. Color of specimen significantly darkened due to preservation issues.
A. *T. archambaulti* male, dorsal; B. *T. archambaulti* male, ventral; C. *T. archambaulti* male, lateral; D. *T. archambaulti* female, dorsal; E. *T. archambaulti* female, ventral; F. *T. archambaulti* female, lateral.

Figure 14: *Tayshaneta bullis* (Cokendolpher, 2004), Up the Creek Cave, Camp Bullis, Bexar County, Texas (holotype AMNH, paratype TMM), habitus.
A. *T. bullis* male holotype, dorsal; B. *T. bullis* male holotype, ventral; C. *T. bullis* male holotype, lateral; D. *T. bullis* female paratype, dorsal; E. *T. bullis* female paratype, ventral; F. *T. bullis* female paratype, lateral.

Figure 15: *Tayshaneta coeca* (Chamberlin and Ivie, 1942), Heidrich's Cave, Comal County, Texas (AMNH), habitus.

A. *T. coeca* male holotype, dorsal; B. *T. coeca* male holotype, ventral; C. *T. coeca* male holotype, lateral; D. *T. coeca* female paratype, dorsal; E. *T. coeca* female paratype, ventral; F. *T. coeca* female paratype, lateral.

Figure 16: *Tayshaneta concinna* (Gertsch, 1974), Lost Gold Cave, Travis County, Texas (AMNH), habitus.
A. *T. concinna* male holotype, dorsal; B. *T. concinna* male holotype, ventral; C. *T. concinna* male holotype, lateral.

Figure 17: *Tayshaneta devia* (Gertsch, 1974), MacDonald Cave, Travis County, Texas (CASC), habitus.
A. *T. devia* male, dorsal; B. *T. devia* female, dorsal; C. *T. devia* female holotype, ventral; D. *T. devia* male, lateral; E. . *T. devia* female, lateral.

Figure 18: *Tayshaneta emeraldae* **sp. nov.**, Emerald Sink, Val Verde County, Texas (AMNH), habitus.
A. *T. emeraldae* male, dorsal; B. *T. emeraldae* male, ventral; C. *T. emeraldae* male, lateral; D. *T. emeraldae* female, dorsal; E. *T. emeraldae* female, ventral; F. *T. emeraldae* female, lateral.

Figure 19: *Tayshaneta fawcetti* **sp. nov.**, Fawcett's Cave, Val Verde County, Texas (CASC), habitus.
A. *T. fawcetti* male, dorsal; B. *T. fawcetti* male, ventral; C. *T. fawcetti* male, lateral; D. *T. fawcetti* female, dorsal; E. *T. fawcetti* female, ventral; F. *T. fawcetti* female, lateral.

Figure 20: *Tayshaneta grubbsi* **sp. nov.**, Litterbarrel Cave, Val Verde County, Texas (AMNH), habitus. Color of specimen significantly darkened due to preservation issues.
A. *T. grubbsi* male holotype, dorsal; B. *T. grubbsi* male holotype, ventral; C. *T. grubbsi* male holotype, lateral.

Figure 21: *Tayshaneta madla* **sp. nov.**, Madla's Cave, Bexar County, Texas (CASC), habitus.
A. *T. madla* female, dorsal; B. *T. madla* female, ventral; C. *T. madla* female, lateral.

Figure 22: *Tayshaneta microps* (Gertsch, 1974), Government Canyon Bat Cave, Bexar County, Texas (CASC), habitus.
A. *T. microps* male, dorsal; B. *T. microps* male, ventral; C. *T. microps* male, lateral; D. *T. microps* female, dorsal; E. *T. microps* female, ventral; F. *T. microps* female, lateral.

Figure 23: *Tayshaneta myopica* (Gertsch, 1974), Tooth Cave, Travis County, Texas (CASC), habitus.
A. *T. myopica* male, dorsal; B. *T. myopica* male, ventral; C. *T. myopica* male, lateral; D. *T. myopica* female, dorsal; E. *T. myopica* female, ventral; F. *T. myopica* female, lateral.

Figure 24: *Tayshaneta oconnori* **sp. nov.**, Fern Cave, Hays County, Texas (AMNH), habitus.

A. *T. oconnori* male holotype, dorsal; B. *T. oconnori* male holotype, ventral; C. *T. oconnori* male holotype, lateral.

Figure 25: *Tayshaneta paraconcinna* (Cokendolpher and Reddell, 2001), Camp 6 Cave Number 1, Fort Hood, Bell County, Texas (TMM), habitus.
A. *T. paraconcinna* male, dorsal; B. *T. paraconcinna* male, ventral; C. *T. paraconcinna* male, lateral; D. *T. paraconcinna* female, dorsal; E. *T. paraconcinna* female, ventral; F. *T. paraconcinna* female, lateral.

Figure 26: *Tayshaneta sandersi* **sp. nov.**, District Park Cave, Travis County, Texas (CASC), habitus.
A. *T. sandersi* female holotype, dorsal; B. *T. sandersi* female holotype, ventral; C. *T. sandersi* female holotype, lateral.

Figure 27: *Tayshaneta sprousei* **sp. nov.**, Constant Sorrow Cave, Camp Bullis, Bexar County, Texas (TMM), habitus.
A. *T. sprousei* male holotype, dorsal; B. *T. sprousei* male holotype, ventral; C. *T. sprousei* male holotype, lateral.

Figure 28: *Tayshaneta valverdae* **sp. nov.**, Oriente Milestone Molasses Bat Cave, Val Verde County, Texas (AMNH), habitus.
A. *T. valverdae* male holotype, dorsal; B. *T. valverdae* male holotype, ventral; C. *T. valverdae* male holotype, lateral.

Figure 29: *Tayshaneta vidrio* **sp. nov.**, 400 Foot Cave, Brewster County, Texas (AMNH), habitus.
A. *T. vidrio* male holotype, dorsal; B. *T. vidrio* male holotype, ventral; C. *T. vidrio* male holotype, lateral.

Figure 30: *Tayshaneta whitei* **sp. nov.**, Lithic Ridge Cave, Bexar County, Texas (CASC), habitus.
A. *T. whitei* male, dorsal; B. *T. whitei* male, ventral; C. *T. whitei* male, lateral; D. *T. whitei* female, dorsal; E. *T. whitei* female, ventral; F. *T. whitei* female, lateral.

Figure 31: Morphology of *Tayshaneta* right male palpi in dorsal view, showing differences in tarsal shape.
A. *T. myopica* (Gertsch, 1974), Scoot Over Cave, Williamson County, Texas; B. *T. devia* (Gertsch, 1974), Stovepipe Cave, Travis County, Texas; C. *T. microps* (Gertsch, 1974), Bexar County, Texas; D. *T. fawcetti* **sp. nov.**, Fawcett's Cave, Val Verde County, Texas; E. *T. vidrio*, **sp. nov.**, 400 foot Cave, Brewster County (RTS damaged), Texas; F. *T. madla* **sp. nov.**, Madla's Drop Cave, Bexar County, Texas.

Figure 32: General morphology of *Tayshaneta* male palpi, showing differences in retrolateral tibial spine.
A. *T. myopica* (Gertsch, 1974), Scoot Over Cave, Williamson County, Texas; B. *T. devia* (Gertsch, 1974), Stovepipe Cave, Travis County, Texas; C. *T. microps* (Gertsch, 1974),

Bexar County, Texas; D. *T. fawcetti* **sp. nov.**, Fawcett's Cave, Val Verde County, Texas; E. *T. grubbsi*, **sp. nov.**, Litterbarrel Cave, Val Verde County, Texas; F. *T. madla* **sp. nov.**, Cave Number 189, Bexar County, Texas.

Figure 33: *Tayshaneta anopica* (Gertsch, 1974), Cobb's Cave, Williamson County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 34: *Tayshaneta archambaulti* **sp. nov.**, Grapevine Ranch Cave, Hays County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 35: *Tayshaneta bullis* (Cokendolpher, 2004), Up the Creek Cave, Camp Bullis, Bexar County, Texas (TMM), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Apical.

Figure 36: *Tayshaneta coeca* (Chamberlin and Ivie, 1942), Heidrich's Cave, Comal County, Texas (AMNH), male right palp.
A. Retrolateral; B. Ventral; C. Tarsus, dorsal; D. Retrolateral, embolus; E. Ventroapical; F. Retrolateral tibial spine.

Figure 37: *Tayshaneta concinna* (Gertsch, 1974), Lost Gold Cave, Travis County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 38: *Tayshaneta devia* (Gertsch, 1974), MacDonald Cave, Travis County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 39: *Tayshaneta emeraldae* **sp. nov.**, Emerald Sink, Val Verde County, Texas (AMNH), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 40: *Tayshaneta fawcetti* **sp. nov.**, Fawcett's Cave, Val Verde County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Ventrolateral; D. Retrolateral tibial spine; E. Ventroapical; F. Retrolateral, embolus.

Figure 41: *Tayshaneta grubbsi* **sp. nov.**, Litterbarrel Cave, Val Verde County, Texas (AMNH), male right palp.

A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Apical.

Figure 42: *Tayshaneta madla* **sp. nov.**, Madla's Cave, Bexar County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Embolus.

Figure 43: *Tayshaneta microps* (Gertsch, 1974), Government Canyon Bat Cave, Bexar County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 44: *Tayshaneta myopica* (Gertsch, 1974), Tooth Cave, Travis County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Embolus.

Figure 45: *Tayshaneta oconnori* **sp. nov.**, Fern Cave, Hays County, Texas (TMM), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 46: *Tayshaneta paraconcinna* (Cokendolpher and Redell, 2001), Fern Cave, Hays County, Texas (TMM), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 47: *Tayshaneta sandersi* **sp. nov.**, Whirlpool Cave, Travis County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Retroventral; D. Retrolateral, embolus; E. Ventroapical; F. Apical.

Figure 48: *Tayshaneta sprousei* **sp. nov.**, Constant Sorrow Cave, Camp Bullis, Bexar County, Texas (TMM), male right palp.
A. Ventral; B. Ventral sclerite; C. Tarsus, dorsal; D. Retrolateral, embolus; E. Ventroapical; F. Apical.

Figure 49: *Tayshaneta valverdae* (Gertsch, 1974), Oriente Milestone Molasses Bat Cave, Val Verde County, Texas (AMNH), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Proapical.

Figure 50: *Tayshaneta vidrio* **sp. nov.**, 400 foot Cave, Brewster County, Texas (AMNH), male right palp.

A. Retrolateral; B. Ventral; C. Prolateral; D. Embolus; E. Ventroapical; F. Ventral sclerite.

Figure 51: *Tayshaneta whitei* **sp. nov.**, Lithic Ridge Cave, Bexar County, Texas (CASC), male right palp.
A. Retrolateral; B. Ventral; C. Prolateral; D. Retrolateral, embolus; E. Ventroapical; F. Embolus.

Figure 52: Female genitalia for *Tayshaneta* species.
A. *T. anopica* (Gertsch, 1974), Corn Cobb's Cave, Williamson County, Texas; B. Eggsac of *T. anopica* (Gertsch, 1974), Corn Cobb's Cave, Williamson County, Texas; C. *T. archambaulti* **sp. nov.**, Grapevine Cave, Hays County, Texas; D. *T. bullis* (Cokendolpher, 2004), Up the Creek Cave, Bexar County, Texas; E. *T. coeca* (Chamberlin and Ivie, 1942), Natural Bridge Caverns, Hays County, Texas; F. *T. concinna* (Gertsch, 1974), Lost Gold Cave, Travis County, Texas.

Figure 53: Female genitalia for *Tayshaneta* species.
A. *T. devia* (Gertsch, 1974), MacDonald Cave, Travis County, Texas; B. *T. emeraldae* **sp. nov.**, Emerald Sink, Val Verde County, Texas; C. *T. fawcetti* **sp. nov.**, Fawcett's Cave, Val Verde County, Texas; D. *T. madla* **sp. nov.**, Madla's Cave, Bexar County, Texas; E. *T. microps* (Gertsch, 1974), Government Canyon Bat Cave, Bexar County, Texas; F. *T. myopica* (Gertsch, 1974), Tooth Cave, Travis County, Texas.

Figure 54: Female genitalia for *Tayshaneta* species.
A. *T. paraconcinna* (Cokendolpher and Reddell, 2001), Figure 8 Cave, Fort Hood, Bell County, Texas; B. *T. sandersi* **sp. nov.**, District Park Cave, Travis County, Texas; C. *T. valverdae* (Gertsch, 1974), Love Creek Ranch, Bandera County, Texas; D. *T. vidrio* **sp. nov.**, 400 foot Cave, Brewster County, Texas; E. *T. whitei* **sp. nov.**, Lithic Ridge Cave, Bexar County, Texas.

Figure 55: Distribution map showing morphotypes within *Tayshaneta myopica* (Gertsch, 1974). A. Tooth Cave; B. Goat Cave; C. McNeil Bat Cave; D. Jester Estates Caves; E. Steiner Telephone Pole Cave; F. Geode Cave.

Figure 56: Distribution map for *T. anopica* (Gertsch, 1974), *T. concinna* (Gertsch, 1974), *T. sandersi* **sp. nov.**, and *T. devia* (Gertsch, 1974).

Figure 57: Distribution map for *T. myopica* (Gertsch, 1974) and *T. paraconcinna* (Cokendolpher and Reddell, 2001).

Figure 58: Distribution map for *T. archambaulti* **sp. nov.** *T. coeca* (Chamberlin and Ivie, 1942), and *T. oconnori* **sp. nov.**

Figure 59: Distribution map for *T. madla* **sp. nov.** *T. bullis* (Cokendolpher, 2004), *T. microps* (Gertsch, 1974), *T. sprousei* **sp. nov.** and *T. whitei* **sp. nov.**

Figure 60: Distribution map for *T. emeraldae* **sp. nov.**, *T. fawcetti* **sp. nov.**, *T. grubbsi* **sp. nov.**, *T. valverdae* (Gertsch, 1974), and *T. vidrio* **sp. nov.**

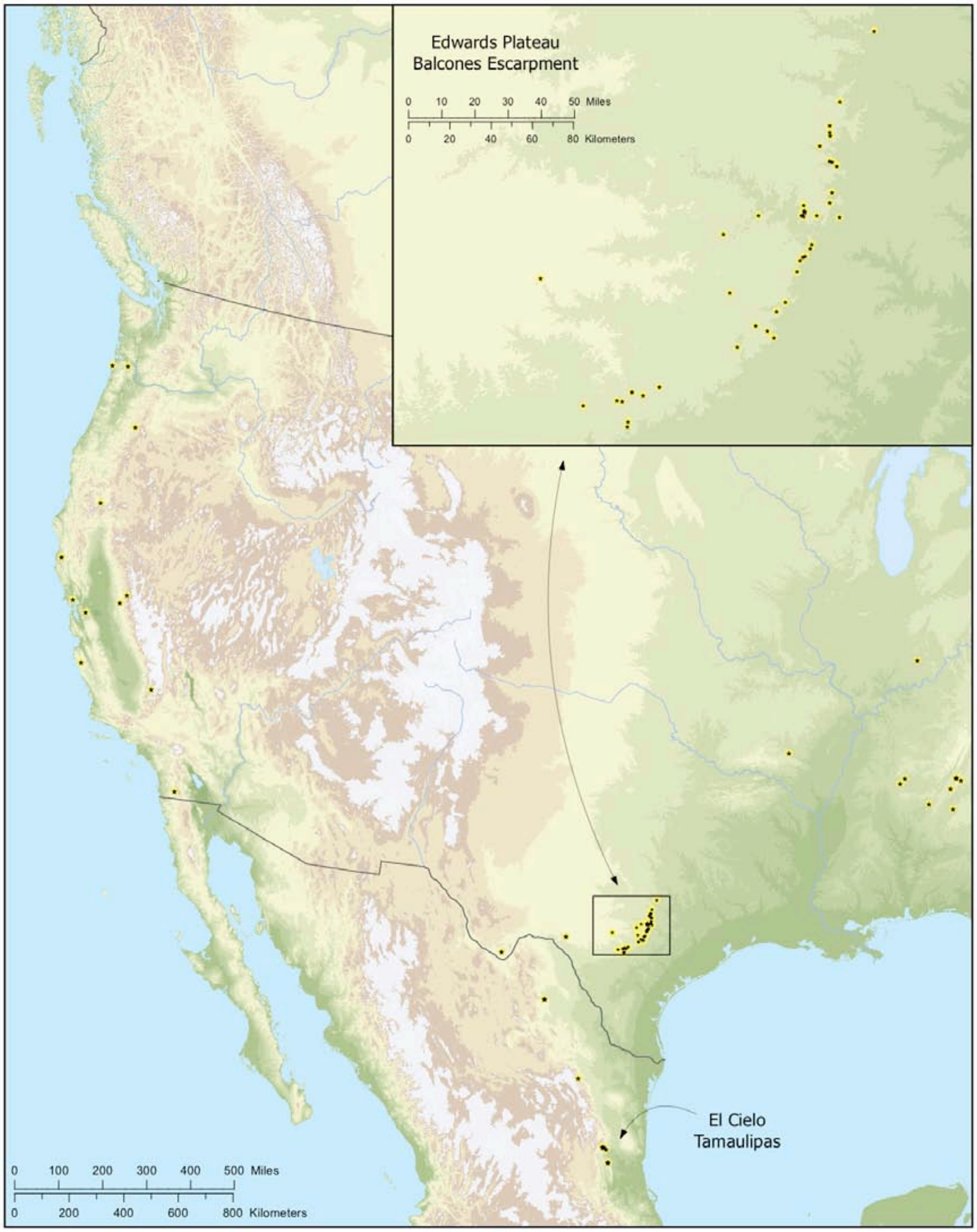
Figure 61: Distribution map for undetermined *Tayshaneta* species.

Figure 62: Distribution of *Tayshaneta* species in Travis and Williamson Counties superimposed on Karst Faunal Regions (KFR's).

Figure 63: Distribution of *Tayshaneta* species in Bexar County superimposed on Karst Faunal Regions.


A
B
C
D
E


A
B
C
D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Balcones Escarpment
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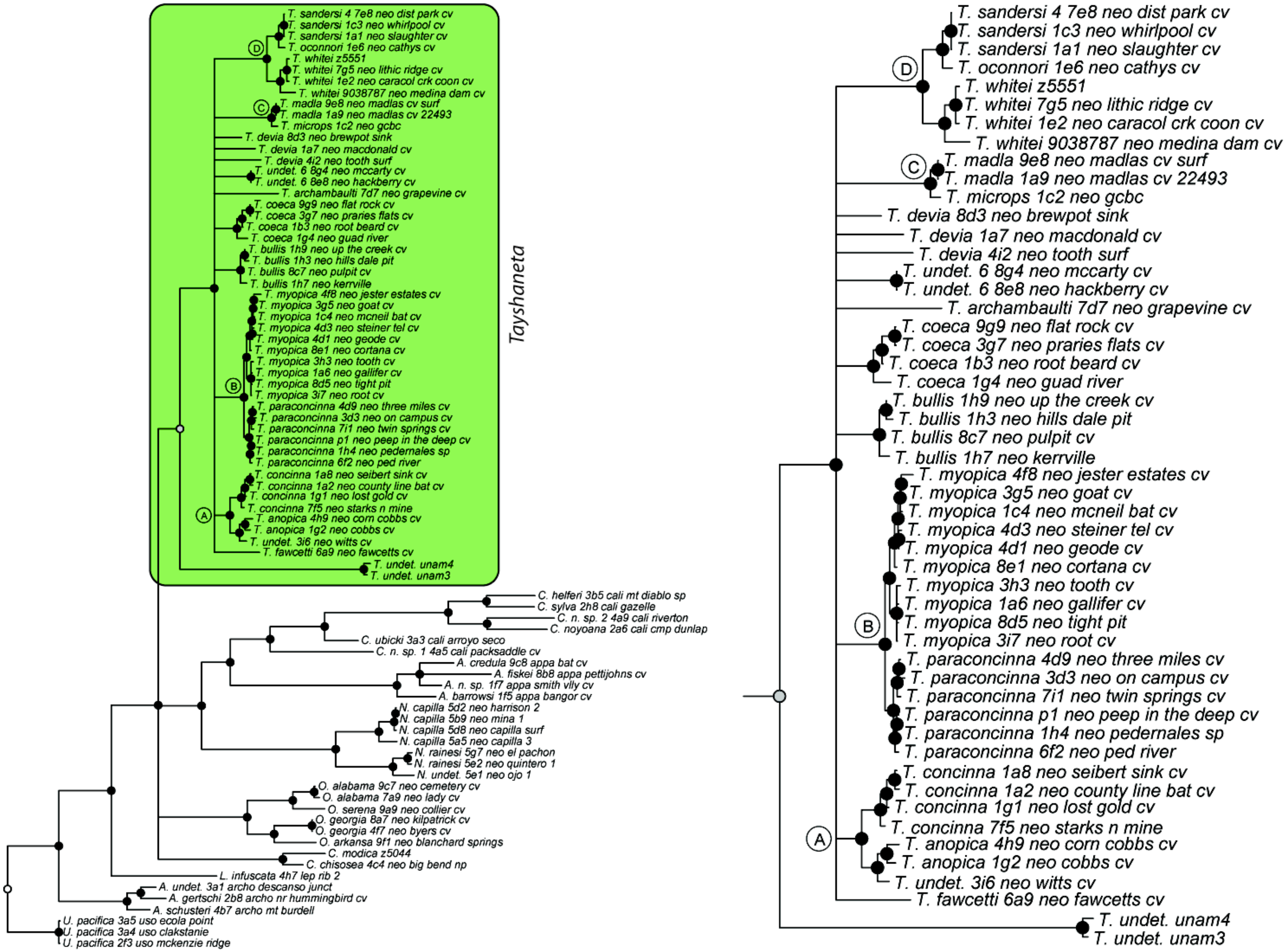
0 20 40 60 80 Kilometers
El Cielo
Tamaulipas
0 100 200 300 400 500 Miles
0 200 400 600 800 Kilometers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D
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T. whitei 7g5 neo lithic ridge cv
T. whitei 1e2 neo caracol crk coon cv
T. whitei 9038787 neo medina dam cv
C
T. madla 9e8 neo madlas cv surf
T. madla 1a9 neo madlas cv 22493
T. microps 1c2 neo gcbc
T. devia 8d3 neo brewpot sink
T. devia 1a7 neo macdonald cv
T. devia 4i2 neo tooth surf
T. undet. 6 8g4 neo mccarty cv
T. undet. 6 8e8 neo hackberry cv
T. archambaulti 7d7 neo grapevine cv
T. coeca 9g9 neo flat rock cv
T. coeca 3g7 neo praries flats cv
T. coeca 1b3 neo root beard cv
T. coeca 1g4 neo guad river
T. bullis 1h9 neo up the creek cv
T. bullis 1h3 neo hills dale pit
T. bullis 8c7 neo pulpit cv
T. bullis 1h7 neo kerrville
T. myopica 4f8 neo jester estates cv
T. myopica 3g5 neo goat cv
T. myopica 1c4 neo mcneil bat cv
T. myopica 4d3 neo steiner tel cv
T. myopica 4d1 neo geode cv
T. myopica 8e1 neo cortana cv
T. myopica 3h3 neo tooth cv
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B
T. myopica 8d5 neo tight pit
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T. paraconcinna 3d3 neo on campus cv
T. paraconcinna 7i1 neo twin springs cv
T. paraconcinna p1 neo peep in the deep cv
T. paraconcinna 1h4 neo pedernales sp
T. paraconcinna 6f2 neo ped river
T. concinna 1a8 neo seibert sink cv
T. concinna 1a2 neo county line bat cv
T. concinna 1g1 neo lost gold cv
A
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T. anopica 1g2 neo cobbs cv
T. undet. 3i6 neo witts cv
T. fawcetti 6a9 neo fawcetts cv
T. undet. unam4
T. undet. unam3
Tayshaneta
C. helferi 3b5 cali mt diablo sp
C. sylva 2h8 cali gazelle
C. n. sp. 2 4a9 cali riverton
C. noyoana 2a6 cali cmp dunlap
C. ubicki 3a3 cali arroyo seco
C. n. sp. 1 4a5 cali packsaddle cv
A. credula 9c8 appa bat cv
A. fiskei 8b8 appa pettijohns cv
A. n. sp. 1f7 appa smith vlly cv
A. barrowsi 1f5 appa bangor cv
N. capilla 5d2 neo harrison 2
N. capilla 5b9 neo mina 1
N. capilla 5d8 neo capilla surf
N. capilla 5a5 neo capilla 3
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N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
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O. serena 9a9 neo collier cv
O. georgia 8a7 neo kilpatrick cv
O. georgia 4f7 neo byers cv
O. arkansa 9f1 neo blanchard springs
C. modica z5044
C. chisosea 4c4 neo big bend np
L. infuscata 4h7 lep rib 2
A. undet. 3a1 archo descanso junct
A. gertschi 2b8 archo nr hummingbird cv
A. schusteri 4b7 archo mt burdell
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T. undet. 6 8g4 neo mccarty cv
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T. paraconcinna 1h4 neo pedernales sp
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T. concinna 1a8 neo seibert sink cv
T. concinna 1a2 neo county line bat cv
T. concinna 1g1 neo lost gold cv
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T. concinna 7f5 neo starks n mine
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T. anopica 1g2 neo cobbs cv
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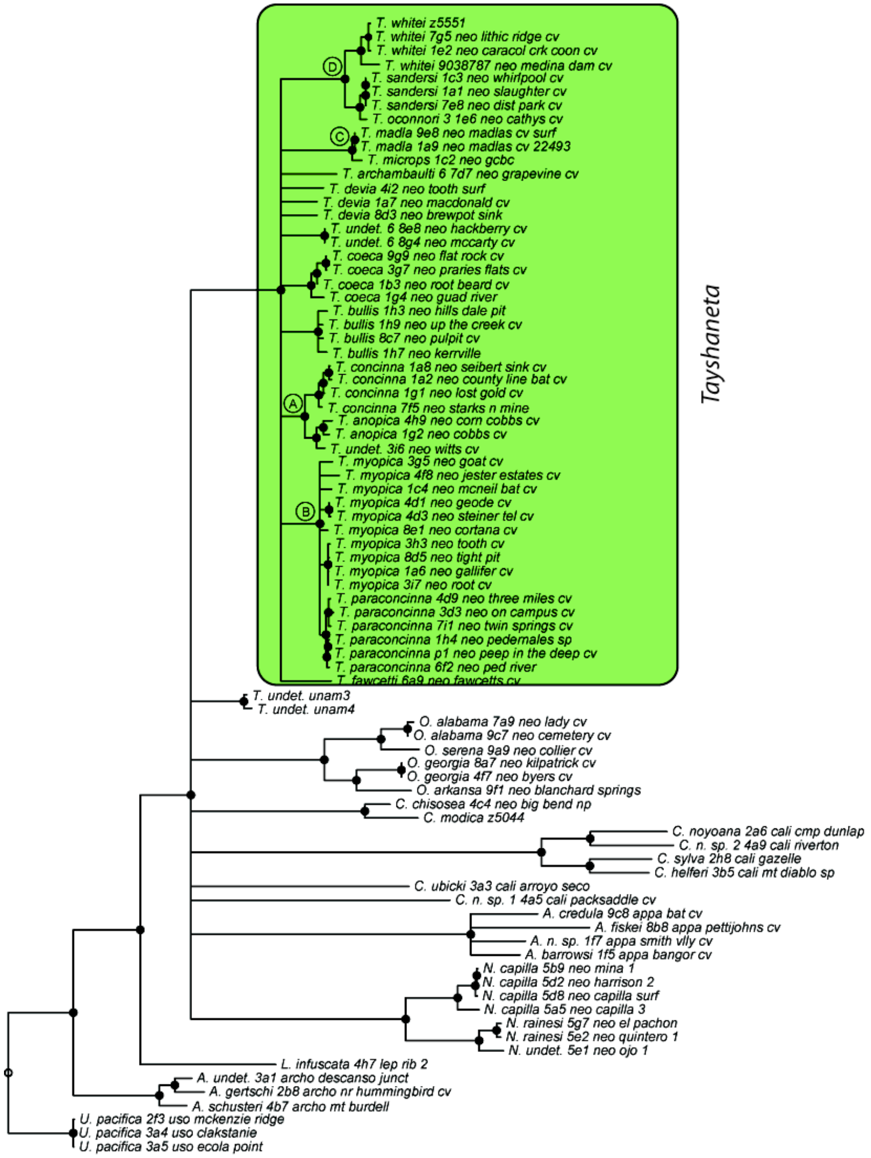
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C. modica z5044
C. noyoana 2a6 cali cmp dunlap
C. n. sp. 2 4a9 cali riverton
C. sylva 2h8 cali gazelle
C. helferi 3b5 cali mt diablo sp
C. ubicki 3a3 cali arroyo seco
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N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
L. infuscata 4h7 lep rib 2
A. undet. 3a1 archo descanso junct
A. gertschi 2b8 archo nr hummingbird cv
A. schusteri 4b7 archo mt burdell
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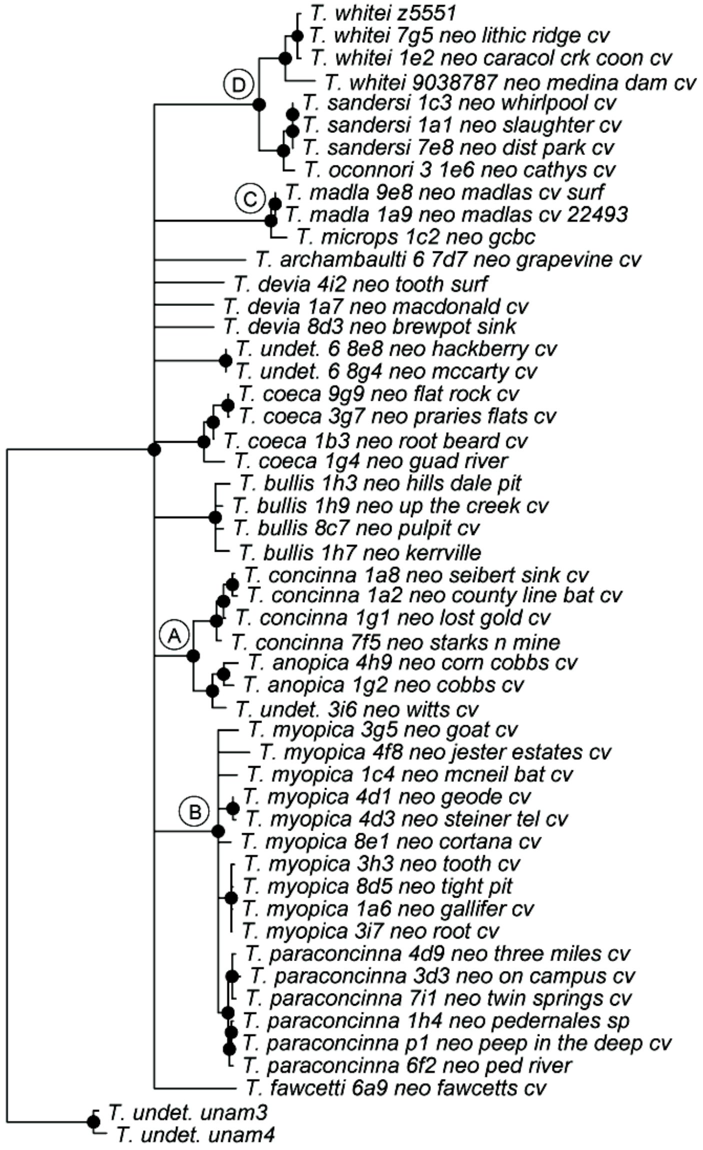
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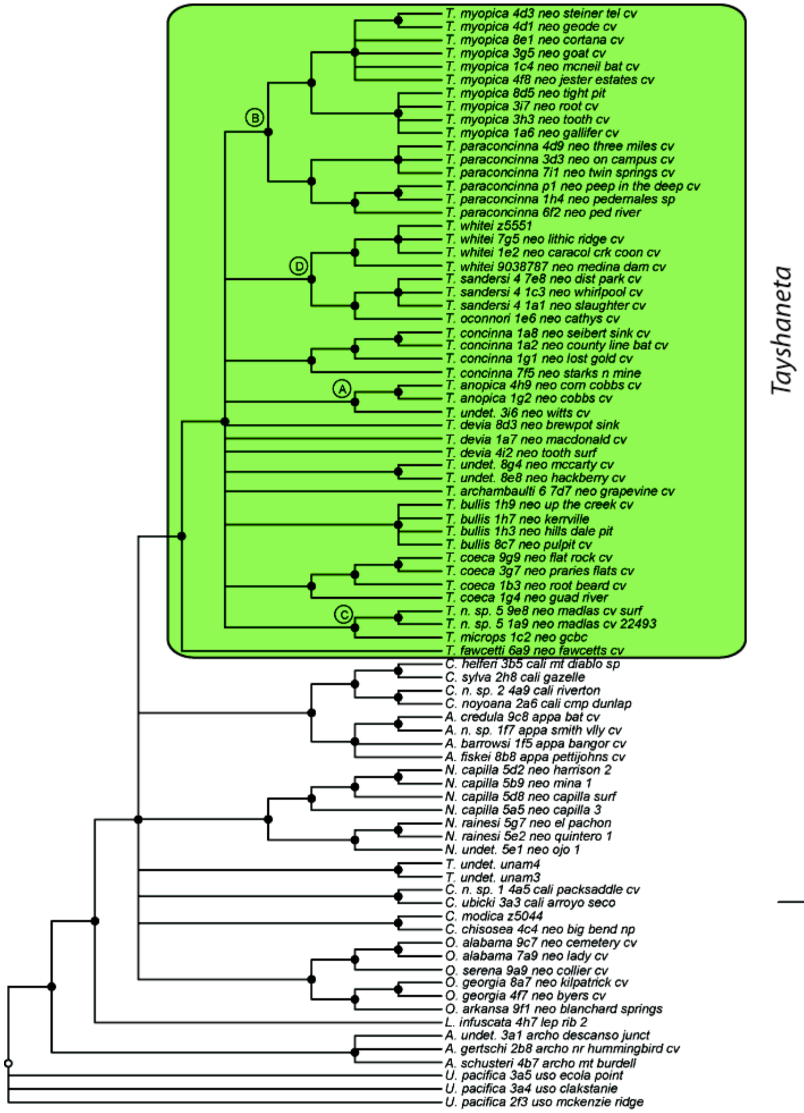
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T. coeca 1g4 neo guad river
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T. n. sp. 5 1a9 neo madlas cv 22493
T. microps 1c2 neo gcbc
T. fawcetti 6a9 neo fawcetts cv
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C. sylva 2h8 cali gazelle
C. n. sp. 2 4a9 cali riverton
C. noyoana 2a6 cali cmp dunlap
A. credula 9c8 appa bat cv
A. n. sp. 1f7 appa smith vlly cv
A. barrowsi 1f5 appa bangor cv
A. fiskei 8b8 appa pettijohns cv
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N. capilla 5b9 neo mina 1
N. capilla 5d8 neo capilla surf
N. capilla 5a5 neo capilla 3
N. rainesi 5g7 neo el pachon
N. rainesi 5e2 neo quintero 1
N. undet. 5e1 neo ojo 1
T. undet. unam4
T. undet. unam3
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C. ubicki 3a3 cali arroyo seco
C. modica z5044
C. chisosea 4c4 neo big bend np
O. alabama 9c7 neo cemetery cv
O. alabama 7a9 neo lady cv
O. serena 9a9 neo collier cv
O. georgia 8a7 neo kilpatrick cv
O. georgia 4f7 neo byers cv
O. arkansa 9f1 neo blanchard springs
L. infuscata 4h7 lep rib 2
A. undet. 3a1 archo descanso junct
A. gertschi 2b8 archo nr hummingbird cv
A. schusteri 4b7 archo mt burdell
U. pacifica 3a5 uso ecola point
U. pacifica 3a4 uso clakstanie
U. pacifica 2f3 uso mckenzie ridge
B
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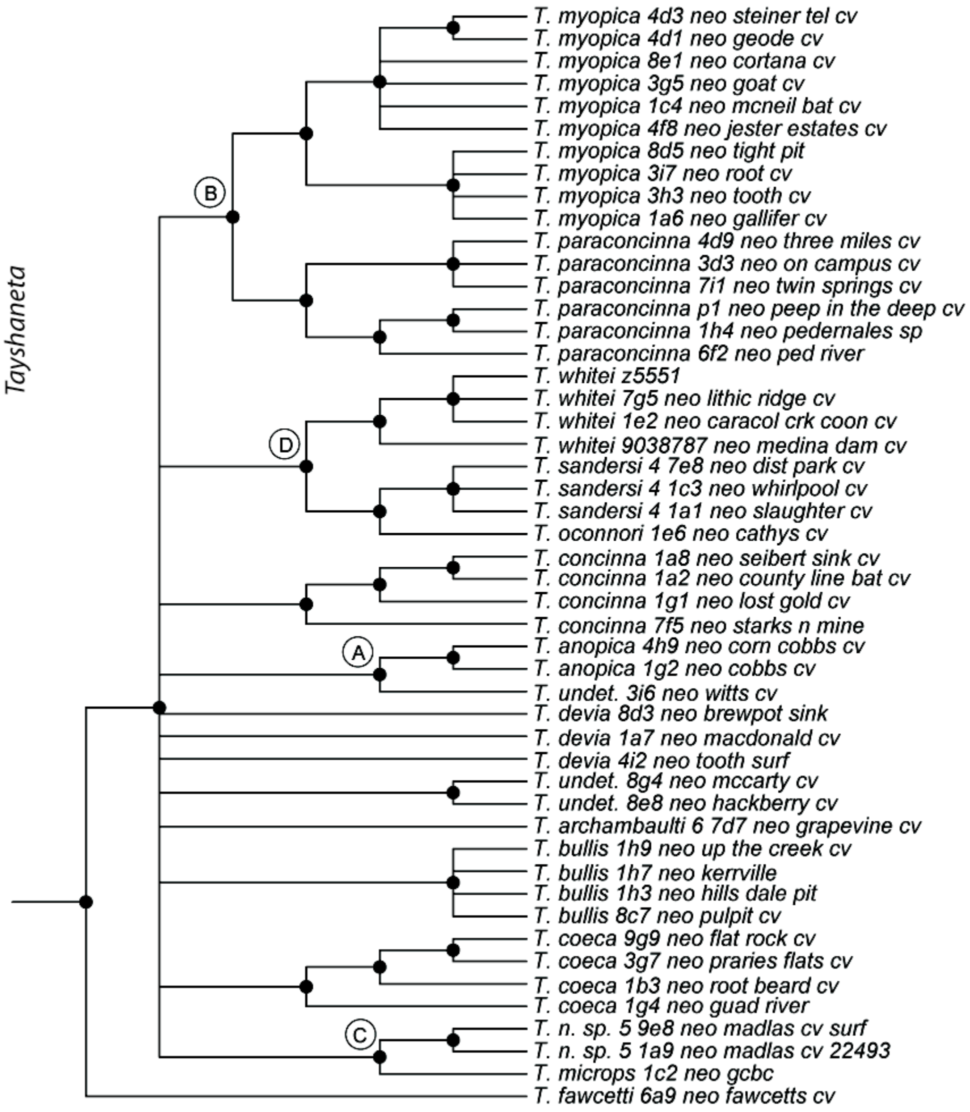
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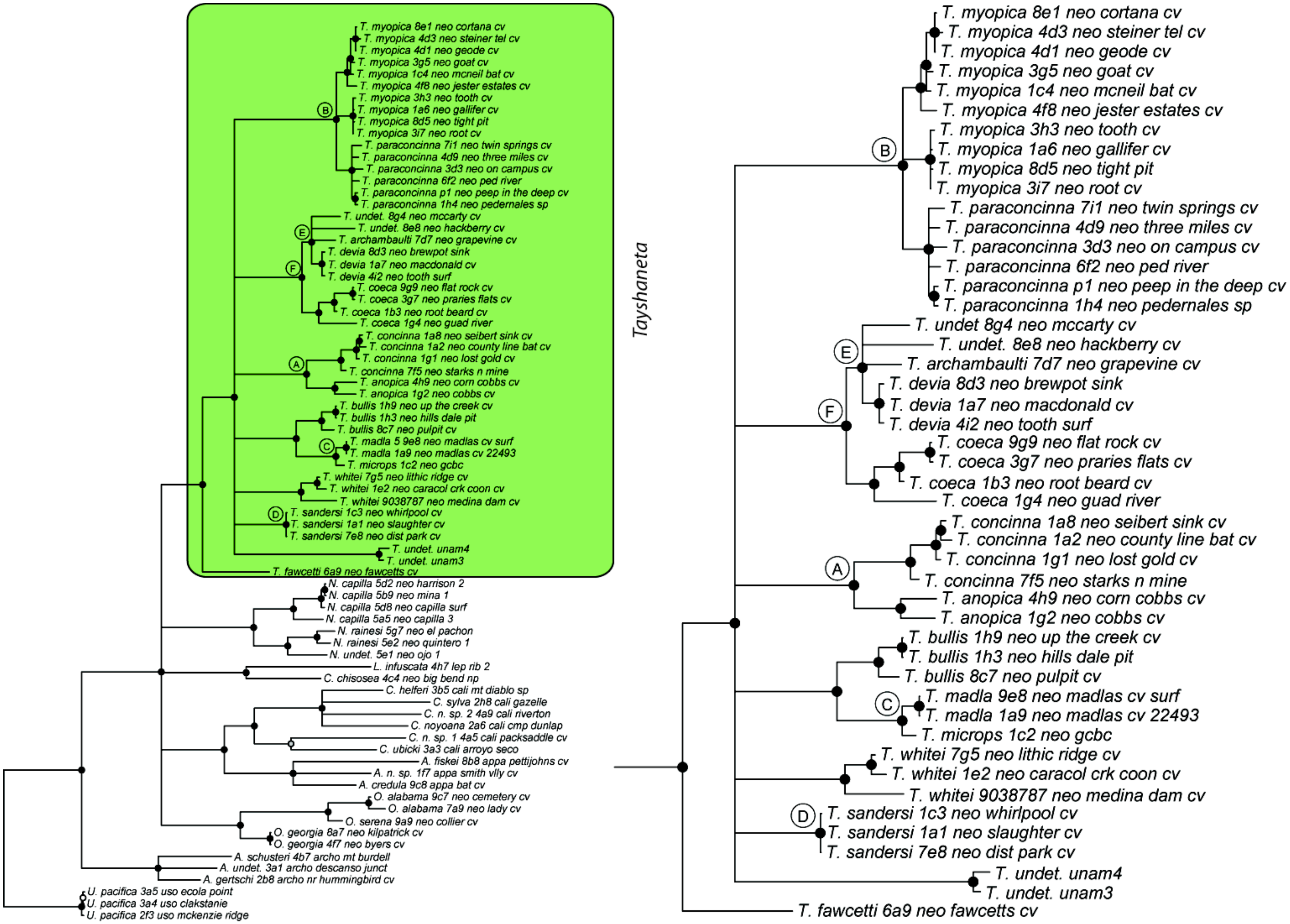
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C. chisosea 4c4 neo big bend np
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C. n. sp. 2 4a9 cali riverton
C. noyoana 2a6 cali cmp dunlap
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O. serena 9a9 neo collier cv
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U. pacifica 2f3 uso mckenzie ridge
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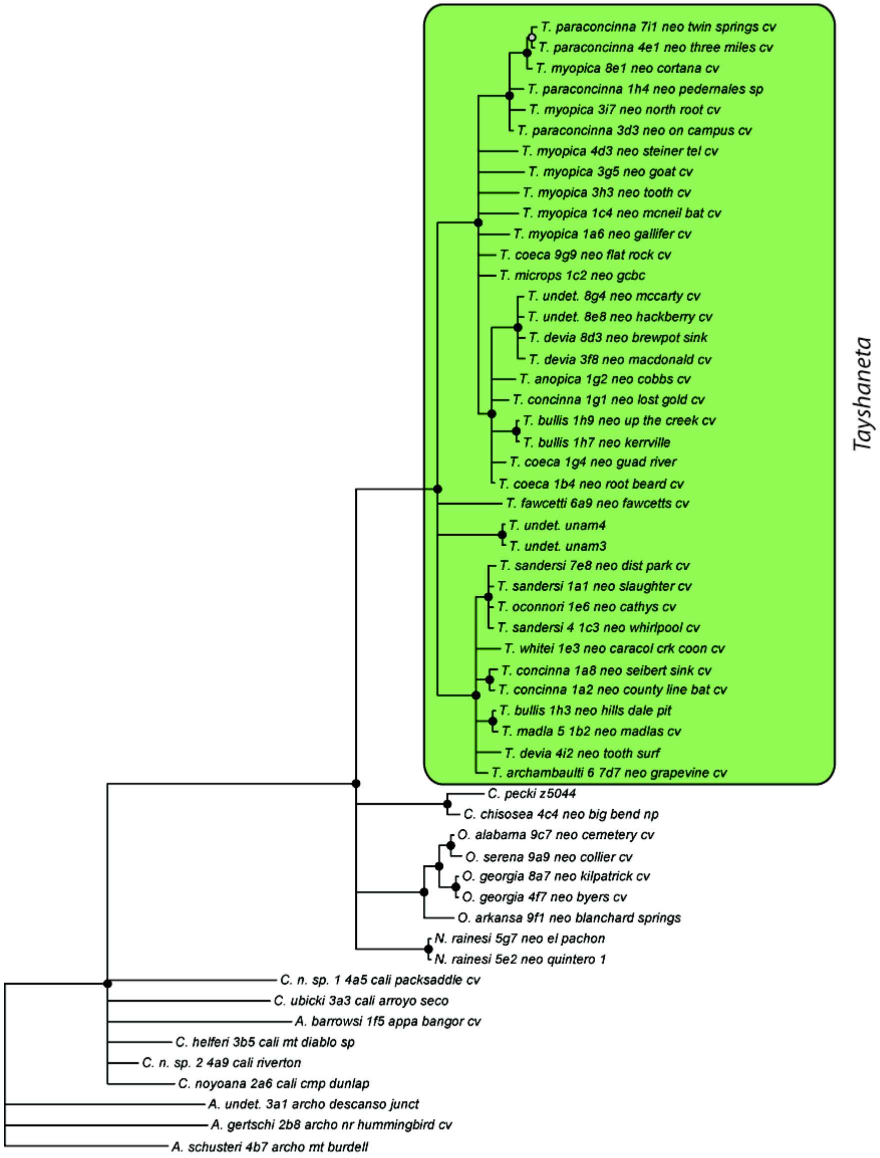
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T. undet. unam3
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T. oconnori 1e6 neo cathys cv
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T. concinna 1a2 neo county line bat cv
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T. devia 4i2 neo tooth surf
T. archambaulti 6 7d7 neo grapevine cv
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C. chisosea 4c4 neo big bend np
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O. georgia 4f7 neo byers cv
O. arkansa 9f1 neo blanchard springs
N. rainesi 5g7 neo el pachon
N. rainesi 5e2 neo quintero 1
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C. ubicki 3a3 cali arroyo seco
A. barrowsi 1f5 appa bangor cv
C. helferi 3b5 cali mt diablo sp
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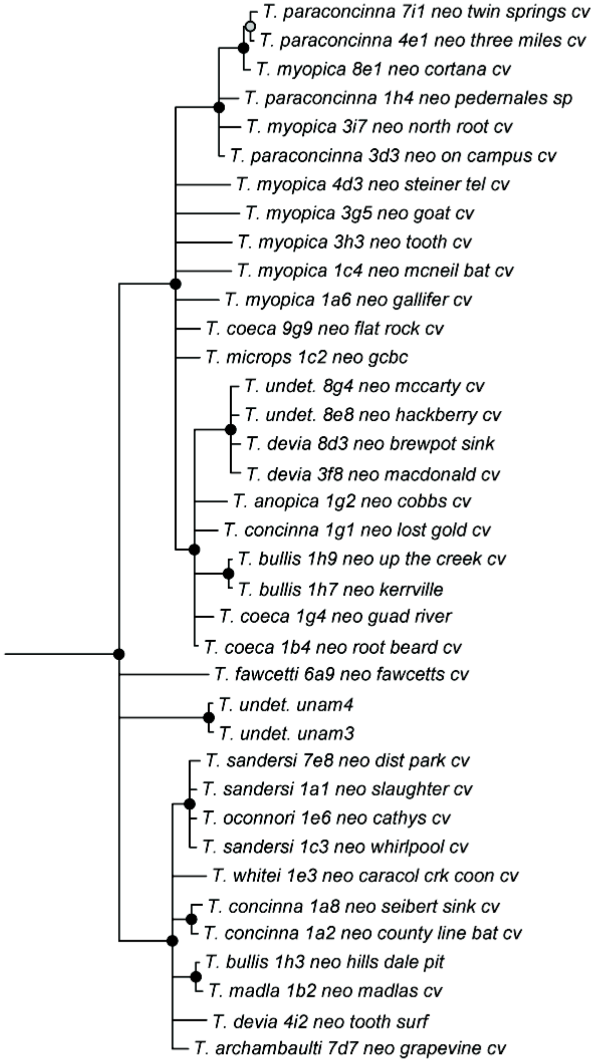
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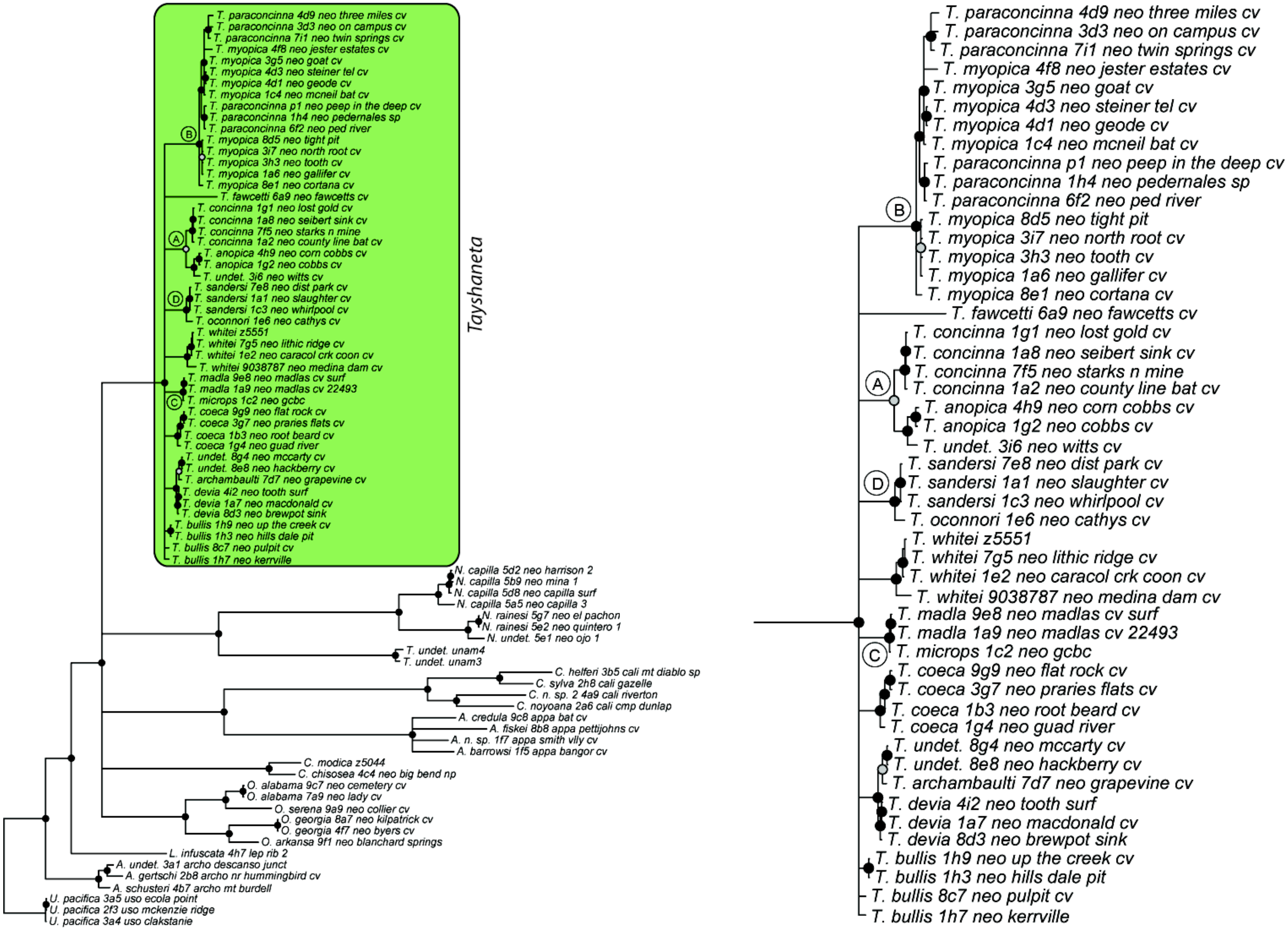

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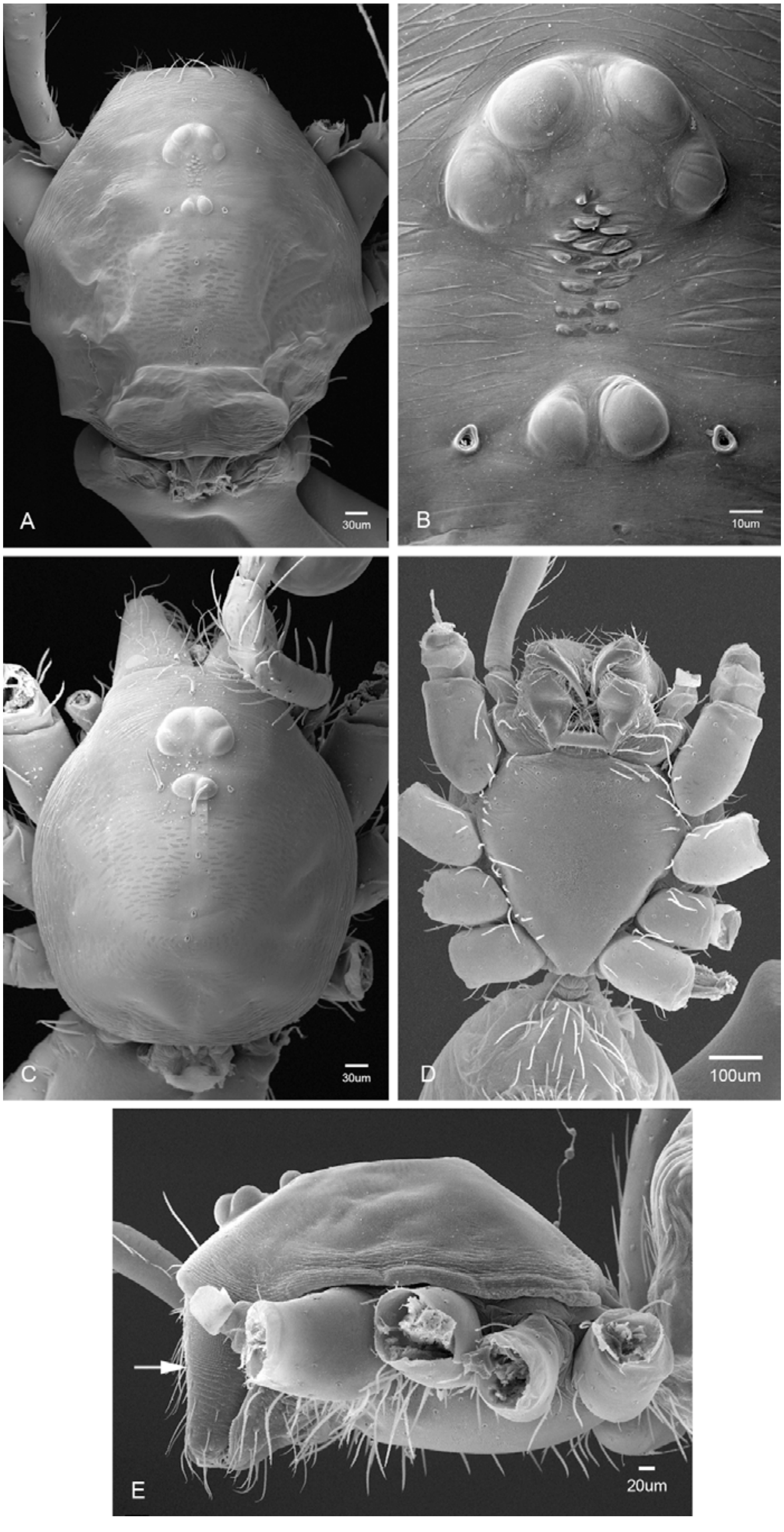
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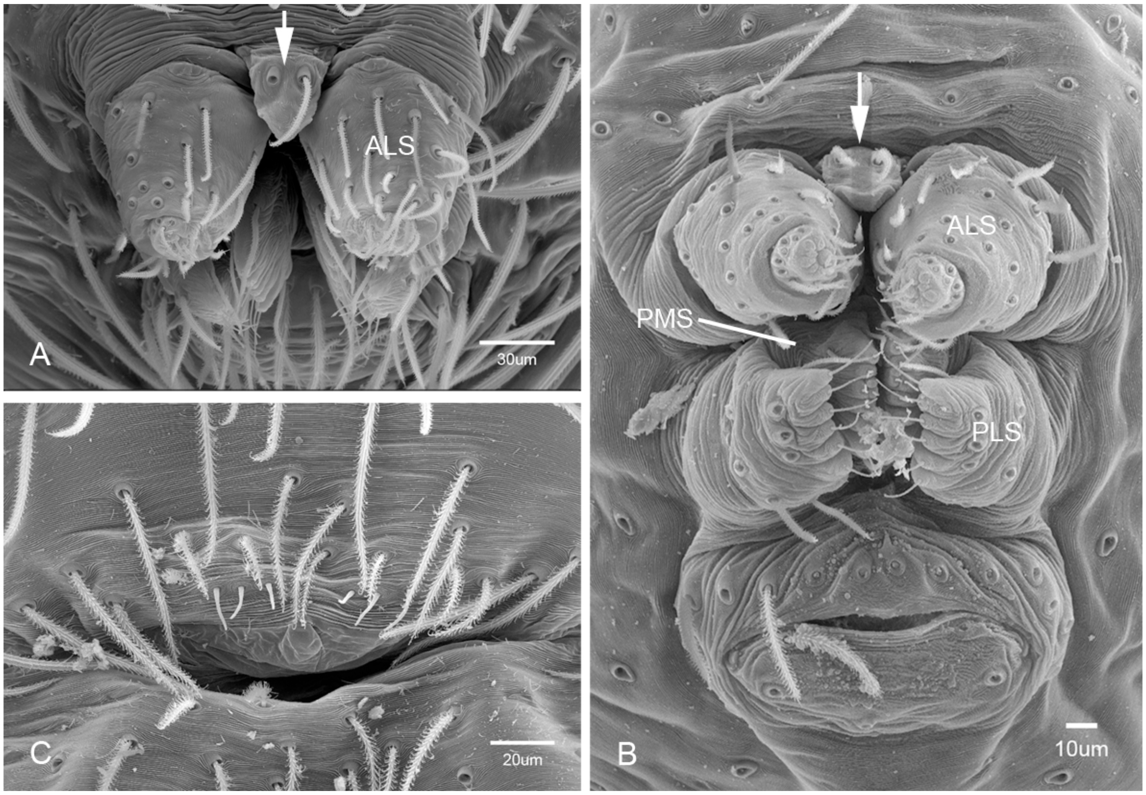
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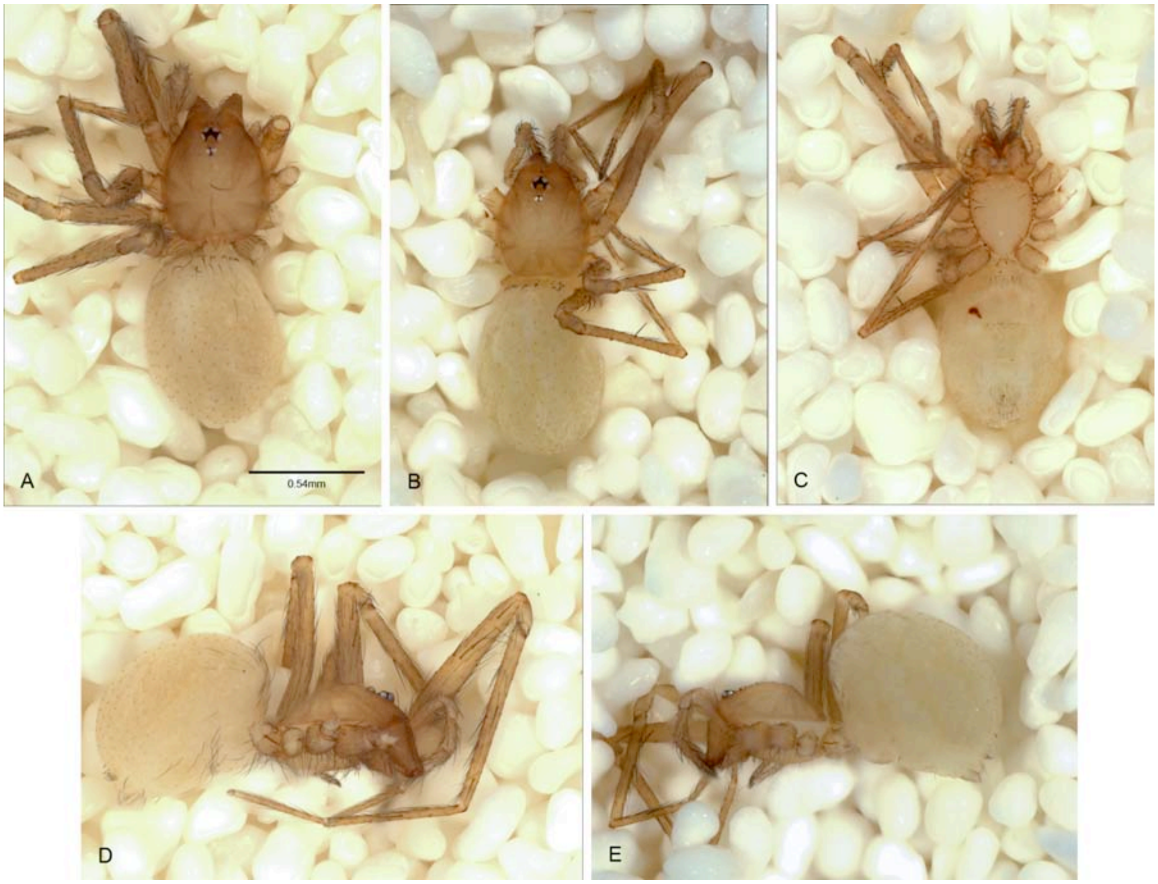
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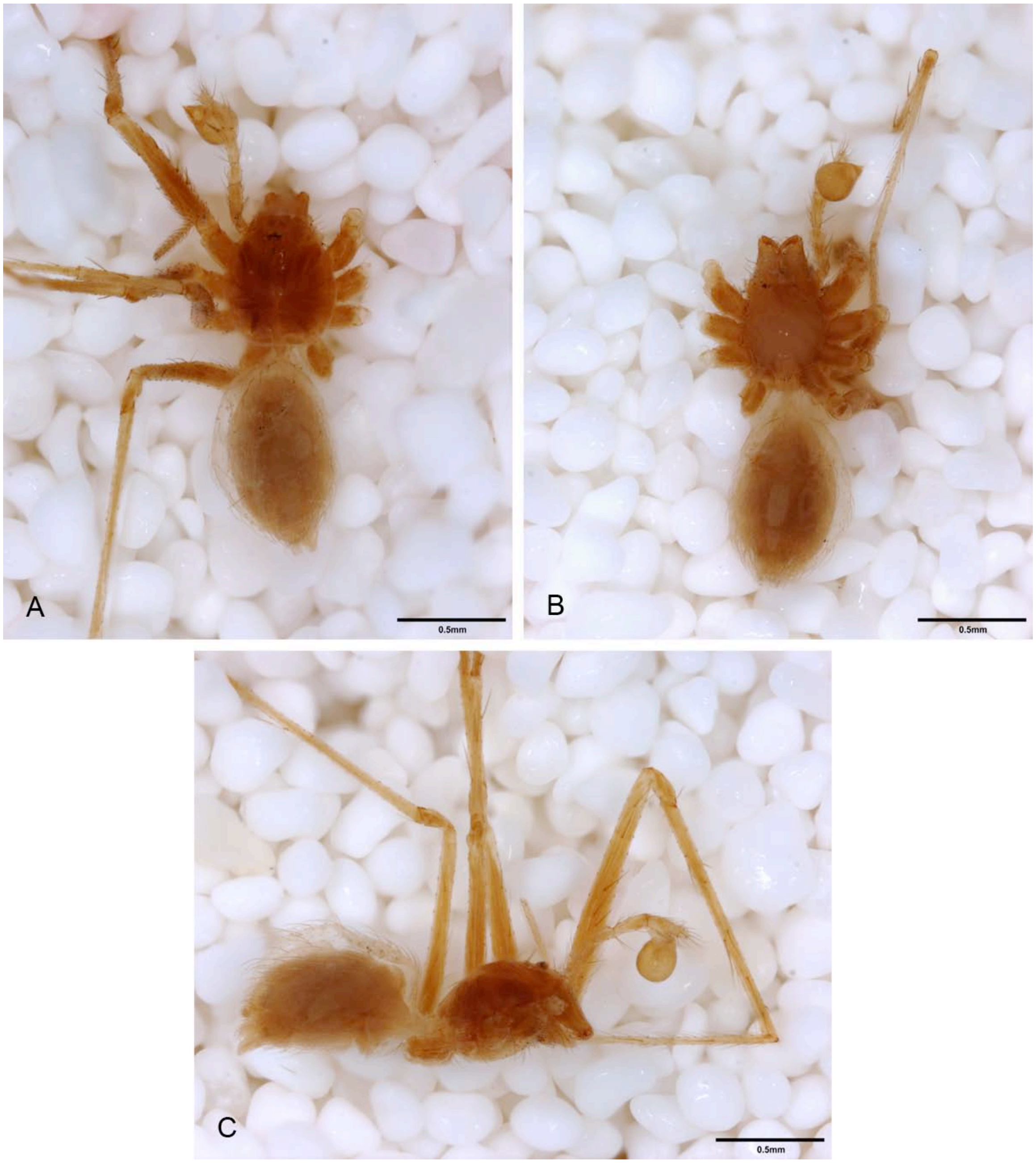
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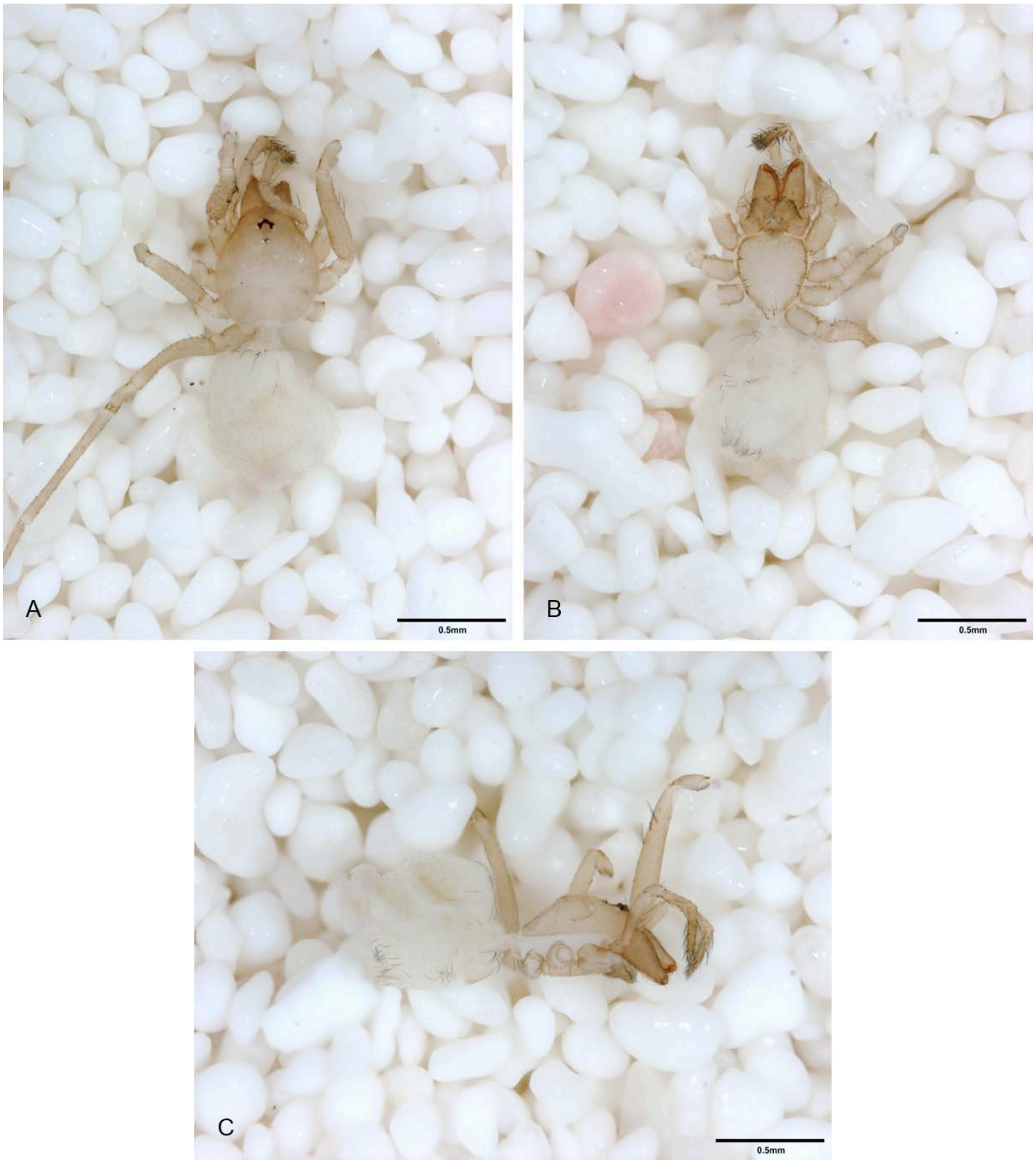
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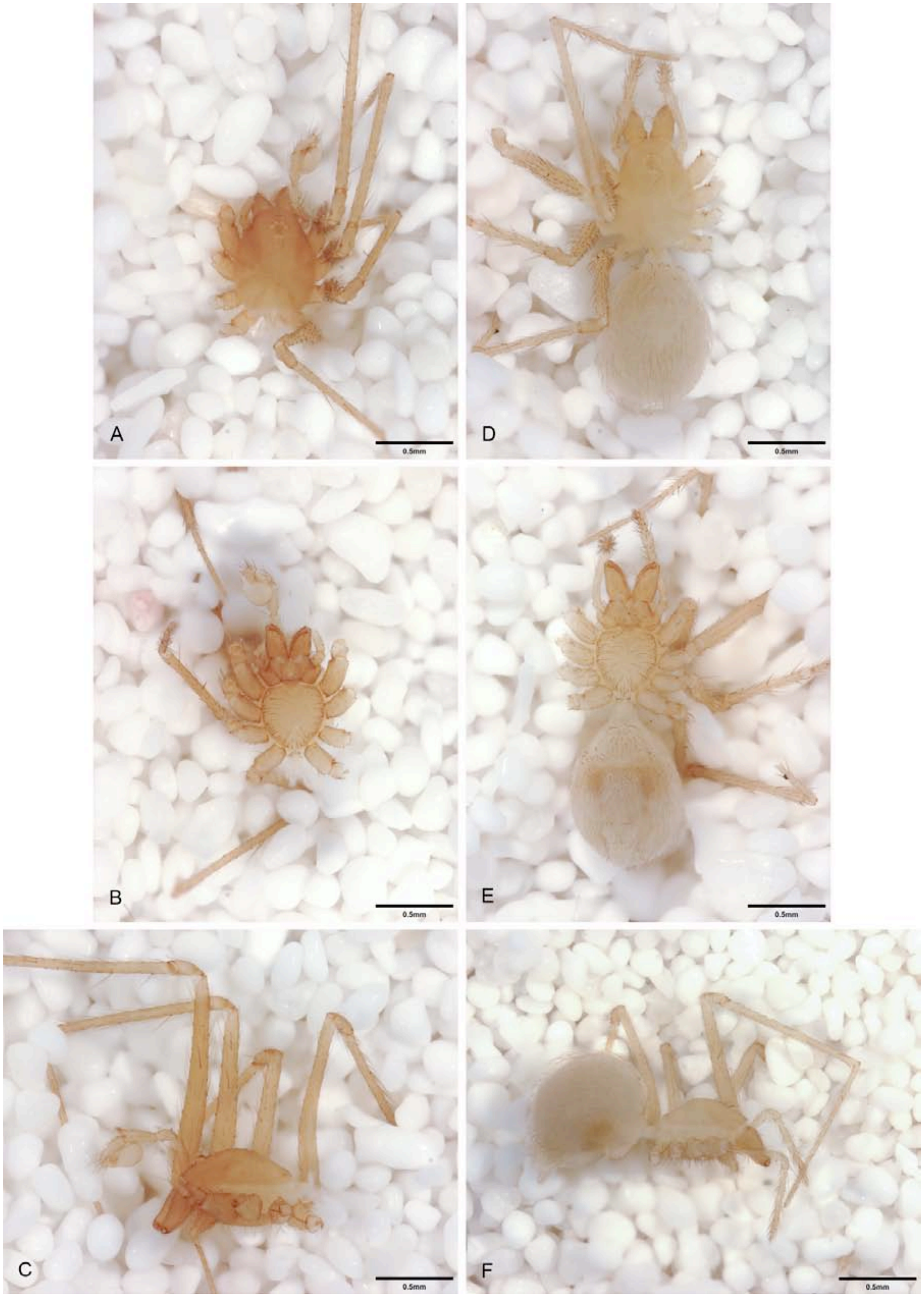
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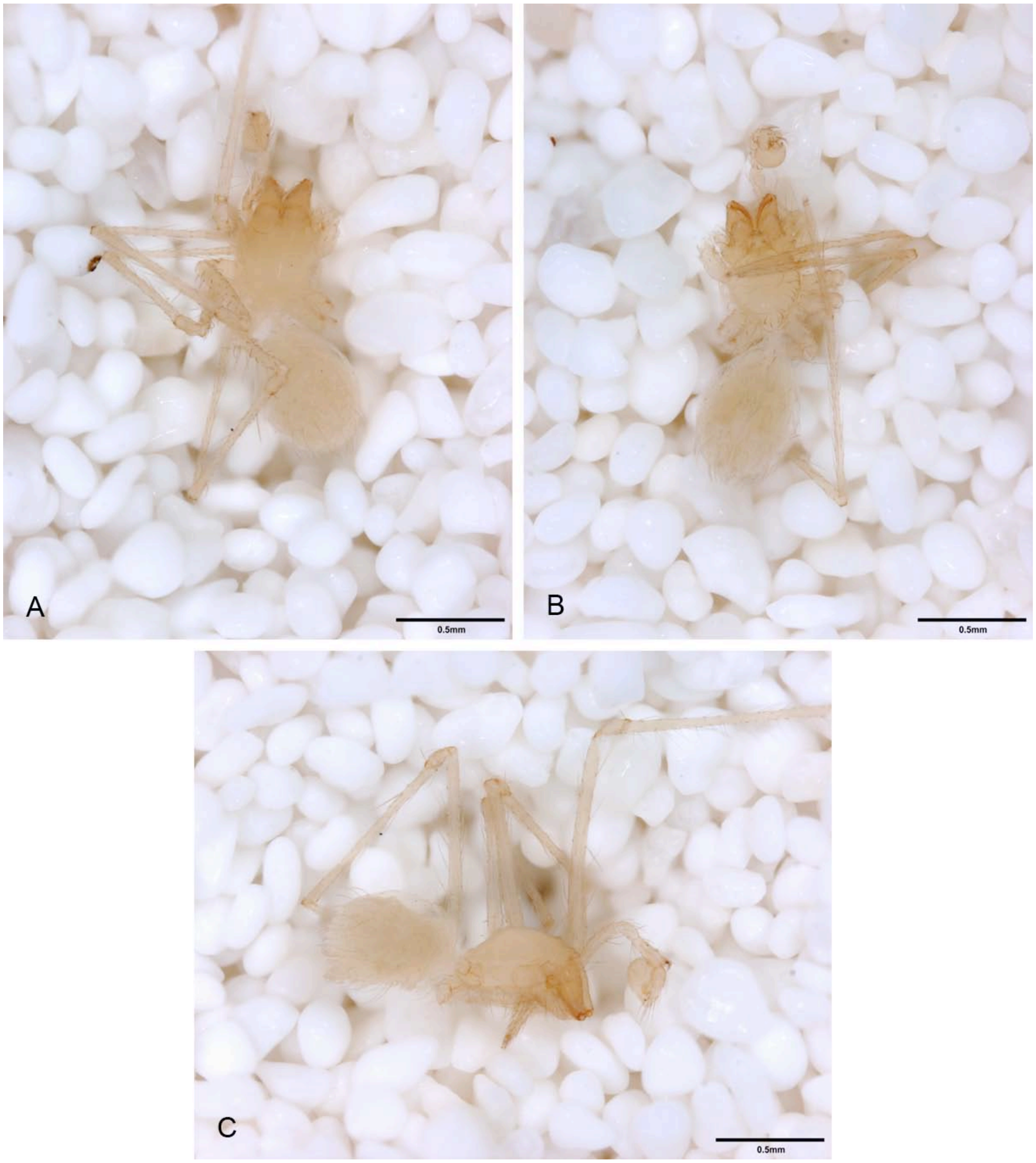
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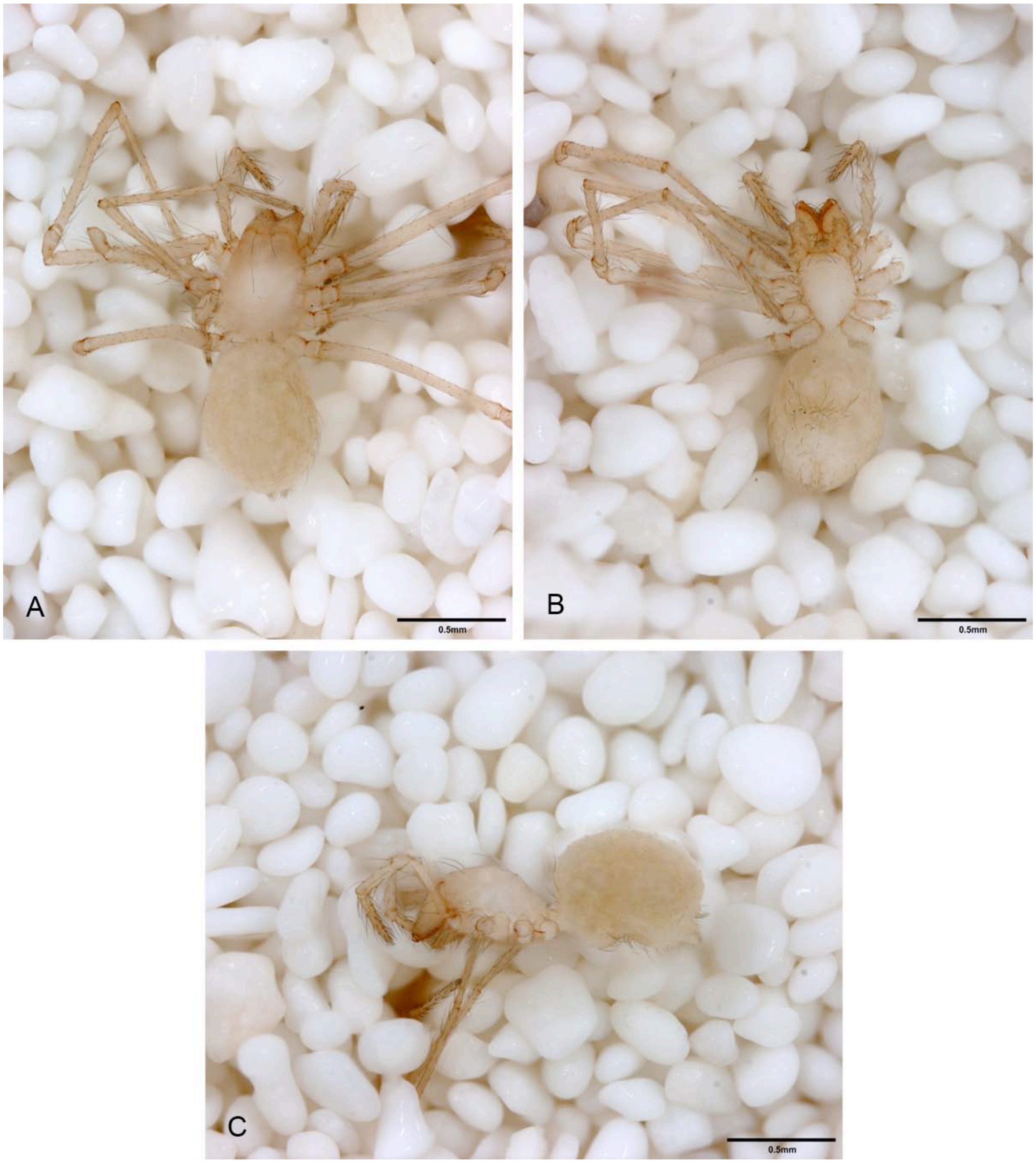
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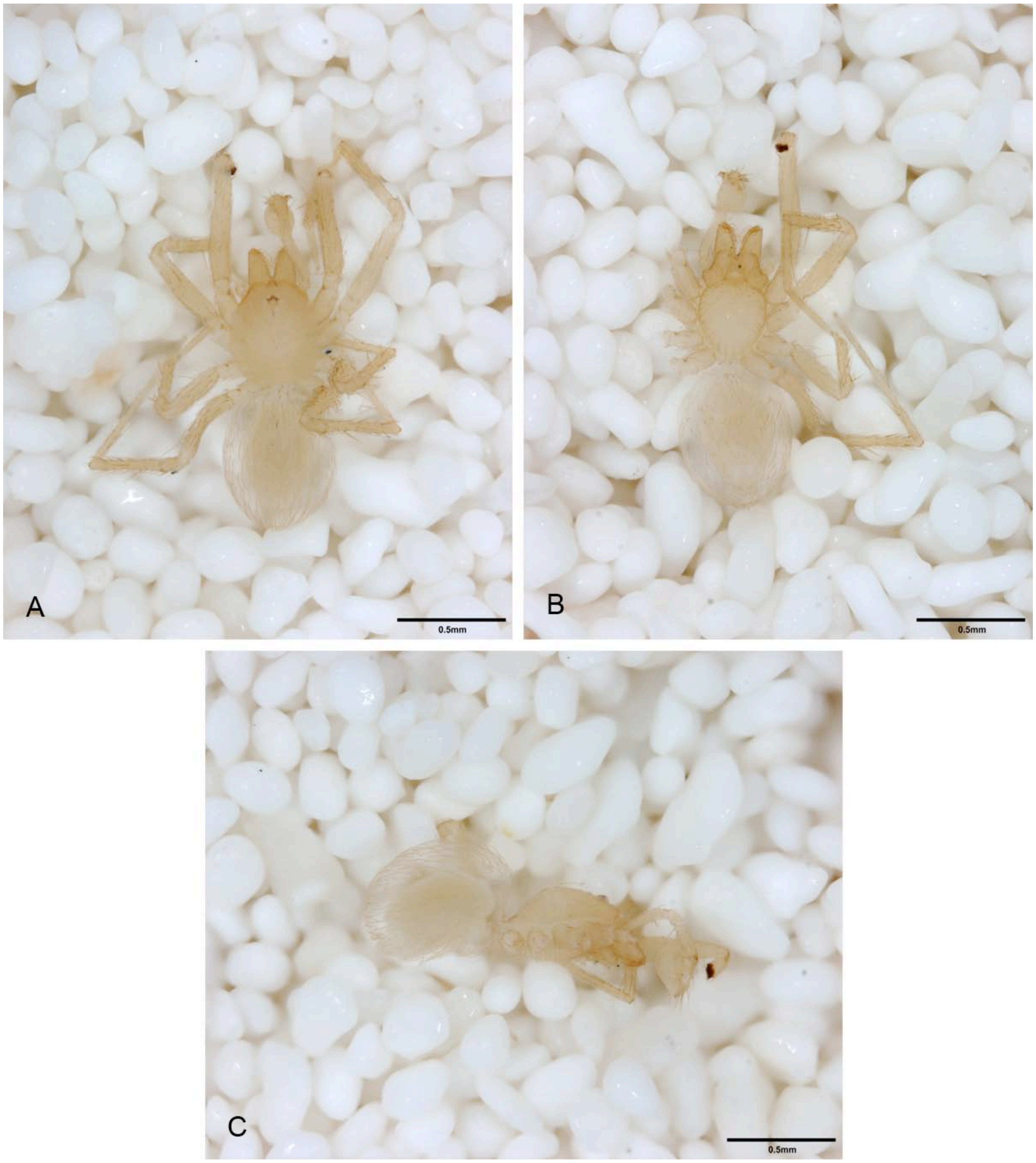
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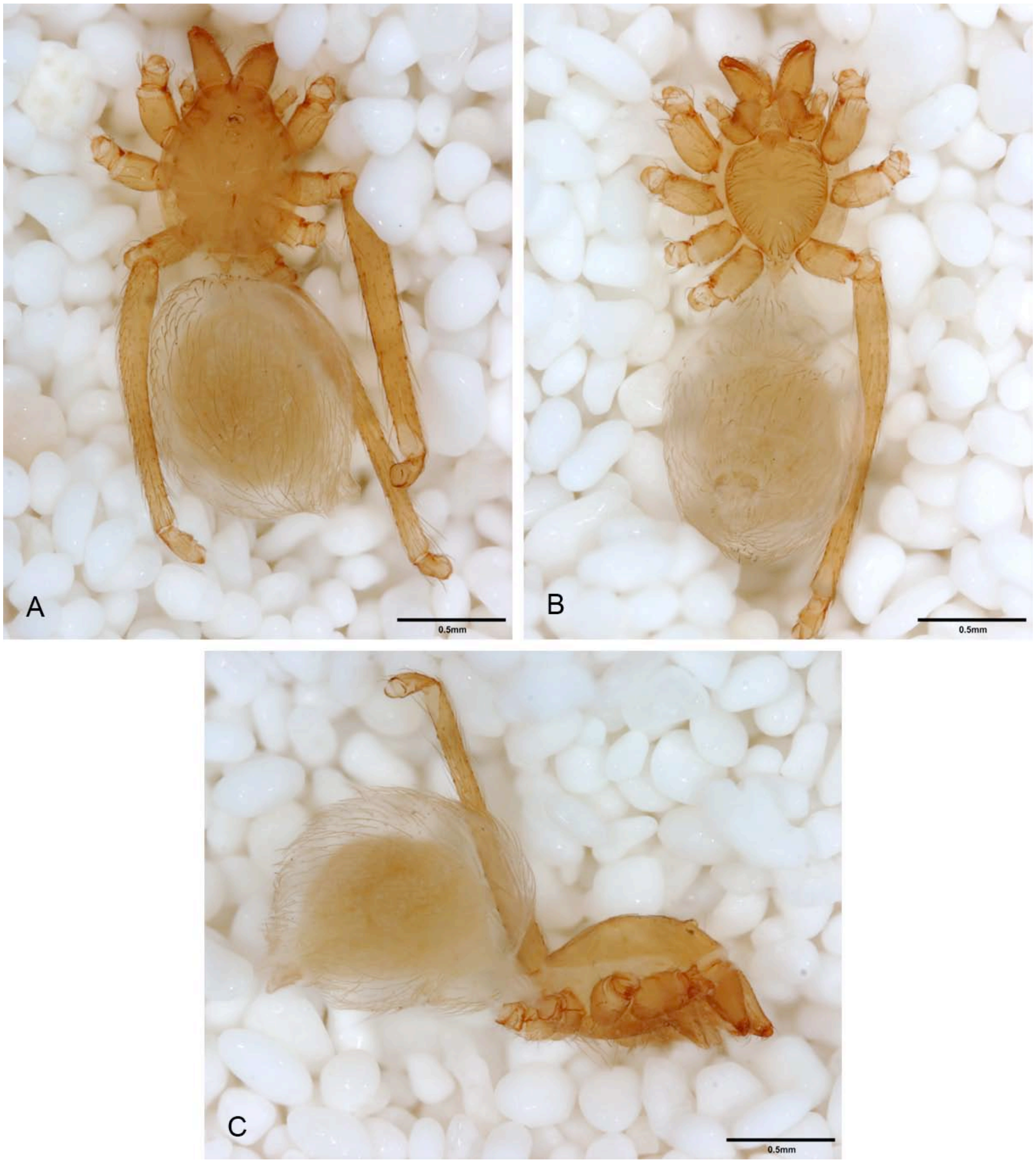
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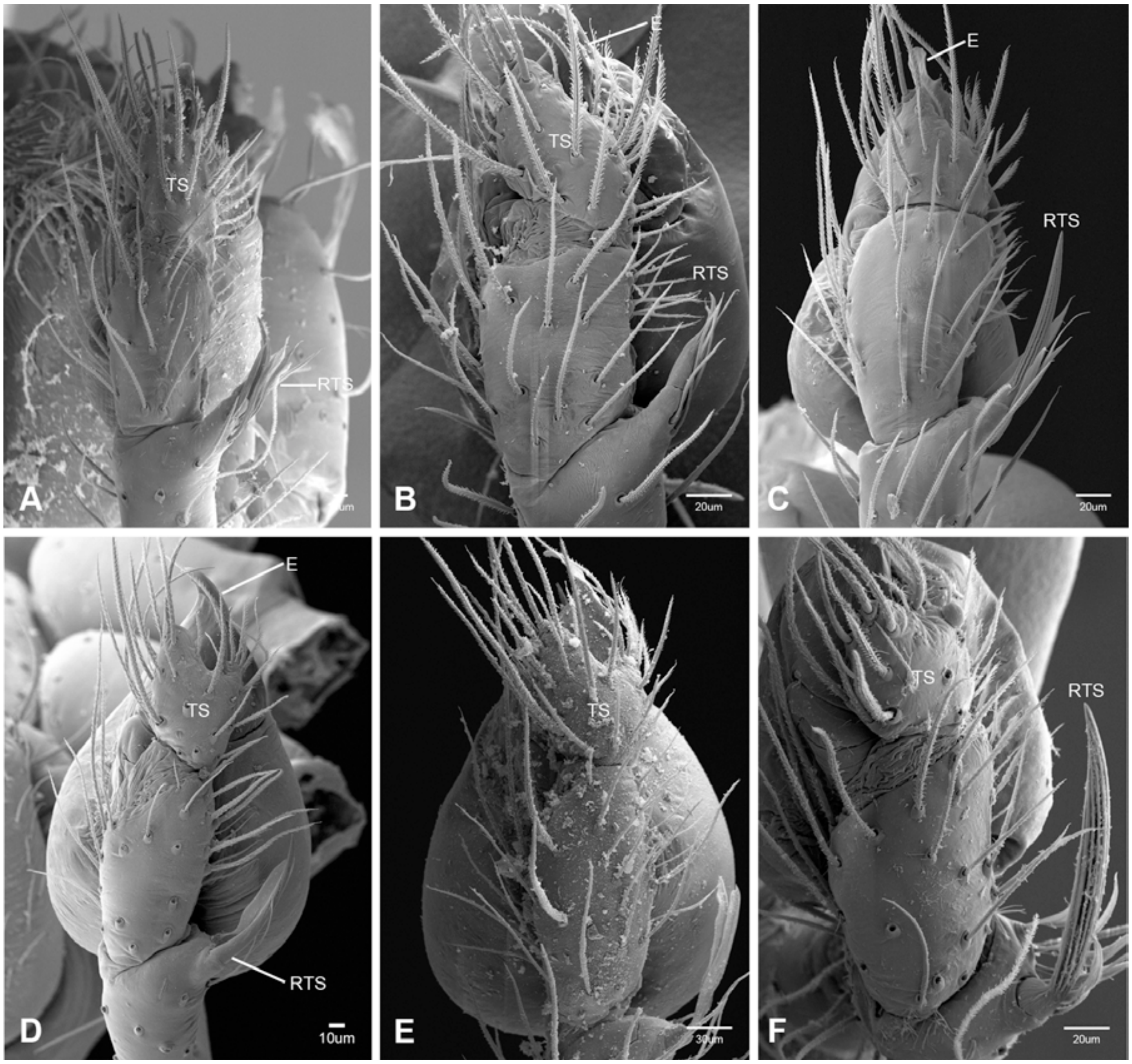
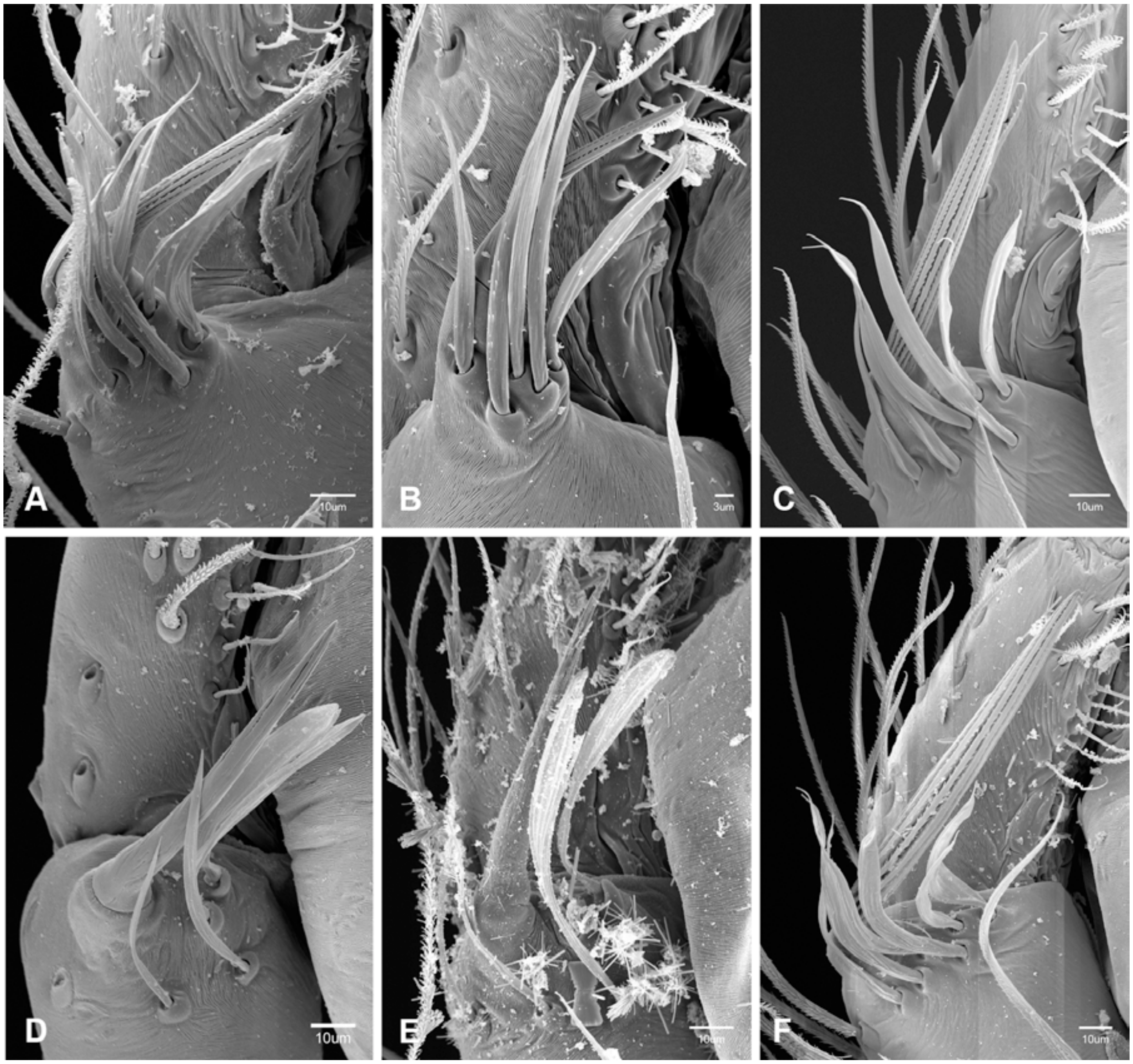
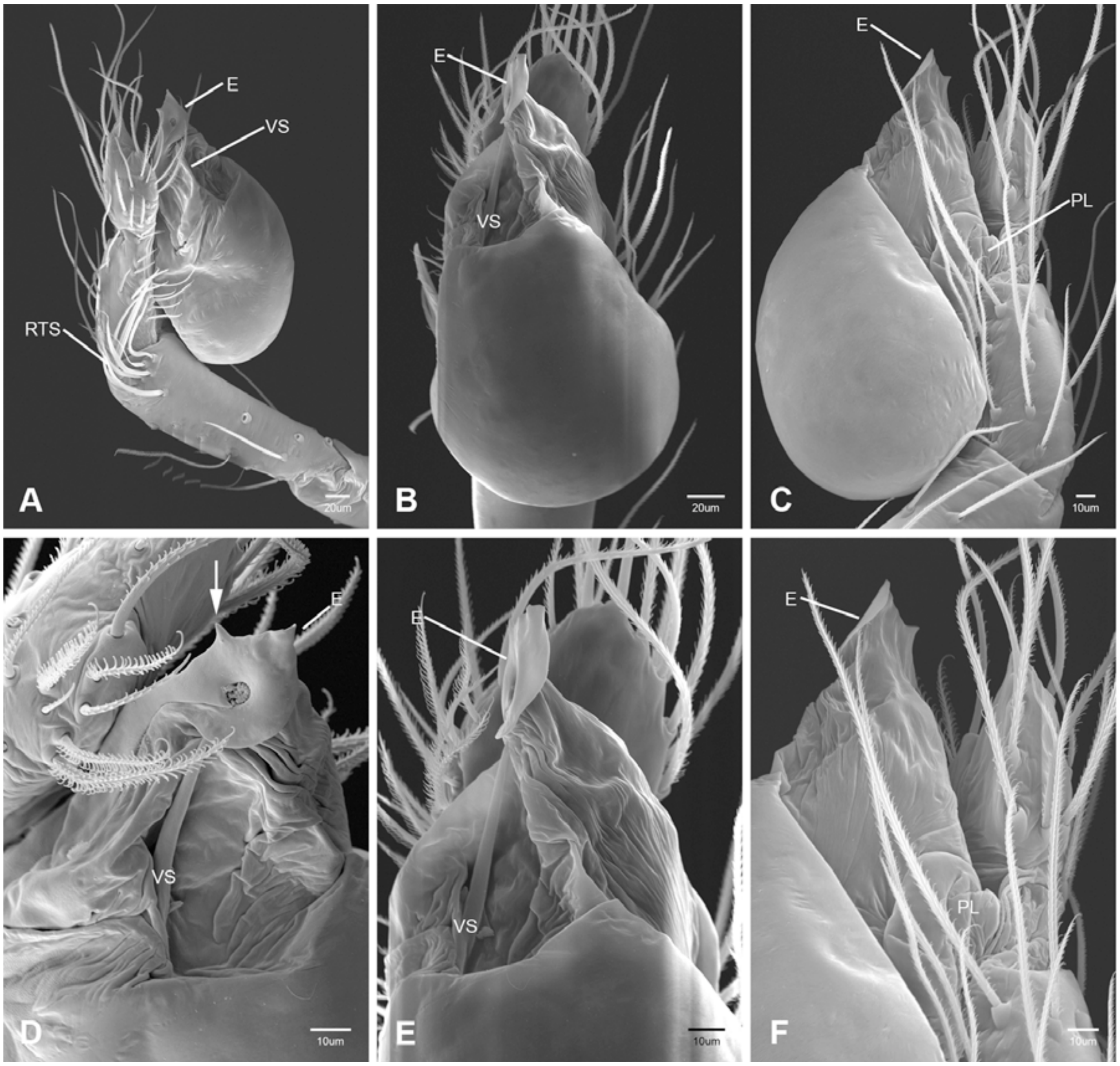
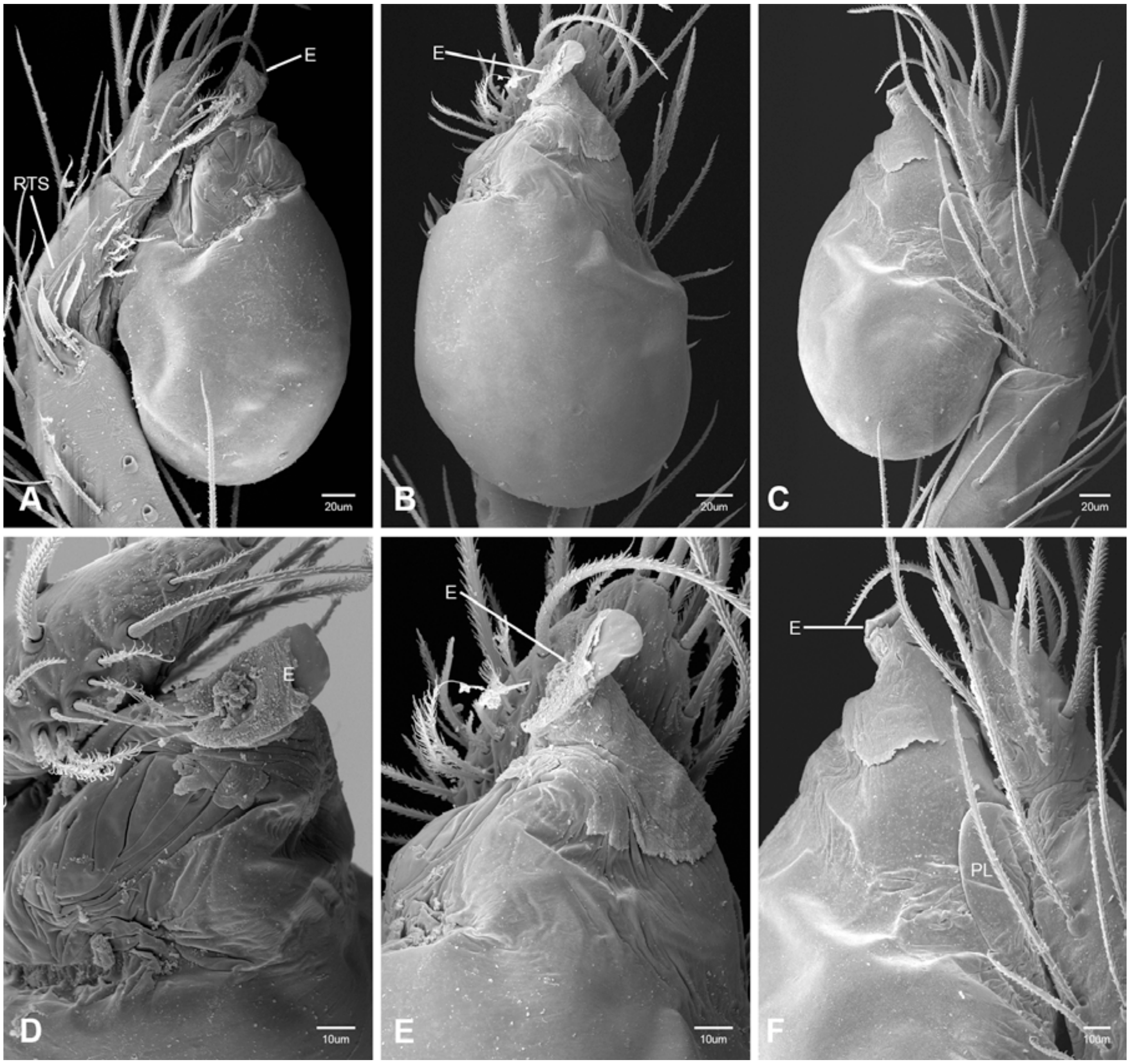
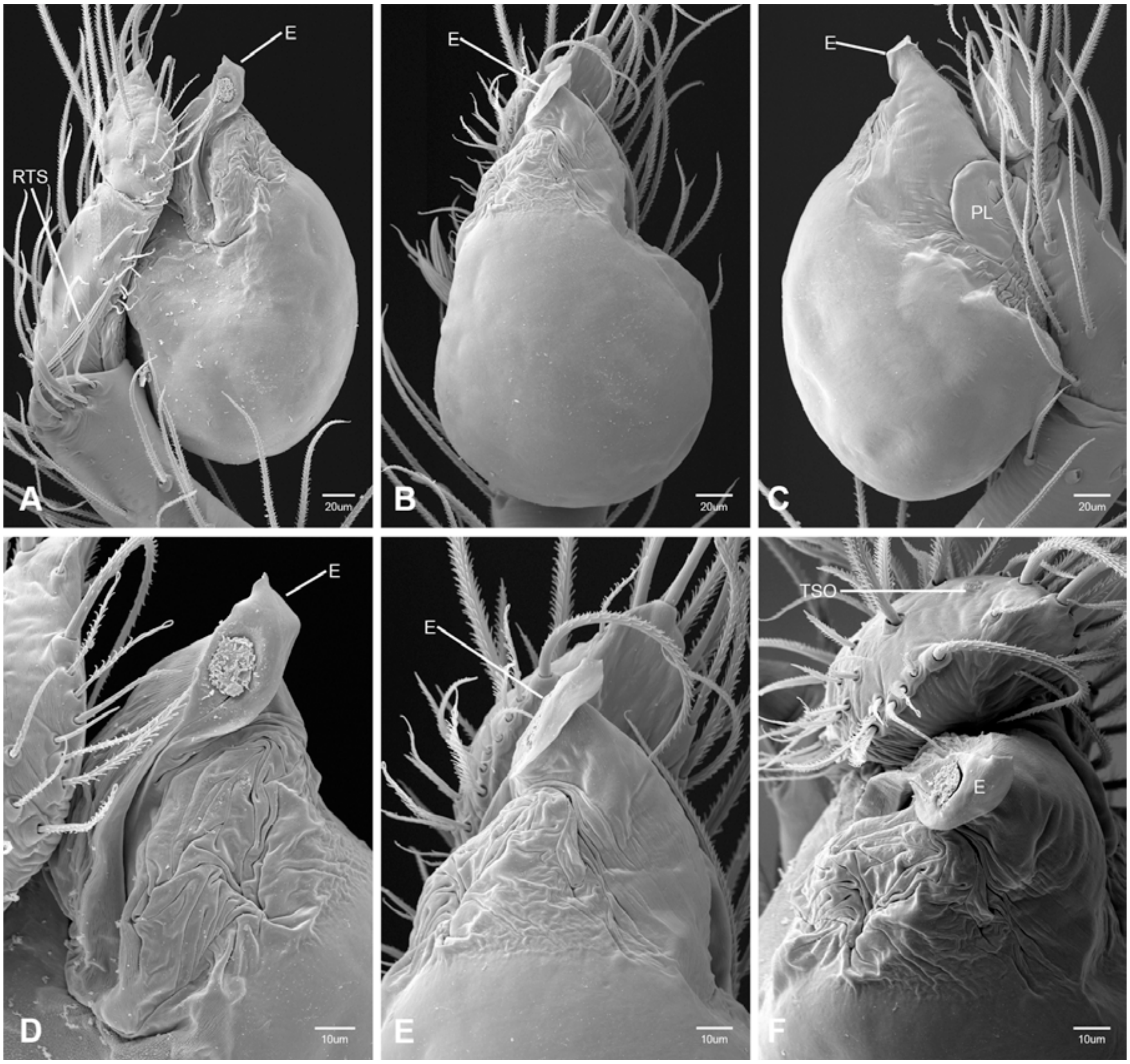
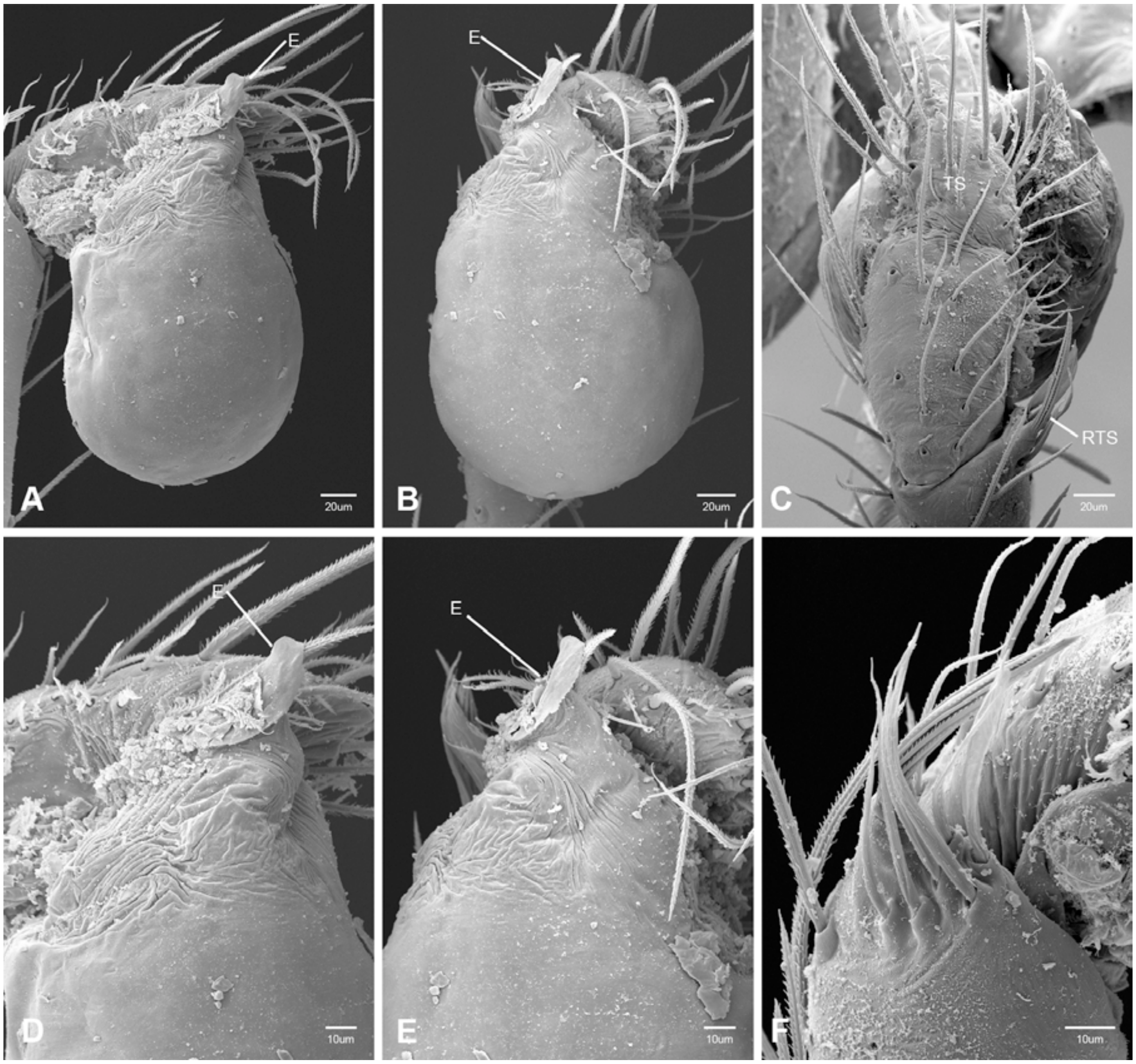

TS
RTS
A
E
TS
RTS
B
20um
E
RTS
C
20um
E
TS
RTS
D
10um
TS
E
30um
TS
RTS
F
20um

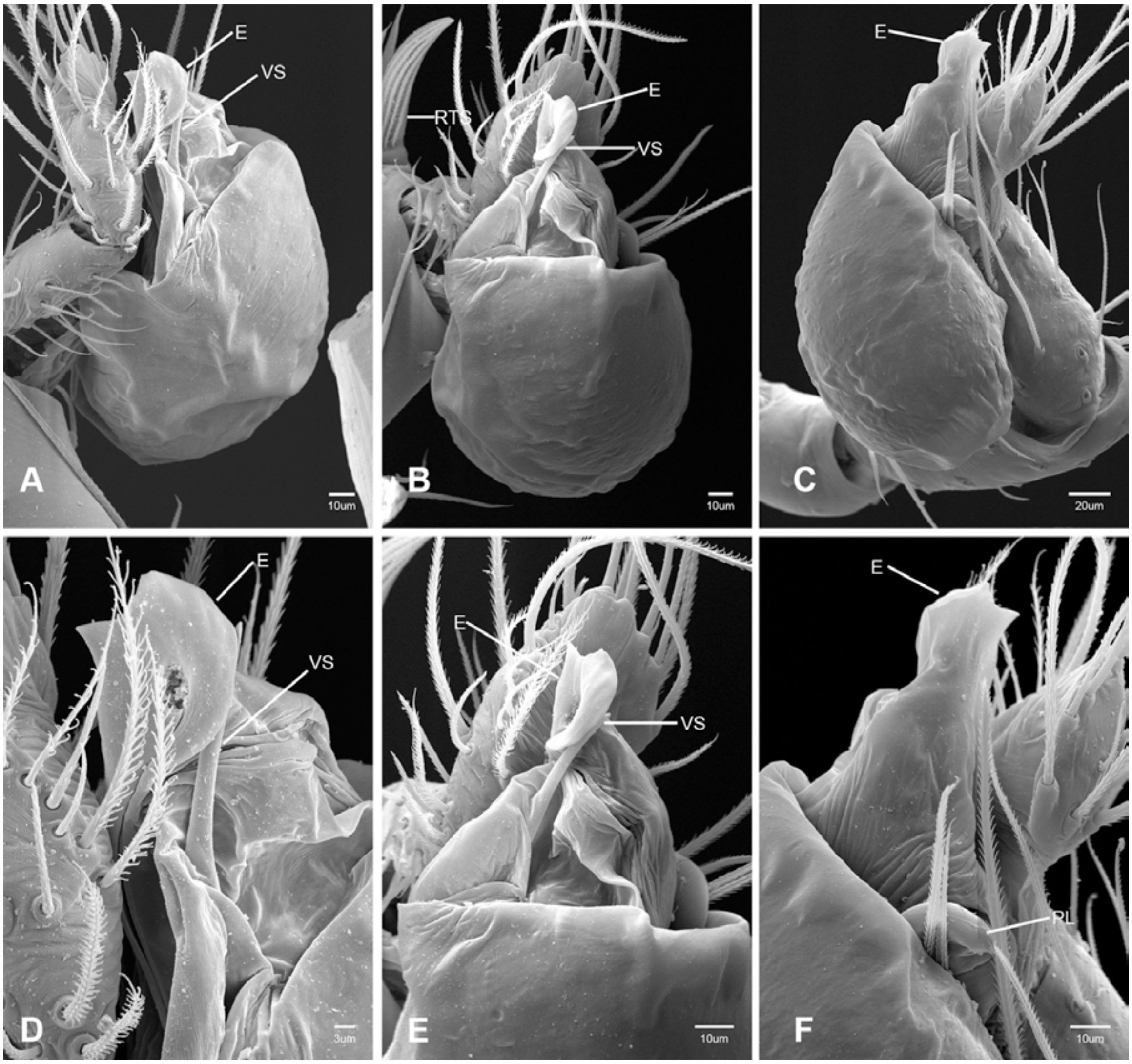

A
10um
B
3um
C
10um
D
10um
E
10um
F
10um

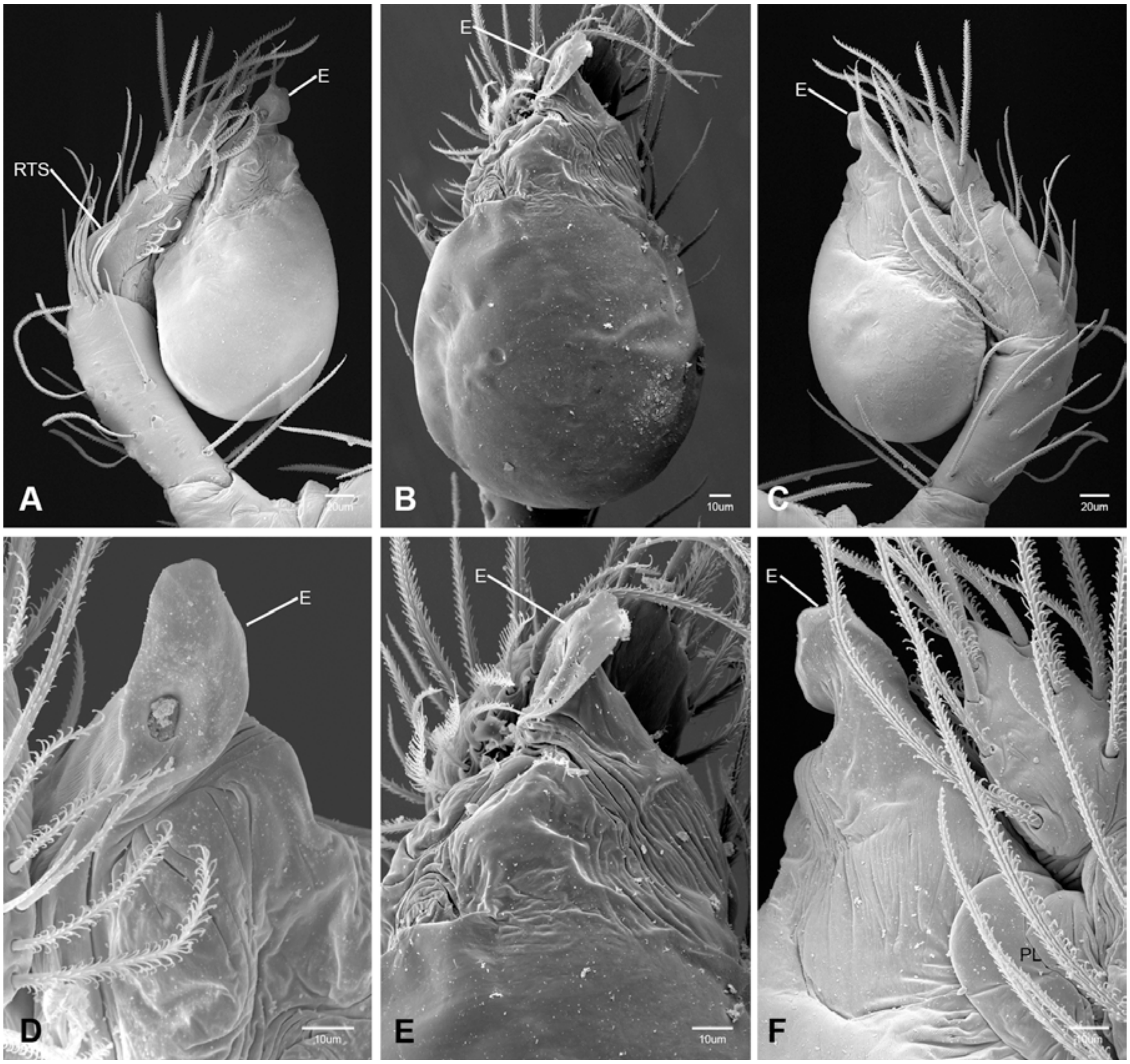

E
VS
RTS
A
20um
E
VS
B
20um
E
PL
C
10um
E
VS
D
10um
E
VS
E
10um
E
PL
F
10um


E
RTS
A
20um
E
B
20um
C
20um
E
D
10um
E
E
10um
E
PL
F
10um

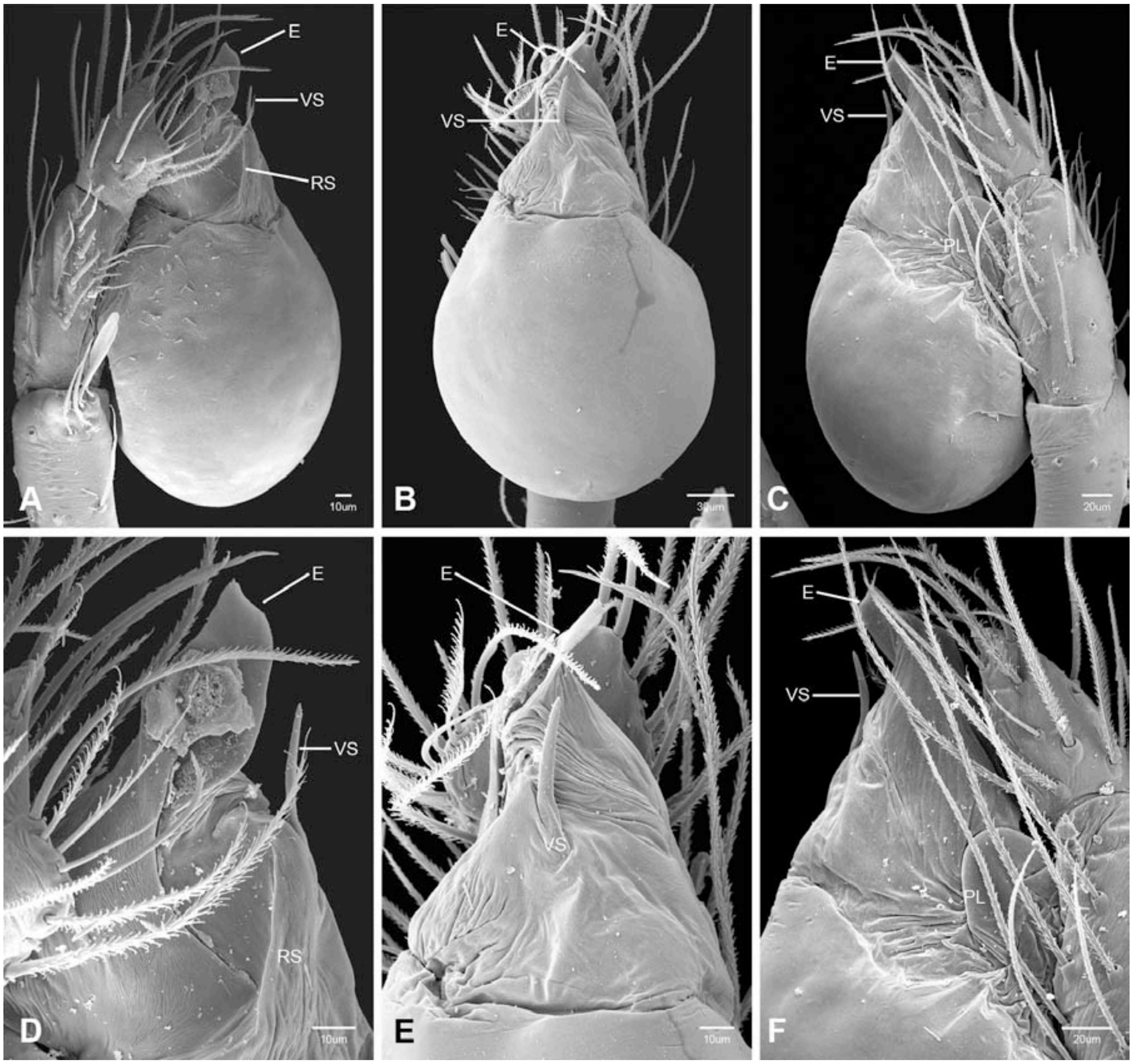

E
RTS
A
20um
E
B
20um
E
PL
C
20um
E
D
10um
E
E
10um
TSO
E
F
10um

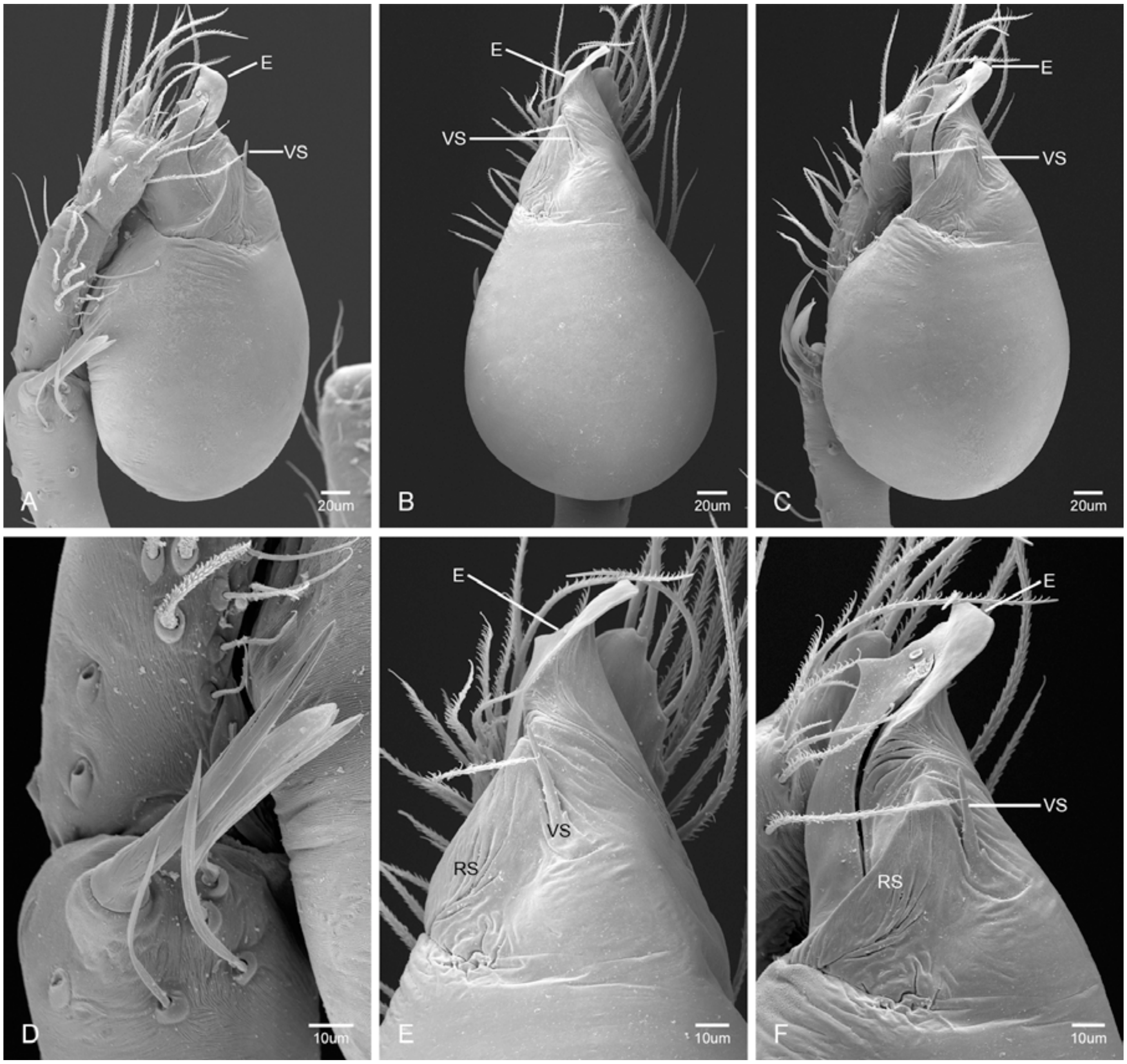

E
A
20um
E
B
20um
TS
RTS
C
20um
E
D
10um
E
E
10um
F
10um

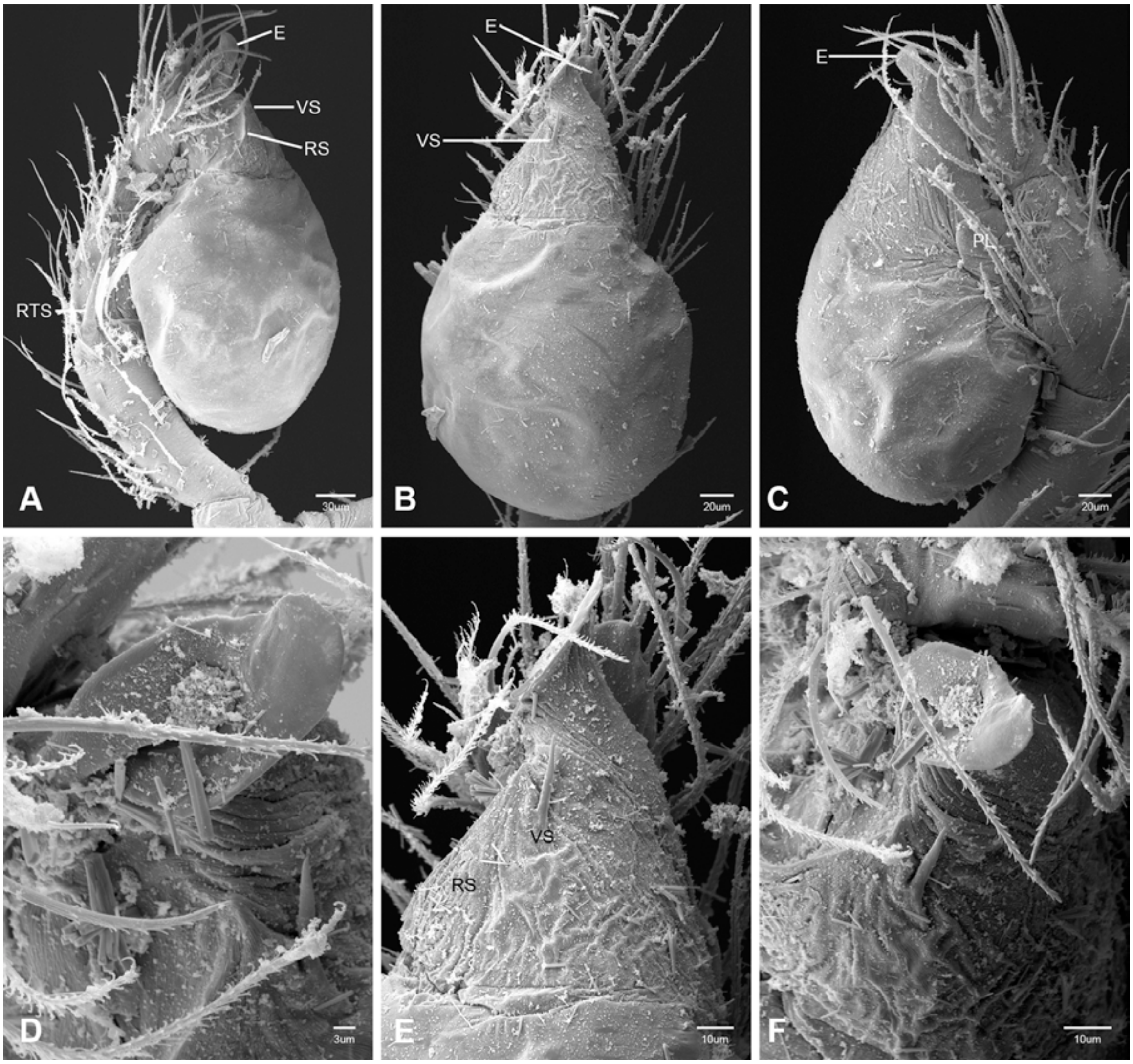

E
VS
A
10um
RTS
E
VS
B
10um
E
C
20um
E
VS
D
3um
E
VS
E
10um
E
PL
F
10um

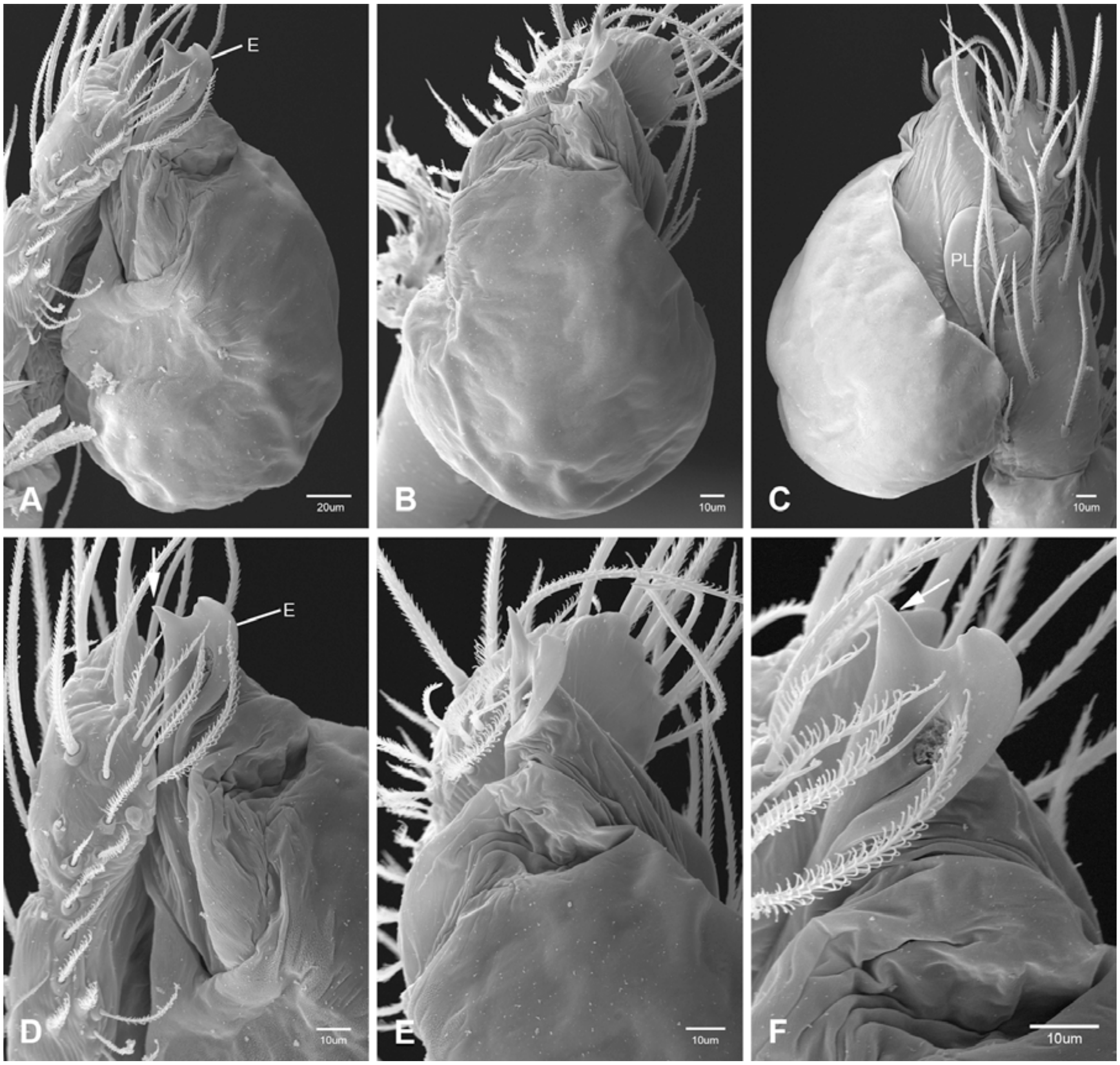


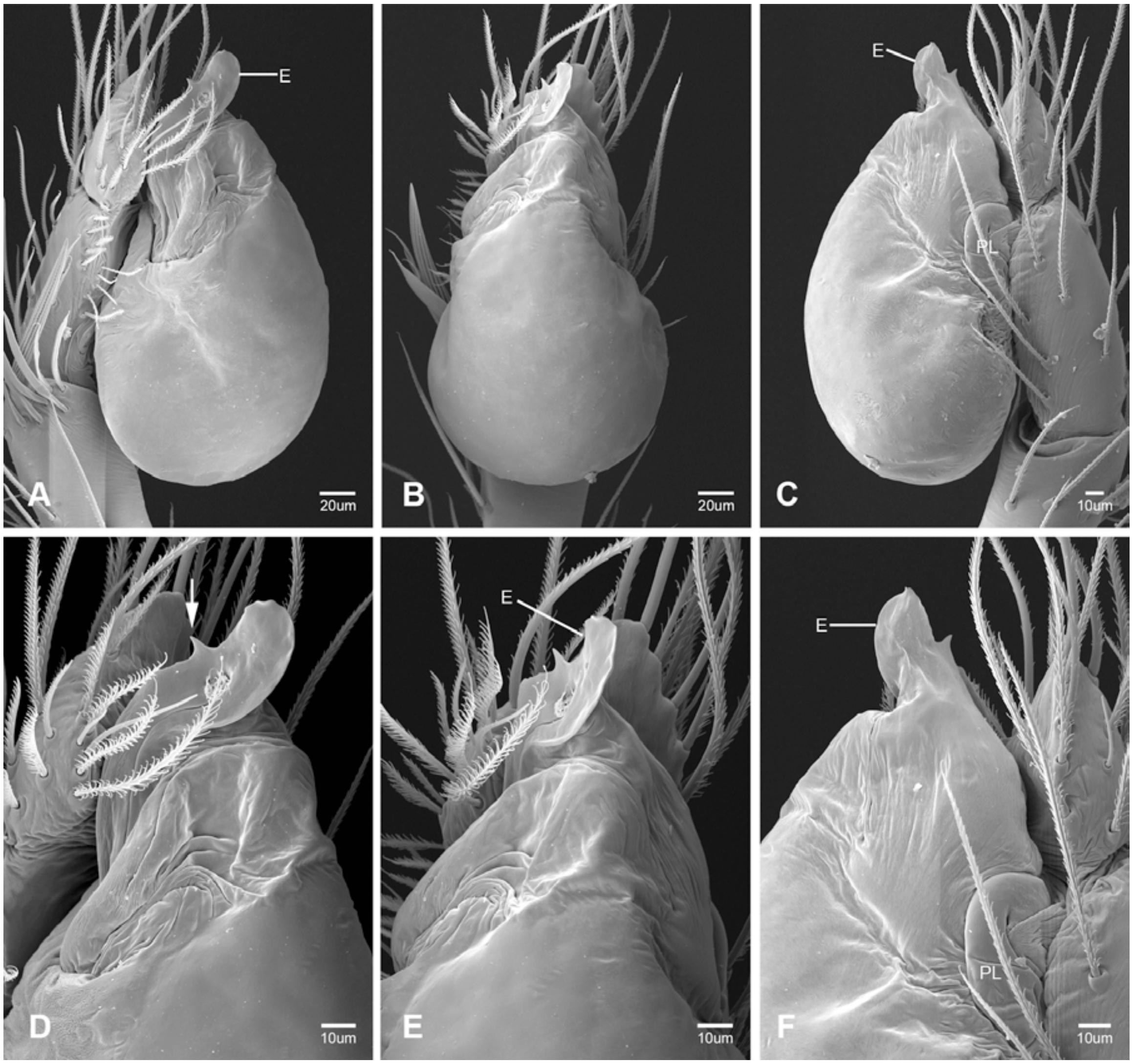
E
RTS
A
20um
E
B
10um
E
C
20um
E
D
10um
E
E
10um
E
PL
F
10um

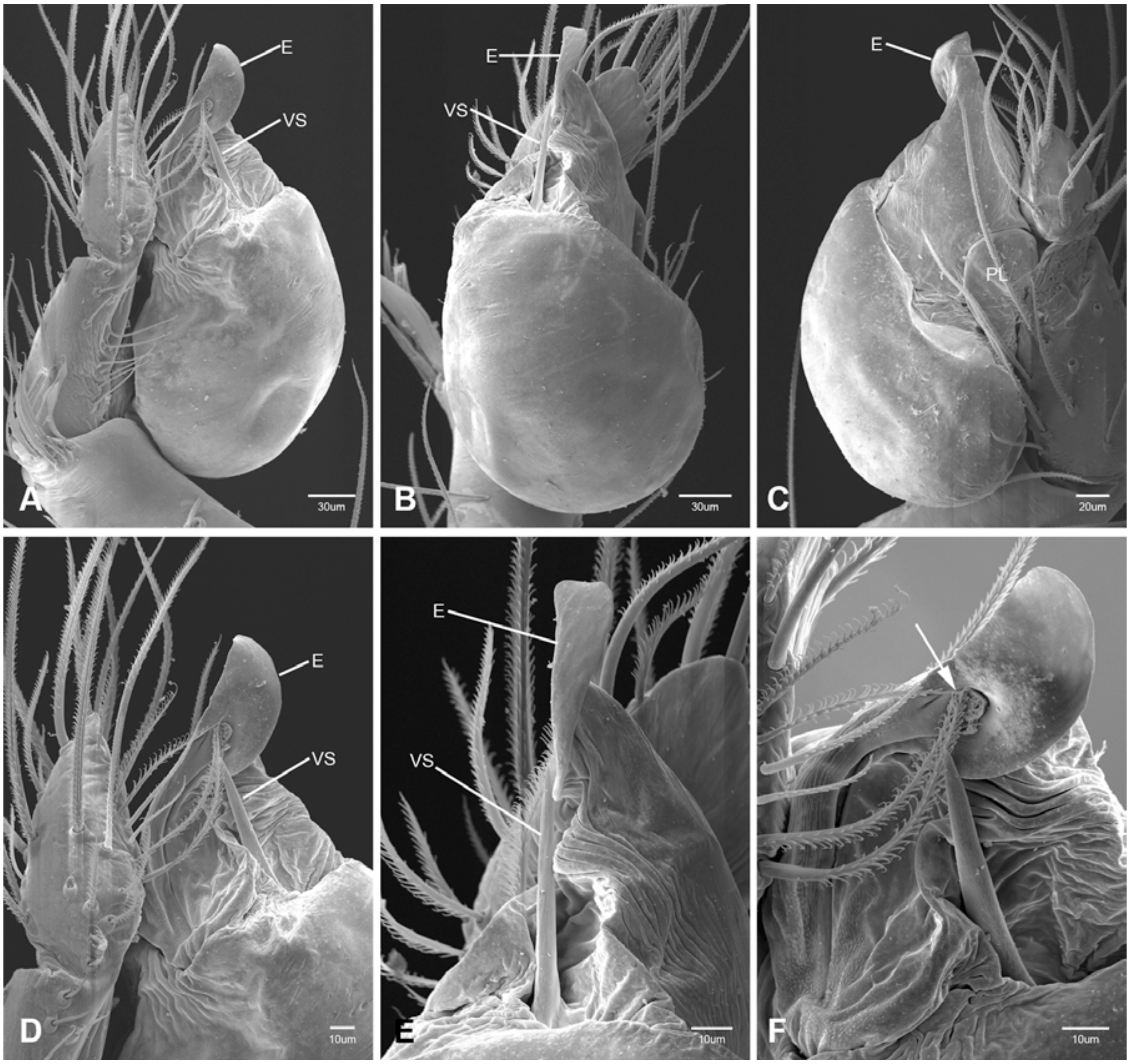

E
VS
RS
A
10um
E
VS
B
30um
E
VS
PL
C
20um
E
VS
RS
D
10um
E
VS
E
10um
E
VS
PL
F
20um

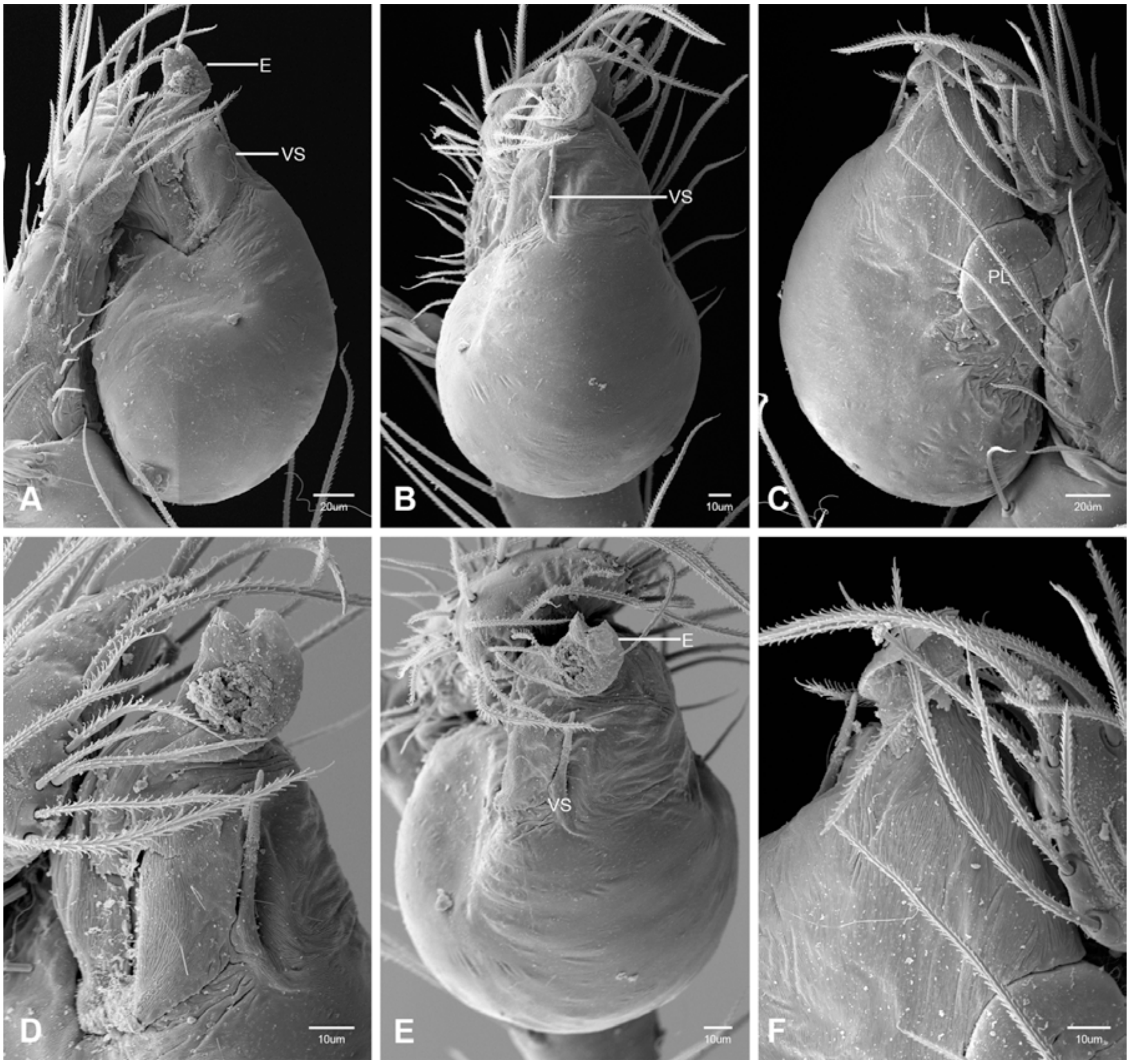

E
VS
A
20um
E
VS
B
20um
E
VS
C
20um
D
10um
E
VS
RS
E
10um
E
VS
RS
F
10um

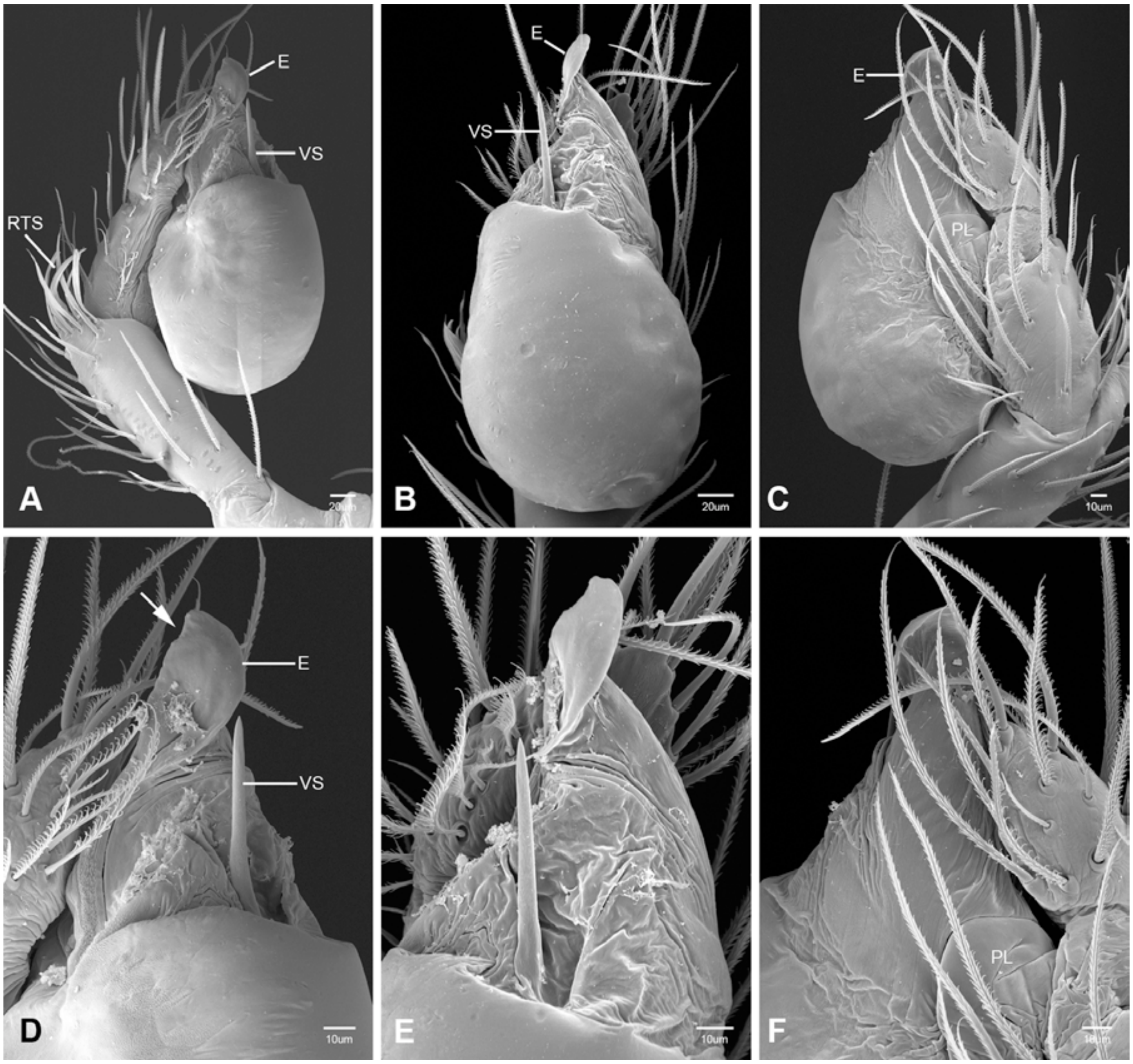

E
VS
RS
RTS
A
30um
E
VS
B
20um
E
PL
C
20um
D
3um
VS
RS
E
10um
F
10um

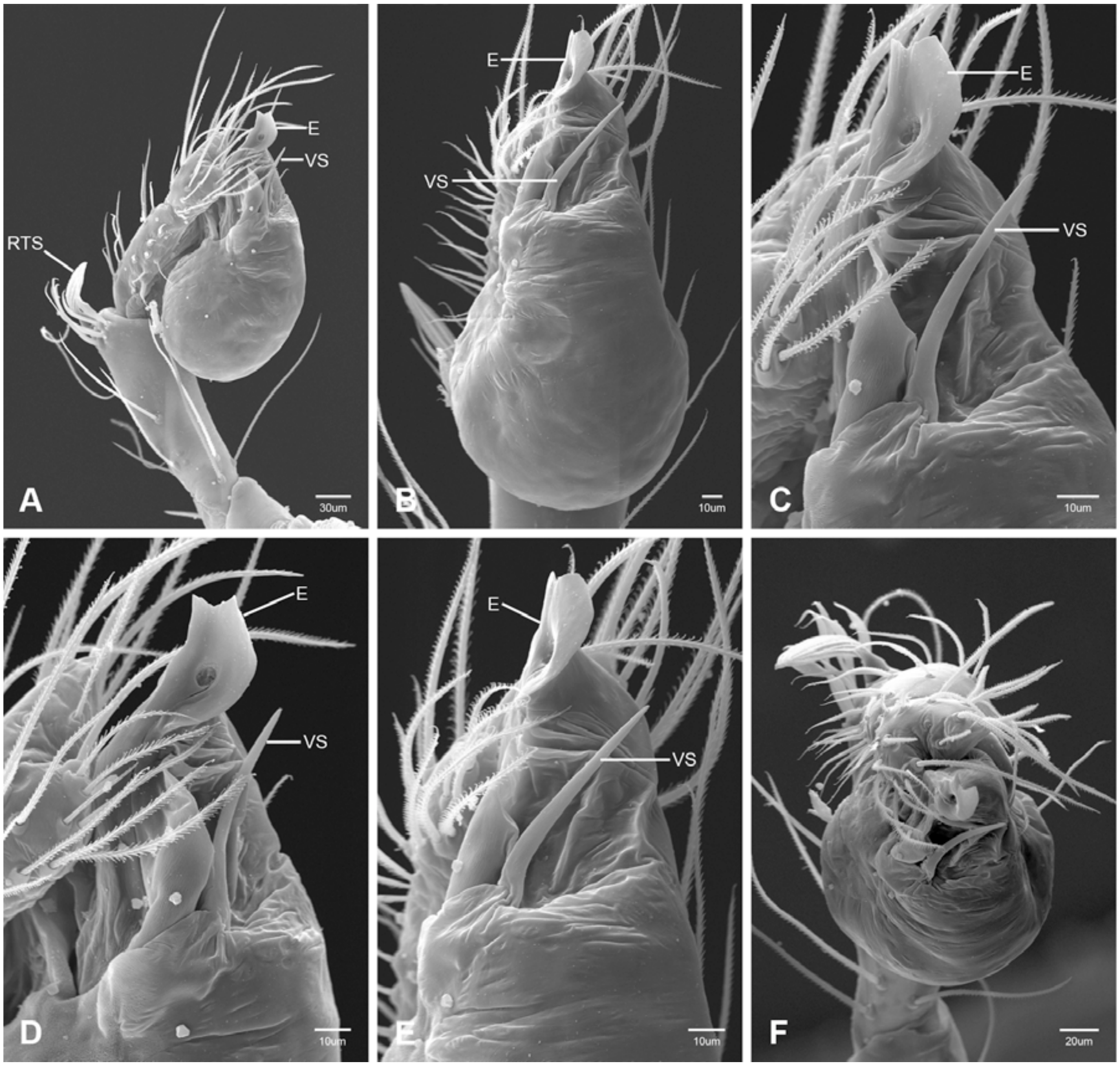

E
A
20um
B
10um
PL
C
10um
E
D
10um
E
10um
F
10um

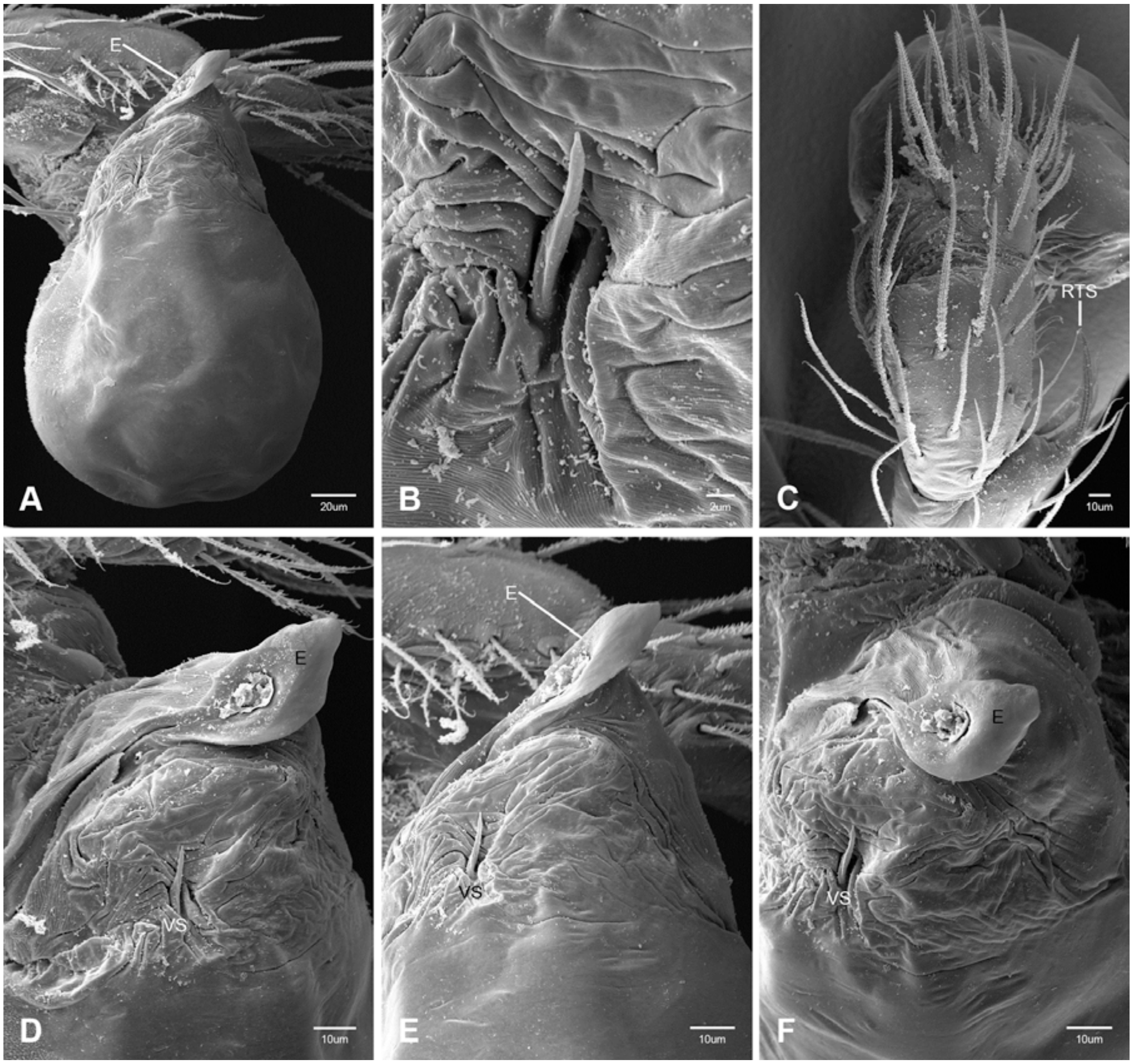

E
A
20um
B
20um
E
PL
C
10um
D
10um
E
E
10um
E
PL
F
10um

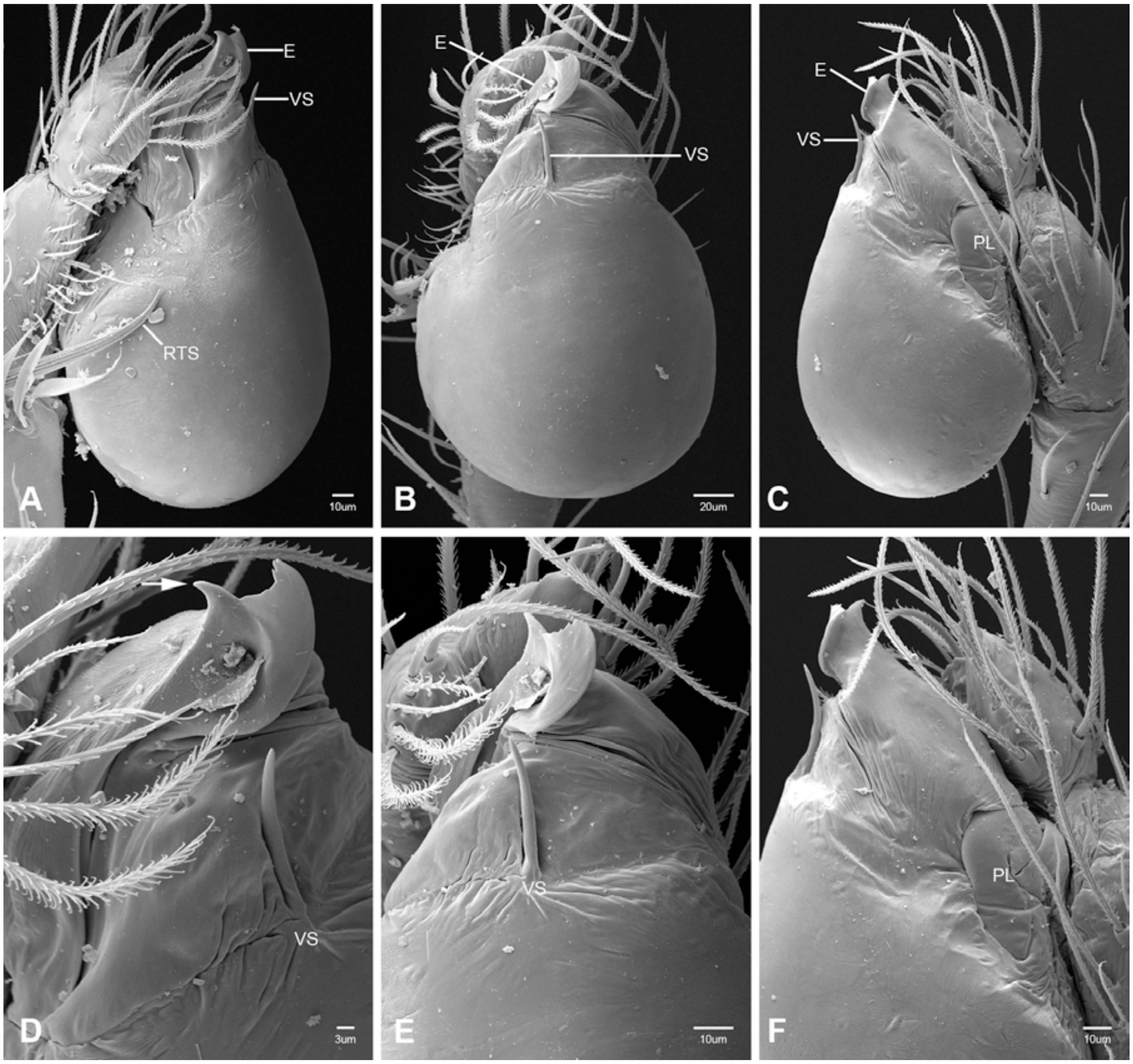

E
VS
A
30um
E
VS
B
30um
E
PL
C
20um
E
VS
D
10um
E
VS
E
10um
F
10um

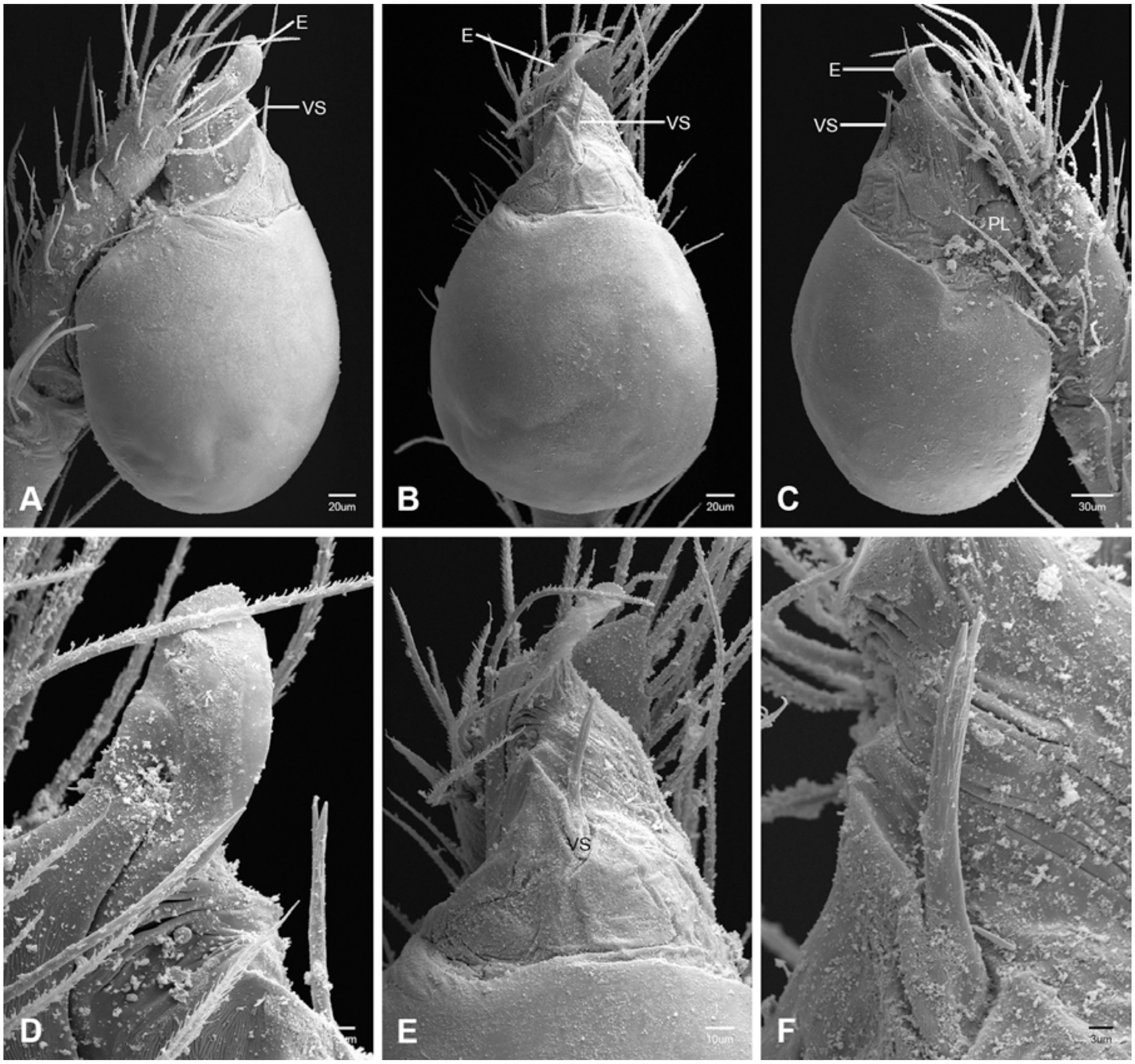

E
VS
20um
A
VS
10um
B
PL
20um
C
10um
D
E
VS
10um
E
10um
F

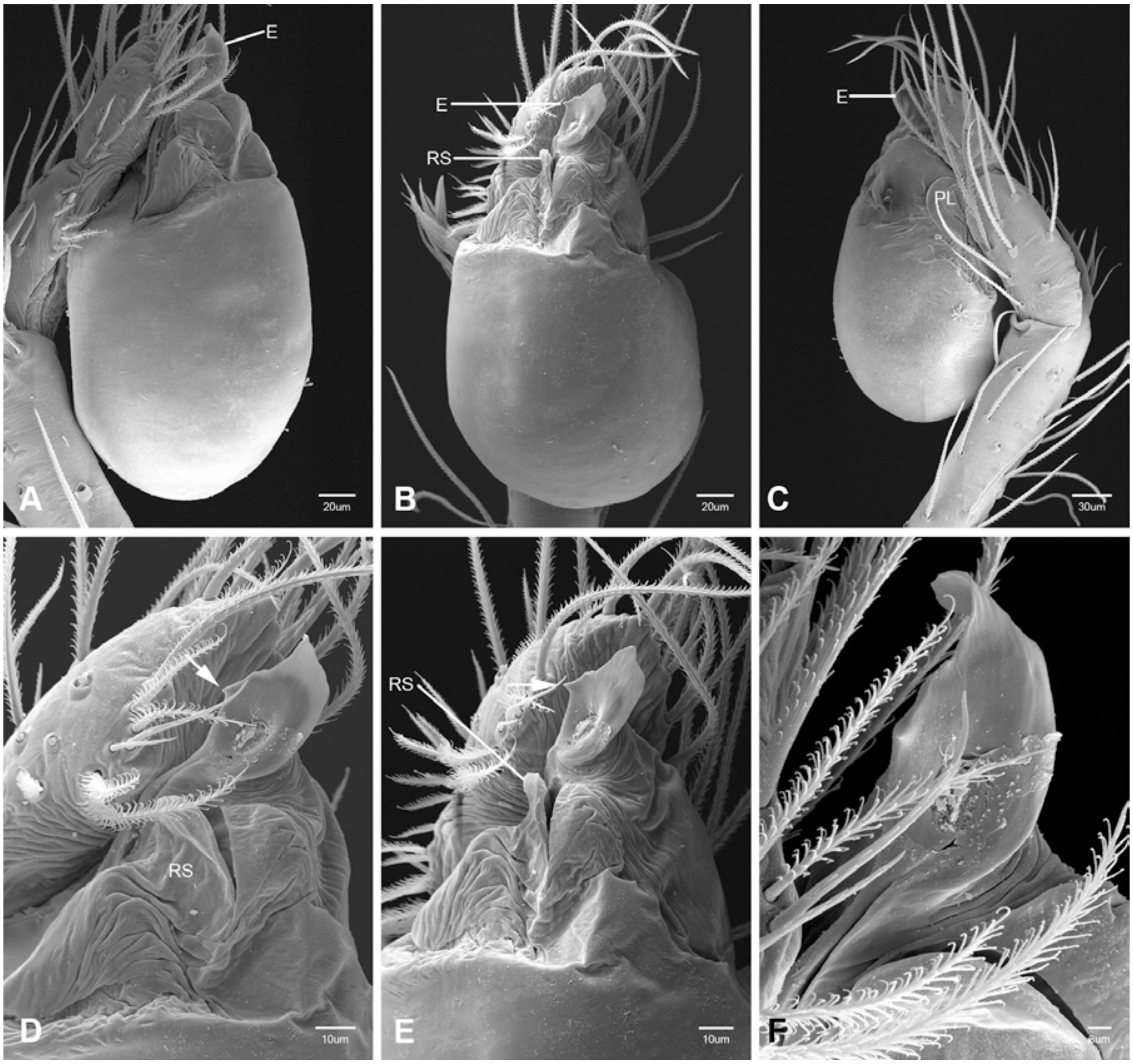

E
VS
RTS
A
20um
E
VS
B
20um
E
PL
C
10um
E
VS
D
10um
E
10um
PL
F
10um

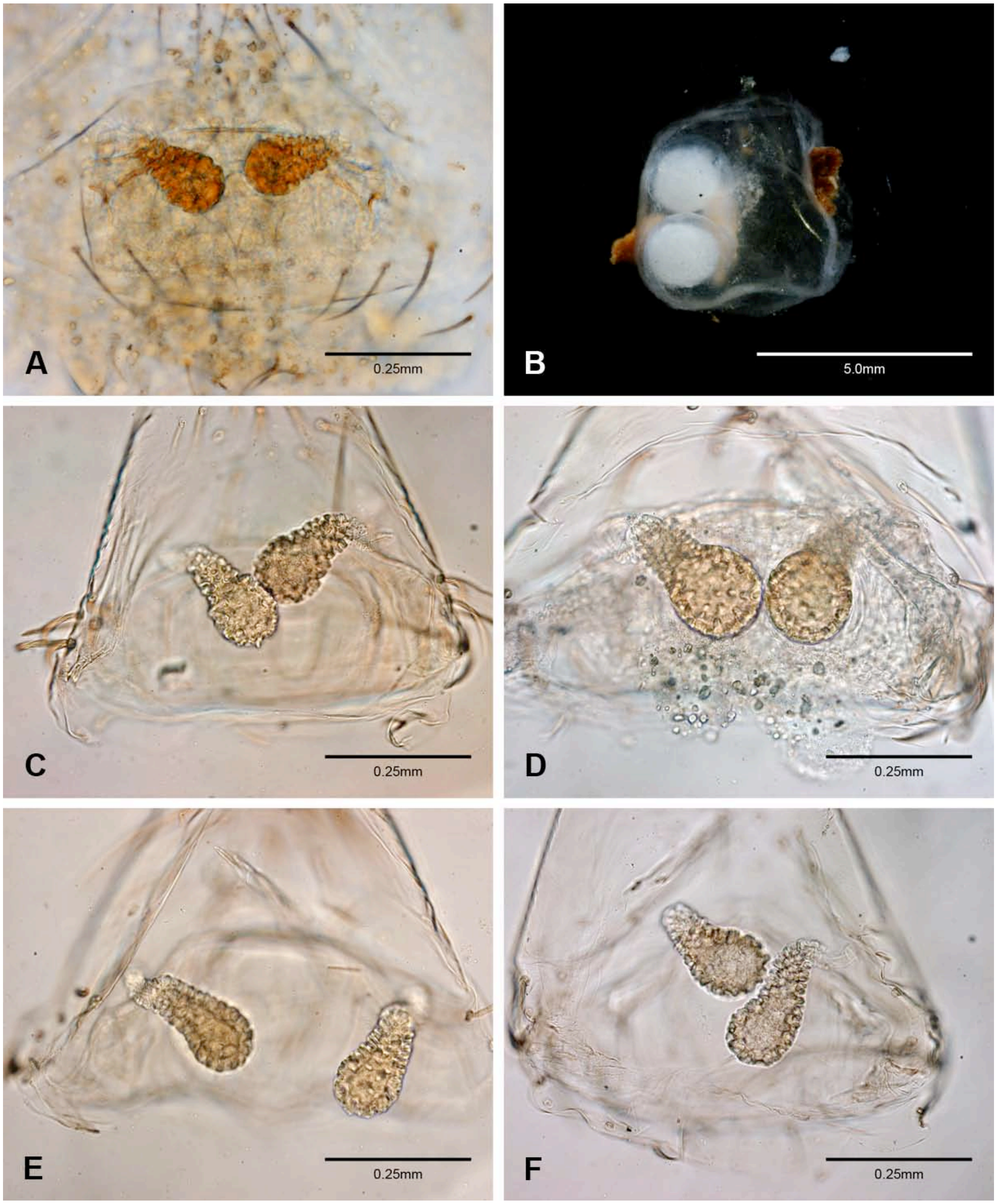

A
E
VS
RTS
30um
B
E
VS
10um
C
E
VS
10um
D
E
VS
10um
E
E
VS
10um
F
20um

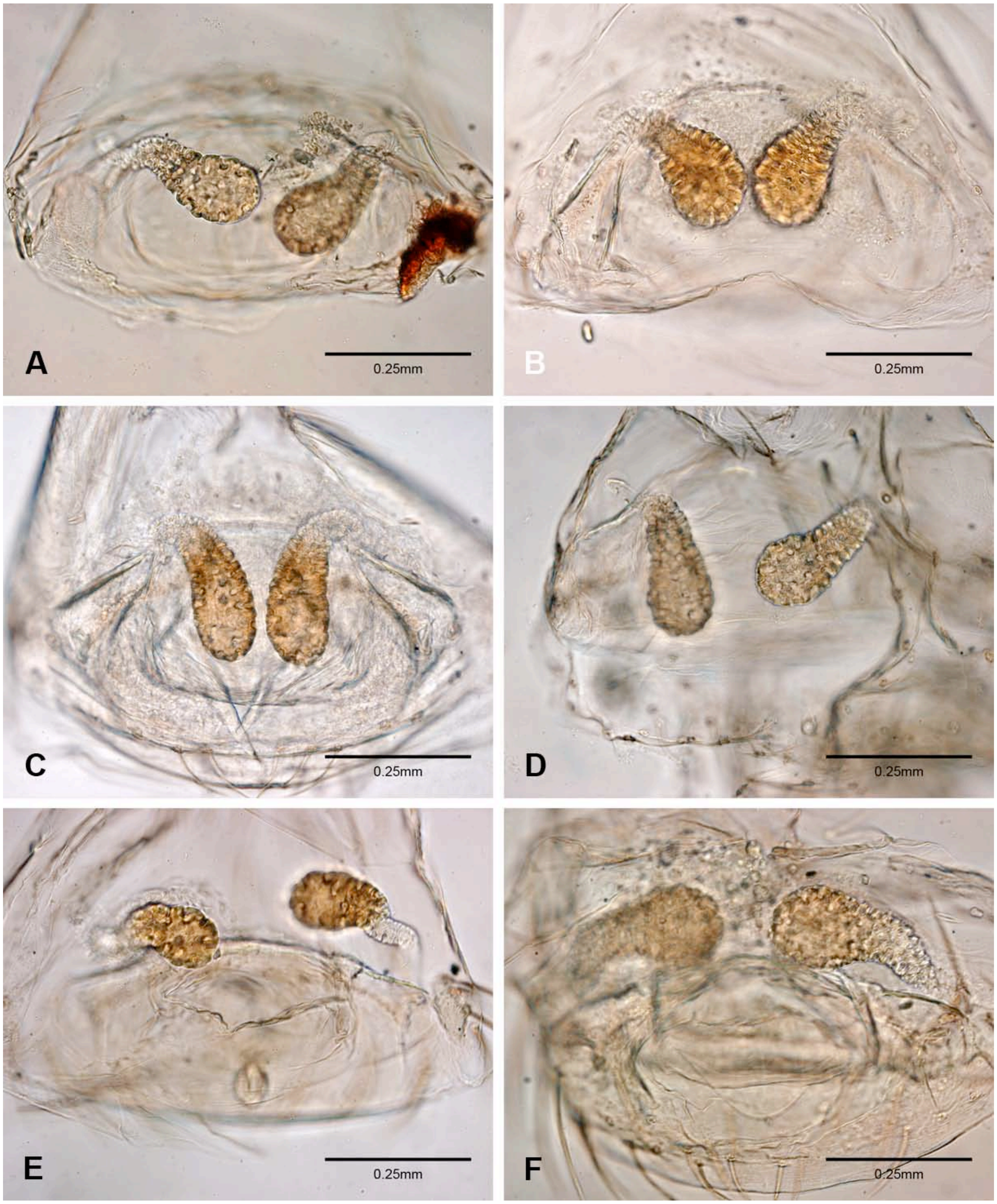

E
A
20um
B
2um
RTS
C
10um
E
VS
D
10um
E
VS
E
10um
E
VS
F
10um

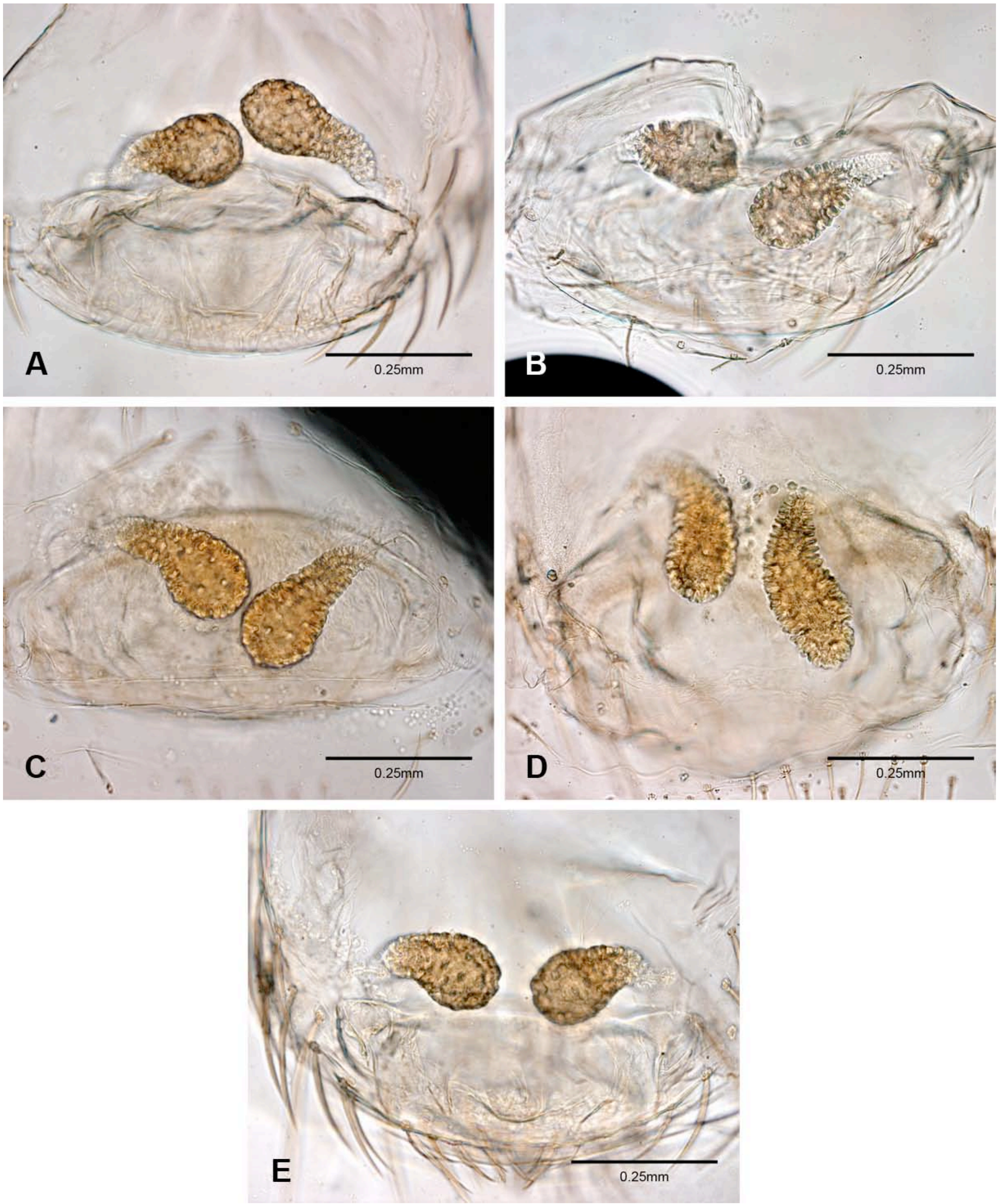

E
VS
RTS
A
10um
E
VS
B
20um
E
VS
PL
C
10um
VS
D
3um
VS
E
10um
PL
F
10um

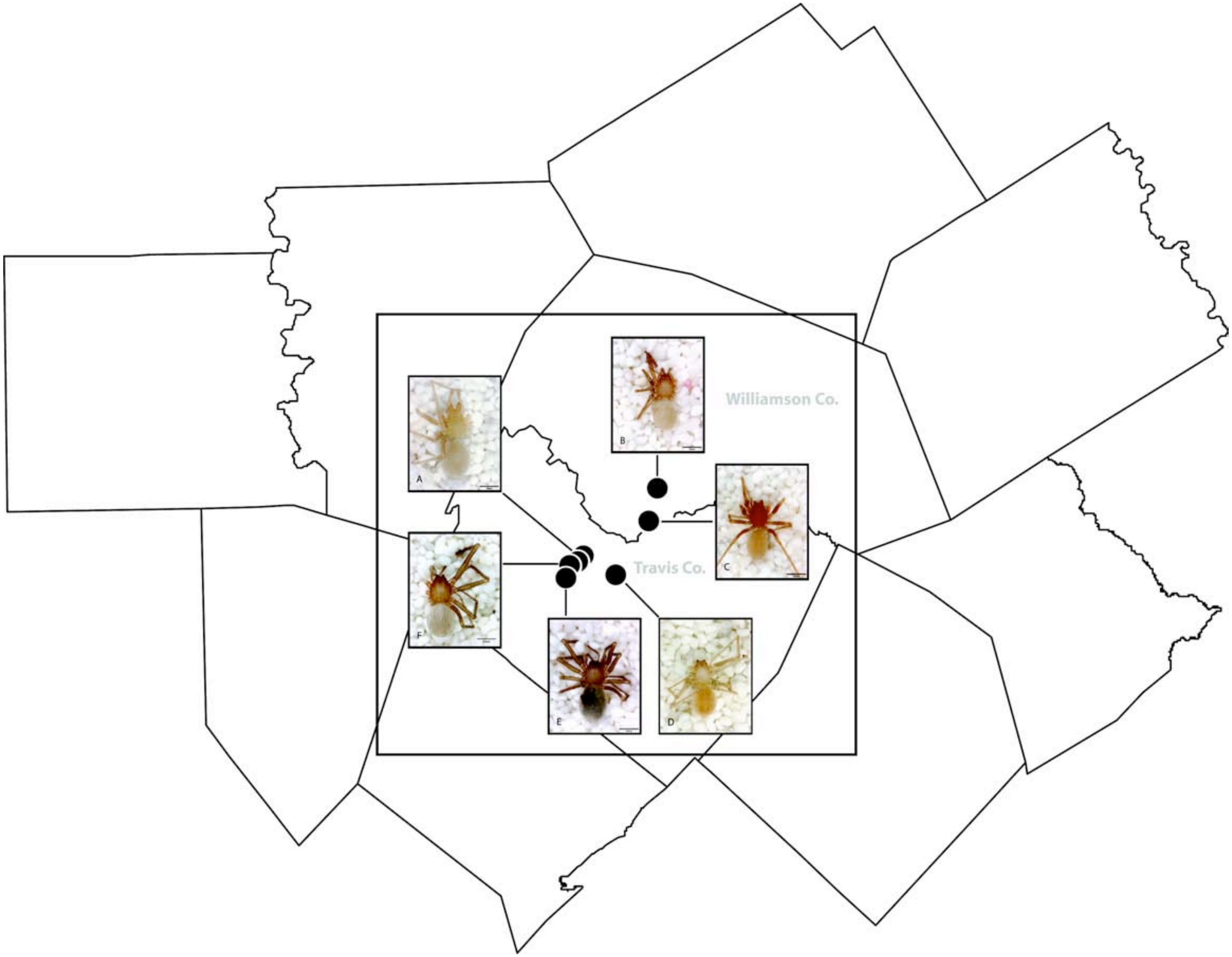

E
VS
20um
A
E
VS
20um
B
E
VS
PL
30um
C
D
VS
10um
E
3um
F

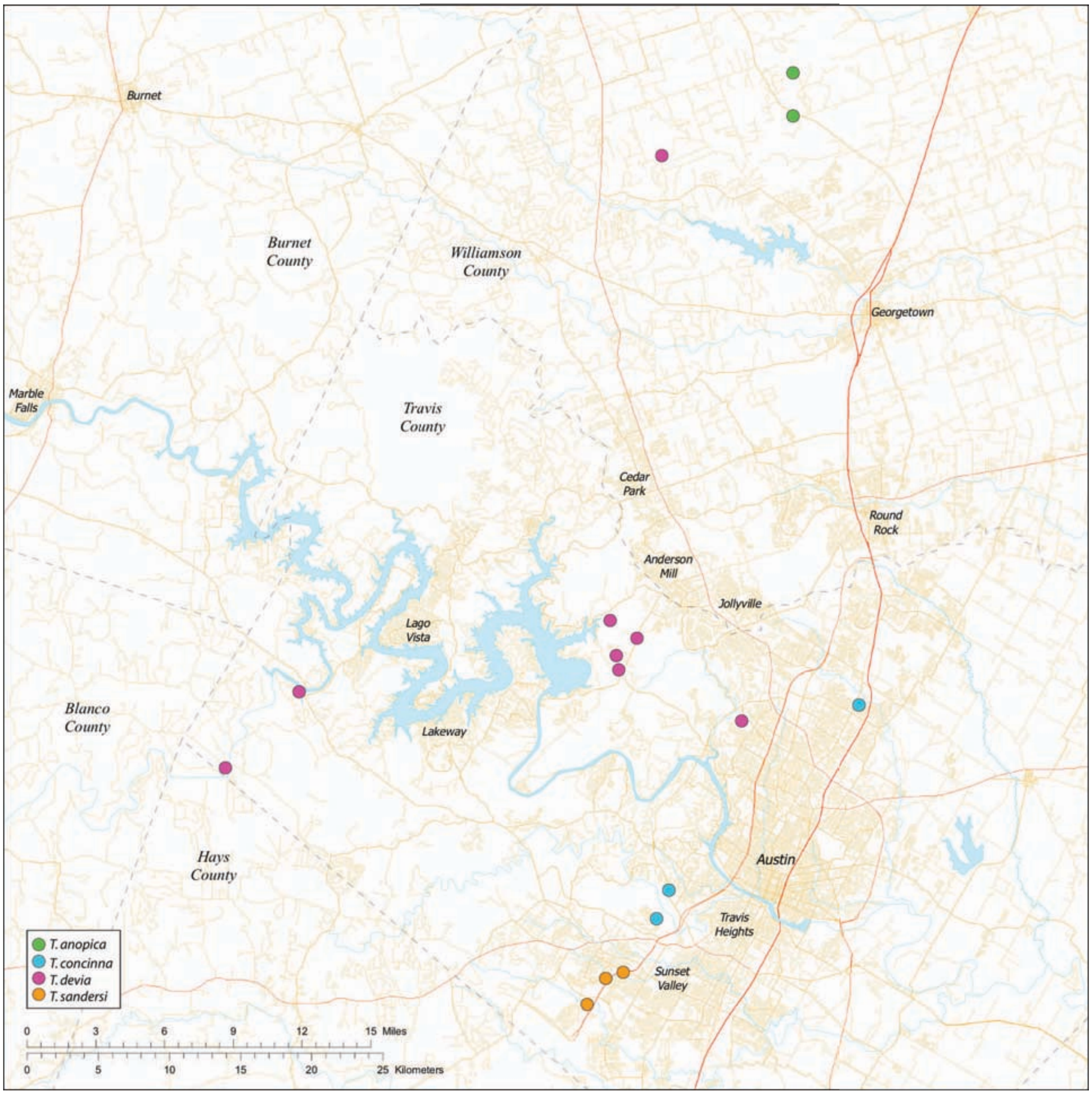

E
A
20um
E
RS
B
20um
E
PL
C
30um
RS
D
10um
RS
E
10um
F
5um

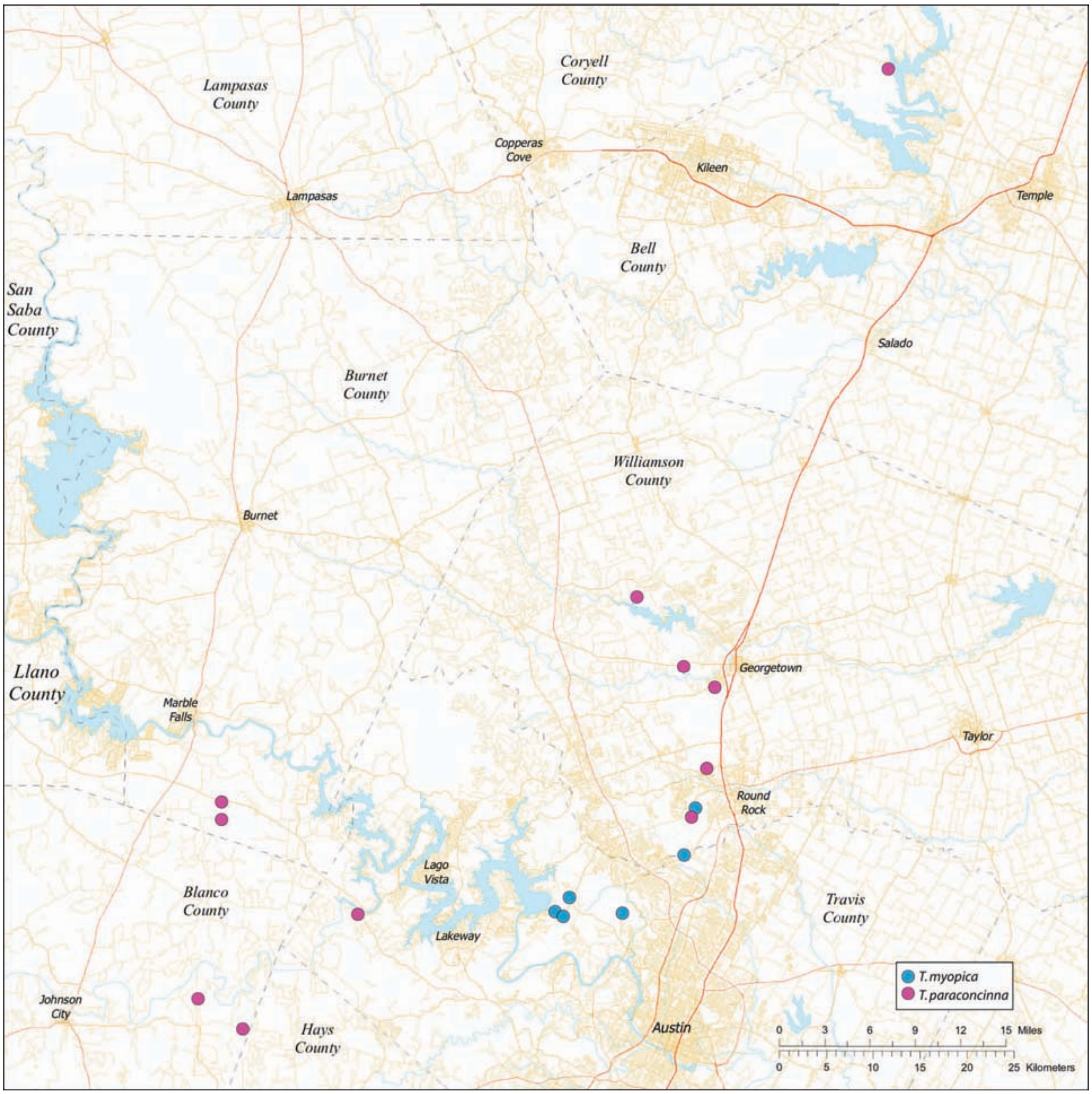

A
0.25mm
B
5.0mm
C
0.25mm
D
0.25mm
E
0.25mm
F
0.25mm

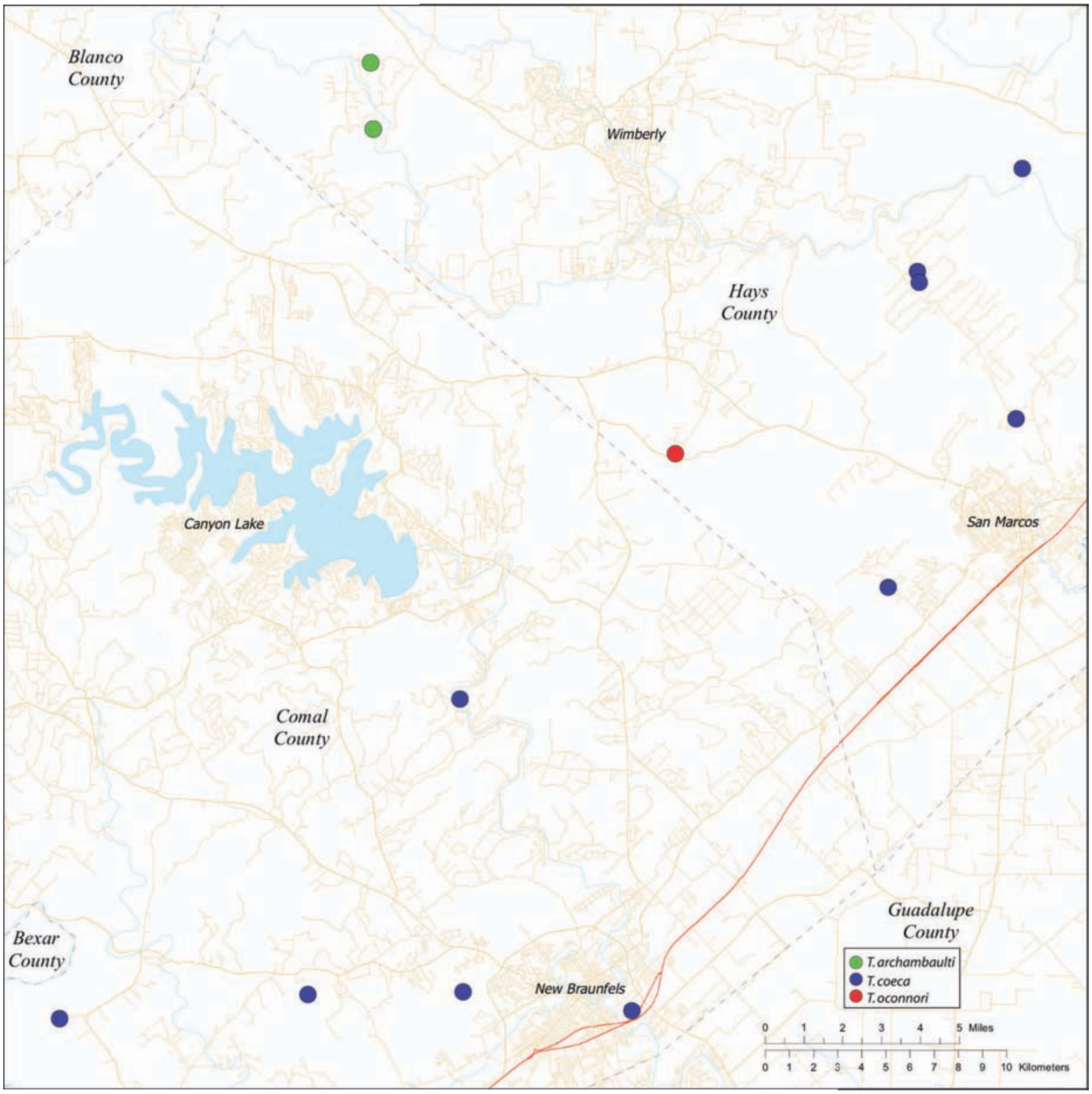

A
0.25mm
B
0.25mm
C
0.25mm
D
0.25mm
E
0.25mm
F
0.25mm

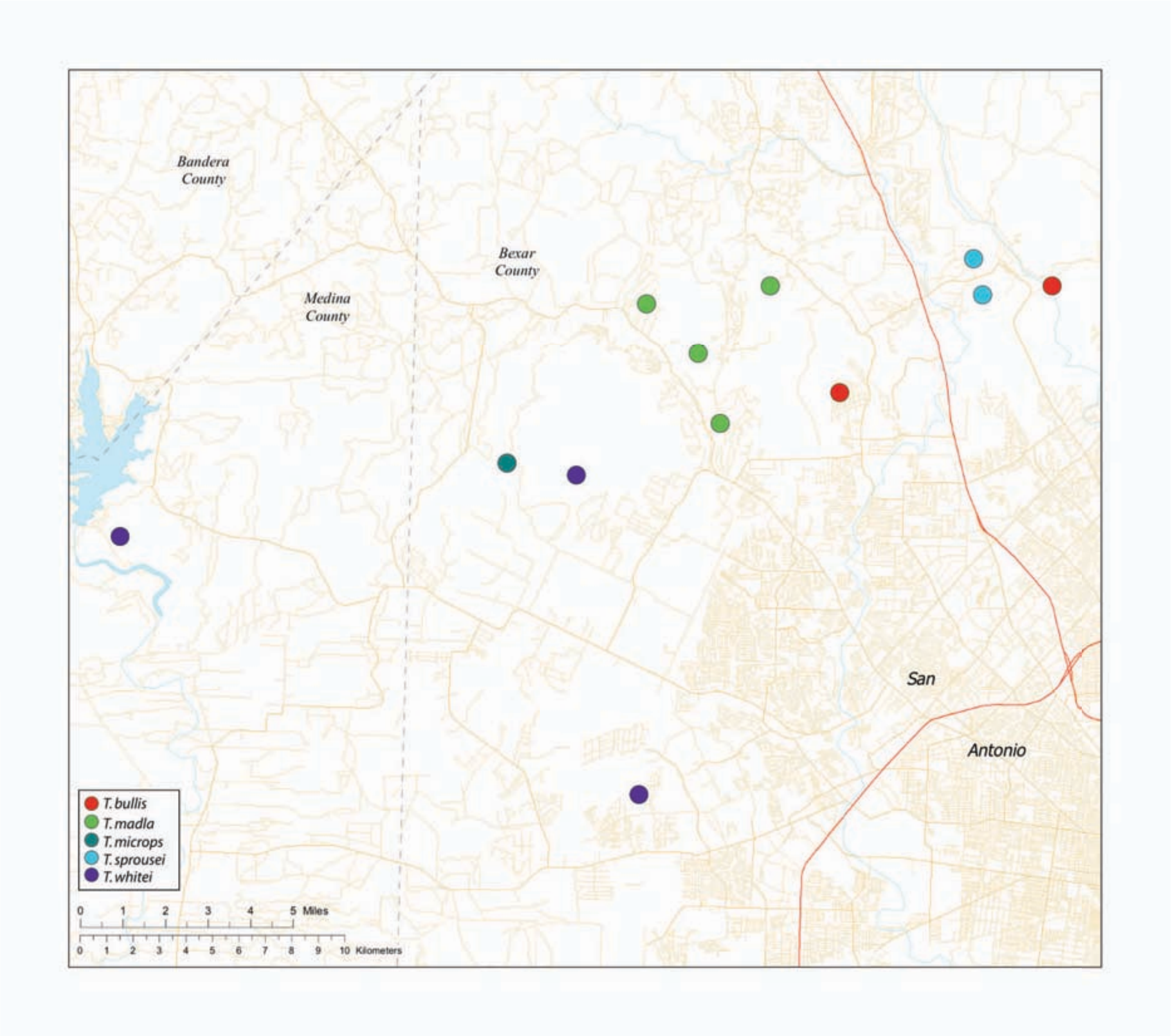

A
0.25mm
B
0.25mm
C
0.25mm
D
0.25mm
E
0.25mm

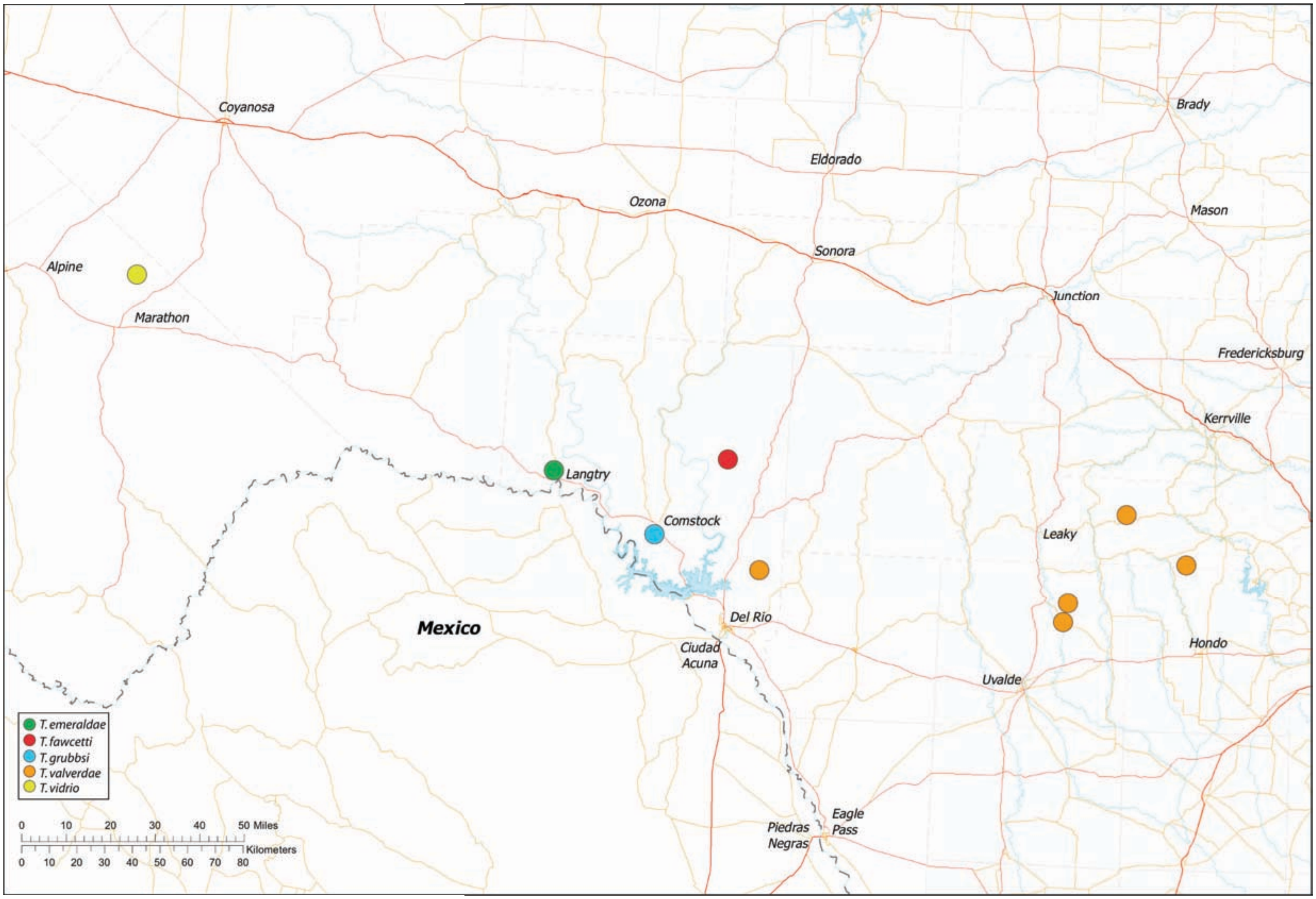

Williamson Co.
Travis Co.
A
B
C
D
E
F


Burnet
Burnet County
Williamson County
Georgetown
Marble Falls
Travis County
Cedar Park
Round Rock
Anderson Mill
Jollyville
Lago Vista
Lakeway
Blanco County
Hays County
Austin
Travis Heights
Sunset Valley
T. anopica
T. concinna
T. devia
T. sandersi
0 3 6 9 12 15 Miles
0 5 10 15 20 25 Kilometers

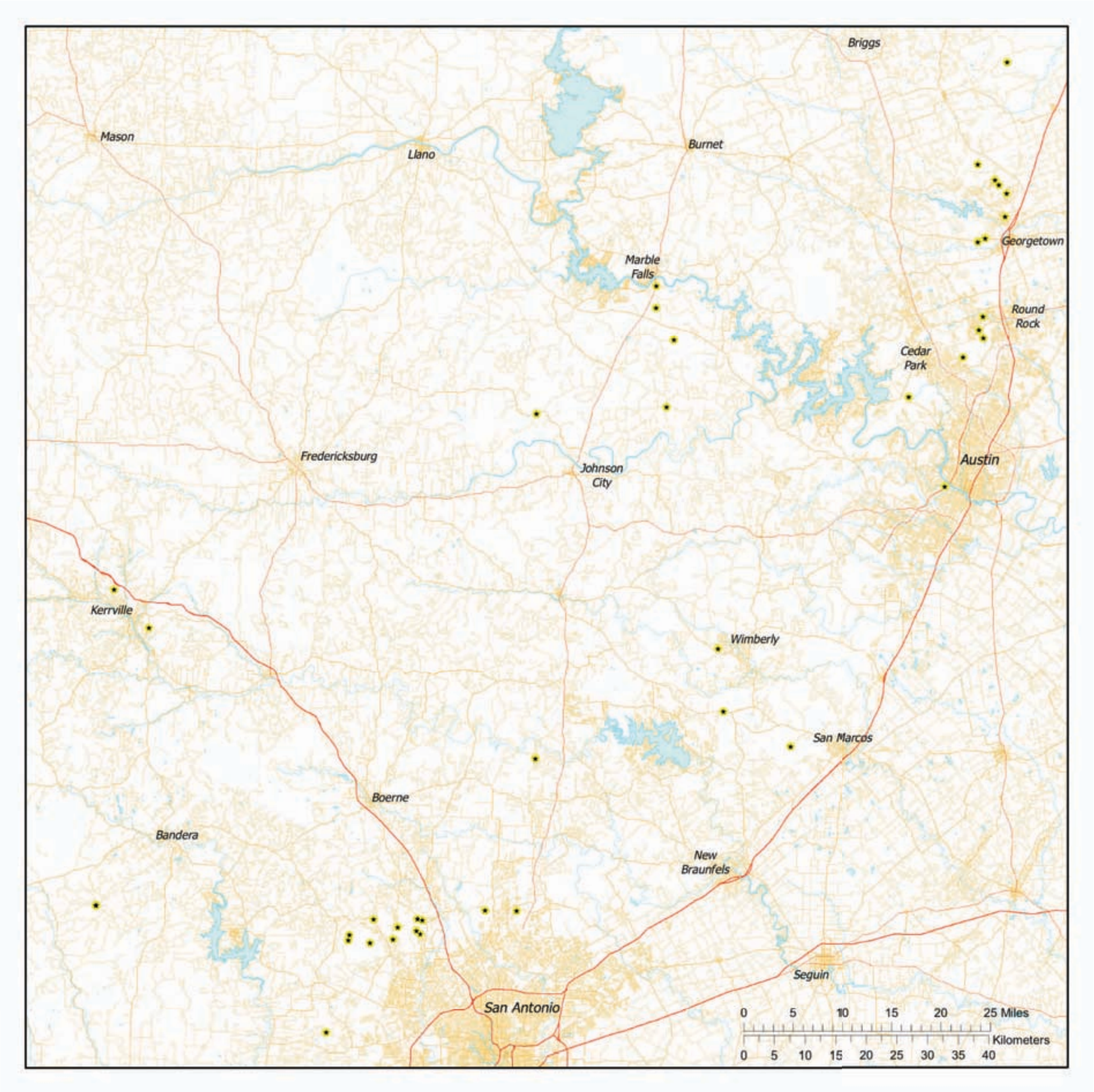

Coryell County
Lampasas County
Copperas Cove
Kileen
Lampasas
Temple
Bell County
San Saba County
Salado
Burnet County
Williamson County
Burnet
Georgetown
Llano County
Marble Falls
Taylor
Round Rock
Lago Vista
Blanco County
Travis County
Lakeway
● T. myopica
● T. paraconcinna
Johnson City
Hays County
Austin
0 3 6 9 12 15 Miles
0 5 10 15 20 25 Kilometers

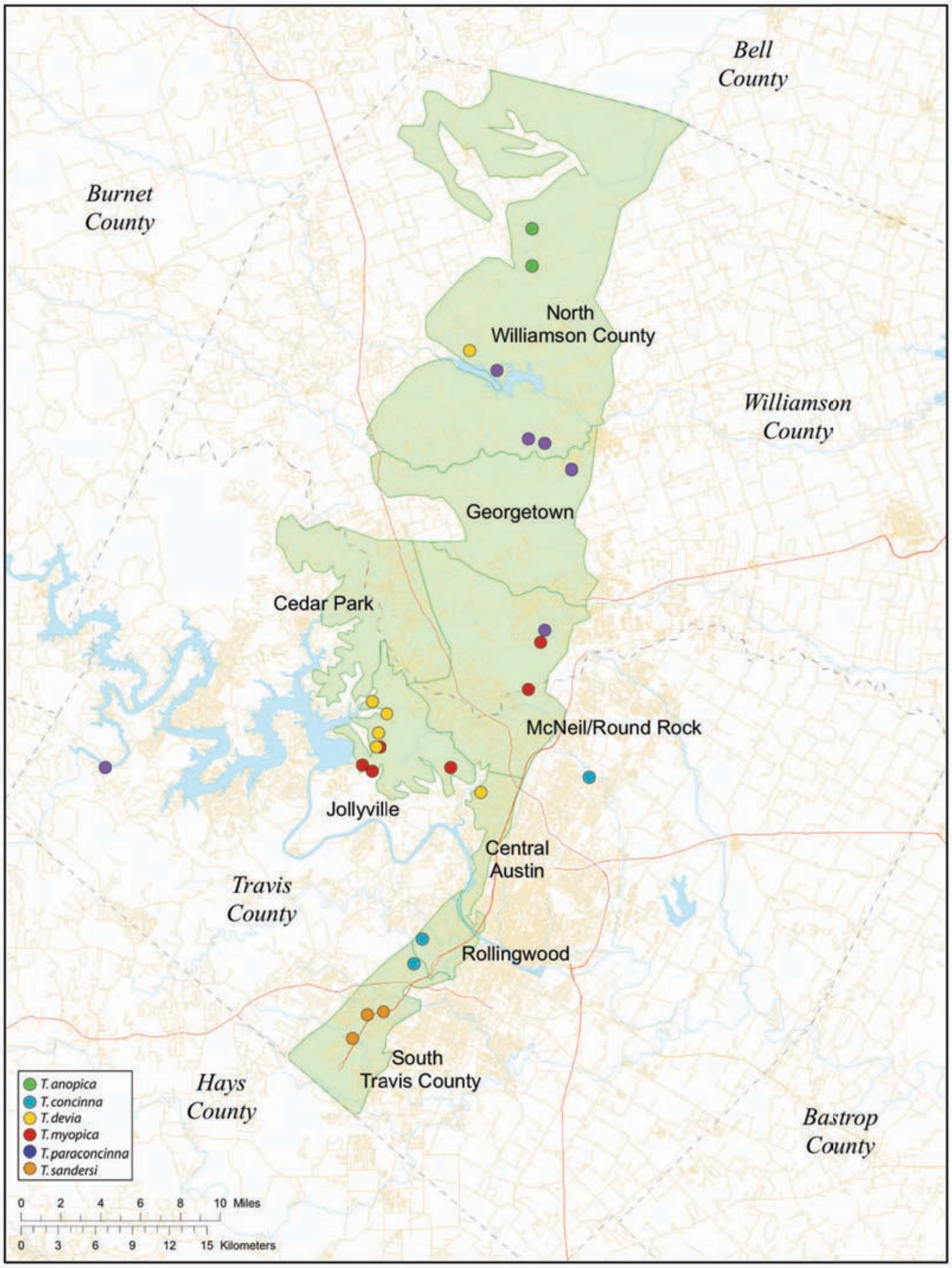

Blanco County
Wimberly
Hays County
Canyon Lake
San Marcos
Comal County
Guadalupe County
Bexar County
New Braunfels
T. archambaulti
T. coeca
T. oconnori
0 1 2 3 4 5 Miles
0 1 2 3 4 5 6 7 8 9 10 Kilometers

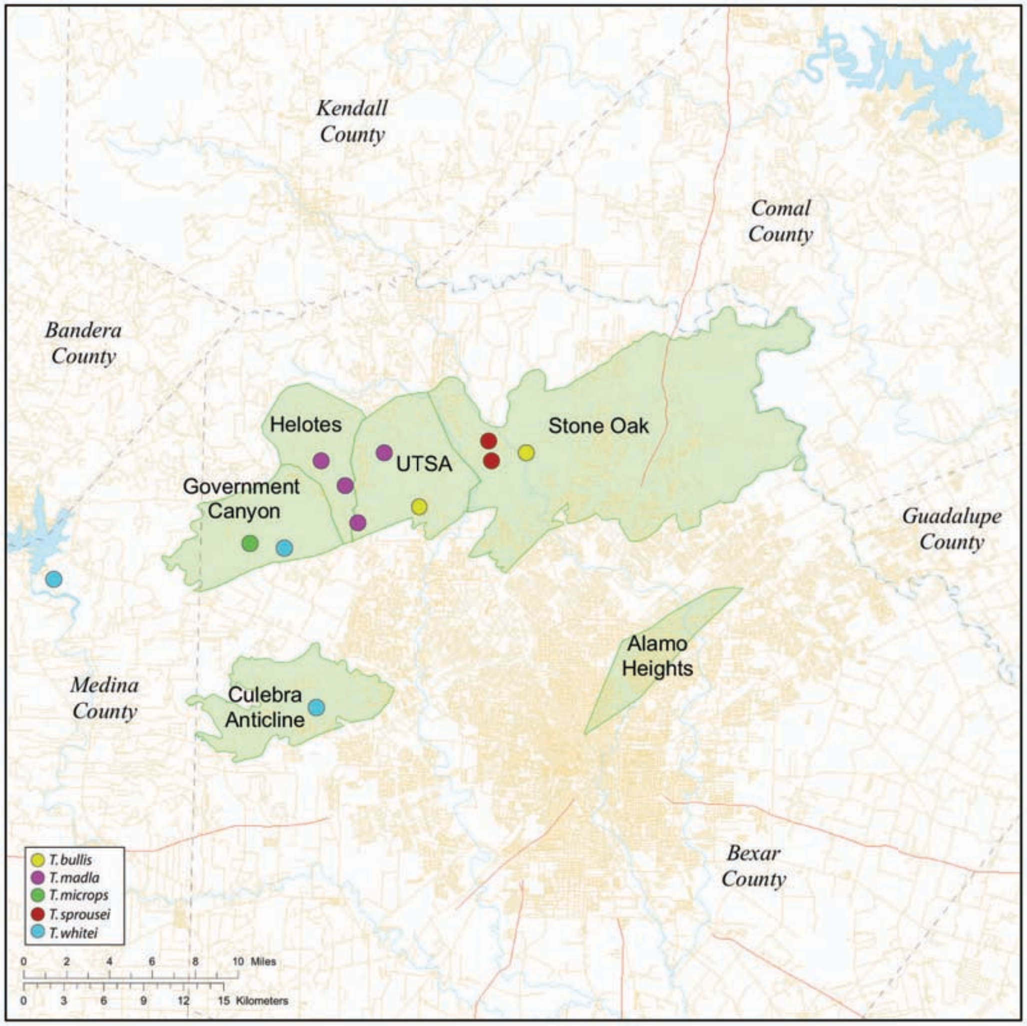

Bandera County
Medina County
Bexar County
San Antonio
T. bullis
T. madla
T. microps
T. sprousei
T. whitei
0 1 2 3 4 5 Miles
0 1 2 3 4 5 6 7 8 9 10 Kilometers



Coyanosa
Brady
Eldorado
Ozona
Mason
Sonora
Alpine
Marathon
Junction
Fredericksburg
Kerrville
Langtry
Comstock
Leaky
Del Rio
Mexico
Hondo
Ciudad Acuna
Uvalde
Eagle Pass
Piedras Negras
● T. emeraldae
● T. fawcetti
● T. grubbsi
● T. valverdae
● T. vidrio
0 10 20 30 40 50 Miles
0 10 20 30 40 50 60 70 80 Kilometers


Briggs
Mason
Llano
Burnet
Georgetown
Marble Falls
Round Rock
Cedar Park
Fredericksburg
Johnson City
Austin
Kerrville
Wimberly
San Marcos
Boerne
Bandera
New Braunfels
Seguin
San Antonio
0 5 10 15 20 25 Miles
Kilometers
0 5 10 15 20 25 30 35 40


Bell
County
Burnet
County
North
Williamson County
Williamson
County
Georgetown
Cedar Park
McNeil/Round Rock
Jollyville
Central
Austin
Travis
County
Rollingwood
South
Travis County
Hays
County
Bastrop
County
T. anopica
T. concinna
T. devia
T. myopica
T. paraconcinna
T. sandersi
0 2 4 6 8 10 Miles
0 3 6 9 12 15 Kilometers



Kendall County
Comal County
Bandera County
Helotes
UTSA
Stone Oak
Government Canyon
Guadalupe County
Alamo Heights
Medina County
Culebra Anticline
Bexar County
T. bullis
T. madla
T. microps
T. sprousei
T. whitei
0 2 4 6 8 10 Miles
0 3 6 9 12 15 Kilometers