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Cover photo: Amblypigid female carrying pupae of *Pseudogaurax* (Diptera: Chloropidae) that were egg parasitoids of her egg case as larvae (see page 1). Photo by Kristie Reddick and Jessica Honaker.

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REVIEW

Death comes on two wings: a review of dipteran natural enemies of arachnids

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Abstract. Though the best known natural enemies of arachnids are Hymenoptera, Diptera also form an important group of arachnid enemies, attacking 31 spider families in all three suborders of Araneae, as well as members of the Acari, Amblypygi and Scorpiones. Some species of Bombyliidae, Chloropidae, Drosophilidae, Ephydridae, Phoridae and Sarcophagidae are known to attack eggs of several families of arachnids, acting as predators, parasitoids and/or parasites of egg sacs. Alternatively, members of Acroceridae and Tachinidae are internal parasitoids, attacking juvenile and/or adult spiders. One species of Sarcophagidae is reported as a predator of individual Liphistiidae (Mesothelae) spiders. We summarize the available information on all lineages of Diptera known to attack arachnids, including predators, parasites, kleptoparasites and parasitoids. A table including host records pertaining to the aforementioned dipteran families is presented. Particular emphasis is given to Acroceridae, the only lineage of Diptera known to develop exclusively on arachnids, and one of the most significant groups of natural enemies of spiders.

Keywords: Araneae, parasitoid, spider egg sacs, scorpions, amblypygids

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1. INTRODUCTION

Some of the best known natural enemies of arachnids belong to the order Hymenoptera, with species either feeding on the individual arachnid, or on its eggs. Several groups of Hymenoptera develop on arachnid hosts, including wasps in the families Diapriidae, Eulophidae, Eupelmidae, Eurytomidae, Ichneumonidae, Platygastridae sensu lato, Pompilidae, Pteromalidae and Sphecidae (Fitton et al. 1987; Noyes 2016). Hymenopteran parasitoids and predators exhibit a breadth of life strategies, including species that feed in cocooned spider egg masses, endoparasitoids that develop individually within eggs, external koinobiont parasitoids of mobile spiders, and idiobionts that paralyze one or more spiders as prey (Austin 1985; Gauld & Dubois 2006).

Species in the order Diptera are also significant natural enemies of arachnids. As opposed to the large taxonomic diversity of hymenopteran arachnid enemies, dipteran parasites, parasitoids and predators of arachnids are restricted to fewer families and vary considerably in their mode of action. All species of Acroceridae and a single species of Tachinidae are internal parasitoids of juvenile or adult spiders, while a few members of the Chloropidae, Drosophilidae, Ephydridae, Phoridae and Sarcophagidae are known to attack egg sacs of several arachnids, acting as parasitoids and/or predators of arachnid eggs (Clausen 1940; Vincent 1985; Schlinger 1987; Marshall 2012). One species of Sarcophagidae is a predator of Mesothelae spiders, attacking both adult and immature prey (Schwendinger & Pape 2000).

Although a clear cut distinction between predator and parasite is not always possible in nature, the three extremes of the spectrum (i.e., true parasite vs. true predator vs. true parasitoid) can be easily distinguished. Predators are organ-

isms that consume one or multiple prey during their lifetime, thus establishing a relationship that positively affects the predator and negatively affects the prey. Parasites, in general, live on/in the body of the organism they feed upon, and in contrast to predators, only take resources from one host, which they tend not to kill. Parasitoids, like parasites, only attack one host, but they enter or attach to their host, feed upon it, and ultimately kill it. Thus, the essential difference between parasites and parasitoids is that parasitoids always kill their hosts, while parasites tend to not kill their hosts. Additionally, the main difference between predators and parasitoids relates to the number of individuals attacked; predators usually kill multiple prey during their lifetime, while parasitoids only kill one host (Price 1980).

Parasitoids are found in five orders of holometabolous insects: Hymenoptera, Diptera, Coleoptera, Lepidoptera, and Neuroptera. Hymenopteran parasitoids account for nearly 78% of the estimated number of species, and consequently have served as models for nearly all recent research on insect parasitoids (Feener & Brown 1997). However, parasitoids in the Hymenoptera represent a single evolutionary lineage in contrast to the hundreds of parasitoid lineages in Diptera, Coleoptera, and other orders (Eggleton & Belshaw 1992). There are over 16,000 species of described dipteran parasitoids, which are distributed in 21 families and represent about 20% of the known parasitoid diversity (Eggleton & Belshaw 1992). Dipteran parasitoids are hypothesized to be derived from over 100 independent lineages, thus offering an unparalleled system for understanding the origin, evolution and diversification of parasitoid life history.

In this review, we summarize the available information on all lineages of Diptera that are known to attack arachnids, including predators, parasites, kleptoparasites and parasitoids. A table summarizing the egg parasitoids and/or predators, as well as internal parasitoids of adults and immature arachnid hosts is presented. Predators and kleptoparasites of individual arachnids were not included in the table because they represent opportunistic rather than adaptive interactions. All species and genus names given in the literature were checked and updated using current dipteran and arachnid taxonomy (Pape & Thompson (2013) and World Spider Catalog (2016) respectively).

2. DIPTERAN NATURAL ENEMIES OF ARACHNIDS

2.1 Predators.—Species of Asilidae are among the best known dipteran predators, but it has been indicated that arachnids do not comprise a significant portion of robber fly diet, making up less than 2% of all their consumed prey (Dennis et al. 2012). Robber flies are found worldwide and may occasionally take spiders as prey, especially species in the asilid genera *Daspletis* Loew, 1858, *Efferia* Coquillett, 1893, *Euscelidia* Westwood, 1850, *Holopogon* Loew, 1847, *Laphystia* Loew, 1847, *Psilonyx* Aldrich, 1923 and *Stichopogon* Loew, 1847 (Dennis et al. 2012). Robber flies are recorded to prey on spiders belonging to the suborder Araneomorphae, mainly in the families Agelenidae, Araneidae, Clubionidae, Lycosidae, Salticidae and Theridiidae, among others (Dennis et al. 2012). This suborder comprises species that are generally readily visible, including orbweavers, crab spiders and jumping spiders. In contrast, spiders in the other two suborders of Araneae (Mygalomorphae and Mesothelae) generally have reclusive habits (such as trapdoor and funnel-web spiders) or are highly mobile. There are also smaller dipterans that play a role as predators of small arachnids. For instance, larvae of species in the gall midge genus *Feltiella* Rubsaamen, 1910 (Cecidomyiidae) are specialized predators of all spider mite life stages (Acarina: Tetranychidae), as are many members of the gall midge tribe Lestodiplosini (Gagné 1995). One species of Ceratopogonidae, *Forcipomyia araneivora* Clastrier & Legrand, 1991, also plays a role as an enemy of spiders by feeding directly on their haemolymph (Clastrier & Legrand 1991). Other common dipteran predators (e.g., Muscidae and several families in Empidoidea) may take arachnids as prey, but no records of these were found.

2.2 Kleptoparasites.—Kleptoparasitism is a form of competition that involves the stealing of a portion of already acquired food items, and is one of the most common types of exploitation between animals. Kleptoparasites steal food that is either already in a predator's possession, or which the predator has already spent energy pursuing and capture by the predator is imminent. In this interaction, the kleptoparasite is benefited and the host may potentially be negatively affected by the loss of food resources (Brockmann & Barnard 1979; Barnard 1984). Some fly species in the families Cecidomyiidae, Ceratopogonidae, Chloropidae, Dolichopodidae, Lonchaeidae, Milichiidae and Phoridae are known kleptoparasites of spiders. These organisms typically exploit cadavers captured by spiders, feeding on the semi-digested prey. In general, spiders most commonly attacked by kleptoparasites are orbweavers (Araneidae and Nephilidae), crab spiders (Thomisidae) and jumping spiders (Salticidae). The most common spider kleptoparasites are species in the genera *Didactylomyia* Felt, 1911 (Cecidomyiidae), *Microphor* Macquart, 1827 (Dolichopodidae), *Desmometopa* Loew, 1866, *Neophyllomyza* Melander, 1913, *Paramyia* Williston, 1897, and *Phyllomyza* Fallen, 1810 (Milichiidae) and *Megaselia* Rondani, 1856 (Phoridae) (Robinson & Robinson 1977; Sivinski & Stowe 1980; Weinmann & Disney 1997; Sivinski et al. 1999; Brake 2000; Brake & von Tschirnhaus 2010; van Helsdingen 2011; Marshall et al. 2015).

Due to their generalistic feeding nature (taking a range of taxa as prey/host), predators and kleptoparasites of individual arachnids were not included in the summary table.

2.3 Egg parasitoids and predators.—A large variety of Diptera attack the eggs of arachnids, either as parasitoids or predators; it is often difficult to distinguish between these alternatives due to the limited number of natural history and rearing observations. Therefore, we have decided not to distinguish between these modes, in order to avoid making incorrect assumptions about poorly known dipteran-spider interactions. Each dipteran family is discussed in more detail below.

2.3.1 Family Bombyliidae: Bombyliidae is a large group of Diptera commonly known as bee flies. Despite the great number of species (over 5,000 valid species), the habits of most immature stages (>80%) are still poorly understood (Yeates & Greathead 1997). Known species are mostly ecto- or endoparasitoids on the larvae and/or pupae of other insects, mainly in the Lepidoptera, Hymenoptera, Coleoptera, Diptera and Neuroptera. The only known exception is *Petrorossia feti* Zaitsev & Charykuliev, 1981, which develops as a parasitoid or predator on egg sacs of oecobiid spiders (Zaitsev & Charykuliev 1981; Yeates & Greathead 1997). It is unknown

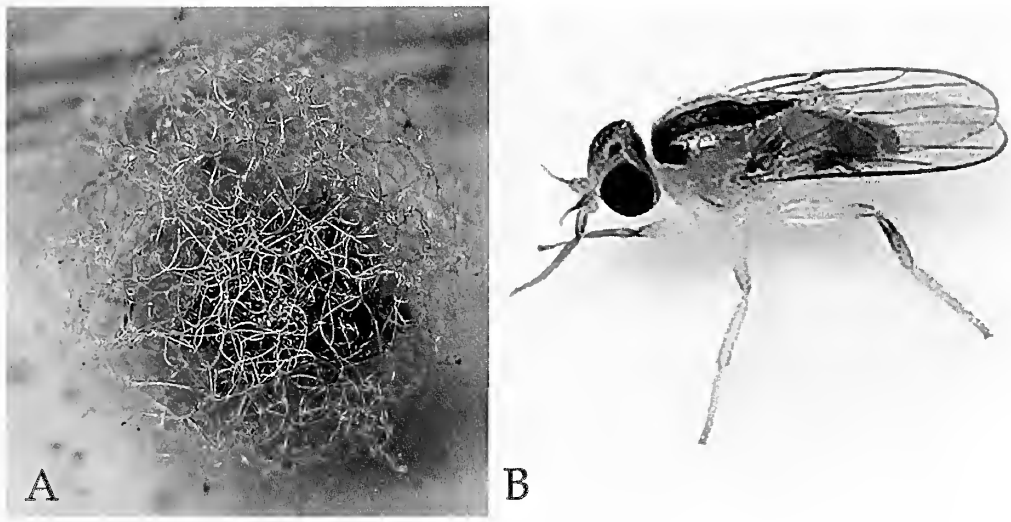

Figure 1.—Chloropidae development on spider egg sac. A. Egg mass of *Mimetus puritanus* Chamberlin, 1923 containing larvae of *Pseudogaurax anchora* (Loew, 1866). B. Adult *P. anchora*. Photos: John R. Maxwell.

whether or not this species has a specific host association with these spiders (Zaitzev & Charykuliev 1981).

2.3.2 Family Chloropidae: Several species of Chloropidae are known to be either parasitoids or predators of arachnid eggs. Genera of chloropids that have been reported as arachnid egg predators include *Conioscinella* Duda, 1929, *Gaurax* Loew, 1863, *Oscinella* Becker, 1909, *Oscinisoma* Lioy, 1864, *Pseudogaurax* Malloch, 1915, *Siphonella* Macquart, 1835, and *Tricimba* Lioy, 1864 (Barnes et al. 1992). Eason et al. (1967), Rollard (1984) and Barnes et al. (1992) provide a review of host records for several groups of Diptera and Hymenoptera, including chloropids. Several species of *Gaurax* and *Pseudogaurax* are suggested to be parasitoids of arachnid eggs (including amblypygids (Viquez & de Armas 2009; Chapin & Hebet 2016)) and have been raised from a variety of host eggs (see details in Table I) (Figs. 1 & 2). However, very little is known about the life histories of most of these species, and there is an indication that the larvae do not complete their development on a single egg, consuming a few or several eggs and, as such, must be considered as predators (Barnes et al. 1992). Some species are apparently opportunists, utilizing a variety of host species or even hosts of different orders, including lepidopteran cocoons and mantid oothecae. *Pseudogaurax signatus* (Loew, 1876) has been suggested as a biocontrol agent of black widow spiders, *Latrodectus* Walckenaer, 1805, since many specimens have been reared from egg sacs of this spider (Barnes et al. 1992; Vetter et al. 2012), with infestation rates reported to range from 6% (Vetter et al. 2012) to 40%, and estimated spider mortality >90% (Barnes et al. 1992). Female *P. signatus* flies lay the eggs on the surface of the host egg sac. Once hatched, larvae enter the egg sacs and consume multiple eggs, developing inside the sac.

2.3.3 Family Drosophilidae: Most species of Drosophilidae feed on decaying fruit and fungal material, as well as on fresh sap and nectar from flowers. Species in the subgenus *Titanochaeta* Knab, 1914 (genus *Scaptomyza* Hardy, 1850), however, differ from all other drosophilids in being parasitoids (or predators) of spider eggs. Unlike the remaining species of *Scaptomyza*, species in the subgenus *Titanochaeta* exhibit a slender, sharply pointed, stylet-like ovipositor, which is likely an adaptation to a lifestyle as a spider egg sac parasitoid or predator (O'Grady et al. 2003). The group is endemic to Hawaii and comprises 11 species known to develop on spider egg sacs (Wirth 1952; Eason et al. 1967; O'Grady et al. 2003). Little biological information is available on the host usage of species of *Titanochaeta*, but available rearing data indicate a preference for spiders in the family Thomisidae (Hardy 1965; Lapoint et al. 2013). Further study is needed in order to investigate the number of eggs consumed by each individual, thus confirming whether species of *Titanochaeta* are predators or parasitoids of spider eggs.

2.3.4 Family Ephydridae: The vast majority of species of Ephydridae feed primarily on autotrophic microorganisms such as algae (Foote 1984). One exception is *Trimerina madizans* (Fallen, 1813), which has been indicated as an egg parasitoid of marsh-inhabiting spiders (Wirth et al. 1987). The fly has been reported to attack egg sacs of the linyphiid *Hypselistes florens* (O. Pickard-Cambridge, 1875) (Wirth et al. 1987). However, it has been shown that each fly larva consumes on average six eggs of *H. florens* during its development (Foote 1984); in this case, the species is better regarded as a predator rather than a parasitoid.

2.3.5 Family Phoridae: Although most species of Phoridae associated with arachnids are merely saprophagous, some are known to be associated with living rather than dead arachnids. Most of these are predators of arachnid eggs. However, specimens of *Apocephalus borealis* Brues, 1924 have been reared from black widow egg sacs, *Latrodectus mactans* (Fabricius, 1775), (Araneae: Theridiidae), and this has been suggested to be a case of true parasitism, although further research is needed for proper confirmation (Disney 1994). Several species in *Megaselia* Rondani, 1856 and *Phalacrotophora* Enderlein, 1912 (Fig. 3) are known to prey on eggs of spiders in the families Araneidae (*Argiope* Audouin, 1826, *Gasteracantha* Sundevall, 1833, and *Larinioides* Caporiacco, 1934), Linyphiidae (*Pityohyphantes* Simon, 1929), Salticidae (*Phidippus* C. L. Koch, 1846), Tetragnathidae (*Meta* C. L. Koch, 1836) and Theridiidae (*Enoplognatha* Pavesi, 1880,

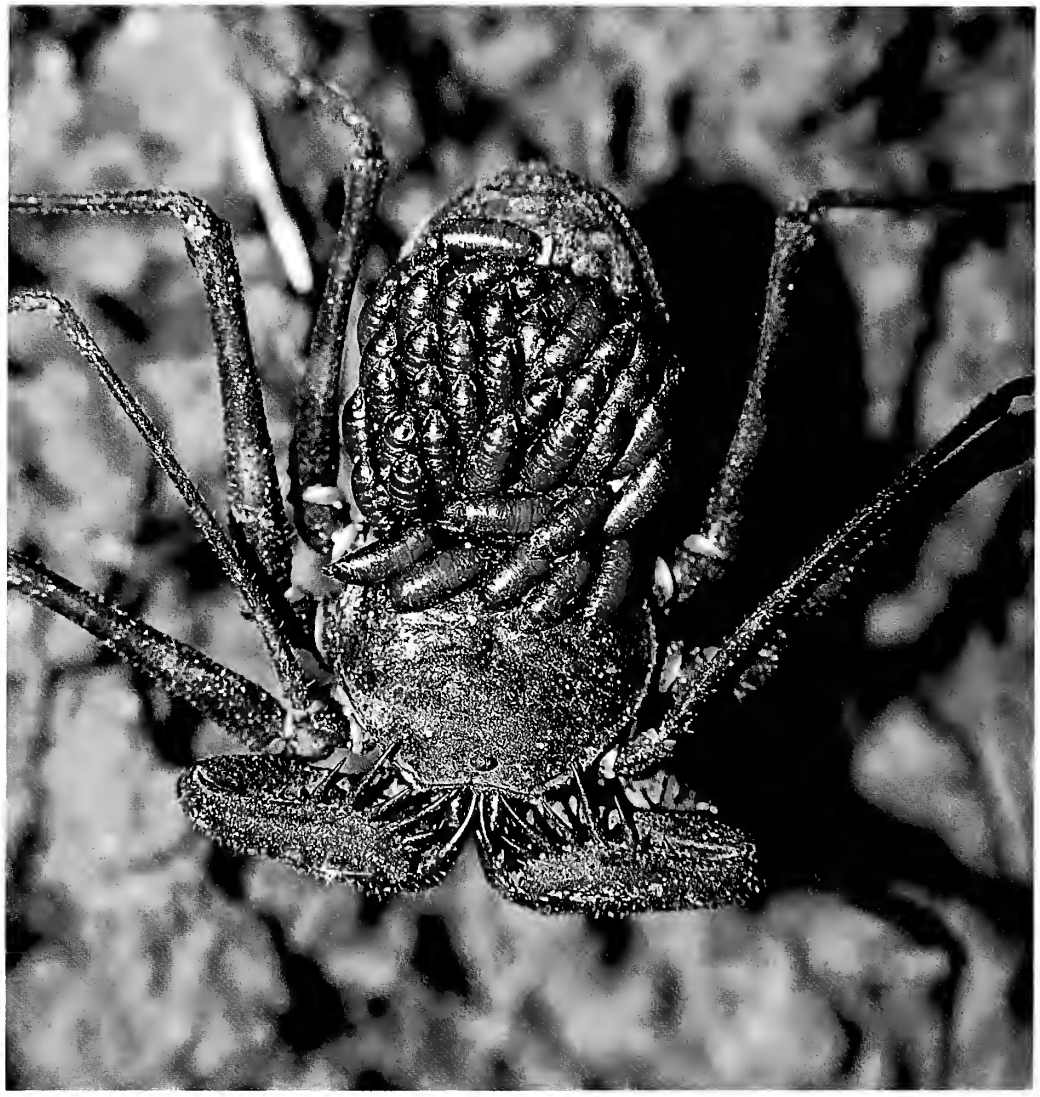

Figure 2.—Amblypigid female carrying pupae of *Pseudogaurax* (Diptera: Chloropidae) that were egg parasitoids of her egg case as larvae. Photographed at the Soltis Center, San Juan de Peñas Blancas, San Ramón, Costa Rica, by Kristie Reddick and Jessica Honaker.

Latrodectus and *Robertus* O. Pickard-Cambridge, 1879) (Disney & Evans 1980; Disney 1982, 1994, 1999).

2.3.6 Family Sarcophagidae: Sarcophagidae is a large family of Diptera with species exhibiting a breadth of habits and life histories. Most species are generalist scavengers and insect predators, while some species are kleptoparasites of solitary bees and wasps (Pape et al. 2012). Several species in the genus *Sarcophaga* Meigen, 1826 are spider egg parasitoids or predators (e.g., Eason et al. 1967; Auten 1925; Prakash & Pandian 1977; Austin 1985; Souza Lopes 1985; Cantrell 1986; Hieber & Uetz 1990). However, as in the dipteran families mentioned above, more research is needed in order to confirm whether these species are parasitoids or predators. Sehwendinger & Pape (2000) reported an unusual case of a predatory species of *Metopia* Meigen, 1803, a genus that mostly comprises kleptoparasites in nests of solitary aculeate Hymenoptera (Pape 1986). Larvae of *Metopia sinensis* Pape, 1986 apparently kill the spider host and complete most of their larval life on the carcass, behaving more like predators rather than parasites (following Price 1980).

2.3.7 Family Tachinidae: As discussed below, tachinids are well known as parasitoids of a range of insects. However, there is only a single record of a tachinid attacking spider eggs, a specimen of *Tachina* Meigen, 1803 which had been reared from egg sacs of the araneid *Larinioides cornutus* (Clerck, 1757) (Bertkau 1880).

2.4 Endoparasitoids.—The majority of dipteran endoparasitoids of arachnids are species of the family Acroceridae, which have exclusively been reared from a variety of spider families. There are also a few examples from other Diptera families (Phoridae, Sarcophagidae and Tachinidae). The specific details of the behaviors in each case are given below.

2.4.1 Family Acroceridae: Species of Acroceridae are commonly called spider flies due to their tight relationship with spiders as internal parasitoids. They are sometimes also referred to as small-headed flies in reference to the disproportionately small heads of some species. Spider flies represent a morphologically heterogeneous assemblage of lineages, currently classified into three subfamilies (Acrocerinae, Panopinae and Philopotinae), 55 genera and approximately 530

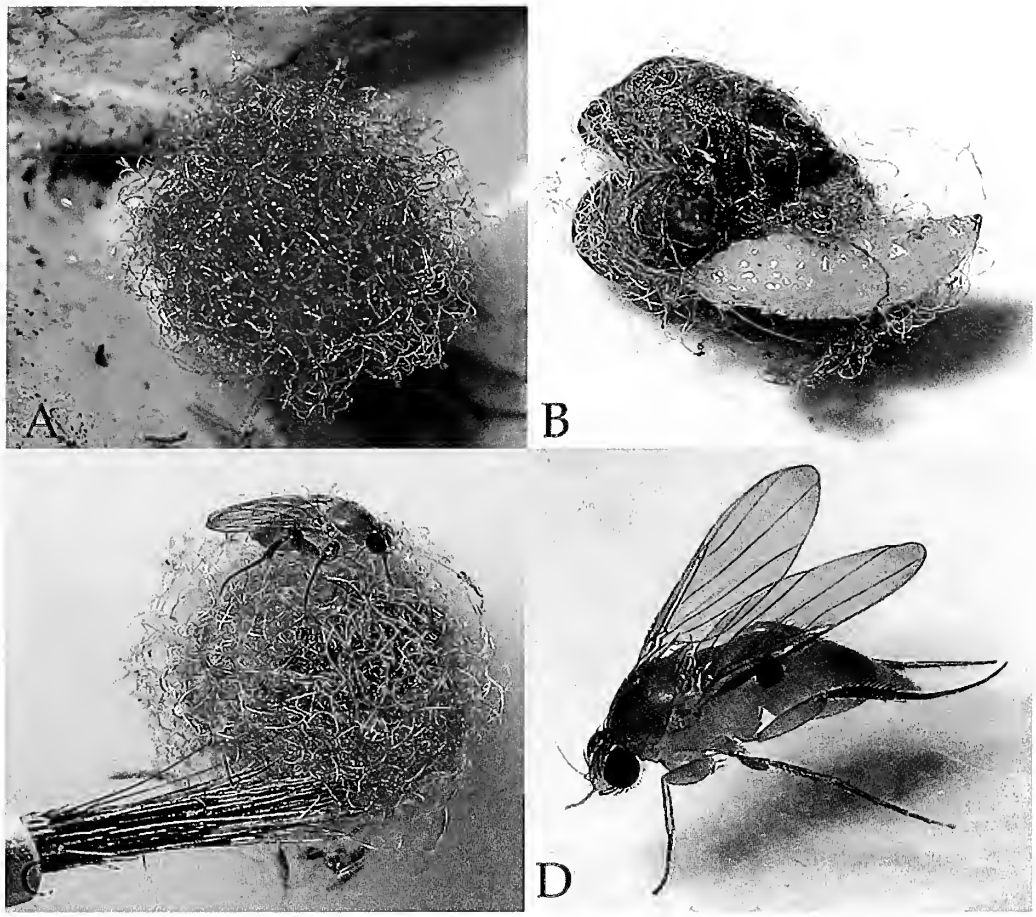

Figure 3.—Phoridae development on spider egg sac. A. Egg mass of *Mimetus puritanus* Chamberlin, 1923. B. Pupae and larva of *Phalacrotophora epeirae* (Brues, 1902). C. Spider egg mass, pupae and adult of *P. epeirae*. D. Adult *P. epeirae*, oblique view. Photos: John R. Maxwell.

species (Schlinger et al. 2013). Adults are morphologically very distinctive, usually with inflated or hunchbacked bodies, and occasionally with metallic coloration. Several species have long, modified mouthparts for nectar feeding and are considered important pollinators (e.g., Goldblatt et al. 1997; Potgieter et al. 1999; Pujol-Luz 2004; Carvalho & Machado 2006; Borkent & Schlinger 2008).

Spider fly larvae attack spiders in the Mygalomorphae (Fig. 4) and Araneomorphae. The only exception to the exclusive endoparasitic mode in Acroceridae is found in the Chilean genus *Carvalhoa* Koçak & Kemal, 2013 (= *Sphaerops* Philippi, 1865), which is reported to remain ectoparasitic on its host spider for at least three weeks (Schlinger 1987). It is still unknown whether the entire lifecycle is spent as an ectoparasite, but Schlinger (1987) reports this ectoparasitic behavior in multiple rearings of later instars of the species.

Records of acrocerids parasitizing Acari are extremely rare (Sferra 1986; Kerr & Winterton 2008), and no spider fly planidium has been reared from living mites to confirm, or identify, the acrocerid species in question. It is likely that the presence of acrocerid first instar larvae in mites is merely accidental parasitism, and the larvae probably do not develop further due to the small size of the mites relative to known acrocerid adults. Acrocerids are known to attack juvenile spiders, but even the smallest known spider hosts are several times larger than mites found in association with acrocerid planidia (Sferra 1986; Kerr & Winterton 2008). In the cases of mite parasitism, it is likely that the planidium is simply indiscriminately adhering to arachnids in an attempt to find a suitable host. In this case, the association between Acroceridae and Acari would not represent a true host-parasitoid relationship.

Generally, adult spider fly females scatter eggs during flight or oviposit large numbers of microtype eggs on twigs, branches or foliage (Schlinger 1987). In most species, oviposition seems to be entirely independent of the presence of a host, though naturally the flies occur in a habitat favorable to spider populations. Females of *Eulonchus* Gerstaecker, 1856 are reported to be attracted to burrows of trapdoor spiders in the genus *Antrodiaetus* Ausserer, 1871. Coyle (1971) reports a case in which, as trapdoor spider burrows were being excavated, a large number of spider flies quickly approached, hovering close to the ground and landing near closed burrow entrances, apparently attracted by some chemical released during the excavation process.

The first-instar acrocerid is a free-living planidium, which actively seeks out a spider host by crawling, looping or jumping, with the aid of well-developed setae, spines and a caudal suction disk (Schlinger 1981). Planidia in the genus *Acrocera* Meigen, 1803, however, differ from all other spider

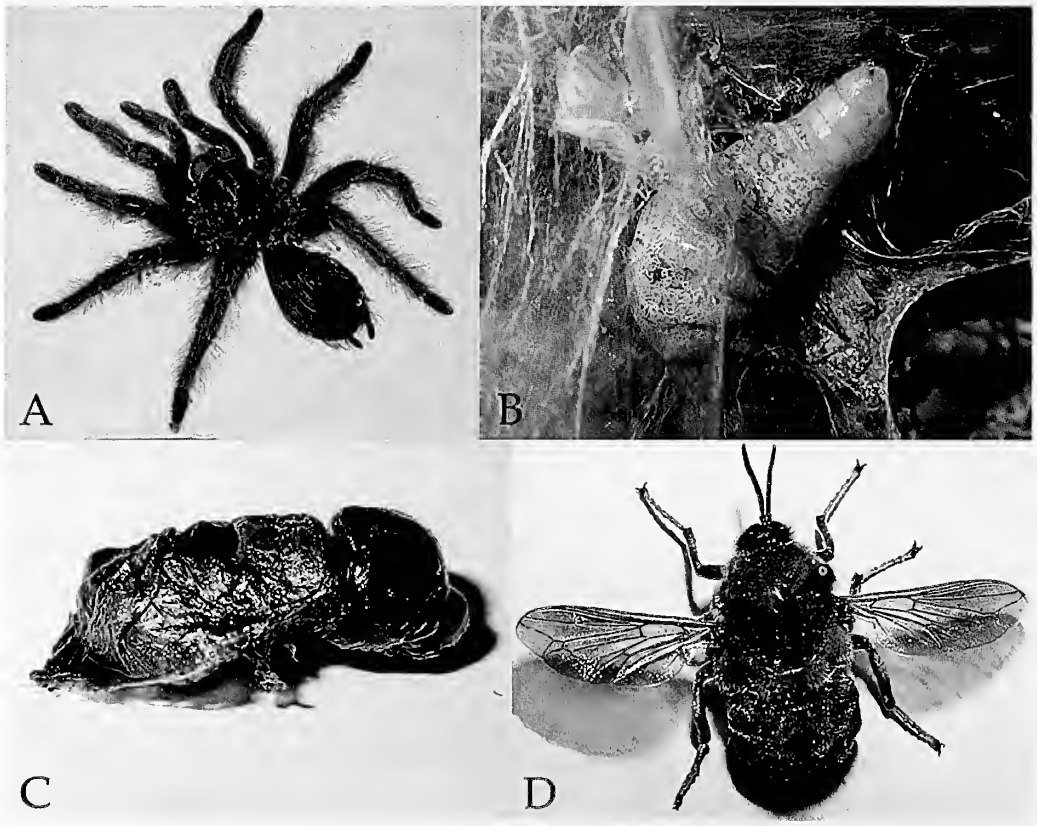

Figure 4.—Acroceridae development in the spider host. A. Spider host, *Aphonopelma duplex* (Chamberlin, 1925). B. Fourth instar larva of *Ocnaea* sp. C. Pupa of *Ocnaea* sp. D. Adult *Ocnaea* sp. Photos: Dr. A. Alagon.

flies in having a poorly sclerotized body and an abdomen with numerous annulations obscuring the regular body segmentation, as well as the absence of setal pile characteristic of acrocerid planidia (Schlinger 1981). *Acrocera* also exhibits a unique mode of entering its host, in which the first-instar larva injects itself into the spider. Planidia of *Acrocera orbicula* (Fabricius, 1787) have been observed entering a wolf spider through this sophisticated mode, in which first-instars firmly attach themselves to the host's cuticle by the mouthparts, presumably feeding externally for about a week (Overgaard Nielsen et al. 1999; Toft et al. 2012). Rather than entering the spider, the first-instar subsequently molts and the small, flexible, and glabrous second-instar is injected directly into the spider via the wound, leaving the exuvia of the ectoparasitic first-instar covering the site of infection. This mode of host invasion may reduce physical damage to the host in the initial phase of endoparasitism, thus enhancing parasitoid survival (Overgaard Nielsen et al. 1999). More research is needed in order to investigate whether this mechanism for infection is also present in other Acroceridae lineages.

Most host records for Acroceridae involve rearing of mature larvae from parasitized spiders, and observations of infestation of the host by the planidium stage are rare. The planidium presumably enters the host directly through the cuticle of the cephalothorax, opisthosoma or leg joints (Schlinger 1981, 1987; Nartshuk 1997), but these apparently have not been verified by direct observations. Acrocerid larvae eventually locate themselves in the opisthosoma and attach their posterior spiracle to the spider's book lung for respiration (Schlinger 1981, 1987). Schlinger (1987) proposed that upon entering the host, the larva may enter a state of diapause that can last for several months (Acrocerinae) up to 10 years (Panopinae), and, upon cessation of diapause, the actively feeding larva completes its life cycle relatively quickly (days to weeks), undergoing up to four instars. McQueen (1983) observed wolf spiders in the genus *Geolycosa* Montgomery, 1904 parasitized by *Pterodontia* Gray, 1832 spider flies and stated that infected spiders carry the larvae for approximately a year until they are entirely consumed by the parasitoid. However, further evidence is needed to support the hypothesis of diapause within the host and to verify the actual number of larval instars in Acroceridae, because the typical number of instars in lower brachyceran flies is three.

Many parasites and parasitoids have evolved remarkable strategies to manipulate the behavior of their hosts in order to promote their own survival and reproduction. These behavioral manipulations may include alterations in phototaxis, locomotion, foraging and defensive behaviors (Moore 2002). Most spider hosts of acrocerids, however, do not exhibit any obvious external indication of parasitism, although there are reports of enlargement of the spider's opisthosoma due to the presence of spider fly larvae (e.g., Lamore 1960; Barraclough & Croucamp 1997). It has been repeatedly reported that the host displays some abnormal, agitated behavior during the final stages of parasitism, in which the spiders walk aimlessly and incessantly scratch the lateral portions of the opisthosoma with the legs, presumably where the parasitoid is located (Cady et al. 1993; Barneche et al. 2013). In some species,

especially in the Mygalomorphae, the emergence of the parasite seems to correspond with the premolting behavior of the spider (e.g., Montgomery 1903; Cady et al. 1993; Barneche et al. 2013). However, a causative relationship between the production of the premolting web and parasitoid emergence can only be speculative at this time, but the presence of hook-like processes on the head and/or abdomen of the spider fly larva, which are supposedly used as attachment to the web, suggests that this is not coincidental. Lamore (1960) reported an example in which a larva of *Ogcodes dispar* (Macquart, 1855) parasitizing a basilica spider, *Mecynogea lemniscata* (Walckenaer, 1841), hung itself on the spider web while also hanging on to the spider on one end for a while, then released its hold on the exoskeleton in order to pupate. The last instar acrocerid larva typically only kills the host shortly prior to emergence, when it consumes the entire contents of the host body, leaving an empty, unbroken exoskeleton (Schlinger 1987; Nartshuk 1997).

While super-parasitism is common in early instars, usually only a single acrocerid adult ultimately emerges from its host (Cady et al. 1993; Overgaard Nielsen et al. 1999). Multiple emergences of larvae from a single host are more likely found in Panopinae, which attack large Mygalomorphae spiders capable of sustaining multiple parasitoids (Schlinger 1987; Cady et al. 1993).

Host records for acrocerids parasitizing spiders are known for at least 60 species, recorded from about 25 spider families (Schlinger 1987). Schlinger (1987, table 24) presented an extensive list of spider taxa parasitized by acrocerids, while Winterton et al. (2007) mapped host use onto a DNA-based phylogeny of the family. These studies clearly demonstrate that Panopinae are host-specific to Mygalomorphae spiders (Fig. 4), while Acrocerinae and Philopotinae are host-specific to the Araneomorphae. Only the genera *Acrocera* and *Carvalhoa* have been reared from Haplogynae spiders, while Philopotinae and all remaining Acrocerinae have only been recorded to attack Entelegynae. The cosmopolitan genera *Acrocera*, *Ogcodes* Latreille, 1797 and *Pterodontia* have been reared from numerous hosts in multiple spider families, but most geographically restricted and species-poor genera tend to be more host-specific, generally attacking only a single spider family (Schlinger 1987). Strict host specificity between particular acrocerid and spider species seems to be rare, but some trends are evident where host preference generally follows spider guilds instead of lineages (Schlinger 1987; Cady et al. 1993). Spiders most susceptible to parasitism by Acroceridae belong to guilds of cursorial or fossorial species (e.g., Mygalomorphae: Antrodiaetidae, Ctenizidae, Migidae, Theraphosidae; Araneomorphae: Anyphaenidae, Clubionidae, Lycosidae, Salticidae, Thomisidae), or those that occupy sac, tangle or funnel-like web retreats that are close to the ground, have webs with many connections to vegetation, or visit surrounding vegetation or substrate frequently (e.g., Agelenidae, Amaurobiidae, some Araneidae, Dipluridae, Segestriidae) (Schlinger 1987; Cady et al. 1993; Overgaard Nielsen et al. 1999). There are very few records of acrocerids parasitizing true web-dwelling spiders and exceptions typically involve comb-footed spiders (e.g., Theridiidae), where the spider may still be proximal to the substrate (e.g., Lamore 1960).

2.4.2 Family Sarcophagidae: As discussed above, the majority of members of Sarcophagidae are generalist scavengers and insect predators (Pape et al. 2012). However, there is one example of a sarcophagid acting as an endoparasitoid of a scorpion. *Sarcophaga dux* (Thomson, 1869), a species generally considered to be of forensic importance, was found to attack the Chinese scorpion *Mesobuthus martensii* (Karsch, 1879) (Scorpiones: Buthidae). Multiple larvae (3–6) attacked more than 50 individuals of this scorpion species, with more than 100 flies emerging as adults by the end of the study (Shi et al. 2015).

2.4.3 Family Tachinidae: Species of Tachinidae are internal parasitoids on a wide range of arthropod hosts. The most commonly used hosts are phytophagous insects, primarily Lepidoptera, Coleoptera, Hymenoptera, Heteroptera, and Orthoptera. Several genera of tachinids attack non-insect arthropods, including centipedes and scorpions (Stireman et al. 2006). There is a single record of a spider serving as a tachinid host (Vincent 1985). Two tachinid larvae in the genus *Lypha* Robineau-Desvoidy, 1830 emerged from the abdomen of immature individuals of *Antrodiaetus riversi* (O. Pickard-Cambridge, 1883) in the laboratory. The two larvae pupated outside of the host but neither adult emerged. Other known hosts of *Lypha* species are Lepidoptera in the families Gelechiidae and Tortricidae, and it is likely that the two spiders may have been accidental hosts that did not manage to survive and become adults. Vincent (1985) reported rearing over 340 spiders, which were examined and inspected for signs of parasitism, and only two contained larval tachinids.

The tachinid *Spilochaetosoma californicum* Smith, 1917 has been found to be an endoparasitoid of two Nearctic scorpions, *Anuroctonus phaiodactylus* (Wood, 1863) and *Paravaejovis spinigerus* (Wood, 1863) (Scorpiones: Vaejovidae). Multiple larvae of *S. californicum* emerged from wild caught individuals of both species and it is likely that this tachinid is a general parasitoid of burrowing scorpions (Williams et al. 1994).

3. CONCLUSION

In this review we summarized the available information on all lineages of Diptera known to attack arachnids, including predators, parasites, kleptoparasites and parasitoids. A summary table (Table 1) containing over 200 host records for eight families of Diptera attacking 36 arachnid families is included. Even though hymenopterans are among the best known natural enemies of arachnids, species of Diptera clearly also comprise a large component of arachnid enemies, attacking families in four orders of arachnids and all three suborders of Araneae.

A single species of Sarcophagidae, one species of Tachinidae and all species of Acroceridae are internal parasitoids, attacking juvenile and/or adult arachnids. Spider flies (family Acroceridae) comprise the only lineage of Diptera known to develop exclusively on arachnid hosts, representing some of the most significant natural enemies of spiders. Multiple species of Chloropidae, Drosophilidae, Ephydridae, Phoridae and Sarcophagidae are known to attack eggs of 11 families of arachnids, acting as predators and/or parasitoids of arachnid egg sacs (see Table I). Some of these species are known to be true predators, while some are known to be true parasitoids. However, in most cases, the life history strategy is not clear,

Table 1.—Host records for the known natural enemies of arachnids in the order Diptera, organized by arachnid order and family. Due to their generalist feeding habits, predators and kleptoparasites of individual arachnids were not included. Host stage exploited by the dipteran is noted as egg, adult, immature or stage unknown (Adult/Immature). EIS = E.I. Schlinger Collection database record.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Amblypygi	Phrynidae	*Paraphrynus laevifrons* (Pocock, 1894)	Adult	Chloropidae	*Pseudogaurax* sp.	Viquez & De Armas 2009
		Phrynus pseudoparvulus Armas & Viquez, 2001	Adult	Chloropidae	*Pseudogaurax* sp.	Viquez & De Armas 2009
Araneae	Agelenidae	*Agelenopsis naevia* (Walckenaer, 1841)	Adult/ Immature	Acroceridae	*Turbopsebius sulphuripes* (Loew)	Melander 1902
		Agelenopsis oregonensis Chamberlin & Ivie, 1935	Adult/ Immature	Acroceridae	*Acrocera bakeri* Coquillett	Schlinger 1987
		Agelenopsis sp.	Adult/ Immature	Acroceridae	*Acrocera melanderi* Cole	EIS database
		Agelenopsis sp.	Adult/ Immature	Acroceridae	*Ogcodes dispar* (Macquart)	Schlinger 1987
		Agelenopsis sp.	Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Guarisco 1990
		Barronopsis sp.	Adult/ Immature	Acroceridae	*Acrocera bimaculata* (Loew)	Schlinger 1987
		Coras montanus (Emerton, 1890)	Adult/ Immature	Acroceridae	*Acrocera bimaculata* (Loew)	Cady et al. 1993
		Coras montanus	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	Sabrosky 1948
		Coras montanus	Adult/ Immature	Acroceridae	*Turbopsebius sulphuripes* (Loew)	Cady et al. 1993
		Eratigena sicana (Brignoli,1976)	Adult/ Immature	Acroceridae	*Ogcodes* sp.	Brignoli 1976
		Hololena curta (McCook, 1894)	Adult/ Immature	Acroceridae	*Acrocera subfasciata* Westwood	EIS database
		Hololena curta	Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1960
		Hololena curta	Adult and immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
		Hololena curta	Immature	Acroceridae	*Turbopsebius diligens* (Osten Sacken)	Schlinger 1952
		Hololena sp.	Adult/ Immature	Acroceridae	*Acrocera melanderi* Cole	Cole 1969
		Hololena sp.	Adult/ Immature	Acroceridae	*Acrocera subfasciata* Westwood	Schlinger 1987
		Rualena sp.	Adult/ Immature	Acroceridae	*Turbopsebius diligens* (Osten Sacken)	Schlinger 1987
		Textrix denticulata (Olivier, 1769)	Adult/ Immature	Acroceridae	*Acrocera sanguinea* Meigen	Koch 1872
Araneae	Amaurobiidae	*Amaurobius erberi* (Keyserling, 1893)	Immature	Acroceridae	*Acrocera orbicula* (Fabricius)	Kehlmaier & Almeida 2014
		Amaurobius sp.	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
		Callobius benuetti (Blackwall, 1846)	Adult/ Immature	Acroceridae	*Acrocera fasciata* Wiedemann	Emerton 1890
		Undetermined genus	Adult/ Immature	Acroceridae	*Megalybus pictus* Philippi	Schlinger 1987
		Undetermined genus	Adult/ Immature	Acroceridae	*Thyllis* sp.	Schlinger 2003
Araneae	Amphinectidae	*Metaltella* sp.	Adult/ Immature	Acroceridae	*Holops cyaneus* Philippi	Schlinger 1987
Araneae	Antrodiaetidae	*Aliatypus californicus* (Banks, 1896)	Adult/ Immature	Acroceridae	*Eulonchus tristis Loew*	Coyle & Icenogle 1994
		Aliatypus erebus Coyle, 1974	Adult	Acroceridae	*Eulonchus tristis* Loew	Coyle & Icenogle 1994

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Antrodiaetidae	*Aliatypus* sp.	Adult/ Immature	Acroceridae	*Eulonchus tristis* Loew	Schlinger 1987
		Antrodiaetus riversi (O. Pickard-Cambridge, 1883)	Adult/ Immature	Acroceridae	*Eulonchus sapphirinus* Osten Sacken	EIS database
		Antrodiaetus riversi	Adult/ Immature	Acroceridae	*Eulonchus* sp.	Vincent 1986
		Antrodiaetus riversi	Adult	Tachinidae	*Lypha* sp.	Vincent 1985
		Antrodiaetus unicolor (Hentz, 1842)	Adult/ Immature	Acroceridae	*Eulonchus marialiciae* Brimley	Coyle 1971; Adler et al 1997
		Antrodiaetus sp.	Adult/ Immature	Acroceridae	*Eulonchus* sp.	Schlinger 1987
Araneae	Anyphaenidae	*Anyphaena californica* (Banks, 1904)	Adult/ Immature	Acroceridae	*Ogcodes* sp.	Cady et al. 1993
		Wulfila saltabundus (Hentz, 1847)	Adult/ Immature	Acroceridae	*Ogcodes borealis* Cole	Sabrosky 1948
		Wulfila saltabundus	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Sabrosky 1948
Araneae	Araneidae	*Alpaida veniliae* (Keyserling,1865)	Egg	Chloropidae	*Pseudogaurax cingulatus* Sabrosky	Sabrosky 1966
		Araneus angulatus Clerck, 1757	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Davidson 1896
		Araneus ejusmodi (Boesenberg & Strand, 1906)	Egg	Chloropidae	*Gaurax chiyokae* (Kanmiya)	Kanmiya 1972, 1983
		Araneus gemma (McCook, 1888)	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Pierce 1942
		Argiope aemula (Walckenaer, 1841)	Egg	Phoridae	*Megaselia araneivora* Goto	Goto 1985
		Argiope argentata (Fabricius,1775)	Egg	Sarcophagidae	*Sarcophaga davidsonii* Coquillett	Davidson 1894
		Argiope aurantia Lucas, 1833	Egg	Phoridae	*Megaselia* sp.	Kaston & Jenks 1937
		Argiope aurantia	Egg	Chloropidae	*Pseudogaurax anchora* (Loew)	Kaston & Jenks 1937
		Argiope aurantia	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Coquillet 1898
		Argiope aurantia	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Lockley & Young 1993
		Argiope aurantia	Egg	Sarcophagidae	*Sarcophaga litsingeri* (Shinonaga & Barrion)	Davidson 1896
		Argiope catenulata (Doleschall, 1859)	Egg	Sarcophagidae	*Sarcophaga litsingeri* (Shinonaga & Barrion)	Shinonaga & Barrion 1980
		Argiope pulchella Thorell, 1881	Egg	Sarcophagidae	*Sarcophaga banksi* Senior-White	Prakash & Pandian 1977
		Argiope trifasciata (Forsskål, 1775)	Egg	Sarcophagidae	*Tricharaea* (*Sarcophagula*) Thomson	de Armas & Garcia 1986
		Argiope sp.	Egg	Phoridae	*Megaselia argiopephaga* Disney	Disney 1982
		Cyrtophora moluccensis (Doleschall, 1857)	Egg	Sarcophagidae	*Sarcophaga arachnivora* (Lopes)	Cantrell 1986
		Cyrtophora moluccensis	Egg	Sarcophagidae	*Sarcophaga cyrtophorae* (Cantrell)	Cantrell 1986
		Cyrtophora moluccensis	Egg	Sarcophagidae	*Sarcophaga reposita* (Lopes)	Cantrell 1986

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Araneidae	*Gasteracantha cancriformis* (Linnaeus, 1785)	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Muma & Stone 1971
		Gasteracantha cancriformis	Egg	Chloropidae	*Pseudogaurax lancifer* (Coquillett)	Hall 1937
		Larinioides cornutus (Clerck, 1757)	Egg	Chloropidae	*Conioscinella frontella* (Fallen)	Krijger 1910
		Larinioides cornutus	Egg	Chloropidae	*Oscinella halterata* (Lamb)	Auten 1925
		Larinioides cornutus	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Auten 1925
		Larinioides cornutus	Egg	Tachinidae	*Tachina* sp.	Bertkau 1880
		Larinioides sclopetarius (Clerck, 1757)	Egg	Chloropidae	*Oscinella halterata* (Lamb)	Auten 1925
		Larinioides sclopetarius	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Brues 1902, 1903; Auten 1925
		Larinioides sclopetarius	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	King 1916
		Larinioides sclopetarius	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Auten 1925
		Mecynogea lemniscata (Walckenaer, 1841)	Adult	Acroceridae	*Ogcodes dispar* Macquart	Lamore 1960
		Metepeira atascadero Piel, 2001	Egg	Sarcophagidae	*Sarcophaga lindae* (Lopes)	Hieber & Uetz 1990
		Metepeira incrassata O. Pickard-Cambridge, 1903	Egg	Sarcophagidae	*Sarcophaga lindae* (Lopes)	Hieber & Uetz 1990
		Neoscona nautica (L. Koch, 1875)	Egg	Chloropidae	*Gaurax chiyokae* (Kanmiya)	Kanmiya 1972, 1983
		Ordgarius magnificus (Rainbow, 1897)	Egg	Sarcophagidae	*Sarcophaga arachnivora* (Lopes)	Souza Lopes 1985
		Singa nitidula C. L. Koch, 1844	Egg	Chloropidae	*Conioscinella frontella* (Fallen)	Vachon 1952
		Zygiella x-notata (Clerck, 1757)	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	Holl et al. 1983
		Undetermined genus	Egg	Phoridae	*Megaselia longifurca* (Lundbeck)	Disney 1999
Araneae	Clubionidae	*Clubiona leucaspis* (Simon, 1932)	Immature	Acroceridae	*Ogcodes reginae* Trojan	Kehlmaier & Almeida 2014
		Clubiona putris nom. dub. C. L. Koch, 1839	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Emerton 1890
		Clubiona putris nom. dub.	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Menge 1866
		Clubiona sp.	Immature	Acroceridae	*Acrocera orbicula* (Fabricius)	Millot 1938
Araneae	Ctenizidae	*Bothriocyrtum californicum* (O. Pickard-Cambridge, 1874)	Adult/ Immature	Acroceridae	*Ocnaea smithi* Sabrosky	Jenks 1938, 1940
		Cyrtocarenum cunicularium (Olivier, 1811)	Adult/ Immature	Acroceridae	*Astomella hispaniae* Lamarck	Brauer 1869
Araneae	Desidae	*Matachia ramulicola* Dalmas, 1917	Adult/ Immature	Acroceridae	*Ogcodes brunneus* (Hutton)	Dumbleton 1940
Araneae	Dipluridae	*Linothele cousini* (Simon, 1889)	Adult/ Immature	Acroceridae	*Lasia ecuadorensis* Bequaert	Schlinger 1987
Araneae	Euctenizidae	*Aptostichus stanfordianus* Smith, 1908	Adult/ Immature	Acroceridae	*Eulonchus smaragdinus* Gerstaecker	Schlinger 1987

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Eutichuridae	*Cheiracanthium punctorium* (Villers, 1789)	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Krehenwinkel et al. 2016
		Cheiracanthium sp.	Adult/ Immature	Acroceridae	*Ogcodes croucampi* Barraclough	Barraclough & Croucamp 1997
		Cheiracanthium sp.	Immature	Acroceridae	*Ogcodes* sp.	Schlinger 2003
Araneae	Gnaphosidae	*Herpyllus* sp.	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
		Zelotes sp.	Adult/ Immature	Acroceridae	*Acrocera melanderi* Cole	Schlinger 1987
		Zelotes sp.	Adult/ Immature	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Nielsen 1932
Araneae	Linyphiidae	*Hypselistes florens* (O. Pickard-Cambridge, 1875)	Egg	Ephydridae	*Trimerina madizans* (Fallen)	Wirth et al. 1987
		Pityohyphantes costatus (Hentz, 1850)	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Manuel 1984
Araneae	Liphistiidae	*Liphistius lahu* Schwendinger, 1998	Adult/ Immature	Sarcophagidae	*Metopia sinensis* Pape	Schwendinger & Pape 2000
		Liphistius sp.	Adult	Sarcophagidae	*Metopia sinensis* Pape	Schwendinger & Pape 2000
Araneae	Lycosidae	*Alopecosa accentuata* (Latreille, 1817)	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Eason et al. 1967
		Alopecosa barbipes (Sundevall, 1833)	Adult	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Locket 1930
		Alopecosa barbipes	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Locket 1930
		Alopecosa kochi (Keyserling, 1877)	Immature	Acroceridae	*Ogcodes melampus* (Loew)	Schlinger 1960
		Geolycosa domifex (Hancock, 1899)	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	McQueen 1978, 1983
		Lycosa godeffroyi L. Koch, 1865	Immature	Acroceridae	*Ogcodes basalis* (Walker)	Humphreys 1976
		Lycosa godeffroyi	Immature	Acroceridae	*Pterodontia melli* Erichson	Humphreys 1976
		Pardosa alacris (C. L. Koch, 1833)	Adult	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Langer 2005
		Pardosa distincta (Blackwall, 1846)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Sabrosky 1948
		Pardosa lapidicina Emerton, 1885	Adult/ Immature	Acroceridae	*Acrocera fasciata* Wiedemann	Eason 1966
		Pardosa lapidicina	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Eason 1966
		Pardosa littoralis Banks, 1846	Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Kaston 1937
		Pardosa littoralis	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Kaston 1937
		Pardosa lugubris (Walckenaer, 1802)	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	de Jong et al. 2000
		Pardosa milvina (Hentz, 1844)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Eason et al. 1967
		Pardosa milvina	Immature	Acroceridae	Undetermined genus	Allard & Robertson 2003
		Pardosa prativaga (L. Koch, 1870)	Immature	Acroceridae	*Acrocera orbicula* (Fabricius)	Toft et al. 2012
		Pardosa pullata (Clerck, 1757)	Adult/ Immature	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Duffey 2000
		Pardosa pullata	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Schlinger 1987
		Pardosa pullata	Adult/ Immature	Acroceridae	*Ogcodes rufoabdominalis* Cole	Eason et al. 1967
		Pardosa saxatilis (Hentz, 1844)	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Kaston 1937

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Lycosidae	*Pardosa sternalis* (Thorell, 1877)	Adult/ Immature	Acroceridae	*Acrocera convexa* Cole	Schlinger 1987
		Pardosa sternalis	Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1960
		Pardosa sternalis	Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1960
		Pardosa sternalis	Adult/ Immature	Acroceridae	*Pterodontia misella* Osten Sacken	Schlinger 1987
		Pardosa tuoba Chamberlin, 1919	Adult/ Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1987
		Pardosa utahensis Chamberlin, 1919	Adult/ Immature	Acroceridae	*Ogcodes rufoabdominalis* Cole	Capelle 1966
		Pardosa vancouveri Emerton, 1917	Adult/ Immature	Acroceridae	*Acrocera convexa* Cole	Schlinger 1987
		Pirata sedentarius Montgomery, 1904	Adult/ Immature	Acroceridae	*Ogcodes dispar* (Macquart)	Eason et al. 1967
		Schizocosa crassipes (Walckenaer, 1837)	Adult/ Immature	Acroceridae	*Acrocera fasciata* Wiedemann	Montgomery 1903, Johnson 1915
		Schizocosa ocreata (Hentz, 1844)	Adult/ Immature	Acroceridae	*Acrocera fasciata* Wiedemann	Montgomery 1903, Johnson 1915
		Schizocosa rovneri Uetz & Dondale, 1979	Adult/ Immature	Acroceridae	*Ogcodes borealis* Cole	Cady et al. 1993
		Schizocosa rovneri	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Cady et al. 1993
		Tigrosa helluo (Walckenaer, 1837)	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Eason et al. 1967
		Trochosa hispanica Simon, 1870	Adult/ Immature	Acroceridae	*Ogcodes lautereri* Chvala	Canzoneri & Hansen 1996
		Trochosa terricola Thorell, 1856	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	King 1916
Araneae	Migidae	*Moggridgea crudeni* Hewitt, 1913	Adult/ Immature	Acroceridae	*Astomella capensis* Schlinger	Barraclough 1984
Araneae	Mimetidae	*Mimetus notius* Chamberlin, 1923	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Guarisco 2001
Araneae	Miturgidae	*Griswoldia* sp.	Immature	Acroceridae	*Thyllis crassa* (Fabricius)	Schlinger 1987
		Griswoldia sp.	Adult/ Immature	Acroceridae	*Thyllis* sp.	Schlinger 2003
Araneae	Nephilidae	*Nephila clavipes* (Linnaeus, 1767)	Egg	Chloropidae	*Pseudogaurax higginsi* Sabrosky	Barnes et al. 1992
		Nephila clavipes	Egg	Chloropidae	*Pseudogaurax mexoculatus* Sabrosky	Barnes et al. 1992
		Nephila inaurata (Vinson, 1863)	Egg	Chloropidae	*Pseudogaurax coyleae* Cogan	Cogan 1977
		Nephila pilipes (Fabricius, 1793)	Egg	Chloropidae	*Pseudogaurax seguyi* (Sabrosky)	Sabrosky 1990
Araneae	Oecobiidae	*Uroctea limbata* (C. L. Koch, 1843)	Egg	Bombyliidae	*Petrorossia feti* Zaitsev & Charykuliev	Zaitzev & Charykuliev 1981
Araneae	Oxyopidae	*Oxyopes lineatus* Latreille, 1806	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	Schlinger 1987
		Oxyopes salticus Hentz, 1845	Adult/ Immature	Acroceridae	*Ogcodes dispar* (Macquart)	Eason et al. 1967
		Oxyopes salticus	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Eason et al. 1967
Araneae	Philodromidae	*Philodromus aureolus* (Clerck, 1757)	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Auten 1925

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Philodromidae	*Philodromus cespitum* (Walckenaer, 1802)	Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	Kehlmaier et al. 2012
		Philodromus cespitum	Egg	Chloropidae	*Oscinella halterata* (Lamb)	Auten 1925
		Philodromus cespitum	Egg	Sarcophagidae	*Sarcophaga sexpunctata* (Fabricius)	Auten 1925
		Philodromus sp.	Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1960
Araneae	Phyxelididae	*Ambohima sublima* Griswold, 1990	Immature	Acroceridae	*Thyllis* sp.	Schlinger 2003
Araneae	Plectreuridae	*Kibramoa* sp.	Adult/ Immature	Acroceridae	*Acrocera arizonensis* Cole	Schlinger 1987
Araneae	Salticidae	*Aelurillus v-insignitus* (Clerck, 1757)	Adult	Acroceridae	*Ogcodes pallipes* Latreille	Millot 1938
		Aelurillus v-insignitus (Clerck)	Adult/ Immature	Acroceridae	*Ogcodes varius* Latreille	Séguy 1926
		Cobanus sp.	Adult/ Immature	Acroceridae	*Terphis* sp.	Schlinger 1987
		Cosmophasis bitaeniata (Keyserling, 1882)	Adult/ Immature	Acroceridae	*Ogcodes basalis* (Walker)	Schlinger 1987
		Cosmophasis bitaeniata	Adult/ Immature	Acroceridae	*Ogcodes doddi* Wandolleck	Wandolleck 1906, Dodd 1906
		Eris militaris (Hentz, 1845)	Immature	Acroceridae	*Acrocera* sp.	Larrivée & Borkent 2009
		Evarcha jucunda (Lucas, 1846)	Immature	Acroceridae	*Ogcodes reginae* Trojan	Kehlmaier & Almeida 2014
		Habronattus hallani (Richman, 1973)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Heliophanus sp.	Immature	Acroceridae	*Ogcodes pallipes* Latreille	Millot 1938
		Heliophanus sp.	Immature	Acroceridae	*Ogcodes zonatus* Erichson	Millot 1938
		Lyssomaninae gen. sp.	Adult/ Immature	Acroceridae	*Ogcodes guttatus* (Costa)	Schlinger 1987
		Metaphidippus manni (Peckham & Peckham, 1901	Adult/ Immature	Acroceridae	*Pterodontia vix* Townsend	Schlinger 1987
		Metaphidippus sp.	Adult/ Immature	Acroceridae	*Acrocera bulla* Westwood	Schlinger 1987
		Metaphidippus sp.	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Schlinger 1987
		Pelegrina aeneola (Curtis, 1892)	Adult/ Immature	Acroceridae	*Acrocera bulla* Westwood	Beckwith et al. 1987
		Pelegrina aeneola	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Beckwith et al. 1987
		Pelegrina aeneola	Adult/ Immature	Acroceridae	*Ogcodes borealis* Cole	Schlinger 1987
		Pelegrina proterva (Walckenaer, 1837)	Immature	Acroceridae	*Ogcodes eugonatus* Loew	Larrivée & Borkent 2009
		Pelegrina proterva	Immature	Acroceridae	*Ogcodes melampus* Loew	Larrivée & Borkent 2009
		Phidippus ardens Peckham & Peckham, 1901	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Schlinger 1987
		Phidippus audax (Hentz, 1845)	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Jones 1940
		Phidippus comatus Peckham & Peckham, 1901	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Schlinger 1987

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Salticidae	*Phidippus johnsoni* (Peckham & Peckham, 1883)	Adult/ Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1987
		Phidippus johnsoni	Adult/ Immature	Acroceridae	*Ogcodes boharti* Schlinger	Schlinger 1987
		Phidippus johnsoni	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Phidippus octopunctatus (Peckham & Peckham, 1883)	Egg	Sarcophagidae	*Sarcophaga davidsonii* Coquillett	Coquillet 1892; Davidson 1896
		Phidippus princeps (Peckham & Peckham, 1883)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Phidippus regius C. L. Koch, 1846	Egg	Phoridae	*Phalacrotophora epeirae* (Brues)	Manuel 1984
		Phidippus rimator nom. dub. (Walckenaer, 1837)	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Phidippus sp.	Adult/ Immature	Acroceridae	*Acrocera* sp.	Schlinger 1987
		Phlegra fasciata (Hahn, 1826)	Immature	Acroceridae	*Ogcodes pallipes* Latreille	Millot 1938
		Sassacus sp.	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Sidusa sp.	Adult/ Immature	Acroceridae	*Terphis* sp.	Schlinger 2003
Araneae	Segestriidae	*Ariadna maxima* (Nicolet, 1849)	Adult/ Immature	Acroceridae	*Carvalhoa appendiculata* Philippi	Schlinger 1987
Araneae	Tetragnathidae	*Meta menardi* (Latreille, 1804)	Egg	Phoridae	*Megaselia melanocephala* (Roser)	Decou-Burghele 1961
		Tetragnatha sp.	Egg	Chloropidae	*Pseudogaurax silbergliedi* Sabrosky	Sabrosky 1990
		Tetragnatha sp.	Egg	Chloropidae	*Siphonella* sp.	Kintner 1935
Araneae	Theraphosidae	*Acanthoscurria sternalis* Pocock, 1903	Immature	Acroceridae	*Exetasis jujuyensis* Gillung	Barneche et al. 2013
		Aphonopelma duplex (Chamberlin, 1925)	Adult/ Immature	Acroceridae	*Ocnaea* sp.	Alagon & Odell 2004
		Aphonopelma hentzi (Girard, 1852)	Adult/ Immature	Acroceridae	*Lasia purpurata* Bequaert	Baerg 1958; Eason et al. 1967
		Aphonopelma sp.	Adult/ Immature	Acroceridae	*Ocnaea* sp.	Schlinger 1987
		Chaetopelma sp.	Adult/ Immature	Acroceridae	*Astomella gravis* Erichson	Schlinger 1987
		Grammostola actaeon (Pocock, 1903)	Adult	Acroceridae	*Exetasis* sp.	Vellard 1934
		Lasiodora klugi (C. L. Koch, 1841)	Immature	Acroceridae	*Exetasis eickstedtae* Schlinger	Eickstedt 1971; Schlinger 1972
		Phrixotrichus scrofa (Molina, 1788)	Immature	Acroceridae	*Arrhynchus maculatus* Schlinger	Schlinger 1968
Araneae	Theridiidae	*Enoplognatha ovata* (Clerck, 1757)	Adult/ Immature	Acroceridae	*Ogcodes gibbosus* (Linnaeus)	Pichka 1977
		Enoplognatha sp.	Egg	Phoridae	*Megaselia tenebricola* Schmitz	Evans 1969
		Enoplognatha sp. or *Robertus* sp.	Egg	Phoridae	*Megaselia angusta* Wood	Disney & Evans 1980; Disney 1999
		Enoplognatha sp. or *Robertus* sp.	Egg	Phoridae	*Megaselia longifurca* (Lundbeck)	Disney & Evans 1980; Disney 1999

Table 1.—Continued.

Host order	Host family	Arachnid host	Host stage	Fly family	Fly parasitoid/ parasite/predator	Reference
Araneae	Theridiidae	*Latrodectus geometricus* C.L. Koch, 1841	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Vetter et al. 2012
		Latrodectus hesperus Chamberlin & Ivie, 1935	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Vetter et al. 2012
		Latrodectus mactans (Fabricius, 1775)	Egg	Phoridae	*Apocephalus borealis* Brues	Disney 1994
		Latrodectus mactans	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Davidson 1896
		Latrodectus mactans	Egg	Chloropidae	*Pseudogaurax* sp.	Baerg 1959
		Parasteatoda tepidariorum (L. Koch, 1841)	Egg	Chloropidae	*Pseudogaurax signatus* (Loew)	Kaston & Jenks 1937
		Robertus sp.	Egg	Phoridae	*Megaselia tenebricola* Schmitz	Disney & Evans 1980
		Steatoda palomara Chamberlin & Ivie, 1935	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
Araneae	Thomisidae	*Diaea* sp.	Adult/ Immature	Acroceridae	*Ogcodes nitens* (Hutton)	Schlinger 1987
		Mecaphesa sp.	Immature	Acroceridae	*Ogcodes eugonatus* Loew	Cokendolpher et al. 1979
		Misumena vatia (Clerck, 1757)	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	de Jong et al. 2000
		Thomisus onustus (Walckenaer, 1806)	Adult/ Immature	Acroceridae	*Ogcodes fumatus* (Erichson)	de Jong et al. 2000
		Xysticus cunctator Thorell, 1877	Immature	Acroceridae	*Ogcodes adaptatus* Schlinger	Schlinger 1960
		Xysticus cunctator	Immature	Acroceridae	*Ogcodes melampus* (Loew)	Schlinger 1960
		Xysticus luctuosus (Blackwall, 1836)	Adult/ Immature	Acroceridae	*Ogcodes pallipes* Latreille	Trojan 1956
		Xysticus montanensis Keyserling1887	Immature	Acroceridae	*Ogcodes borealis* Cole	Schlinger 1960
		Xysticus montanensis	Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1960
		Xysticus sp.	Adult/ Immature	Acroceridae	*Ogcodes eugonatus* (Loew)	Schlinger 1987
		Undetermined genus	Egg	Drosophilidae	*Scaptomyza (Titanochaeta)* 11 spp.	Wirth 1952; Hardy 1965; Lapoint et al. 2013
Araneae	Trachelidae	*Trachelas mexicanus* Banks, 1898	Adult/ Immature	Acroceridae	*Ogcodes pallidipennis* (Loew)	Schlinger 1987
Araneae	Unknown	Undetermined genus	Egg	Phoridae	*Megaselia oviaraneae* Disney	Disney 1999
Scorpiones	Buthidae	*Centruroides margaritatus* (Gervais, 1841)	Adult/ Immature	Sarcophagidae	*Sarcodexia sternodontis* Townsend	Townsend 1893
		Mesobuthus martensii (Karsch, 1879)	Adult/ Immature	Sarcophagidae	*Sarcophaga dux* Thomson	Shi et al. 2015
Scorpiones	Vaejovidae	*Anuroctonus phaiodactylus* (Wood, 1863)	Adult	Tachinidae	*Spilochaetosoma californicum* Smith	Williams et al. 1994
		Vaejovis spinigerus (Wood, 1863)	Adult/ Immature	Tachinidae	*Spilochaetosoma californicum* Smith	Williams et al. 1994
Trombidiformes	Anystidae	Undetermined genus	Adult/ Immature	Acroceridae	Undetermined genus	Kerr & Winterton 2008
Trombidiformes	Erythraeidae	*Abrolophus* sp.	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	Sferra 1986
Trombidiformes	Trombidiidae	*Podothrombium* sp.	Adult/ Immature	Acroceridae	*Pterodontia flavipes* Gray	Sferra 1986

and deeper investigation is needed in order to verify whether the species in question are predators, parasitoids, or both.

In general, there is still much to be learned about the interactions between Diptera and the arachnids they attack. Many more large rearing studies of spiders and other arachnids would be the best approach to fill this gap in knowledge, as the majority of reports of natural enemies are the result of individual incidental rearings. Unfortunately, there are still large numbers of arachnid species that we know almost nothing about in terms of their habits, habitats, mating behavior and natural enemies. This lack of basic natural history information seriously limits the ability of arachnologists and dipterists to address these issues, though this problem is not limited to these groups or questions (Tewksbury et al. 2014; Barrows et al 2016). It is imperative that we as biologists spend time observing our chosen study organisms in their natural environment, if we are to have any hope of both discovering and understanding the ecological web of organisms that covers our planet.

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Integrating fossil and extant lineages: an examination of morphological space through time (Araneae: Archaeidae)

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Abstract. The integration of fossil and extant lineages in evolutionary analyses allows for morphological change to be examined over long periods of time. This study explores how fossil archaeid species compare with extant species in terms of morphological diversity. By adding additional data for fossil species, this study builds upon the total evidence phylogenetic data matrix and the carapace/chelicerae measurements of an earlier analysis. Phylogenetic analyses recovered a monophyletic Archaeidae crown-group, and there is some support for a monophyletic fossil clade. However, analyses did not recover a monophyletic Archaeidae: the fossil *Lacunauchenius* Wunderlich, 2008 fell outside of the remaining archaeids, although its placement was only weakly supported. Fossil archaeids are morphologically diverse, and compared to extant species, occupy a novel morphological space characterized by shorter features. There has been a shift through time towards the more elongated features of the extant species. Given the unique morphologies of the fossil species, it is likely that fossil archaeids occupied unique niches that are no longer occupied by extant species.

Keywords: Morphology, evolution, phylogenetics, Palpimanoidea, arachnid

The fossil record offers the possibility to examine morphological change over long periods of time, and the integration of fossil and extant lineages in phylogenetic analysis is crucial for examining trait evolution (Slater et al. 2012). The fossil record suggests that palpimanoid spiders were possibly more diverse and more widespread in the past, having several lineages known only from fossils (Petrunkevitch 1942; Eskov & Wunderlich 1995; Selden et al. 2008; Wunderlich 2008). Archaeidae, in particular, is a palpimanoid family that has an unusual distribution and a well-documented fossil record: fossil archaeids are known from only the Northern Hemisphere, while extant lineages occur only in the Southern Hemisphere, restricted to Madagascar, Australia, and South Africa (Forster & Platnick 1984). A divergence dating study that included fossil and extant taxa concluded that the split between the extinct northern and extant southern faunas likely relates to Pangaea breaking into Gondwana and Laurasia in the Jurassic (Wood et al. 2013). So, it appears that archaeids were once more widespread, but are now restricted to relictual areas. However, within their present day distributions the extant clades have diversified, with the timing of diversification in Australia congruent with Miocene aridification (Rix & Harvey 2012b), and in South Africa possibly congruent with Miocene uplift of the Great Escarpment (Wood et al. 2015). Diversification in the Madagascan clade may be due to geoclimatic events that are more ancient than the Miocene, with repeated climatic events leading to the build-up of sympatric species in montane, rainforest areas (Wood et al. 2015).

Archaeid spiders are morphologically bizarre: these spiders have an extremely modified carapace that is extended and tubular in structure, that encircles the cheliceral bases, and gives archaeids the appearance of a "neck" and "head" (Fig. 1). This unusual morphology directly relates to their predatory behaviors: the modified carapace allows for highly maneuverable chelicerae that are used to attack their spider prey at a distance (Forster & Platnick 1984; Wood et al. 2012). There is a diversity of "neck" shapes among archaeids, with "necks" of varying degrees of elongation, from long and constricted to short and stout, with different morphs independently evolving within the family (Wood et al. 2007). The morphological diversity in the carapace and chelicerae shape in the extant clades seems to directly relate to the diversification patterns mentioned above: the Madagascan clades show an increased rate of morphological trait evolution compared to the Australian and South African clades (Wood et al. 2015). It may be that trait divergence is increased in the Madagascan clades due to species living in sympatry, as has been found in *Percina* darters (Carlson et al. 2009).

While previous studies in archaeids incorporated fossils in order to date divergence events and to understand phylogenetic relationships, the fossils were not incorporated into the studies of trait evolution and morphological diversity. Here, I specifically focus on the fossil archaeid species (Table 1), which come from Bitterfield amber (age disputed, from Eocene to Miocene), Baltic amber (Eocene age), and Burmese amber (Cretaceous age), as well as compression fossils from Inner-Mongolia (Jurassic age). Using the total evidence dataset from Wood et al. (2015), which is the most comprehensive archaeid phylogenetic study to date, I add several fossil taxa to the matrix, scoring them for morphological characters, and I also take morphological measurements for the fossil lineages. The motivation for this study is to explore how the morphological space in archaeid spiders has changed over time.

METHODS

Phylogenetic analysis and divergence dating.—In order to examine the evolutionary history of living and extinct archaeids, a phylogenetic analysis and a divergence dating analysis were executed using the total evidence data matrix modified from Wood et al. (2015). This data matrix contains living and fossil archaeids, with the living taxa scored for both molecular and morphological characters and the fossil taxa scored only for morphological characters. The four known extant genera from Madagascar, Australia and South Africa, are represented in this matrix: *Eriauchenius* Cambridge, 1881,

Austrarchaea Forster & Platnick, 1984, *Afrarchaea* Forster & Platnick, 1984 and *Zephyrarchaea* Rix & Harvey, 2012a, as well as the monophyletic "Gracilicollis Group" (Wood 2008) that is currently considered part of *Eriauchenius*. Five fossil genera (out of 11 fossil genera in total) were represented in this matrix: *Archaea* Koch & Berendt, 1854, *Burmesarchaea* Wunderlich, 2008, *Baltarchaea* Eskov, 1992, *Myrmecarchaea* Wunderlich, 2004, and *Patarchaea* Selden, Huang & Ren, 2008. For the current study, two additional genera represented by three additional fossil species were added to the matrix: *Lacunauchenius speciosus* Wunderlich, 2008, *Saxonarchaea dentata* Wunderlich, 2004, and *Saxonarchaea diabolica* Wunderlich, 2004 (see Table 1 for a list of the fossil specimens used in this study). Archaeids belong to the Palpimanoidea (Wood et al. 2012): the outgroup taxa included 13 terminals representing the remaining four Palpimanoidea families plus one species in the family Austrochilidae, and the resulting tree was rooted with one species of Haplogynae (family Segestriidae). The new matrix, with the inclusion of 3 fossil taxa and with duplicate taxa pruned, had a total of 77 terminals. The final concatenated matrix had 5584 characters, consisting of: 111 morphological characters (reduced from the original 126 when phylogenetically uninformative characters were excluded); 658 base pairs (bp) for the mitochondrial protein-coding gene Cytochrome c Oxidase subunit 1 (COI); 328 bp for the nuclear protein-coding gene Histone-H3 (H3); and 2572 bp and 1915 bp, respectively, for the ribosomal nuclear genes 18S and 28S.

The morphology-only portion of the data set was analyzed under parsimony using TNT version 1.5 (Goloboff et al. 2008): characters were treated as unweighted and non-additive ("unordered"), and gaps were treated as missing (command 'nstates nogaps'). Uninformative characters were inactivated (command 'xinact'). Optimal trees were searched using random addition sequences to generate Wagner trees, followed by the tree-bisection reconnection (TBR) algorithm, making 1000 replications and saving up to 10 trees per replication (command 'mult = tbr replic 1000 hold 10'). To examine clade support values, jackknife calculations were performed on group frequencies with the probability of elimination set to $P = 0.36$, consisting of 1000 pseudoreplicates of 10 random addition sequences, followed by 10 iterations of TBR and retaining 10 trees per replicate (command: 'mult: no ratchet replic 10 tbr hold 10; resample jak replic 1000;').

To examine the timing of divergence, a time-calibrated phylogeny was created using Bayesian methods by treating archaeid fossil taxa as non-contemporaneous tips following the methods of Pyron (2011) and Wood et al. (2013). This analysis was performed using the combined molecular and morphological dataset. For each terminal fossil, the geological stage and reference are listed in Table 1. The fossil tip date was treated as a uniform distribution spanning the entire estimated age range of the fossil species. There is dispute around the age of the Bitterfeld amber deposits (Dunlop 2010), with age estimations ranging from the Eocene to the Oligocene. Because of this, the tip date for the two species of *Saxonarchaea* Wunderlich, 2004 was broad, being set to 23–49 Ma. The root age was constrained, being treated as a normal distribution with a mean of 225 Ma with soft upper and lower bounds (standard deviation = 30; 5–95% bounds = 175.7–274.3 Ma), based on the age of the oldest Araneomorphae fossil (Selden et al. 1999). The breadth of this prior constraint was intentionally large to contain the true age of Araneomorphae divergence and so as not to bias the study. The mean node ages and their 95% Bayesian credible interval (CI) were estimated using a relaxed clock model implemented in BEAST version 1.8.2 (Drummond et al. 2012). The data partitions and nuclear substitution models were the same as the Wood et al. (2015) divergence dating analysis: partition 1 = morphology, set to a standard discrete Markov model (Lewis 2001); partition 2 = COI codon position 3, set to a Hasegawa-Kishino-Yano (HKY) model; partition 3 = COI codon positions 1 and 2 and H3, set to a HKY model; and partition 4 = 18S and 28S, set to a K80+I+G model. The molecular clock model was set to relaxed, uncorrelated lognormal and the tree prior was set to speciation, birth–death process. Two MCMC analyses were run for 50 million generations, sampling the chain every 1000 generations. Log files were visualized in Tracer version 1.4 (Rambaut et al. 2014) to ensure that the effective sample size of the combined log files

Figure 1.—Archaeid spiders: A. *Eriauchenius* sp., male, lateral view, legs removed. B. *Archaea paradoxa*, male, from Baltic amber, Eocene age, anterior view. Scale bars = 0.5 mm.

Table 1.—List of fossil vouchers measured for trait analyses and used for gathering morphological data for phylogenetic analysis. The deposit where the fossils originated, the deposit age, and references are also listed. Museum abbreviations: GPIH = Geologisch-Paläontologisches Institut der Universität Hamburg; JW = Joerg Wunderlich private collection; SMF = Senckenberg Research Institute and Natural History Museum, Frankfurt; SMNS = Staatliches Museum für Naturkunde, Stuttgart; ZMB = Museum für Naturkunde, Berlin. An asterisk (*) denotes a fossil that did not have a museum voucher number, so the number reported was created specifically for this study. The *Myrmecarchaea* specimen is likely *M. pediculus*, based on the presence of a constriction in the "neck."

Species	Voucher material	Species reference	Deposit	Deposit age	Reference for deposit age
Archaea paradoxa	GPIH: S2117 ♂; S791 ♂; S3934 ♂; S3955 ♂; S5935 ♂; S5974 ♀ ZMB: MB.A-1669 ♀ SMNH: BB-A4000 ♀ SMF: F567/BB/AR/ARC/CJW ♂; Be34 ♂; F564/BB/AR/ARC/CJW ♂; F566/BB/AR/ARC/CJW ♂; F565/BB/AR/ARC/CJW ♂; HWood_035* ♂; HWood_042* ♂; HWood_044* ♂	Koch & Berendt, 1854	Baltic amber	Eocene, 44-49 Ma	Ritzkowski (1997)
Baltarchaea conica	JW: F2171/BB/AR/CJW ♀	Koch & Berendt, 1854	Baltic amber	Eocene, 44-49 Ma	Ritzkowski (1997)
Burmesarchaea grimaldii	AMNH: Bu-256 ♂	Penney, 2003	Burmese amber	Cretaceous, 88-95 Ma	Penney, 2003
Lacunauchenius speciosus	JW: F1923/BU/AR/CJW ♂	Wunderlich, 2008	Burmese amber	Cretaceous, 88-95 Ma	Penney, 2003
Myrmecarchaea sp. (*pediculus?*)	SMF: F1132/BB/AR/ARC/CJW, juvenile	Wunderlich, 2004	Baltic amber	Eocene, 44-49 Ma	Ritzkowski (1997)
Patarchaea muralis	Character scoring and measurements taken from published figures.	Selden, Huang & Ren, 2008	Inner Mongolia, compression fossil	Middle Jurassic, 161-176 Ma	Chen et al. 2004; Gao & Ren, 2006
Saxonarchaea dentata	SMF, Görlitz section: 07/36290, F558/BB/AR/ARC/CJW ♀	Wunderlich, 2004	Bitterfield amber	Disputed: Eocene to Oligocene, 23-49 Ma	Dunlop & Giribet, 2003; Dunlop, 2010
Saxonarchaea diabolica	SMF: F556/BB/AR/ARC/CJW ♀	Wunderlich, 2004	Bitterfield amber	Disputed: Eocene to Oligocene, 23-49 Ma	Dunlop & Giribet, 2003; Dunlop, 2010

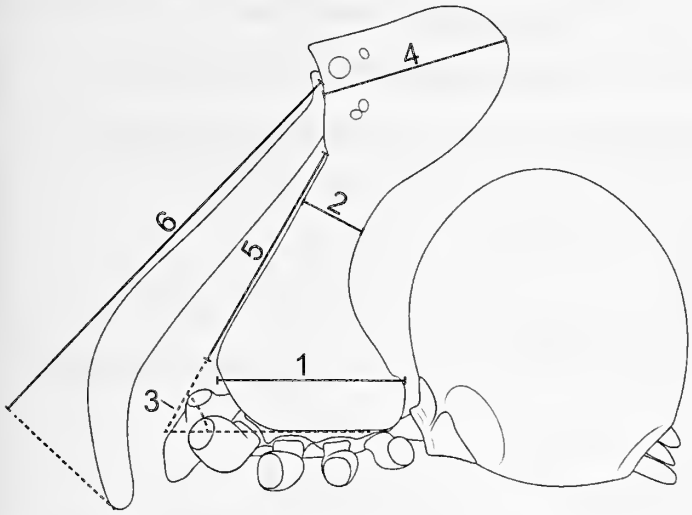

Figure 2.—Diagram showing the measured morphological traits (reproduced from Wood et al. 2015): 1, carapace length; 2, carapace constriction; 3, carapace angle; 4, "head" length; 5, "neck" length; 6, chelicerae length. Measurement 7 (femur I length) not shown.

reached 200 for all parameters (Drummond et al. 2006). The burn-in (20%) was removed from each independent run and the resulting tree files were combined.

Measurement data and morphological evolution.—Wood et al. (2015) measured seven traits of the cephalothorax and one measurement of standard length per species for 51 extant species (Fig. 2). The same measurements were made for the eight fossil taxa included in the phylogeny and were added to the Wood et al. (2015) data matrix (see supplemental information for the measurements of all taxa: online at http://dx.doi.org/10.1636/JoA-S-16-039.s1). The measurements were as follows: (1) carapace length; (2) carapace constriction, defined as the depth from anterior to posterior of the narrowest portion of the "neek" in the lateral habitus view; (3) carapace angle, defined as the angle between the posterior edge of the lateral side of the carapace (the portion above coxae II and III) and the anterior edge of the "neck" in the lateral view; (4) anterior "head" length, defined as the length between the clypeus and the posterior edge of the "head," taken perpendicular to the cheliceral foramen in the dorsal view; (5) "neck" length, defined as the length from the bottom edge of the cheliceral foramen to the bottom edge of the carapace, taken in the anterior view; (6) chelicerae length; and (7) length of femur I. Carapace width was used as the measurement for size. These traits were selected because of their ecological and functional significance in predatory attacks (Wood 2008; Wood et al. 2012). Measurements for *Archaea paradoxa* C. L. Koch & Berendt, 1854 and *Patarchaea muralis* Selden, Huang & Ren, 2008 were taken from 16 and 3 specimens, respectively, and were averaged, and the remaining fossil species measurements, due to specimen availability, were taken from only one specimen (Table 1), with the following exceptions: (1) *P. muralis* was not physically examined and measurements were taken from published images; (2) the carapace width measurement for *Saxonarchaea dentata* was taken from a value reported in the literature (Wunderlich 2004), as the amber shape prevented a dorsal view of the carapace; and (3) the carapace width measurement for *Lacunauchenius speciosus* was based on an average measurement of carapace width from the dorsal, anterior and ventral views, as the amber was cloudy and precluded a perfect view of the carapace width in the dorsal view. Using the combined data set for all species, all traits were natural log transformed and, when more than one specimen was available, were averaged. The effect of size was removed by performing a phylogenetic linear regression on each measurement against the size measurement, and then retaining the residual values for each species (Revell 2009). The size-corrected residuals were used as inputs for a phylogenetically corrected principal components (PC) analysis and the resulting eigenstructure and scores were extracted for each species. Two fossil specimens were further removed from the PC analysis, as *Lacunauchenius speciosus* is likely not an archaeid (see phylogenetic results and discussion), and *Patarchaea muralis* was missing some measurements.

RESULTS

Phylogenetic analysis and divergence dating.—The results reported here deal only with the additional fossil taxa newly added for the current study; see Wood et al. (2015) for results and a discussion of trait evolution and diversification in the extant clades. Parsimony analysis of the morphological data recovered 940 trees of 190 steps that were summarized as a strict consensus tree (Fig. 3). For the total evidence, Bayesian, divergence dating analysis, there were moderate amounts of rate heterogeneity, meaning that the data are not clock-like: the mean coefficient of variation was 1.051 and the mean ucld.stdev was 0.859. There was not strong evidence for autocorrelation (mean covariance = 0.152). The resulting summary chronogram is presented in Fig. 4.

Both phylogenetic analyses recover the crown-group archaeids (jackknife support = jk = 96; posterior probability = pp = 0.78), with fossil lineages falling outside. Both analyses did not recover a monophyletic Archaeidae: in the morphology-only analysis the fossil *Lacunauchenius* Wunderlich, 2008 fell outside of the remaining archaeids, although its placement was not supported; in the total evidence analysis the fossils *Lacunauchenius* and *Patarchaea* fell outside the remaining archaeids, with *Lacunauchenius* being sister to Mecysmaucheniidae (pp = 0.65), and with *Patarchaea* falling within Palpimanoidea (pp = 1.0). The total evidence analysis recovered a monophyletic stem-group fossil archaeid clade (pp = 0.89) consisting of the following species: *Archaea paradoxa*, *Baltarchaea conica* (C. L. Koch & Berendt, 1854), *Burmesarchaea grimaldii* (Penney, 2003), *Myrmecarchaea* sp., *Saxonarchaea dentata* and *Saxonarchaea diabolica*. Posterior probability values were low for relationships within the stem-group clade, likely reflecting a paucity of defining synapomorphies.

Mean divergence values indicate that Archaeidae (excluding *Lacunauchenius* and *Patarchaea*) originated in the Jurassic-Triassic (mean = 200 Ma, 95% CI = 159–241), with the Southern Hemisphere crown-group splitting off from the Northern Hemisphere stem-group in the Jurassic (mean = 173 Ma, 95% CI = 136–211). The stem-group clade containing the Baltic, Bitterfeld and Burmese amber species began to diversify during the Cretaceous (mean = 134 Ma, 95% CI = 95–178).

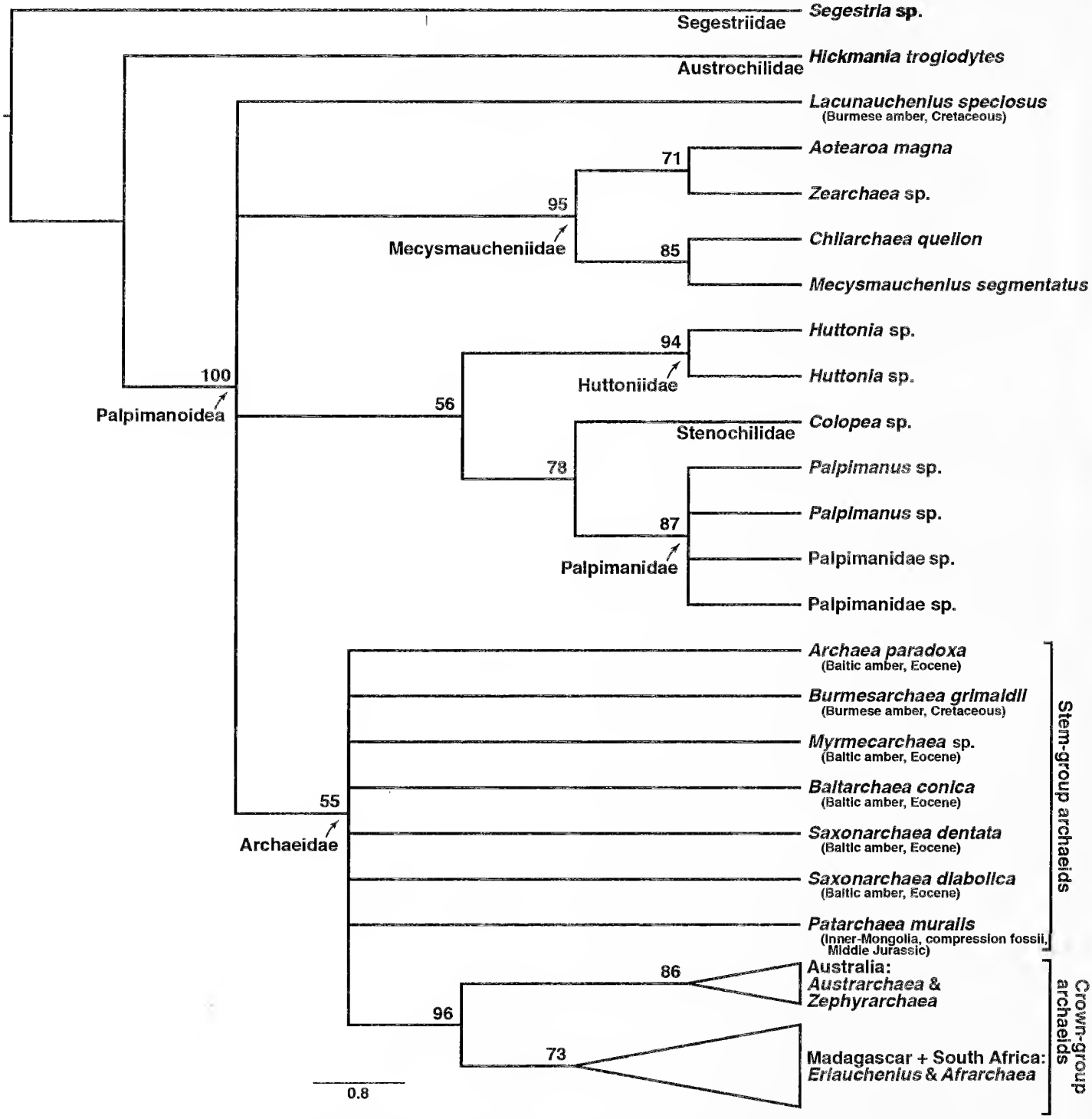

Figure 3.—Strict consensus tree summarizing 940 most parsimonious trees of 190 steps, obtained using TNT v.1.5, based on 111 morphological characters, with an outgroup of *Segestria* sp. The Australian and the Madagascar + South Africa clades are each a polytomy containing 7 species and 45 species, respectively. Node values represent jackknife support.

Morphological evolution.—The first three morphological PC axes had eigenvalues greater than one, and explained 52.3%, 16.3%, and 15.1% of the data (combined 83.7%). PC1 showed variation between archaeid species with elongated features (chelicerae, carapace length and height ("necks"), legs and "heads"), with "necks" that are constricted, compared to species with shorter features and thicker "necks." PC2 described the variation between species with shorter heads and smaller carapace lengths, and with more constricted and more upright "necks," compared to species with elongated heads and longer carapace lengths, with "necks" that are more tilted and less constricted. PC3 showed variation from one extreme of having shorter legs, shorter "heads," and more upright carapaces, to species with longer legs, longer "heads," and more tilted carapaces. Results are summarized in Table 2, and for PC1 and PC2, in Fig 5.

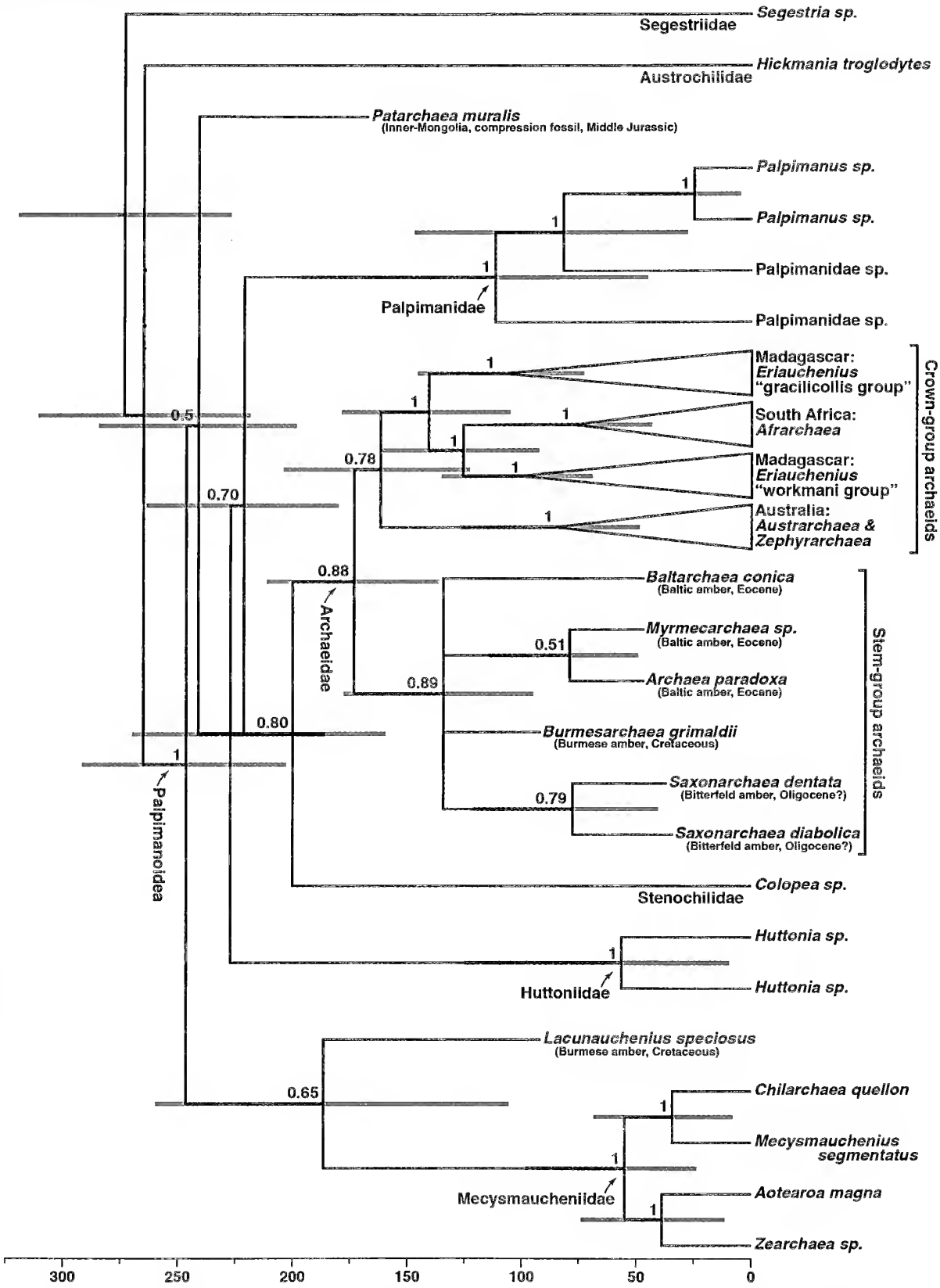

Figure 4.—Total evidence phylogeny from Bayesian analysis of the molecular and morphological data, with branch lengths drawn to reflect BEAST divergence age estimations. Error bars reflect the 95% Bayesian credible interval. Node values represent posterior probabilities, with branches with values less than 0.5 collapsed. Scale at bottom = millions of years before present.

Table 2.—Resulting eigenvalues and eigenvectors for the first three axes from the principal components analysis.

Trait	Eigenvalue	% Variation explained	Carapace length	Carapace constriction	Carapace angle	"Head" length	"Neck" length	Chelicerae length	Femur I length
PC1	3.66	52.3	0.39	−0.33	0.00	0.31	0.47	0.50	0.42
PC2	1.14	16.3	−0.37	−0.61	0.55	−0.42	0.07	−0.01	0.10
PC3	1.06	15.1	0.06	0.18	0.68	0.53	0.18	−0.06	−0.43

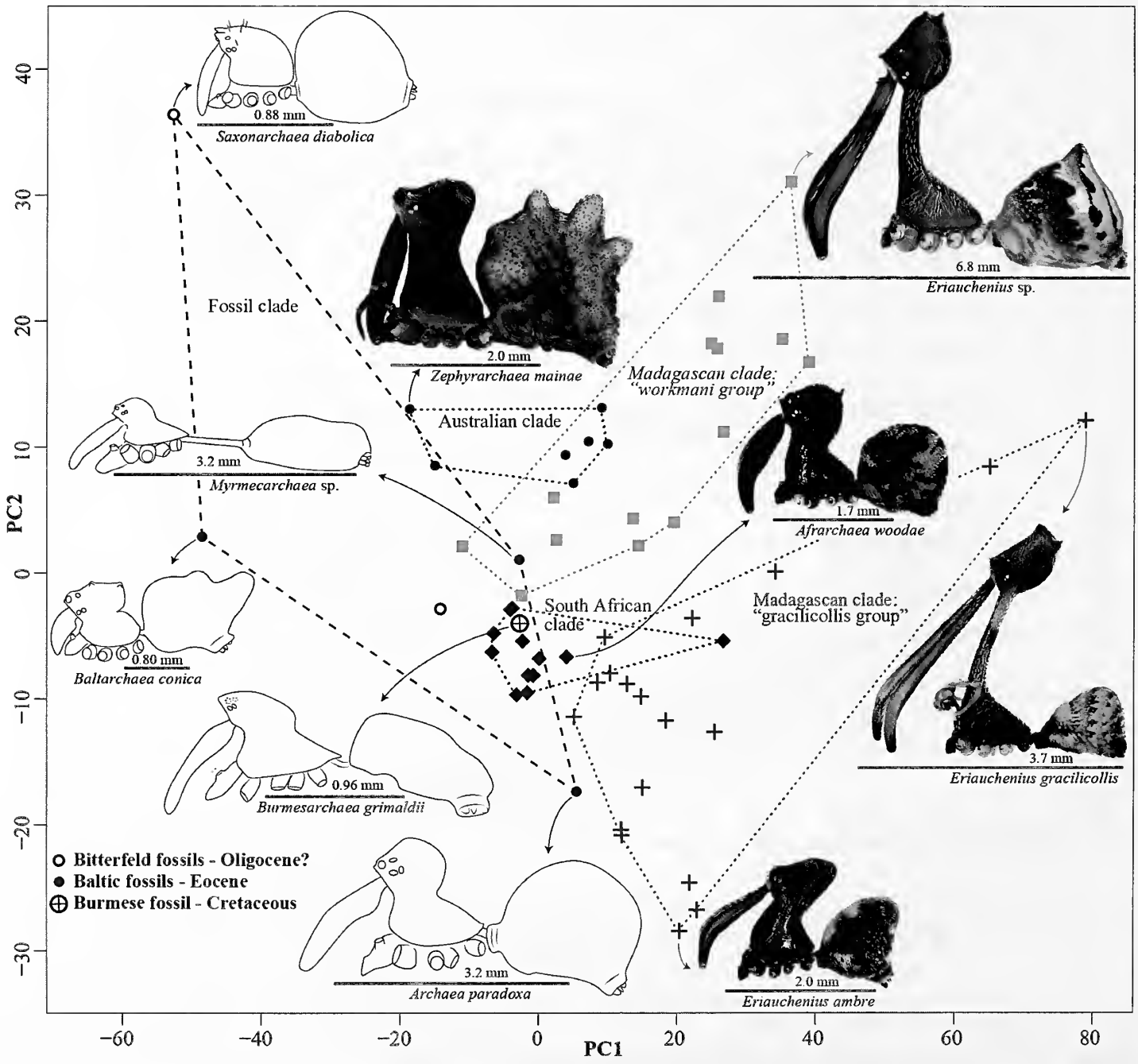

Figure 5.—Morphospace plot of the first two principal components for seven phylogenetically size-corrected traits (PC1 and PC2 explain 52.3% and 16.3% of the data), for 51 extant and 6 fossil species. A dashed line circumscribes the fossil clade and dotted lines circumscribe the four extant clades. Body shapes of 5 fossil and 5 living species are shown, lateral view, legs removed, not to scale, with the scale bar equaling the length of the first femur. Dashed lines marking some eyes in *Burmesarchaea grimaldii* are approximations. The following fossil specimens were excluded from the PC analysis and morphospace plot: *Patarchaea muralis* is missing some measurements due to fossil preservation; *Lacunauchenius speciosus* is likely not an archaeid. The image from the Australian clade, *Zephyrarchaea mainae*, is taken from Rix et al. (2011).

The oldest fossil, *Burmesarchaea grimaldii*, of Cretaceous age, sits close to the center of the morphospace plot (Fig. 5) and overlaps with the extant clades. The next time slice represented by the Baltic amber fossils of Eocene age, shows an expansion into novel morphospace, towards more negative values in PC1. The Bitterfeld amber species of Oligocene age (although the age is disputed) remain within the vicinity of the Baltic amber species, on the left side of the morphospace plot, yet still expanding into novel morphospace. In the final time slice, the present, there has been a dramatic shift, with the extant species occupying the right side of the morphospace plot towards larger values in PC1, showing little overlap with the fossil clade.

DISCUSSION

Evolutionary relationships.—Wood et al. (2013) recovered an estimated divergence date for the split between the Northern Hemisphere fossils and the Southern Hemisphere extant clade that is consistent with the vicariance hypothesis that archaeid divergence is related to Pangaea splitting into Gondwana and Laurasia 180 Ma (Smith et al. 2004). As discussed in Wood et al. (2012), there are several characters that are unique to the extant clade: (1) a tubercle on the posterior edge of the sternum is present, which may be used for stridulation; (2) the posterior edge of the carapace is truncated in extant archaeids, rather than the tapering off seen in the fossil archaeids; (3) extant archaeids, unlike their extinct relatives, have a spine or protuberance on the anterior surface of their chelicerae; (4) the distal portion of the chelicerae is curved towards the posterior in extant archaeids, whereas in fossil archaeids the chelicerae are straight; and (5) extant archaeids have a brush of hairs on the palp tarsi, unlike fossil archaeids which have stridulatory picks that likely interact with the stridulatory file. These traits support the monophyly of the extant archaeids. Based on the morphology-only, parsimony analysis, it is unclear whether the fossil archaeids are a monophyletic or paraphyletic group. However, the total evidence, Bayesian analysis recovered a monophyletic fossil clade that had reasonable branch support (pp = 0.89). A monophyletic fossil clade further supports the vicariance hypothesis of a distinct northern and southern fauna that diverged due to Pangaea breaking into a northern Laurasia and a southern Gondwana.

The current study does not find strong support for relationships among the fossils, which is likely due to the paucity of derived fossil characters, as well as the high amount of missing data due to fossil preservation. Regarding the oldest fossil, *Patarchaea muralis*, dated to be of Jurassic age, the parsimony phylogenetic analysis with only morphological data recovered this species as falling within Archaeidae, although with low support (jk = 55). On the other hand, in the Bayesian, total evidence analysis, this taxon did not fall with the other archaeids, rendering Archaeidae paraphyletic. The lack of a well-supported placement of this taxon makes sense because this is a compression fossil with many missing characters. This differs from the findings of Wood et al. (2015), which recovered *Patarchaea* as monophyletic with the remaining archaeids. This discrepancy may be due to the different taxon sampling in each study, particularly the inclusion of the fossil *Lacunauchenius speciosus* in the present study (see below). I believe *Patarchaea* should remain in Archaeidae until additional evidence suggests otherwise.

Regarding the placement of *Lacunauchenius speciosus*, from Burmese amber deposits dated to be of Cretaceous age, the morphology-only, parsimony analysis did not recover a well-supported placement within Palpimanoidea. The total evidence, Bayesian analysis placed *L. speciosus* as sister to the Mecysmaucheniidae, although not well supported (pp = 65). It is not unreasonable that this species is a stem mecysmaucheniid: *L. speciosus* has greatly elongated hairs on the inner margins of the chelicerae, a trait that occurs only in mecysmaucheniids and in the malkarid lineages that were previously considered Pararchaeidae (Wood et al. 2012). It is likely that this trait independently evolved in these families based on phylogenetic relationships, with these families being very distantly related (Rix et al. 2008; Wood et al. 2012; Dimitrov et al. 2016). Mecysmaucheniids have a trap-jaw predatory strike, with some species evolving power-amplified cheliceral movements (Wood et al. 2016), and these cheliceral hairs may be functionally equivalent to the trigger-hairs in the trap-jaw ants. Recently, Wunderlich (2015) described additional *Lacunauchenius* species, however, these specimens were not examined for the current study. These fossils as well as future discoveries may shed light on placement of this enigmatic genus.

Morphological evolution.—The morphological fossil diversity in this study is based on only six species: three Baltic amber species, two Bitterfeld amber species, and one Burmese amber species. However, there are around 20 described archaeid fossils (Dunlop et al. 2016), so it is likely that this study underestimates the total amount of morphological diversity in the fossil lineages. Furthermore, the fossil record is incomplete due to preservation and sampling bias. Thus, it is likely the fossil morphological diversity is further underestimated as archaeid species with unique morphologies may have gone extinct without being preserved in the fossil record. Regardless, this study found fossil archaeids to be morphologically diverse, and compared to the extant lineages, morphologically unique. The most dramatic shift through time in morphological space occurs between the fossil species and the extant species. While *Burmesarchaea grimaldii* overlaps with the morphospace of the extant species, the remaining Baltic and Bitterfeld species have novel forms that are no longer represented in the extant lineages. *Myrmecarchaea*, although also overlapping with the morphospace of the extant clades, has an exceptionally long pedicle, and this trait was not measured in this study, as the focus was on carapace/chelicerae morphology. An elongated pedicle is of unknown ecological consequence, although Wunderlich (2004) speculated that *Myrmecarchaea* may have been an ant or wasp mimic.

Assuming that morphological adaptations reflect how species interact with their environment, then morphology can determine ecological niche (Ricklefs & O'Rourke 1975; Arnold 1983; Losos 1990). Thus, the high morphological diversity in fossil archaeids suggests that these extinct species occupied a diversity of niches. The fossil species occupy a different portion of the morphospace plot compared to the extant species (Fig. 5). This difference centers on PC1, which relates to species having, at one extreme, short "necks," legs and chelicerae, and at the other extreme, species having

elongated features. Comparing fossils of the past with extant species of the present, there has been a dramatic shift towards more elongated features. In extant archaeids previous research showed a correlation with body shape and habitat: species with long "necks," chelicerae, and legs occur more often in the vegetation, while species with shorter, more robust "necks," legs and chelicerae are found more often on the ground (Wood et al. 2015). I speculate that different forms occur in different habitats because there may be a different composition of spider fauna in the vegetation compared to on the ground, necessitating longer features in archaeids in order to exploit this prey; alternatively, life in dense leaf litter may constrain morphologies to be compact, whereas in the open vegetation this constraint may be lifted (Wood et al. 2015). Assuming similar evolutionary processes were at play in the past, this suggests that the more compact fossil species, such as *Baltarchaea conica, Saxonarchaea dentata* and *S. diabolica*, may have occurred in greater frequency on the ground. Although *Myrmecarchaea* sp. has a short "neck," this species has very long legs and an elongated pedicle, so it is difficult to infer the past habitat. Given the unique morphologies of the fossil species, it is also likely that in the past archaeids may have also occupied niches that are no longer occupied by extant species.

The archaeid distribution was more cosmopolitan in the past, spanning an array of sites over a vast amount of time. The first fossil record is from the Jurassic of Inner-Mongolia (assuming *Patarchaea* is an archaeid). Archaeids are then documented from the Cretaceous in Burmese amber, from the Eocene in Baltic amber, from the Oliogocene (although the date is disputed) in Bitterfeld amber, and finally, to the present day, occurring only in Australia, Madagascar, and South Africa. This extensive recorded history is quite remarkable given the incomplete nature of the fossil record. Archaeids have persisted for a duration of 165 million years, relatively unchanged considering the vast amount of time that has passed, and have gone extinct in different parts of the world. The most recent extinction is perhaps the most enigmatic: if Bitterfeld amber is assumed to be of Oligocene age, it was only around 25 million years ago that archaeids occurred in the northern parts of Europe. Although the age of Bitterfeld amber is presently disputed, it is likely younger than the Baltic amber of Eocene age, although some researchers suggest that the two deposits could be contemporaneous (Dunlop 2010). The paleoclimate of the Bitterfeld amber forests was likely warm and temperate (Dunlop 2010, and references therein), with overlap in species composition with the Baltic amber forests (Röschmann 1997; Mitov et al. 2015). While the Eocene was a very warm period in Earth's history, with tropical organisms occurring worldwide (Grimaldi & Engel 2005), the Oligocene marked the beginning of a transition to a cooler, more variable climate due to Antarctic glaciation (Ivany et al. 2000; Zachos et al. 2001). Archaeid extinction from northern Europe may have been caused by this climatic transition, similar to what has been found for many other organisms that did not survive the Eocene-Oligocene boundary (Prothero 1994). Presently, the climates in the areas of the world where archaeids occur tend to be warmer, mesie year-round, and more stable (aseasonal) (Fjeldså & Lovett 1997; Jury 2003; Rix & Harvey 2012b). Through the integration of fossil and extant archaeid species our picture of their morphological evolution is more complete: there was a major shift in morphological space from the Oligocene to the present, with unique forms distinct to the Northern and Southern Hemispheres, and with the northern lineages going extinct while the southern lineages persisted.

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Four new genera of funnel-web spiders (Araneae: Agelenidae) from the Baja California Peninsula in Mexico

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Abstract. Four new genera of funnel-web spiders of the family Agelenidae C.L. Koch, 1837 from the Baja California Peninsula, Mexico are described and illustrated. *Bajacalilena* gen. nov. is represented by *B. bolzerni* sp. nov. and *B. clarki* sp. nov. *Cabolena* gen. nov. is represented by *C. huiztocatl* sp. nov., *C. kosatli* sp. nov., and *C. sotol* sp. nov. *Callidalena* gen. nov. is represented by *C. quintin* sp. nov. and *C. tijuana* sp. nov. *Lagunella* gen. nov. is represented by *L. guaycura* sp. nov. Additionally, the males of *Calilena angelena* Chamberlin & Ivie, 1941, *Hololena septata* Chamberlin & Ivie, 1942, and *Rothilena sudcalifornienses* Maya-Morales & Jiménez, 2013 are described for the first time. New records for *C. angelena*, *H. septata*, *R. cochimi* Maya-Morales & Jiménez, 2013, *R. pilar* Maya-Morales & Jiménez, 2013, and *R. sudcalifornienses* are also provided. Molecular analysis of a fragment of cytochrome c oxidase subunit I (COI) provides support for the monophyly of the new genera and facilitated sorting of conspecific males and females. Finally, an identification key to native Nearctic and Neotropical genera of the subfamily Ageleninae is provided.

Keywords: Ageleninae, taxonomy, morphology, barcoding

http://zoobank.org/?lsid=urn:lsid:zoobank.org:pub:AE1C4819-5642-456D-B664-59B3BB33AC55

Agelenidae C.L. Koch, 1837 is one of the most diverse spider families in the world, with 73 genera and 1,201 described species (Bolzern & Hänggi 2016; World Spider Catalog 2016) in two subfamilies: Ageleninae Simon, 1898 and Coelotinae F.O. Pickard-Cambridge, 1893. However, knowledge of true species diversity is often limited, especially in regions where no major biodiversity inventories have been completed (Bolzern & Jäger 2015). In Mexico, recent taxonomic works have resulted in an increase in the number of both genera and species (Maya-Morales & Jiménez 2013, 2016; Bolzern & Hänggi 2016). The Baja California Peninsula (BCP), the second longest peninsula in the world, is a geographically isolated landmass that stretches over 1,000 km (Crews & Hedin 2006). It is a region with a high degree of endemism (Williams 1980; Sissom & Hendrixon 2005; Rebman & Roberts 2012), where the diversity of the family Agelenidae is still underestimated (Roth & Brame 1972).

Banks (1898) described the first species of Agelenidae on the BCP with the female of *Agelena peninsulana* Banks, 1898, and also reported *Tegenaria domestica* (Clerck, 1757). Chamberlin (1924) recorded *Agelenopsis naevia* (Walckenaer, 1841), while Chamberlin & Ivie (1941) transferred *A. peninsulana* to *Calilena* Chamberlin & Ivie, 1941. Later, Roth & Brown (1986) reported *Agelenopsis potteri* (Blackwall, 1846). Recently, Maya-Morales & Jiménez (2013, 2016) described *Rothilena* with six new species from the southern part of the BCP and three new species of *Rualena* Chamberlin & Ivie, 1941 from the northern part of the BCP.

In North America, molecular studies of the subfamily Ageleninae have been carried out mainly with species of *Agelenopsis* Giebel, 1869 (Ayoub & Riechert 2004; Ayoub et al. 2005), and only a dozen species from other genera (e.g. *Barronopsis* Chamberlin & Ivie, 1941, *Calilena*, *Hololena* Chamberlin & Gertsch, 1929, *Novalena* Chamberlin & Ivie, 1942, *Rualena* and *Tegenaria* Latreille, 1804) have been sequenced and are available in GenBank. The barcode gene COI (mitochondrial cytochrome c oxidase subunit I) is useful for species-level taxonomy (Robinson et al. 2009; Blagoev et al. 2016) and for establishing the generic affiliation of agelenid species (Bolzern et al. 2010; Bolzern & Jäger 2015).

The aim of this study was to describe new genera and species of Agelenidae collected from the BCP, using both morphological and molecular characters. We document four new genera and eight new species, and further provide an identification key to native Nearctic and Neotropical genera of the subfamily Ageleninae.

METHODS

Material examined.—Specimens were examined using a stereomicroscope (Carl Zeiss Stemi SR), and measurements were made with a micrometer slide adapted to one lens, and recorded in millimeters. The epigyna of females were dissected in ethanol (70%) and later cleaned with a solution of pancreatin, which digests the soft tissues and leaves the rigid parts intact (Álvarez-Padilla & Hormiga 2007). Drawings of the genitalia were made using a camera lucida adapted to a stereomicroscope (Leica MZ6). Photographs of genitalia were taken at the California Academy of Sciences and Centro de Investigaciones Biológicas del Noroeste with a digital camera adapted to a Leica stereomicroscope. Helicon Focus 6.5.2 software was used for combining digital images. For scanning electron micrographs (SEM; Hitachi S-3000N), specimens were dehydrated in an ethanol series (70%, 80%, 90% and 100%), critical-point dried, and mounted on stubs using copper tape and coated with gold using a sputter coater for 70 s. *In vivo* photographs were taken with a digital camera Sony

Table 1.—GenBank accession numbers of included COI sequences of Agelenidae.

Species	Accession Number
Agelenopsis aperta (Gertsch, 1934)	AY676089
Calilena restricta Chamberlin & Ivie, 1941	DQ628545
Hololena adnexa (Chamberlin & Gertsch, 1929)	DQ628541
Eratigena agrestis (Walckenaer, 1802)	GU682805
Novalena intermedia (Chamberlin & Gertsch, 1930)	DQ628618

Alpha NEX-5N. Distribution maps were created using QGIS 2.8.2 software.

Morphological terminology is based on the criteria of Chamberlin & Ivie (1942), Roth & Brame (1972), Maya-Morales & Jiménez (2013, 2016), and Ramírez (2014). Abbreviations used in the text and figures are as follows: AME, anterior median eyes; ALE, anterior lateral eyes; PME, posterior median eyes; PLE, posterior lateral eyes; C, conductor; Cd, dorsal projection of conductor; Cdi, distal projection of conductor; Ce, ectal projection of conductor; Cm, mesal projection of conductor; Cv, ventral projection of conductor; E, embolus; F, fulcrum; MA, median apophysis; RTA, retrolateral tibial apophysis; RTAb, basal projection of RTA; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; St, subtegulum; T, tegulum; TMP, tegular median process; A, atrium; BG, Bennett's glands; CD, copulatory ducts; CO, copulatory openings; FD, fertilization ducts; S, spurs; Sc, Scape; S1, primary spermathecae; S2, secondary spermathecae. For purposes of nomenclature, the new taxa are authored by Maya-Morales and Jiménez only, with the exception of *Cabolena kosatli*, *C. sotol* and *Lagunella guaycura*, which are authored by Maya-Morales, Jiménez and Palacios-Cardiel.

The specimens studied belong to the following museums and institutions (abbreviations and curators in parentheses): American Museum of Natural History, New York, USA (AMNH, Norman I. Platnick); California Academy of Sciences, San Francisco, USA (CAS, Charles E. Griswold); Colección de Arácnidos del Centro de Investigaciones Biológicas del Noroeste, La Paz, Mexico (CARCIB, María Luisa Jiménez); Orma J. Smith Museum of Natural History at The College of Idaho, Caldwell, ID, USA and Museo de Artrópodos del Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Baja California, Mexico (OJSMNH and CICESE, William H. Clark); and San Diego Natural History Museum, San Diego, USA (SDNHM, Michael A. Wall). Specimens from the CAS are labeled as CASENT, and those from OJSMNH and CICESE are labeled as CIDA and ALBRCIDA, respectively. Additionally, we collected new material from several localities in the State of Baja California Sur (2011–2015), deposited at CARCIB.

Molecular data.—To corroborate the morphologically identified species and verify the accuracy of sex pairing in each species, we sequenced the barcoding fragment of mitochondrial COI. Genomic DNA was extracted using spin-columns and following the protocol of Ivanova et al. (2006). Polymerase chain reaction (PCR) amplification of COI was undertaken using the primers LCO1490: 5′-GGTCAACAAATCATAAAGATATTGG-3′ and HCO2198: 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′ (Folmer et al. 1994). All PCR mixtures contained 3 µl DNA, 0.9 µl of each primer (20 mM), 0.7 µl $MgCl_2$ (50 mM), 1.7 µl PCR buffer (10×), 1 µl dNTP (2.5 mM), 0.7 µl betaine (1 M), and 0.1 µl DNA Taq polymerase (5 U/µl) in a final volume of 15 µl. The PCR cycle was: 3 min at 94°C; five cycles of 30 s at 94°C, 40 s at 45°C, and 1 min at 72°C; 35 cycles of 30 s at 94°C, 40 s at 51°C, and 1 min at 72°C; and a final 5 min at 72°C. Amplified products were checked using 2.0% agarose gel electrophoresis and subsequently sequenced at the University of California Berkeley. The sequences obtained were edited in DNA Baser 4.5 (http://www.DNABaser.com). The sequence data, together with other COI sequences of Agelenidae from GenBank (http://www.ncbi.nlm.nih.gov/genbank) (Table 1), were analyzed using MEGA 6 (Tamura et al. 2013). Haplotypes were determined in DnaSP 5.10 (Librado & Rozas 2009) and genetic (uncorrected) distances among the species were calculated in MEGA. We used jModelTest 2.1.9 (Darriba et al. 2012) to select a best-fit nucleotide substitution model (TIM3+I+G), according to the Akaike information criterion (AIC) and implemented in MrBayes 3.2 (Ronquist et al. 2012) for phylogenetic analysis. Two independent MCMC analyses were run for 10 million generations. Trees were sampled every 100 generations, and a 50% majority rule consensus Bayesian tree was generated with a 25% burnin. Species designations were further tested using the Automatic Barcode Gap Discovery (ABGD) software for primary species delimitation (Puillandre et al. 2012). All sequences generated in this study are deposited in GenBank (Accession numbers KU976337–KU976384).

TAXONOMY

Family Agelenidae C.L. Koch, 1837

Subfamily Ageleninae C.L. Koch, 1837

KEY TO THE NATIVE NEARCTIC AND NEOTROPICAL GENERA OF AGELENINAE

NB. *Neotegenaria* Roth, 1967, represented only by *N. agelenoides* Roth, 1967, was not examined.

1. Eye rows straight or slightly procurved in frontal view 2
– Eyerows strongly procurved in frontal view 3
2. Cheliceral retromargin with three to six teeth; male pedipalp without lateroventral ridge on RTA ..... *Eratigena* Bolzern, Burckhardt & Hänggi, 2013
– Cheliceralretromargin with six or more teeth; male pedipalp with lateroventral ridge on RTA ..... *Tegenaria* Latreille, 1804
3. Male pedipalp with tegular lateral process (= tegular apophysis of Stocks 2009: fig. 20); RTA with one projection (Stocks 2009: fig. 38); epigynum with copulatory ducts long or membranous and plicate (Stocks 2009: fig. 52) 4

– Malepedipalp without tegular lateral process; RTA with two or three projections (Fig. 4e); epigynum with copulatory ducts short and selerotized (Fig. 5d) 7
4. Male pedipalp with tethering membrane and radix (Gering 1953: fig. 4); copulatory ducts membranous and plicate (Stocks 2009: fig. 61) 5
– Malepedipalp without tethering membrane and radix; copulatory ducts long 6
5. Embolus circular (Whitman-Zai et al. 2015: fig. 15); posterior part of epigynum with eoupling cavity (Whitman-Zai et al. 2015: fig. 30); distal segment of PLS two times the length of basal segment ..... *Agelenopsis* Giebel, 1869
– Embolustightly eoiled basally and loosely coiled distally (Stocks 2009: fig. 39); posterior part of epigynum without coupling cavity; distal segment of PLS as long as basal segment ..... *Barronopsis* Chamberlin & Ivie, 1941
6. Embolus forming an eight (Chamberlin & Ivie 1941: fig. 76); embolic process a short hook concealed by embolus; copulatory ducts in spiral ..... *Tortolena* Chamberlin & Ivie, 1941
– Embolusin spiral or sinuous without forming an eight (Stoeks 2009: fig. 14); embolic process large and exposed; copulatory ducts not forming a spiral ..... *Melpomene* O. Pickard-Cambridge, 1898
7. Male pedipalp with tegular median process (Maya-Morales & Jiménez 2016: fig. 124); primary spermathecae longer than wide (Fig. 15b) (spherical in some *Hoffmannilena* species) 8
– Malepedipalp without tegular median process; primary spermathecae elongated (Fig. 4b), spherical (Fig. 9d), folded (Fig. 19b) or wrinkled (Maya-Morales & Jiménez 2016: fig. 61) 11
8. RTA in distal position on tibia (Fig. 22b); embolus originating from basal part of tegulum (Fig. 21a); copulatory ducts surrounding primary spermathecae dorsally (Fig. 21b); secondary spermathecae in anterior part of primary spermatheeae (Fig. 22b) ..... *Lagunella* gen. nov.
– RTAcovering the entire tibia length; embolus originating from median part of tegulum; copulatory ducts not surrounding primary spermathecae dorsally; secondary spermathecae in ectal part of primary spermatheeae 9
9. RTA usually with three projections (Chamberlin & Ivie 1942: fig. 59); epigynum with median plate not differentiated from lateral lobes (Maya-Morales & Jiménez 2016: fig. 89) ..... *Novalena* Chamberlin & Ivie, 1942
– RTAwith two projections (Fig. 16b); epigynum with median plate differentiated from lateral lobes (Fig. 14c) 10
10. RTA with basal projection (Maya-Morales & Jiménez 2016: fig. 120); all structures of epigynal plate strongly sclerotized (Maya-Morales & Jiménez 2016: fig. 130) ..... *Hoffmannilena* Maya-Morales & Jiménez, 2016
– RTAwith dorsal projection (Fig. 16b); some structures of epigynal plate more sclerotized than others (Fig. 12c) ..... *Cabolena* gen. nov.
11. Embolus supported by fulcrum and conductor (Fig. 4a); epigynal atrium partially divided by a septum (Fig. 5e) ..... *Hololena* Chamberlin & Gertsch, 1929
– Embolussupported only by conductor; epigynal atrium without septum 12
12. RTA with dorsal projection flattened longitudinally (Fig. 3b); epigynum with scape (Fig. 3c) ..... *Calilena* Chamberlin & Ivie, 1941
– RTAotherwise; epigynum without seape 13
13. RTA in distal position on tibia (Fig. 17d); atrium occupying the entire plate length (Fig. 18c); primary spermathecae folded or wrinkled (Fig. 19b) 14
– RTAeovering the entire tibia length (Fig. 9a); atrium in anterior part of plate (Fig. 10a); primary spermathecae spherical (Fig. 6d) 15
14. Male pedipalp with membranous fulcrum (Maya-Morales & Jiménez 2016: fig. 43); conductor with two short projeetions (Maya-Morales & Jiménez 2016: fig. 12); epigynal atrium in cavity ..... *Rualena* Chamberlin & Ivie, 1942
– Malepedipalp without membranous fulcrum; conductor folded longitudinally (Fig. 19c); epigynal atrium flat (Fig. 20c) ..... *Callidalena* gen. nov.
15. Embolus in spiral with 1.5 coils (Fig. 9c); conductor membranous and horseshoe-shaped (Fig. 9a); copulatory ducts longer than primary spermathecae (Fig. 8d) ..... *Bajacalilena* gen. nov.
– Embolussinuous (Maya-Morales & Jiménez 2013: fig. 16); conductor sclerotized with three short projections (Fig. 6c); copulatory ducts shorter than primary spermathecae (Fig. 6b) ..... *Rothilena* Maya-Morales & Jiménez, 2013

Genus *Calilena* Chamberlin & Ivie, 1941

Calilena Chamberlin & Ivie, 1941: 603.

Type species.—*Calilena saylori* Chamberlin & Ivie, 1941, by original designation.

Diagnosis.—*Calilena* is diagnosed by the following characters in combination: male pedipalp with a short and almost straight embolus (Fig. 2e); short and membranous fulcrum at the base of embolus (Fig. 3a); conduetor with two projections (Fig. 2a); and RTA covering the entire tibia length (Fig. 3b). Female epigynum with a scape originating from anterior part of atrium and projecting posteriorly (Fig. 3e); primary spermatheeae elongated and L-shaped; secondary spermatheeae in diverticula and conneeted to copulatory ducts; and fertilization ducts short (Fig. 2b, d).

Calilena angelena Chamberlin & Ivie, 1941
(Figs. 2, 3)

Calilena angelena Chamberlin & Ivie, 1941: 607, fig. 51.

Type material.—*Holotype female*: Los Angeles, California, USA (AMNH; not examined).

Material examined.—USA: *California*: 2 ♀, 9.7 km SW. of Victorville, 34°N, 117°W, 9 March 1941, W. Ivie (AMNH). MEXICO: *Baja California*: 1 ♀, Municipality of Tecate, Highway La Rumorosa-Ojos Negros km 35, 32°16′33″N, 116°12′15″W, 1232 m, 3 March 2010, C. Mayorga & L. Cervantes (CARCIB 1925); 1 ♂, Municipality of Ensenada, 8 km NW of Santo Tomás, 31°37′N, 116°27′W, 200 m, pitfall trap, 11 August – 4 September 1982, W.H. Clark (CIDA 91,767); 8 ♂, 1 ♀, same data except 10 August – 4 September 1982 (CIDA 91,793); 1 ♂, 2 ♀, same data except 4 September 1982 – 7 January 1984 (CIDA 91,843).

Diagnosis.—Females of *C. angelena* differ from *C. absoluta* (Gertsch, 1936), *C. adna* Chamberlin & Ivie, 1941, *C. magna* Chamberlin & Ivie, 1941 and *C. siva* Chamberlin & Ivie, 1941 by having the scape reaching the posterior margin of the atrium; from *C. gertschi* Chamberlin & Ivie, 1941 and *C. saylori* by having the scape distally rounded; from *C. arizonica* Chamberlin & Ivie, 1941 and *C. yosemita* Chamberlin & Ivie, 1941 by the having the median plate wider than long; from *C. californica* (Banks, 1896), *C. gosoga* Chamberlin & Ivie, 1941 and *C. restricta* Chamberlin & Ivie, 1941 by having the anterior margin of the median plate slightly pointed; from *C. stylophora* Chamberlin & Ivie, 1941 by having the scape thicker and shorter; and from *C. umatilla* Chamberlin & Ivie, 1941 by having the median plate wider than long (Fig. 3c). Males of *C. angelena* differ from *C. nita* Chamberlin & Ivie, 1941 by having the dorsal part of the RTA occupying more than half the tibia length; from *C. arizonica* and *C. californica* by having the projections of the conductor shorter and thinner; from *C. umatilla* by the less concave distal edge of RTA; and from *C. restricta* and *C. saylori* by having a less curved ventral projection on the conductor (Fig. 3a, b).

Description.—Male (CIDA 91,793): *Coloration:* Carapace yellow, longitudinal symmetrical dark bands irregularly expressed. Ocular region brown. Chelicerae and condyles brown. Endites and labium light brown with white tip. Sternum yellow. Legs yellow, metatarsus-tarsus light brown. Opisthosoma yellow with light brown spots. Spinnerets yellow.

Habitus: Total length 7.13. Carapace length 3.88, width 2.75, cephalic region width 1.43, ocular region width 0.71. Eye diameter: AME 0.15, ALE 0.25, PME 0.13, PLE 0.17. Distance between eyes: AME-AME 0.06, AME-ALE 0.04, AME-PME 0.15, ALE-PLE 0.06, ALE-ALE 0.33, PME-PME 0.12, PME-PLE 0.13. Clypeus height 0.23. Chelicerae with three promarginal teeth and two retromarginal teeth; basal segment length 1.48, fang length 1. Labium wider than long (0.52/0.43). Endites slightly convergent (distance at their base compared to their tips 0.52/0.33). Sternum longer than wide (1.86/1.62). Opisthosoma longer than wide (3.38/2.38). ALS separated by their basal diameter (0.3/0.3), PLS with distal segment longer than basal segment (0.39/0.27).

Legs: Length: I- femur 3.25/ patella-tibia 3.75/ metatarsus 3/ tarsus 2.13; II- 3.13/ 3.5/ 3.13/ 2.13; III- 3.13/ 3.63/ 3.5/ 1.88; IV- 4/ 4.75/ 4.88/ 2.5.

Spination: Femur dorsal I- 1-3-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 1-0-1/ 0-0-1; II- 0-0-1/ 2-2-2/ 1-0-1/ 0; III- 2-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-2-2/ 2-1-2-2/ 0-1-1/ 0-0-1. Number of trichobothria on tarsus: I- 7, II- 7, III- 7, IV- 7.

Pedipalp: Number of dorsal spines: femur 2, tibia 4. Cymbium length 1.39, width 0.7. Embolus almost straight. Fulcrum at the base of embolus. Conductor with two projections, the ventral one with ectal border almost straight and supporting the embolus. RTA covering the entire length of tibia with dorsal projection flattened longitudinally (Figs. 2a, c, e, 3a, b).

Distribution.—California (USA) and Baja California (Mexico).

Genus *Hololena* Chamberlin & Gertsch, 1929

Hololena Chamberlin & Gertsch, 1929: 105.

Type species.—*Hololena mimoides* (Chamberlin, 1919), by original designation.

Diagnosis.—*Hololena* is diagnosed by the following characters in combination: male pedipalp with sinuous embolus that rests on a membranous fulcrum; conductor with two projections (Fig. 4a); RTA covering the entire tibia length; distal projection of RTA with a tooth-shaped subprocess (Fig. 4e); and basal projection of RTA with a tongue-shaped subprocess (Fig. 5a). Female epigynum with an atrium in anterior position of plate and partially divided by a septum, with spurs in posterolateral position (Fig. 5c); copulatory ducts anterior to spherical primary spermathecae; secondary spermathecae in diverticula and connected to copulatory ducts; and fertilization ducts short (Fig. 4b).

Hololena septata Chamberlin & Ivie, 1942
(Figs. 4, 5)

Hololena septata Chamberlin & Ivie, 1942: 214, fig. 36.

Type material.—*Holotype female*: E. of Pine Valley, California, USA, 32°50′N, 116°32′W, collected in juvenile stage, 13 September 1941 (matured 6 October 1941), W. Ivie (AMNH; not examined).

Material examined.—USA: *California*: 1 ♂, San Diego Co., Naval Base Point Loma, 32°42′44.06″N, 117°15′09.04″W, 27 February 2008, Naval Base Point Loma Team (SDNHM a000798); 1 ♀, same data except 32°41′09.02″N, 117°14′28.46″W, 21 December 2009 (SDNHM a000835); 1 ♀, same data except 32°41′09.03″N, 117°14′28.43″W (SDNHM a000836); 1 ♀, same data except 32°41′45.74″N, 117°14′36.24″W (SDNHM a000837); 1 ♀, same data except 32°42′28.64″N, 117°15′14.6″W, 16 November 2009 (SDNHM a000844); 1 ♂, same data except 32°41′34.42″N, 117°14′36.38″W, 21 December 2009 (SDNHM a000840); 1 ♀, same data except 32°42′14.88″N, 117°14′51.24″W (SDNHM a000871); 1 ♂, North Park, September 2008, J. Berrian (SDNHM a000814); 1 ♂, Lemon Grove, 12 December 2008, J. Berrian (SDNHM a000825); 1 ♀, Balboa Park, 2–3 May 2008, J. Berrian (SDNHM a000828). MEXICO: *Baja California*: 1 ♀, Municipality of Ensenada, Highway Ensenada-Tijuana km 14, 31°54′24″N, 116°43′59″W, 1 m, 1 March 2010, C. Mayorga & L. Cervantes (CARCIB 1926); 1 ♀, La Misión, 2 March 1997, J. Berrian (SDNHM a000818); 1 ♀, same data (SDNHM a000817).

Diagnosis.—Females of *H. septata* differ from *H. aduna* Chamberlin & Ivie, 1942, *H. monterea* Chamberlin & Ivie, 1942 and *H. sula* Chamberlin & Ivie, 1942 by having the spurs separated from each other by three times their basal width; from *H. adnexa* (Chamberlin & Gertsch, 1929), *H. altura* Chamberlin & Ivie, 1942, *H. atypica* Chamberlin & Ivie, 1942, *H. barbarana* Chamberlin & Ivie, 1942, *H. curta* (McCook, 1894), *H. dana* Chamberlin & Ivie, 1942, *H. hopi* Chamberlin & Ivie, 1942, *H. lassena* Chamberlin & Ivie, 1942, *H. nedra* Chamberlin & Ivie, 1942, *H. oola* Chamberlin & Ivie, 1942, *H. parana* Chamberlin & Ivie, 1942, *H. santana* Chamberlin & Ivie, 1942, *H. tentativa* (Chamberlin & Gertsch, 1929) and *H. turba* Chamberlin & Ivie, 1942 by having spurs closer to the posterior margin of the epigynal plate; and from *H. furcata* (Chamberlin & Gertsch, 1929), *H. frianta* Chamberlin & Ivie, 1942, *H. hola* (Chamberlin, 1928), *H. madera* Chamberlin & Ivie, 1942, *H. mimoides*, *H. nevada* (Chamberlin & Gertsch, 1929), *H. oquirrhensis* (Chamberlin & Gertsch, 1930), *H. pacifica* (Banks, 1896) and *H. pearcei* Chamberlin & Ivie, 1942 by having the atrium rounded (Fig. 5c). Males of *H. septata* differ from *H. adnexa*, *H. pacifica*, *H. parana*, *H. sidella* Chamberlin & Ivie, 1942 and *H. tulareana* Chamberlin & Ivie, 1942 by having both projections of the conductor more separated; from *H. altura*, *H. lassena*, *H. mimoides*, *H. nedra*, *H. rabana* Chamberlin & Ivie, 1942 and *H. santana* by having a smaller tooth-shaped subprocess on the distal projection of the RTA and a larger tongue-shaped subprocess on the basal projection of the RTA; from *H. curta*, *H. dana* and *H. tentativa* by having the fulcrum smaller than the distal projection of the conductor; from *H. frianta* by having the distal projection of conductor with a tip straight; and from *H. furcata*, *H. hola*, *H. madera*, *H. monterea*, *H. nevada*, *H. oquirrhensis*, *H. pearcei* and *H. sula* by having a basal projection of the RTA with deeper ectal notch (Fig. 5a).

Description.—Male (SDNHM a000814): *Coloration:* Carapace yellow with a black band around the border of thoracic region and two longitudinal symmetrical dark bands on carapace, intensified by brown feathery scale-like setae. Cephalic region with two brown spots behind PME. Chelicerae dark brown. Condyles brown. Endites and labium brown with white tips. Sternum yellow with brown border. Legs yellow, tibia-metatarsus brown. Opisthosoma light brown with dorsal foliage and lateral brown spots. Spinnerets yellow.

Habitus: Total length 8.5. Carapace length 5, width 2.63, cephalic region width 1.9, ocular region width 1.05. Eye diameter: AME and ALE 0.21, PME 0.19, PLE 0.23. Distance between eyes: AME-AME 0.08, AME-ALE 0.08, AME-PME 0.19, ALE-PLE 0.06, ALE-ALE 0.48, PME-PME 0.15, PME-PLE 0.13. Clypeus height 0.35. Chelicerae with three promarginal teeth and two retromarginal teeth; basal segment length 1.9, fang length 0.95. Labium wider than long (0.7/0.61). Endites slightly convergent (distance at their base compared to their tips 0.61/0.39). Sternum longer than wide (2.38/1.9). Opisthosoma longer than wide (4/2.25). ALS separated by less than their basal diameter (0.24/0.3), PLS with distal segment shorter than basal segment (0.3/0.45).

Legs: Length: I- femur 3.75/ patella-tibia 4.63/ metatarsus 3.63/ tarsus 2.25; II- 3.63/ 4.38/ 3.5/ 2.13; III- 3.5/ 4.38/ 3.5/ 2; IV- 4.13/ 5/ 4.75/ 2.38.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 2-1-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0-1-1; II- 0-0-1/ 2-2-2/ 0-1-1/ 0-1-1; III- 2-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-2-2/ 1-1-1-2-2/ 0-1-1/ 0-0-1. Number of trichobothria on tarsus: I- 6, II- 7, III- 7, IV- 6.

Pedipalp: Number of dorsal spines: femur 3, tibia 4. Cymbium length 1.5, width 1. Embolus sinuous. Conductor with two projections with distal one placed in median part of bulb. Fulcrum supporting the embolus with conductor. RTA with distal and basal projections. Basal projection strongly notched ectally with a tongue-shaped subprocess (Figs. 4a, c, e, 5a, b).

Variation.—Females from Baja California have a less conspicuous septum on atrium of epigynal plate and copulatory ducts less curved (Fig. 4b).

Distribution.—California (USA) and Baja California (Mexico).

Genus *Rothilena* Maya-Morales & Jiménez, 2013

Rothilena Maya-Morales & Jiménez, 2013: 443.

Type species.—*Rothilena griswoldi* Maya-Morales & Jiménez, 2013, by original designation.

Diagnosis.—*Rothilena* is diagnosed by the following characters in combination: male pedipalp with a sinuous embolus; conductor with three short projections (Fig. 6c); RTA covering the entire tibia length (Fig. 7b); and distal and dorsal projections of RTA with dorsal and ventral excavations, respectively (Fig. 6e). Epigynum with an atrium in anterior position of plate; hoods covering the copulatory openings; copulatory ducts short; primary spermathecae spherical; secondary spermathecae in diverticula and connected to copulatory ducts; and fertilization ducts short (Fig. 6b, d, f).

Rothilena cochimi Maya-Morales & Jiménez, 2013

Rothilena cochimi Maya-Morales & Jiménez, 2013: 453, figs. 1–3, 20, 21, 32–41.

Record.—MEXICO: *Baja California Sur*: Municipality of Comondú, San José de Comondú (Maya-Morales & Jiménez 2013: 453).

New records.—MEXICO: *Baja California Sur*: 1 ♂, Municipality of Loreto, San Javier, 25°52′16.4″N, 111°32′46.4″W, 415 m, hand collecting, 1 July 2013, C. Palacios & J. Maya (CARCIB 3690); 1 ♂, same data (CARCIB 3691); 1 ♂, same data (CARCIB 3692); 1 ♀, same data (CARCIB 3756); 1 ♂, Cuevas Pintas, 25°58′41.4″N, 111°27′54.6″W, 206 m, hand collecting, 2 July 2013, C. Palacios & J. Maya (CARCIB 3693); 1 ♀, same data (CARCIB 3694). All specimens were collected as juveniles and reared to maturity in the laboratory September–October 2013.

Rothilena pilar Maya-Morales & Jiménez, 2013

Rothilena pilar Maya-Morales & Jiménez, 2013: 457, figs. 4–6, 42–51.

Record.—MEXICO: *Baja California Sur*: Municipality of La Paz, El Pilar (Maya-Morales & Jiménez 2013: 457).

New records.—MEXICO: *Baja California Sur*: 1 ♀, Municipality of La Paz, Rancho El Camarón, 24°19′11.6″N, 110°40′6.9″W, 17 m, hand collecting, 29 June 2013, C. Palacios and J. Maya (CARCIB 3687); 1 ♂, same data

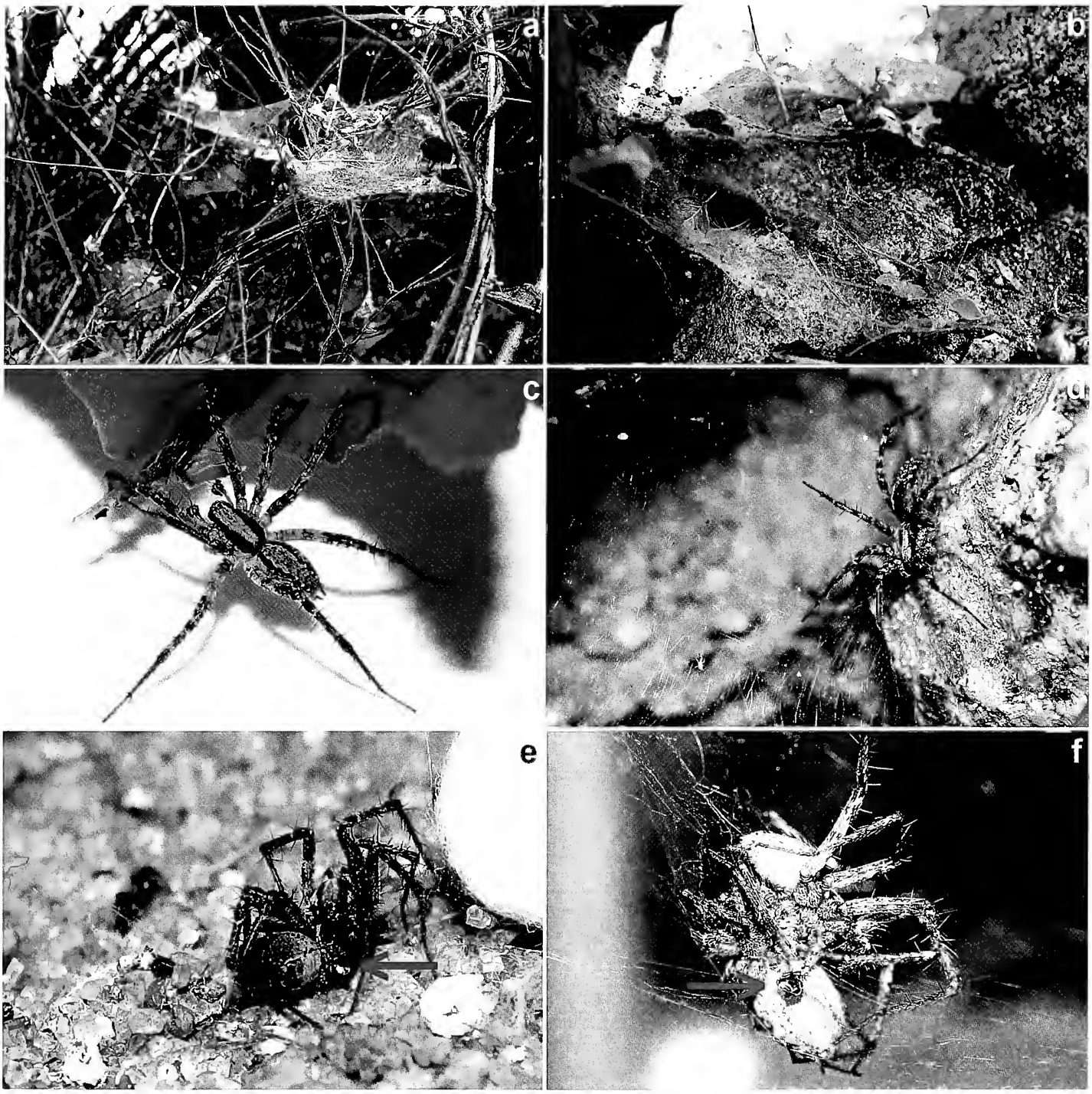

Figure 1.—Agelenids from the Baja California Peninsula (Mexico). a, c, e. *Cabolena huiztocatl* sp. nov. (Punta San Pedro, Baja California Sur). a. Web on vegetation. c. Male. e. Mating pair. b, d. *Rothilena sudcalifornienses* (Sierra Las Cacachilas, Baja California Sur). b. Web on rocks. d. Female on web. f. *R. cochimi* (San Javier, Baja California Sur), mating pair. Arrows indicate expanded bulb.

(CARCIB 3688); 1 ♂, same data (CARCIB 3689). All specimens were collected as juveniles and reared to maturity in the laboratory 1–12 September 2013.

Rothilena sudcalifornienses Maya-Morales & Jiménez, 2013
(Figs. 1b, d, 6, 7)

Rothilena sudcalifornienses Maya-Morales & Jiménez, 2013: 461, figs. 58–63.

Type material.—*Holotype female*: Municipality of La Paz, Biosphere Reserve Sierra La Laguna, Cañón La Burrera, Baja California Sur, Mexico, 1 January 1988, A. Cota (CARCIB 56).

New material examined.—MEXICO: *Baja California Sur*: 1 ♂, Municipality of La Paz, El Comitán, Dr. Laura Arriaga Cabrera Biological Station, 24°05′N, 110°21′W, pitfall trap, 29 September 1992, J.G. Navarrete (CARCIB 3427); 1 ♂, same

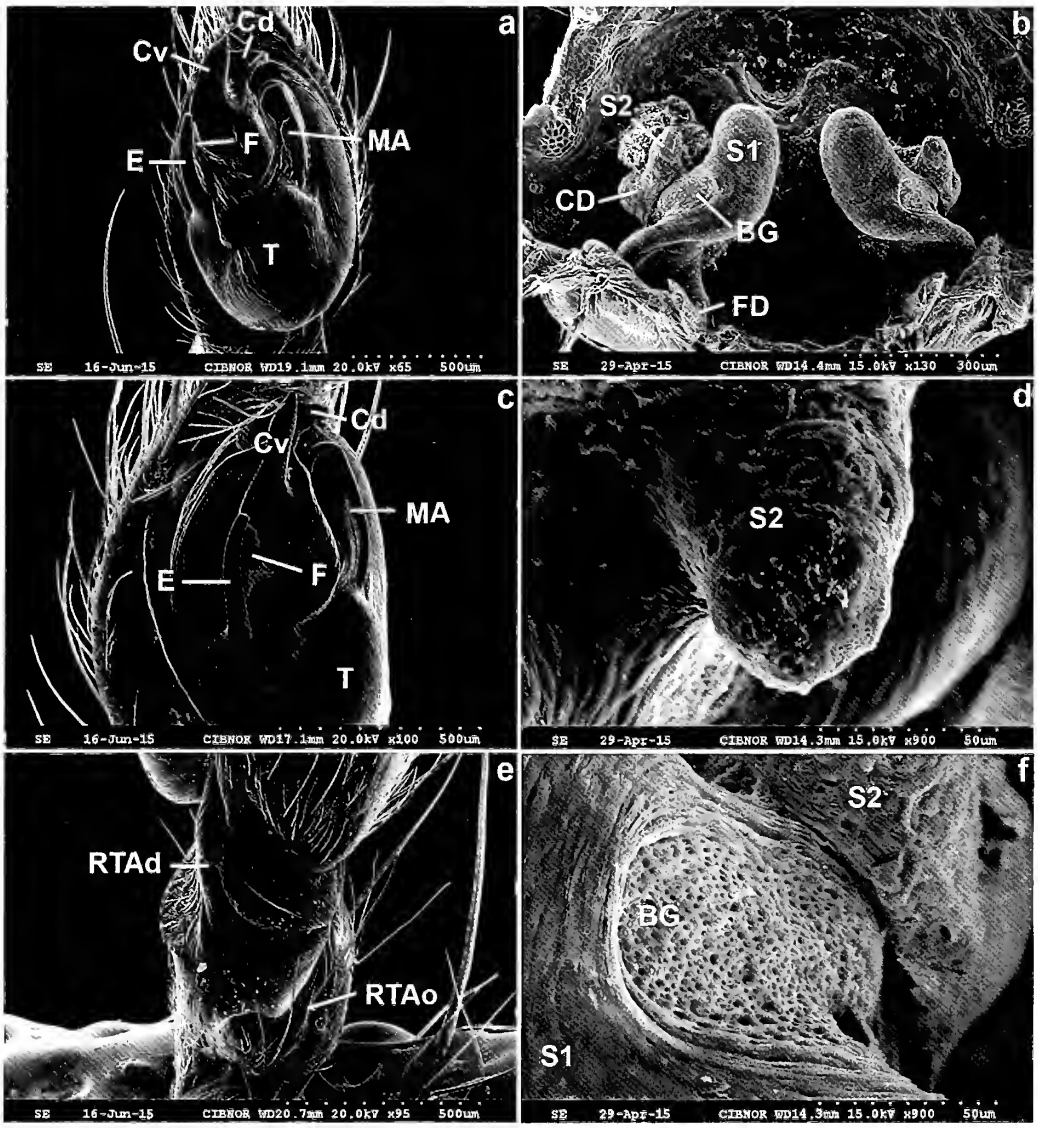

Figure 2.—*Calilena angelena*, genitalia (SEM). a, c, e. Male pedipalp b, d, f. Epigynum. Abbreviations: BG, Bennett's glands; CD, copulatory ducts; Cd, dorsal projection of conductor; Cv, ventral projection of conductor; E, embolus; F, fulcrum; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum.

data (CARCIB 3428); 1 ♂, 1 ♀, same data except 24°07′N, 110°25′W, 20 m, 4 October 2005, G. Nieto & M. Correa (CARCIB 3739); 1 ♂, 1 ♀, same data (CARCIB 3740); 1 ♂, same data (CARCIB 3741); 1 ♂, same data (CARCIB 3742); 3 ♂, same data (CARCIB 3743); 1 ♂, same data except 6 November 2005 (CARCIB 3744); 1 ♂, same data (CARCIB 3745); 1 ♀, Sierra Las Cacachilas, Rancho El Chivato, 24°02′18.7″N, 110°03′20.0″W, 354 m, hand collecting, 2 November 2013, M.L. Jiménez & J. Maya (CARCIB 3695); 1 ♀, same data except 24°02′41.9″N, 110°04′11.4″W, 487 m, 5 November 2013 (CARCIB 3696); 1 ♀, 24°02′41.9″N, 110°04′8.8″W, 478 m, 17 October 2014, C. Palacios, J. Maya & D. Vega (CARCIB 3758); 1 ♀, same data except 24°02′46.1″N, 110°04′4.6″W, 470 m, 21 October 2014 (CARCIB 3760); 1 ♀, same data except 24°02′41.9″N, 110°04′8.8″W, 478 m, 17 October 2014 (CARCIB 3763); 1 ♀, Los Pisos, 24°07′19.3″N, 110°03′49.1″W, 551 m, 19 October 2014, C. Palacios, J. Maya & D. Vega (CARCIB 3759); 1 ♀, same data (CARCIB 3761); 1 ♀, Arroyo Dos Hermanos, 24°03′35.6″N, 110°03′44.8″W, 403 m, 20 October 2014, C. Palacios, J. Maya & D. Vega (CARCIB 3762); 1 ♂, El Triunfo, 23°48′15.7″N, 110°06′43.7″W, 468 m, hand collecting, 18 March 2015, M.L. Jiménez, C. Palacios & J. Maya (CARCIB 3791); 1 ♂, same data except 23°48′4.4″N, 110°06′24.7″W, 484 m (CARCIB 3793); 1 ♂, same data (CARCIB 3794); 1 ♀, same data (CARCIB 3795); 1 ♂, same data (CARCIB 3796); 1 ♂, same data (CARCIB 3797); 1 ♂, same data (CARCIB 3824).

Diagnosis.—Males of *R. sudcaliforniensis* differ from *R. griswoldi* by having a dorsal projection of the RTA ending in a sharp tip (Fig. 6a) and from *R. cochimi* and *R. pilar* by having a dorsal projection of the RTA that is longer and directed ventrally (Fig. 7b). Females differ from all other species by having hoods that are as long as wide.

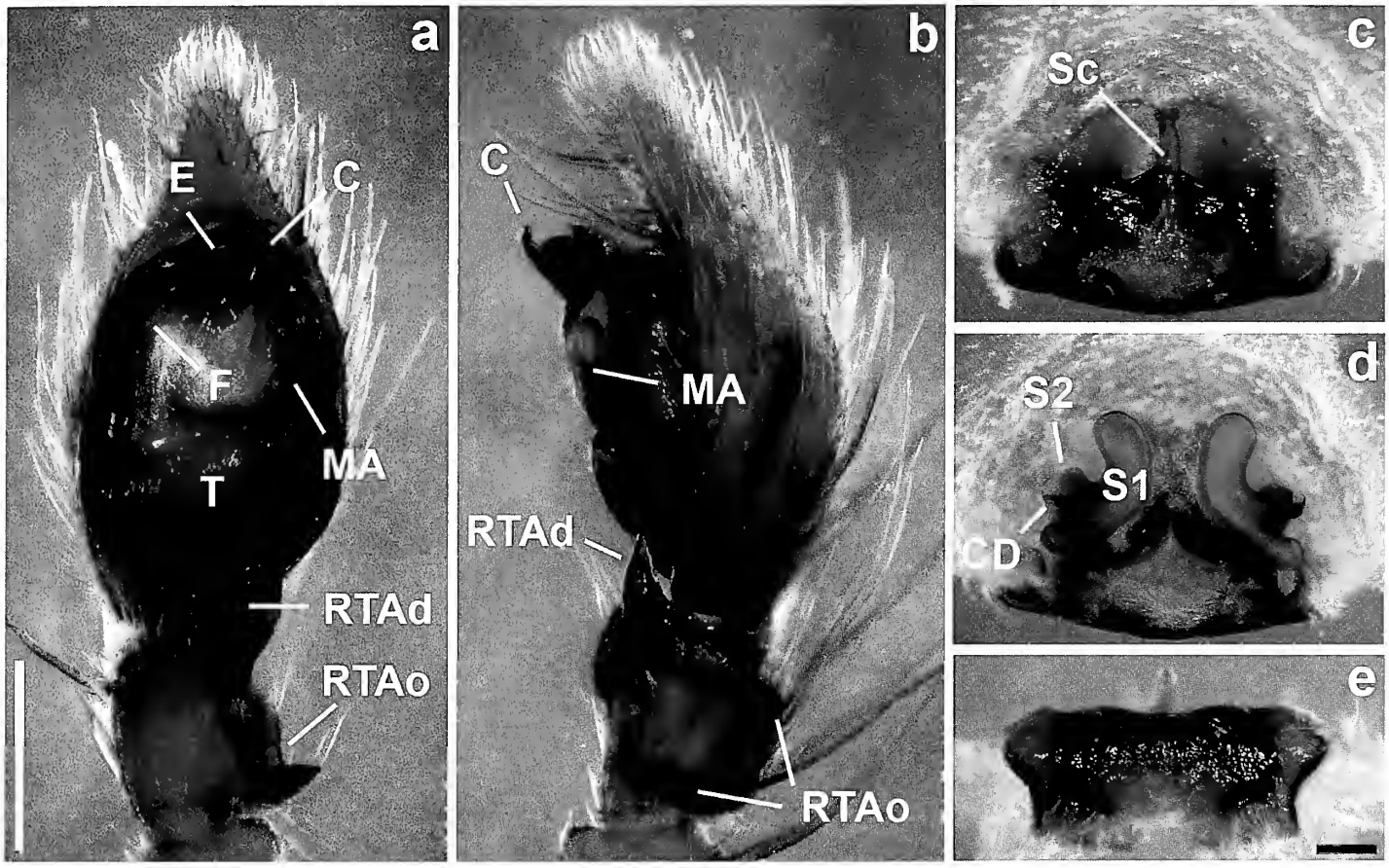

Figure 3.—*Calilena angelena*, genitalia. a, b. Male pedipalp. c–e. Epigynum. a, c. Ventral view. b. Retrolateral view. d. Dorsal view. e. Posterior view. Abbreviations: CD, copulatory ducts; E, embolus; F, fulcrum; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; Sc, scape; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum. Scale bars: a = 0.5 mm; e = 0.15 mm.

Description.—Male (CARCIB 3427): *Coloration:* Carapace light brown with a black band around the border of thoracic region and two longitudinal symmetrical dark bands, intensified by brown feathery scale-like setae. Chelicerae and condyles brown. Endites and labium light brown with white tip. Sternum yellow with brown border. Legs yellow with three rings on femur and one on tibia. Opisthosoma light brown, three anterior brown spots, four pairs of lateral light spots and lateral brown lines. Spinnerets yellow, basal segment of PLS with dark brown spots.

Habitus: Total length 6.38. Carapace length 2.88, width 2.13, cephalic region width 1.06, ocular region width 0.61. Eye diameter: AME, ALE and PLE 0.15, PME 0.13. Distance between eyes: AME-AME 0.02, AME-ALE 0.04, AME-PME 0.12, ALE-PLE 0.02, ALE-ALE 0.25, PME-PME 0.08, PME-PLE 0.08. Clypeus height 0.23. Chelicerae with three promarginal teeth and two retromarginal teeth; basal segment length 1.15, fang length 0.85. Labium wider than long (0.45/0.33). Endites slightly convergent (distance at their base compared to their tips 0.45/0.27). Sternum longer than wide (1.43/1.24). Opisthosoma longer than wide (3.13/1.75). ALS separated by less than their basal diameter (0.21/0.27), PLS with distal segment slightly longer than basal segment (0.45/0.33).

Legs: Length: I- femur 2.62/ patella-tibia 3.31/ metatarsus 2.62/ tarsus 1.77; II- 2.62/ 3.15/ 2.38/ 1.62; III- 2.77/ 3.08/ 2.92/ 1.69; IV- 3.31/ 3.85/ 4.08/ 2.08.

Spination: Femur dorsal I- 1-2-2/ II- 1-3-2/ III- 1-3-2/ IV- 1-2-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 0/ 2-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0; II- 0-0-1/ 2-2-2/ 0-1-1/ 0; III- 2-0-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-2-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 6, II- 6, III- 6, IV- 6.

Pedipalp: Number of dorsal spines: femur 2, tibia 4. Cymbium length 1.09, width 0.64. Embolus sinuous. Conductor with distal and mesal projections beak-shaped, ectal projection rounded. Dorsal projection of RTA ends in a sharp tip and is directed ventrally; anterior margin is straight (Figs. 6a, c, e, 7).

Variation.—The epigynum presents slight differences between localities: the copulatory ducts may be closer to each other in females from El Triunfo and San Antonio; secondary spermathecae are directed laterally in specimens from Sierra La Laguna, El Triunfo, San Antonio, and El Comitán, and anteriorly in specimens from Sierra Las Cacachilas (Fig. 6b, f).

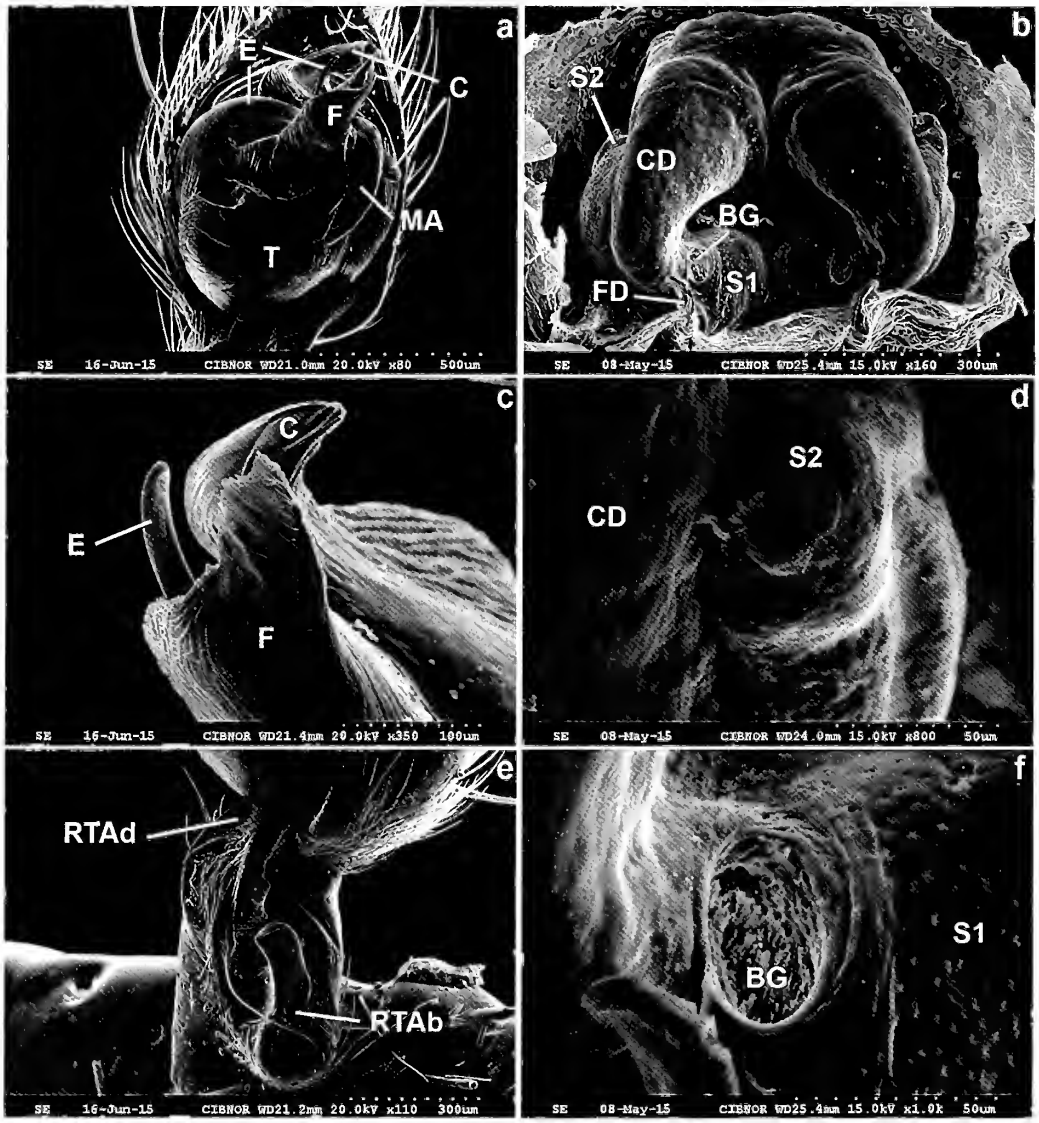

Figure 4.—*Hololena septata*, genitalia (SEM): a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: BG, Bennett's glands; CD, copulatory ducts; Cd, dorsal projection of conductor; Cv, ventral projection of conductor; E, embolus; F, fulcrum; FD, fertilization ducts; MA, median apophysis; RTAb, basal projection of RTA; RTAd, distal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum.

Habitat.—Deciduous lowland forest and desert shrubland. The specimens were found on the ground, between rocks and low vegetation (Fig. 1b, d).

Distribution.—Baja California Sur (Mexico).

Genus *Bajacalilena* Maya-Morales & Jiménez gen. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:60362154-56FF-49D4-BA78-3AB0A9AB32EF

Type species.—*Bajacalilena clarki* sp. nov.

Etymology.—The generic name is derived from the region where the species of the genus are found and are potentially endemic. The gender is feminine.

Diagnosis.—*Bajacalilena* gen. nov. is diagnosed by the following characters in combination: male pedipalp with a coiled embolus supported by a membranous horseshoe-shaped conductor (Fig. 9a); and RTA covering the entire tibia length with distal and dorsal projections. Epigynum with the atrium as a deep cavity and spurs in lateral position (Fig. 8a, b); copulatory openings in lateral position; copulatory ducts larger than primary spermathecae and in two parts (Figs. 8c, 9b); primary spermathecae spherical, adjacent (Fig. 8e) or separated by less than their width (Fig. 8d); secondary spermathecae small and connected to copulatory ducts (Fig. 9b, f); and fertilization ducts short (Fig. 8f).

Bajacalilena gen. nov. differs from *Eratigena* Bolzern, Burckhardt & Hänggi, 2013 and *Tegenaria* by having strongly procurved eye rows in frontal view. *Bajacalilena* gen. nov. shares with *Agelenopsis*, *Barronopsis*, *Melpomene* O. P.-Cambridge, 1898, and *Tortolena* Chamberlin & Ivie, 1941 a strongly modified embolus, and like *Agelenopsis*, *Barronopsis* and *Tortolena*, *Bajacalilena* gen. nov. has a coiled embolus (Fig. 9c). However, *Bajacalilena* gen. nov. differs from these genera by the shape of the median apophysis, which is not

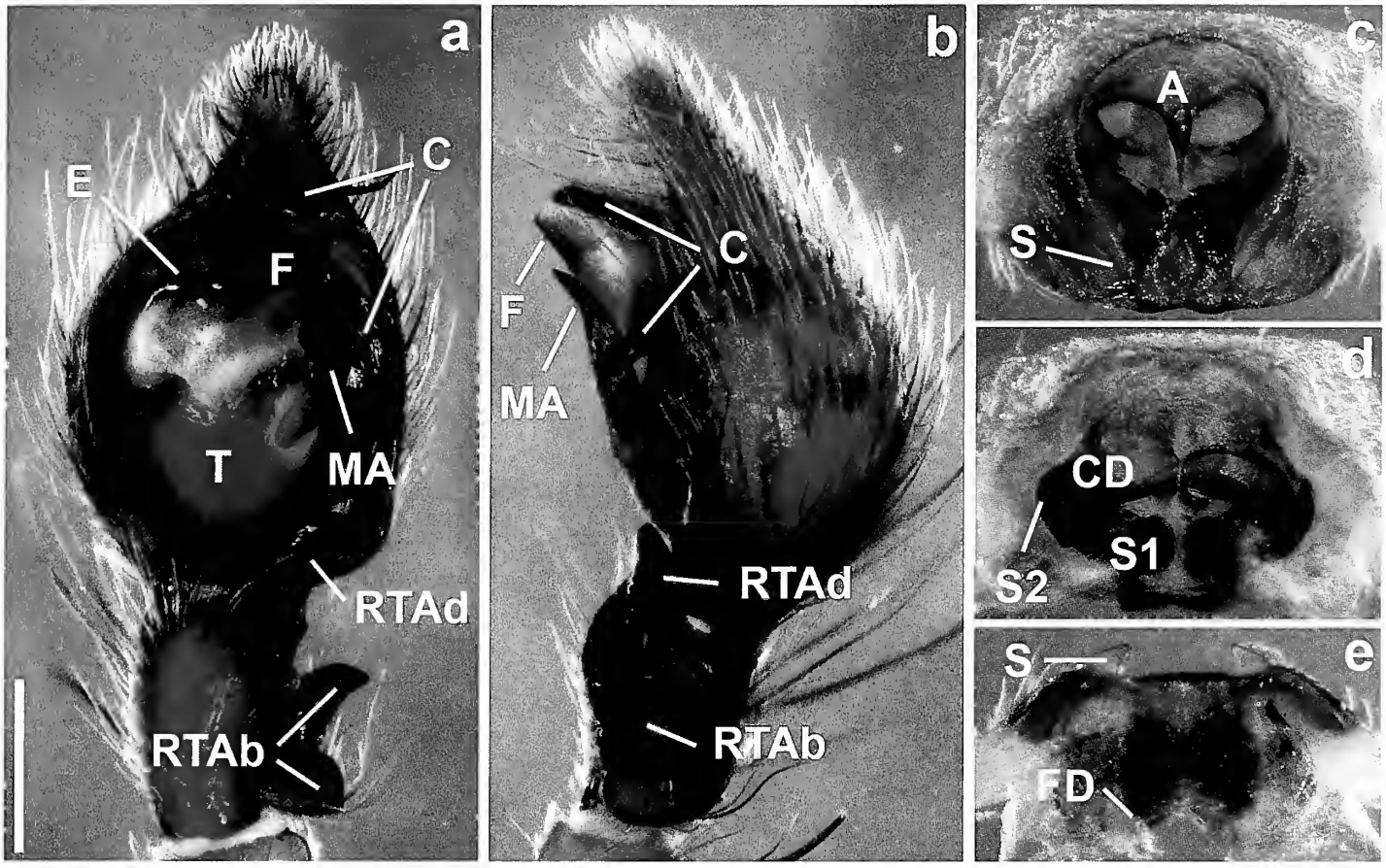

Figure 5.—*Hololena septata*, genitalia. a, b. Male pedipalp. c–e. Epigynum. a, c. Ventral view. b. Retrolateral view. d. Dorsal view. e. Posterior view. Abbreviations: A, atrium; CD, copulatory ducts; E, embolus; F, fulcrum; FD, fertilization ducts; MA, median apophysis; RTAb, basal projection of RTA; RTAd, distal projection of RTA; S, spurs; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum. Scale bar = 0.5 mm.

reduced (Fig. 9a), and by the absence of a tegular lateral process on the male pedipalp. *Bajacalilena* gen. nov. differs from *Hoffmannilena* Maya-Morales & Jiménez, 2016 by the absence of a tegular median process (as in Maya-Morales & Jiménez 2016: fig. 114) and the poorly sclerotized epigynum (as in Maya-Morales & Jiménez 2016: fig. 116); from *Novalena* by the absence of a tegular median process on the male pedipalp (as in Maya-Morales & Jiménez 2016: fig. 87) and having the primary spermathecae spherical; from *Cabolena* gen. nov. by having the embolus coiled and primary spermathecae spherical; from *Lagunella* gen. nov. by having the embolus originating from the median part of the tegulum and the copulatory ducts connected anteriorly to primary spermathecae; from *Calilena* by the absence of both a membranous fulcrum on the male pedipalp (as in Fig. 3a) and a scape on the epigynum (Fig. 3c); from *Hololena* by having the embolus supported by the conductor only and the absence of a median septum on the epigynal atrium (Fig. 5c); from *Rualena* by the absence of a fulcrum on the male pedipalp (as in Maya-Morales & Jiménez 2016: fig. 43) and having the atrium wider than long; from *Rothilena* by having the conductor with two projections and no hoods on the atrium (as in Maya-Morales & Jiménez 2013: fig. 26); and from *Callidalena* gen. nov. by having the embolus coiled and the atrium as an anterior deep cavity.

Description.—Medium sized spiders, 5–11 in total length. Eight eyes. Both eye rows strongly procurved in frontal view. Feathery scale-like setae present on carapace, opisthosoma, pedipalps and legs. Carapace with two longitudinal symmetrical dark bands intensified by feathery setae, a black band around the border of thoracic region, and a clear median band wider on cephalic region. Chelicerae with three promarginal teeth and two retromarginal teeth. Sternum longer than wide. Pedipalp femur with two dorsal spines. Legs with spines. Leg IV the longest. Rings present on femur, patella and tibia. Patella-tibia I longer than carapace in males and usually shorter than carapace in females. Patella I and II with two dorsal spines and one prolateral spine, patella III and VI with two dorsal spines, one prolateral spine, and one retrolateral spine. Leg tarsi with five to six trichobothria. Capsulate tarsal organ in distal position of trichobothrial row. Opisthosoma oval with dorsal foliate pattern and/or posterior chevrons. Colulus divided, represented by few hairs. PLS longest with distal segment as long as or slightly longer than basal segment. Male pedipalp with a distinct coiled embolus supported by a conductor which is membranous and horseshoe-shaped (Fig. 10a). Median apophysis is an elongated, curved membrane

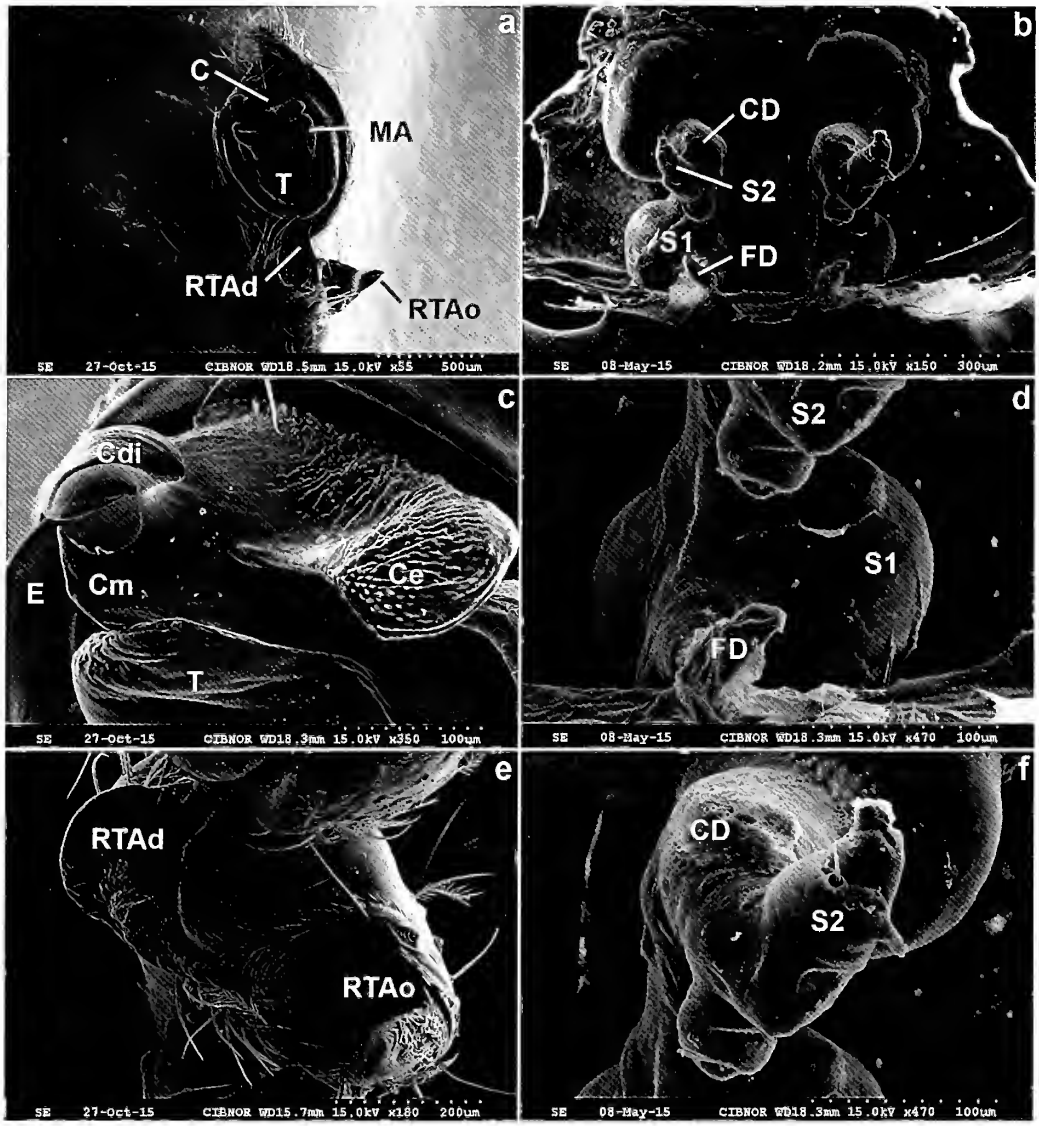

Figure 6.—*Rothilena sudcaliforniensis*, genitalia (SEM). a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: CD, copulatory ducts; Cdi, distal projection of conductor; Ce, ectal projection of conductor; Cm, mesal projection of conductor; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum.

(Fig. 9a). RTA covering the entire tibia length with distal and dorsal projections (Fig. 10c); tibia also with posterodorsal apophysis (Fig. 9b). Epigynal plate wider than long (Fig. 8a). Atrium is a strongly deep cavity without divisions, on anterior part of plate. Lateral hyaline spurs present (Fig. 8b). Copulatory openings at lateral position. Copulatory ducts anterior to spermathecae (Fig. 8d). Spermathecae composed by primary spermathecae and secondary spermathecae. Primary spermathecae spherical (Fig. 9d). Secondary spermathecae are small blind receptacles (diverticula) with primary pores and connected to copulatory ducts (Fig. 9b, f). Fertilization ducts short, originating from the posterior part of epigynum (Fig. 8f).

Distribution.—*Bajacalilena* gen. nov. is distributed in Mexico in the States of Baja California and Baja California Sur (Fig. 23a).

Included taxa.—Two species: *B. bolzerni* sp. nov. and *B. clarki* sp. nov.

Bajacalilena bolzerni Maya-Morales & Jiménez sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:B9D5627B-54AE-40F6-AD71-CBD98866D19C
(Figs. 8a, c, e, 23a)

Type material.—*Holotype female*: Municipality of Ensenada, 3.2 km W. of Ejido Morelos, Baja California, Mexico, 28 December 1978, D. Weissman, R. Love, V. Lee & C. Mullinex (CASENT 9048907). *Paratype female*: MEXICO: *Baja California Sur*: Municipality of Mulegé, Isla Natividad, 5–6 June 1945, B.F. Osorio (AMNH).

Etymology.—The specific name is a patronym in honor of Angelo Bolzern for his contribution to systematics of Agelenidae.

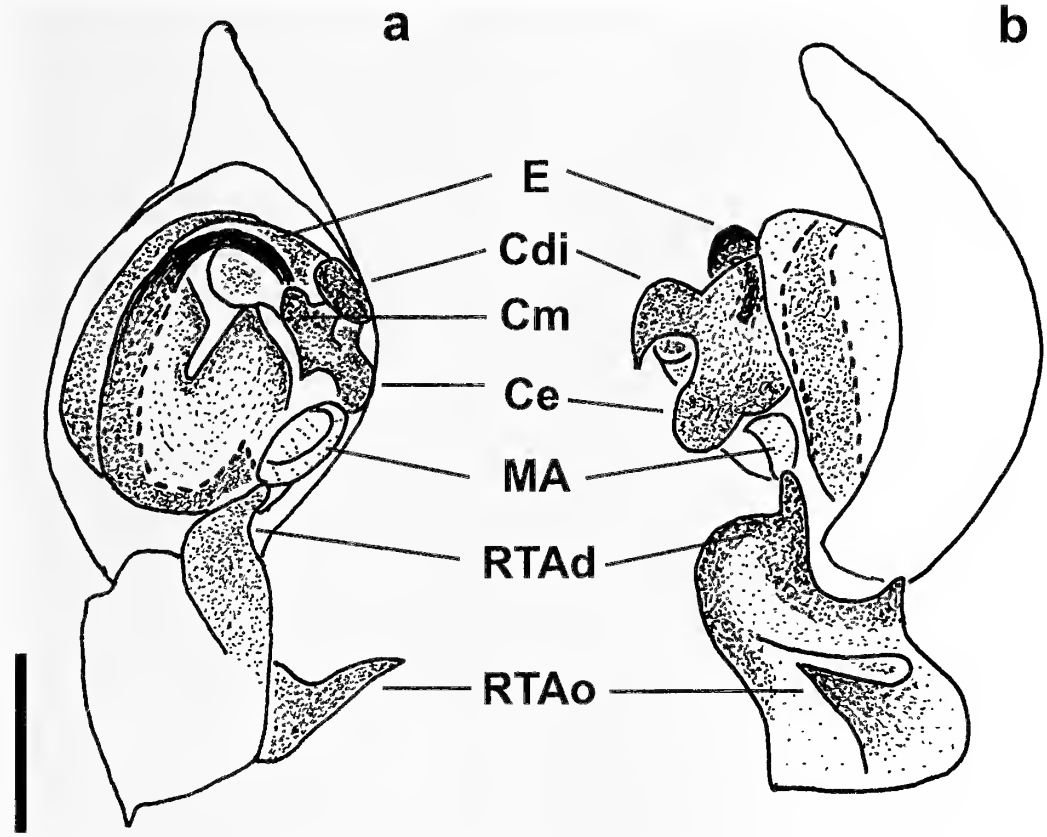

Figure 7.—*Rothilena sudcalifornicnsis*, male pedipalp. a. Ventral view. b. Retrolateral view. Abbreviations: Cdi, distal projection of conductor; Ce, ectal projection of conductor; Cm, mesal projection of conductor; E, embolus; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA. Scale bar = 0.35 mm.

Diagnosis.—*Bajacalilena bolzerni* differs from *B. clarki* sp. nov. by having the primary spermathecae adjacent (Fig. 8e) and copulatory ducts with anterior extensions (Fig. 8c).

Description.—Female (holotype): *Coloration:* Carapace yellow. Chelicerae light brown. Condyles greyish. Endites and labium yellow with white tips and small brown spots. Sternum yellow with brown border and four pairs of brown spots. Legs yellow. Three rings on femur, one on patella, and two on tibia. Opisthosoma orange with an anterior reddish spot, seven pairs of white spots, and several lateral brown spots. Spinnerets yellow, PLS with black borders on basal segments.

Habitus: Total length 7. Carapace length 3.13, width 2, cephalic region width 1.24, ocular region width 0.67. Eye diameter: AME, ALE and PLE 0.15, PME 0.13. Distance between eyes: AME-AME 0.04, AME-ALE 0.04, AME-PME 0.13, ALE-PLE 0.06, ALE-ALE 0.29, PME-PME 0.08, PME-PLE 0.08. Clypeus height 0.25. Chelicerae: basal segment length 1.21, fang length 0.6. Labium wider than long (0.36/0.3). Endites slightly convergent (distance at their base compared to their tips 0.36/0.3). Sternum longer than wide (1.57/1.24). Opisthosoma longer than wide (4.1/2.48). ALS separated by less than their basal diameter (0.24/0.3), PLS with distal segment slightly longer than basal segment (0.52/0.48).

Legs: Length: I- femur 2.15/ patella-tibia 2.69/ metatarsus 1.92/ tarsus 1.38; II- 2.31/ 2.15/ 1.92/ 1.31; III- 2.38/ 2.46/ 2.31/ 1.31; IV- 3.08/ 3.31/ 3.46/ 2.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-2/ IV- 1-2-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 1-1-0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-1-0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-1-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 0-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0; II- 1-0-1/ 2-2-2/ 0-1-1/ 0-0-1; III- 3-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-2-2/ 1-1-1-2-2/ 0-1-1/ 0-0-1. Number of trichobothria on tarsus: I- 5, II- 5, III- 5, IV- 5.

Pedipalp: Dorsal spines on femur: 2. Prolateral spines on tibia: 1-2.

Epigynum: Plate length 0.67, width 1.03. Copulatory ducts with mesal extensions and separated by their width. Primary spermathecae adjacent (Fig. 8a, c, e).

Male: Unknown.

Variation.—Total body length varies between 7 and 7.75 ($n = 2$). Carapace length varies between 3.13 and 3.75 ($n = 2$). Patella-tibia I length varies between 2.69 and 4 ($n = 2$).

Distribution.—Baja California and Baja California Sur (Mexico) (Fig. 23a).

Bajacalilena clarki Maya-Morales & Jiménez sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:527CBDDC-38DB-4CD6-A1DE-1EDEA1E90CD0
(Figs. 8b, d, f, 9, 10, 23a)

Type material.—*Holotype male*: Municipality of Ensenada, 9 km NW. of Rancho Santa Inés, Baja California, Mexico, 29°46′N, 114°46′W, 550 m, pitfall trap, 19 September 1980,

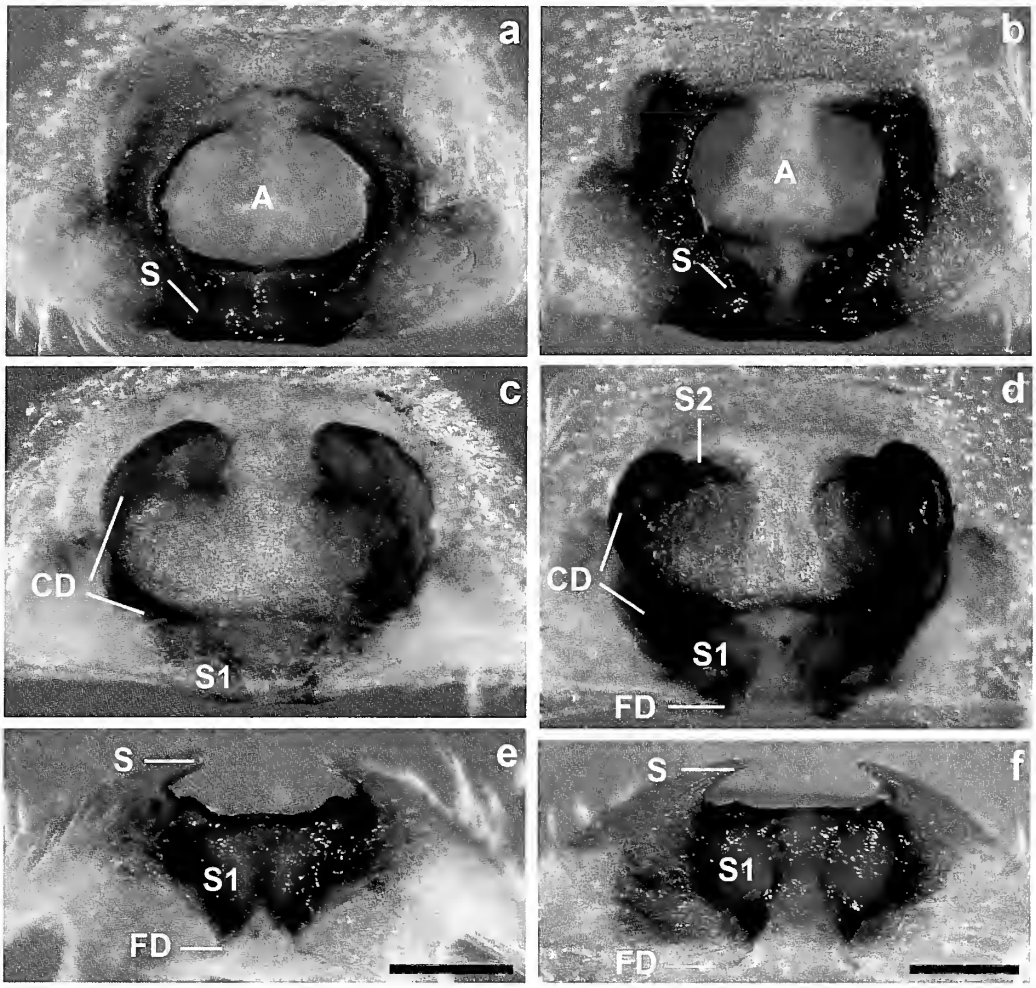

Figure 8.—*Bajacalilena* spp., epigyna. a, c, e. *B. bolzerni* sp. nov. b, d, f. *B. clarki* sp. nov. a, b. Ventral view. c, d. Dorsal view. e, f. Posterior view. Abbreviations: A, atrium; CD, copulatory ducts; FD, fertilization ducts; S1, primary spermathecae; S2, secondary spermathecae. Scale bars = 0.25 mm.

W.H. Clark (CIDA 107,457) (OJSMNH). *Paratypes*: MEXICO: *Baja California*: 1 ♀, Municipality of Ensenada, 66 km E. of El Rosario, Misión San Fernando, 11 January 1965, V. Roth (AMNH); 1 ♀, 12.9 km N. of Laguna Chapala, 16 April 1965, D.Q. Cavagnaro, C.E. Ross, E.S. Ross & V.L. Vesterby (CASENT 9048906); 2 ♂, same data as holotype (CIDA 107,457); 1 ♀, same data as holotype except 17 July 1991 – 26 May 1992 (CIDA 90,622); 5 ♂, same data as holotype except 10 September 1980, P. Finlayson, C. Ross & D. Webster (CIDA 107,413); 1 ♂, same data as holotype except 20 September 1980, C. Ross & P. Finlayson (CIDA 107,420); 2 ♂, 1 ♀, same data as holotype except 18 September 1980, D. Webster & D. Guyot (CIDA 107,465); 1 ♂, same data as holotype except 13 September 1980, P. Finlayson, C. Ross & D. Webster (CIDA 107,466); 1 ♂, 11.7 km E. of El Rosario, 30°04′30″N, 115°37′55″W, 180 m, pitfall trap, 7 February 1982 – 2 April 1985, W.H. Clark & P.E. Blom (CIDA 107,428); 1 ♀, La Ramona camp, Punta Catarina road, hand collecting on ground, 21 March 2005, J. Berrian (SDNHM a000846). *Baja California Sur*: 1 ♂, Municipality of Mulegé, SE. of Mesa El Tecolote, 29°59′N, 113°26′W, 120 m, pitfall trap, 16 March – 8 July 1991, W.H. Clark (ALBRCIDA 83,066); 1 ♀, 7 km N. of Rancho El Tablón, 27°37′N, 113°21′W, 130 m, pitfall trap, 18 March –13 July 1991, W.H. Clark (ALBRCIDA 83,086); 1 ♂, Arroyo San Lorenzo, 26°56′N, 113°47′W, 20 m, pitfall trap, 17 March – 8 July 1991, W.H. Clark (ALBRCIDA 83,091); 1 ♀, foot of Sierra San Francisco, on main road, 8 April 2006, J. Berrian (SDNHM a000845).

Etymology.—The specific name is a patronym in honor of William H. Clark, collector of the holotype, for his work with terrestrial arthropods in North America.

Diagnosis.—*Bajacalilena clarki* differs from *B. bolzerni* by having the primary spermathecae separated (Fig. 9b) and by the absence of mesal extensions on the copulatory ducts (Fig. 8d).

Description.—Male (holotype): *Coloration:* Carapace yellow with central white spot. Chelicerae brown. Condyles light brown. Endites and labium light brown with white tips. Sternum dark brown with a central yellow foliage-shaped band. Legs yellow, patella-tibia with borders dark brown. Opisthosoma light brown with anterior dark brown spot, yellow foliage, and lateral dark brown spots. Spinnerets yellow, basal segment of PLS with black borders.

Habitus: Total length 7.75. Carapace length 4.25, width 2.88, cephalic region width 1.43, ocular region width 0.76. Eye diameter: AME 0.13, ALE, PME and PLE 0.15. Distance

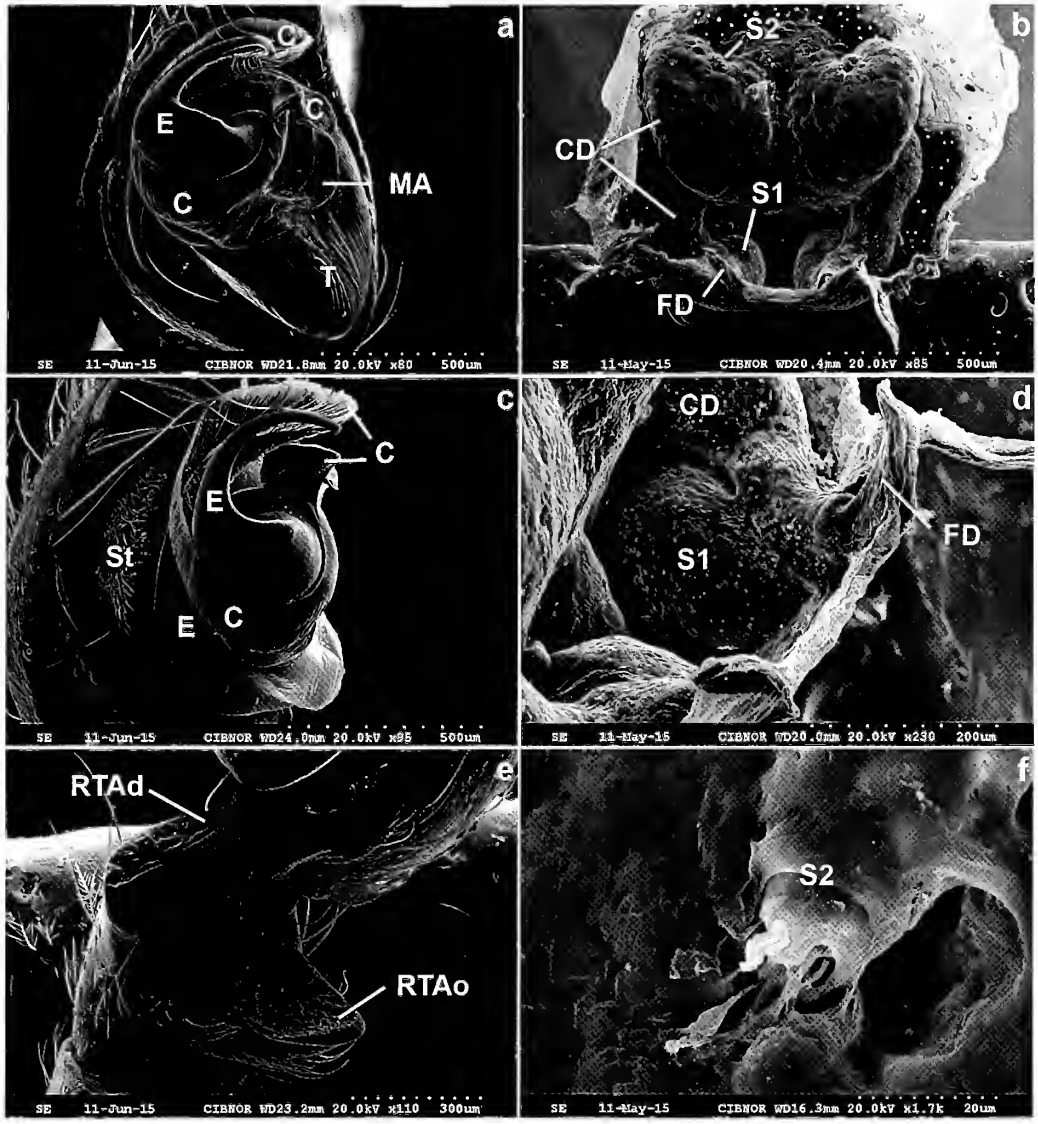

Figure 9.—*Bajacalilena clarki* sp. nov., genitalia (SEM). a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: C, conductor; CD, copulatory ducts; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; St, subtegulum; T, tegulum.

between eyes: AME-AME 0.04, AME-ALE 0.04, AME-PME 0.19, ALE-PLE 0.06, ALE-ALE 0.35, PME-PME 0.08, PME-PLE 0.06. Clypeus height 0.31. Chelicerae: basal segment length 1.67, fang length 0.71. Labium wider than long (0.62/0.52). Endites slightly convergent (distance at their base compared to their tips 0.68/0.38). Sternum longer than wide (1.95/1.52). Opisthosoma longer than wide (4/2.25). ALS separated by less than their basal diameter (0.3/0.36), PLS with distal segment as long as basal segment (0.61/0.61).

Legs: Length: I- femur 3.38/ patella-tibia 4.63/ metatarsus 3.88/ tarsus 2.38; II- 3.5/ 4.38/ 4/ 2.25; III- 3.38/ 4.38/ 4.63/ 2.38; IV- 4.75/ 5.63/ 6.38/ 2.88.

Spination: Femur dorsal I- 1-2-2/ II- 1-3-2/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 1-1-0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-1-0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-1-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0; II- 0/ 2-2-2/ 0-1-1/ 0-1-1; III- 3-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 5, II- 5, III- 5, IV- 6.

Pedipalp: Number of dorsal spines: femur 2, tibia 4. Cymbium length 1.7, width 1. Embolus with one and a half coils. Horseshoe-shaped membranous conductor. RTA with distal and dorsal projections and without excavations (Figs. 9a, c, e, 10).

Female (paratype) (AMNH): *Coloration:* Carapace brown, black spot between AME. Chelicerae reddish and condyles yellow. Endites and labium orange with white tips. Sternum orange with three pairs of black spots. Legs with three rings on femur and two on tibia. Coxa IV with diffuse spot on proximal part. Opisthosoma with an anterior red spot with a pair of lateral white spots that form a foliage and four pairs of black spots. Diffuse black spots laterally and ventrally. Spinnerets yellow.

Habitus: Total length 9. Carapace length 3.88, width 2.63, cephalic region width 1.19, ocular region width 0.71. Eye

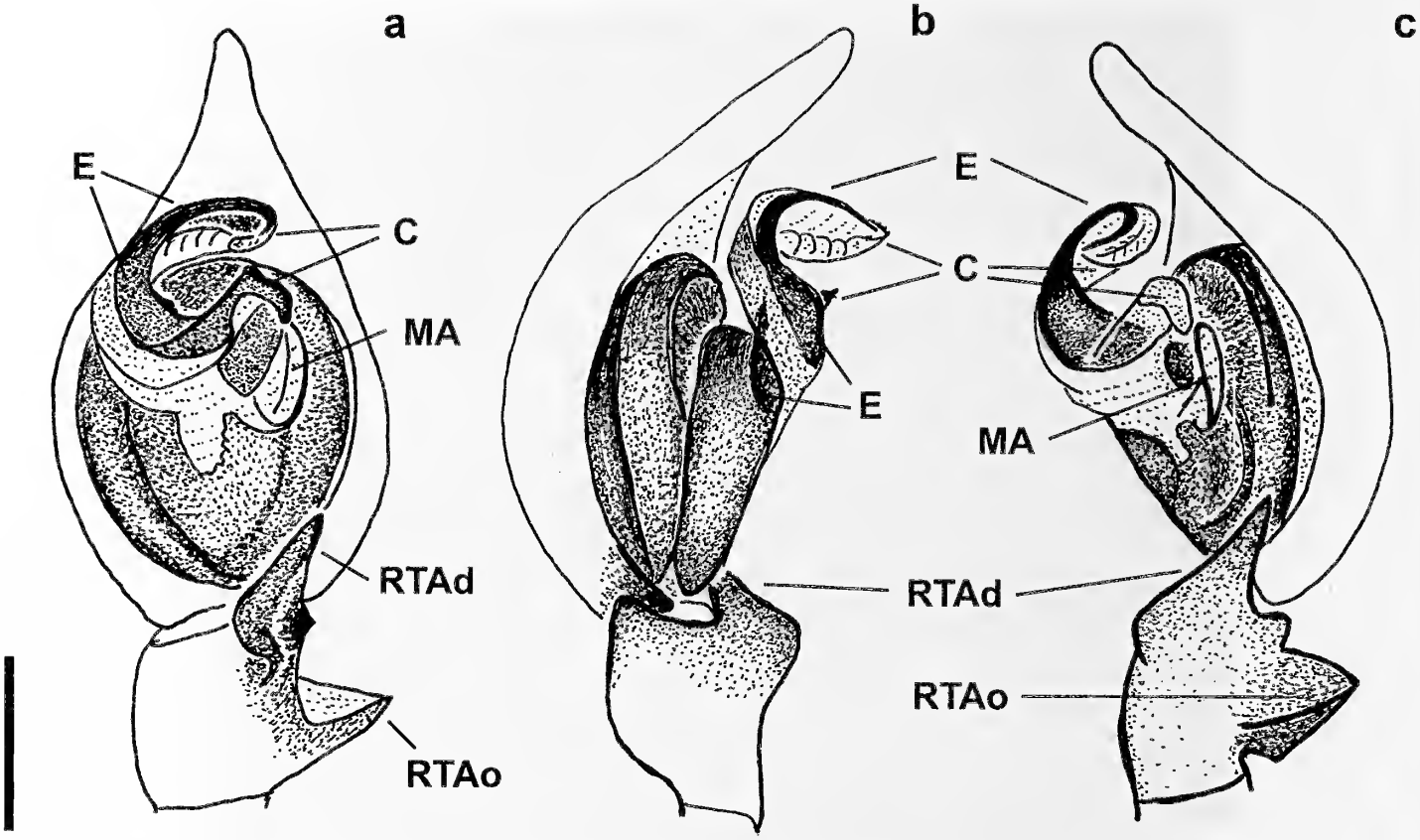

Figure 10.—*Bajacalilena clarki* sp. nov., male pedipalp. a. Ventral view. b. Prolateral view. c. Retrolateral view. Abbreviations: C, conductor; E, embolus; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; T, tegulum. Scale bar = 0.5 mm.

diameter: AME 0.15, ALE 0.17, PME and PLE 0.13. Distance between eyes: AME-AME 0.06, AME-ALE 0.04, AME-PME 0.15, ALE-PLE 0.04, ALE-ALE 0.35, PME-PME 0.1, PME-PLE 0.1. Clypeus height 0.25. Chelicerae: basal segment length 1.43, fang length 0.67. Labium wider than long (0.61/0.45). Endites slightly convergent (distance at their base compared to their tips 0.61/0.39). Sternum longer than wide (1.81/1.52). Opisthosoma longer than wide (5/3.25). ALS separated by less than their basal diameter (0.27/0.33), PLS with distal segment as long as basal segment (0.61/0.61).

Legs: Length: I- femur 2.88/ patella-tibia 3.38/ metatarsus 2.5/ tarsus 1.75; II- 2.88/ 3.38/ 2.5/ 1.5; III- 2.88/ 2.38/ 2.75/ 1.63; IV- 3.13/ 4.38/ 4.38/ 2.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 1-1-0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-1-0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-1-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0-0-1; II- 0/ 1-2-2/ 0-1-1/ 0-0-1; III- 3-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 5, II- 5, III- 5, IV- 5.

Pedipalp: Dorsal spines on femur: 2. Prolateral spines on tibia: 1-2.

Epigynum: Plate length 0.76, width 1.1. Copulatory ducts with anterior part separated by three times their width. Primary spermathecae separated by less than their width (Figs. 8b, d, f, 9b, d, f).

Variation.—Total body length in males varies between 5.75 and 10 ($n = 14$) and in females between 7.5 and 10.38 ($n = 7$). Carapace length in males varies between 2.88 and 5 ($n = 15$) and in females between 2.75 and 4.63 ($n = 7$). Patella-tibia I length in males varies between 3 and 5.25 ($n = 15$) and in females between 3 and 4.25 ($n = 7$).

Distribution.—Baja California and Baja California Sur (Mexico) (Fig. 23a).

Cabolena Maya-Morales & Jiménez gen. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:4E727171-8324-4492-9B62-C33F30C89392

Type species.—*Cabolena kosatli* sp. nov.

Etymology.—The generic name is derived from Los Cabos, the region where the genus is distributed. The gender is feminine.

Diagnosis.—*Cabolena* gen. nov. is diagnosed by the following characters in combination: epigynum with the median field of plate wider posteriorly and clearly differentiated from lateral lobes by epigynal folds or sutures (Figs. 12c, 14c, 16c); eopulatory openings at central position of plate length (Figs. 12c, 16c); copulatory ducts at ventral (Fig. 13d) or mesal (Fig. 11d) position in relation to primary spermathecae; primary spermathecae longer than wide (Figs. 11b, 13b); and secondary spermathecae in diverticula (Fig. 14d). Male pedipalp with simple curved embolus originating at median part of bulb length (Fig. 13a); conductor with two

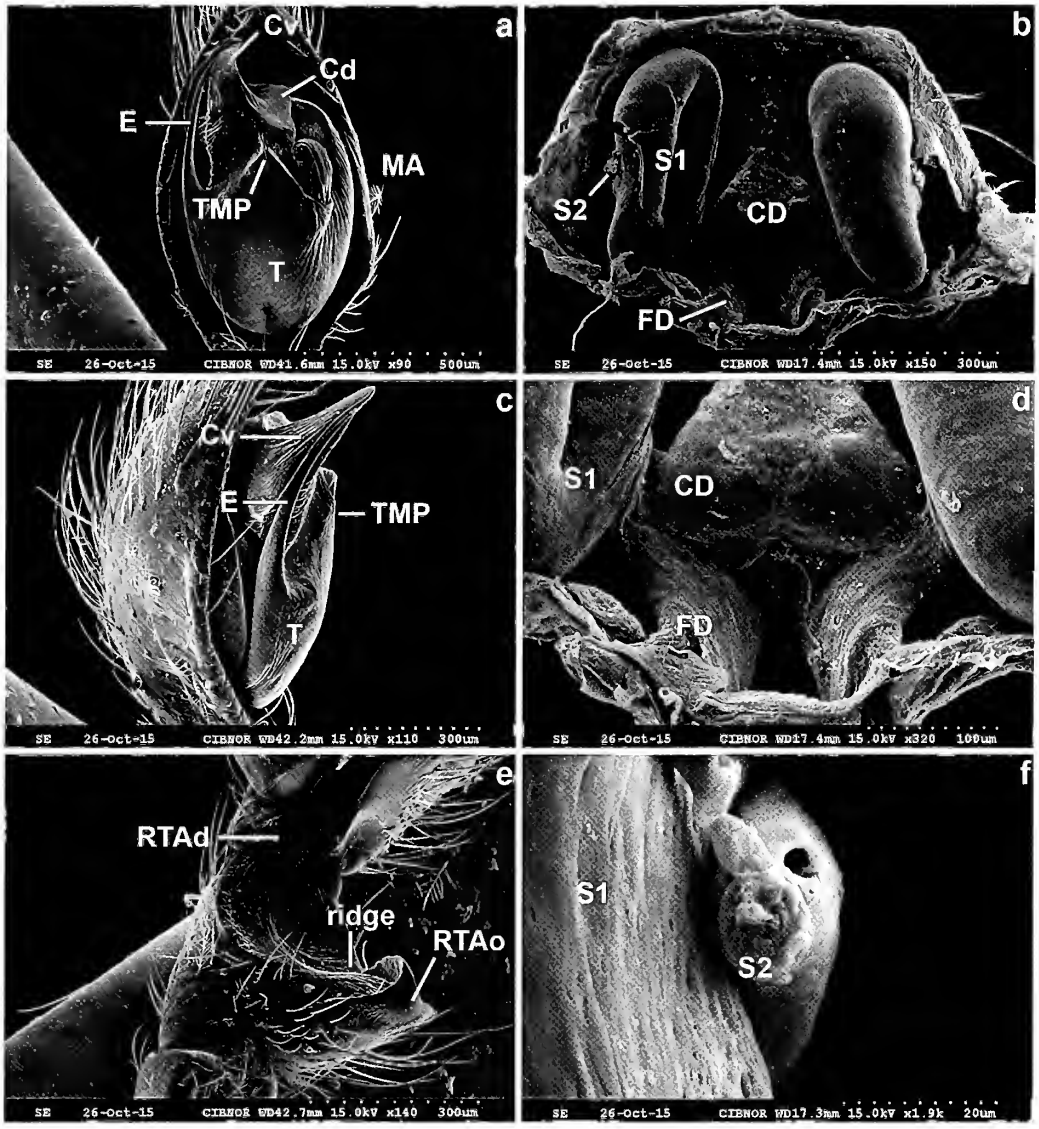

Figure 11.—*Cabolena huiztocatl* sp. nov., genitalia (SEM). a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: CD, copulatory ducts; Cd, dorsal projection of conductor; Cv, ventral projection of conductor; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum; TMP, tegular median process.

projections (Fig. 11a, 15a); and RTA with a ridge on the dorsal projection (Figs. 11e, 15e).

Cabolena gen. nov. differs from *Eratigena* and *Tegenaria* by having strongly procurved eye rows in frontal view; from *Agelenopsis*, *Barronopsis*, *Melpomene* and *Tortolena* by having the embolus slightly curved and by the absence of a tegular lateral process; from *Calilena* by the absence of both a membranous fulcrum on the male pedipalp and a scape on the epigynum; from *Hololena* by having the embolus supported by the conductor only and having the primary spermathecae longer than wide; from *Rualena* by the absence of both a fulcrum and a posterior ridge on the epigynal plate (as in Maya-Morales 2016: fig. 30); from *Rothilena* by having the conduetor with two projections and by the absence of hoods on the atrium; from *Bajacalilena* gen. nov. by having the embolus slightly curved and by the shape of the epigynal plate, which has the median field clearly differentiated from the lateral lobes; and from *Callidalena* gen. nov. by having the conductor with two projections and the primary spermathecae not folded. *Cabolena* gen. nov. also differs from *Bajacalilena* gen. nov., *Callidalena* gen. nov., *Calilena*, *Hololena*, *Rualena*, and *Rothilena* by having three to four retromarginal teeth on the chelicerae. *Cabolena* gen. nov. differs from *Lagunella* gen. nov. by having the embolus short and slightly curved and by the shape of the epigynal plate, which has the median field clearly differentiated from the lateral lobes; from *Novalena* by having a ridge on the dorsal projection of the RTA and copulatory openings separated by less than their width; and from *Hoffmannilena* by having a dorsal projection on the RTA and by the absence of a strongly sclerotized epigynal plate.

Description.—Medium-sized spiders, 4–13 mm total length. Both eye rows strongly procurved in frontal view. Feathery scale-like setae present on carapace, opisthosoma, pedipalps, and legs. Carapace with two longitudinal symmetrical dark

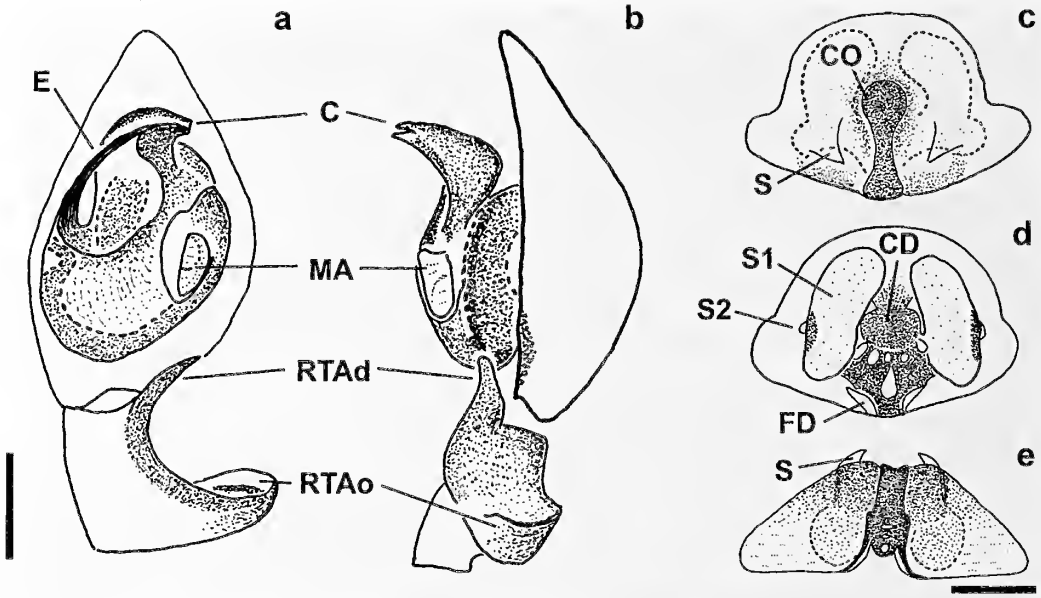

Figure 12.—*Cabolena huiztocatl* sp. nov., genitalia. a, b. Male pedipalp. c–e. Epigynum. a, c. Ventral view. b. Retrolateral view. d. Dorsal view. e. Posterior view. Abbreviations: C, conductor; CD, copulatory ducts; CO, copulatory openings; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S, spurs; S1, primary spermathecae; S2, secondary spermathecae. Scale bars = 0.25 mm.

bands intensified by feathery setae, a black band around the border of thoracic region, and a clear median band wider on cephalic region. Chelicerae with three promarginal teeth and three to four retromarginal teeth. Sternum longer than wide. Pedipalp femur with three dorsal spines. Legs with spines, longer in males than in females. Leg IV the longest. Rings present on femur, patella and tibia. Patella-tibia I longer than carapace in males and usually longer than carapace in females. Patella I and II with two dorsal spines and one prolateral spine, patella III and VI with two dorsal spines, one prolateral spine, and one retrolateral spine. Leg tarsi with five to seven trichobothria. Capsulate tarsal organ in distal position of trichobothrial row. Opisthosoma oval with dorsal foliate pattern and/or posterior chevrons. Colulus divided, represented by few hairs. PLS longest with distal segment usually as long as basal. Male pedipalp with short embolus originating at medium part of tibia length (Fig. 16a). Conductor with two projections (Fig. 11a). Median apophysis an elongated, spoon-shaped membrane (Fig. 14a). RTA covering the entire tibia length with distal and dorsal projections and a ridge (Fig. 15e). Tibia with prolaterodorsal protuberance. Epigynal plate wider than long (Fig. 12c) with median field of plate wider posteriorly and clearly differentiated from lateral lobes by epigynal folds or sutures (Fig. 16c). Anterolateral hyaline spurs present (Fig. 14c). Copulatory openings in central position of plate length (Fig. 14c). Copulatory ducts in ventral (Fig. 13d) or mesal (Fig. 11b) position in relation to primary spermathecae. Primary spermathecae longer than wide (Fig. 16d). Secondary spermathecae in diverticula (Fig. 15d). Fertilization ducts short (Fig. 13b).

Distribution.—*Cabolena* gen. nov. is distributed in Mexico in the State of Baja California Sur (Fig. 23b).

Included taxa.—Three species: C. *huiztocatl* sp. nov., *C. kosatli* sp. nov. and *C. sotol* sp. nov.

Cabolena huiztocatl Maya-Morales & Jiménez sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:64F8B9F5-F8F0-4D46-93FB-88E84CDA1B89
(Figs. 1a, c, e, 11, 12, 23b)

Type material.—*Holotype female*: Municipality of La Paz, Biosphere Reserve Sierra La Laguna, La Cieneguita, Baja California Sur, Mexico, 23°33′06.7″N, 109°59′07.3″W, 1761 m, hand collecting on ground, 4 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1876). *Paratypes*: MEXICO: *Baja California Sur*: 1 ♀, same data as holotype except Las Cascadas, 23°32′58″N, 109°58′55″W, 1748 m, 3 November 2006, M. Correa (CARCIB 2523); 1 ♂, same data as holotype except road to La Palma, 23°33′22.6″N, 109°58′43.5″W, 1818 m, beat sheet, 5 October 2011 (CARCIB 1886); 3 ♀, Municipality of La Paz, Punta San Pedro, 23°23′22.4″N, 110°12′30.2″W, 6 m, hand collecting, 7 February 2013, M.L. Jiménez, C. Palacios & J. Maya (CARCIB 32); 1 ♀, same data (CARCIB 3345); 2 ♀, same data (CARCIB 3611); 2 ♂, same data (CARCIB 3612); 1 ♀, same data except 18 January 2013 (CARCIB 3613); 1 ♀, same data except beat sheet, 28 August 2005, M. Correa (CARCIB 1893); 1 ♂, same data except 7 August 2005, C. Palacios (CARCIB 1903); 1 ♀, same data except 31 August 2005 (CARCIB 1895); 1 ♀, same data except 3 August 2005 (CARCIB 1899).

Other material examined.—MEXICO: *Baja California Sur*: 1 ♀, Municipality of La Paz, Punta San Pedro, 23°23′22.4″N, 110°12′30.2″W, 6 m, hand collecting, 7 February 2013, M.L. Jiménez, C. Palacios & J. Maya (CARCIB 41); 2 ♀, same data (CARCIB 44); 1 ♀, same data (CARCIB 3344); 1 ♀, same data (CARCIB 3420); 1 ♀, same data except beat sheet, 31 August 2005, C. Palacios (CARCIB 1894); 1 ♀, Biosphere Reserve Sierra La Laguna, Cerro Madroñito, 23°32′58″N, 109°58′55″W, beat sheet, 3 November 2006, C. Palacios (CARCIB 2522).

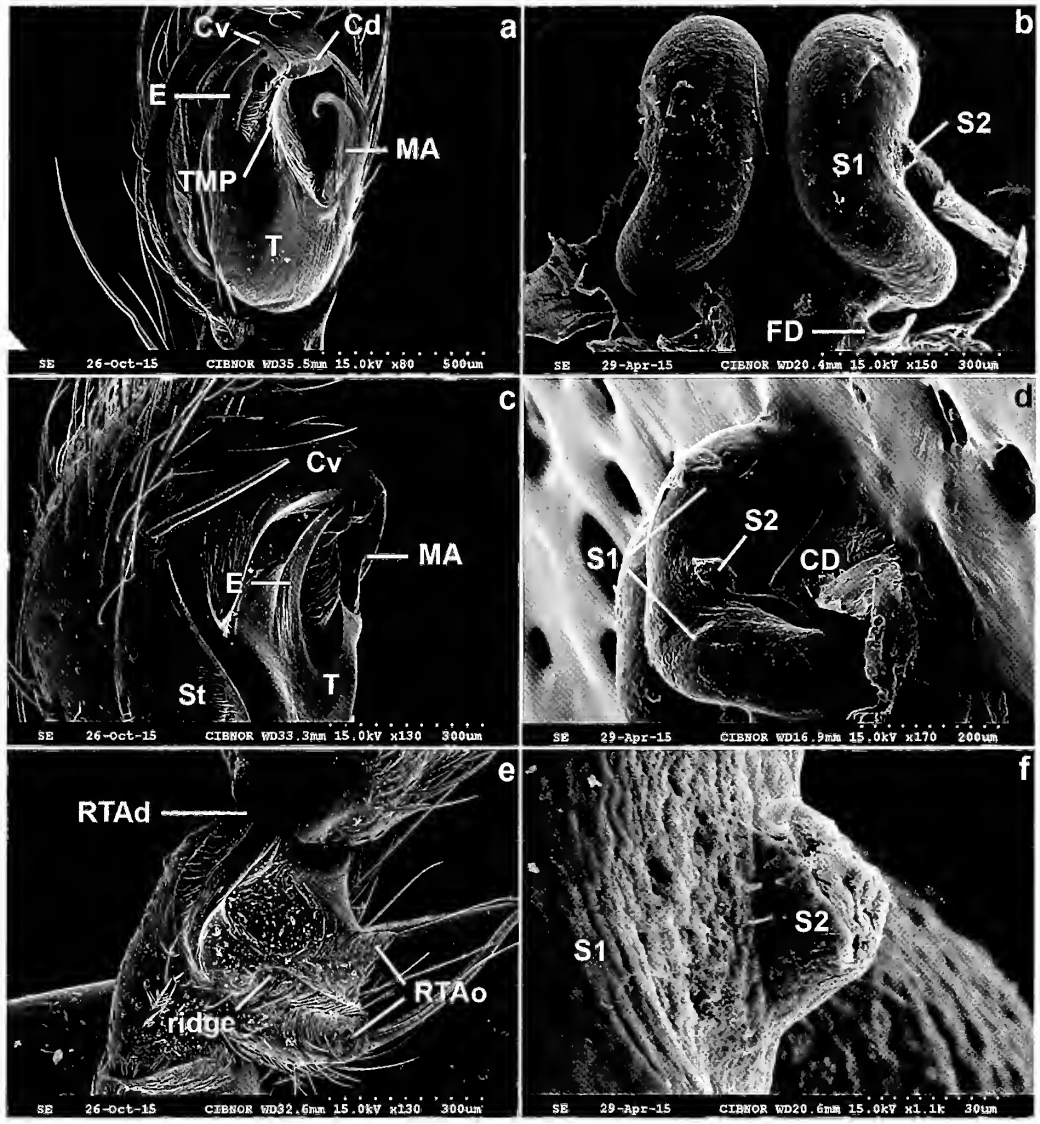

Figure 13.—*Cabolena kosatli* sp. nov., genitalia (SEM). a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: CD, copulatory ducts; Cd, dorsal projection of conductor; Cv, ventral projection of conductor; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; St, subtegulum; T, tegulum; TMP, tegular median process.

Etymology.—The specific name is the Náhuatl word "huiztocatl" which means "spider with spines".

Diagnosis.—Females of this species differ from *C. kosatli* and *C. sotol* by having the median plate of the epigynum strongly sclerotized (Fig. 12c) and by the copulatory ducts, which are clearly visible in dorsal view (Fig. 12d). Males differ from *C. kosatli* by having a conductor with the ventral projection longer than the dorsal one (Fig. 12a); and from *C. sotol* by having one spermophore coil visible through the tegulum (Fig. 12a).

Description.—Female (holotype): *Coloration:* Carapace yellow. Chelicerae and condyles brown. Endites yellow with white tips. Labium greyish with white tips. Sternum greyish with a yellow central band and three pairs of lateral spots. Legs yellow, patella-metatarsus brown. Three black rings on femur, one on patella, and two on tibia. Opisthosoma black, anterior reddish spot, six pairs of lateral yellow spots. ALS yellow with black border, PLS black, distal segment reddish.

Habitus: Total length 7. Carapace length 3.38, width 2.13, cephalic region width 1.15, ocular region width 0.7. Eye diameter: AME 0.12, ALE 0.17, PME and PLE 0.15. Distance between eyes: AME-AME 0.06, AME-ALE 0.06, AME-PME 0.13, ALE-PLE 0.06, ALE-ALE 0.29, PME-PME 0.1, PME-PLE 0.08. Clypeus height 0.17. Chelicerae with three retromarginal teeth; basal segment length 1.12, fang length 0.52. Labium wider than long (0.48/0.39). Endites convergent (distance at their base compared to their tips 0.48/0.21). Sternum longer than wide (1.48/1.19). Opisthosoma longer than wide (3.5/2.13). ALS separated by less than their basal diameter (0.12/0.3), PLS with distal segment as long as basal segment (0.36/0.36).

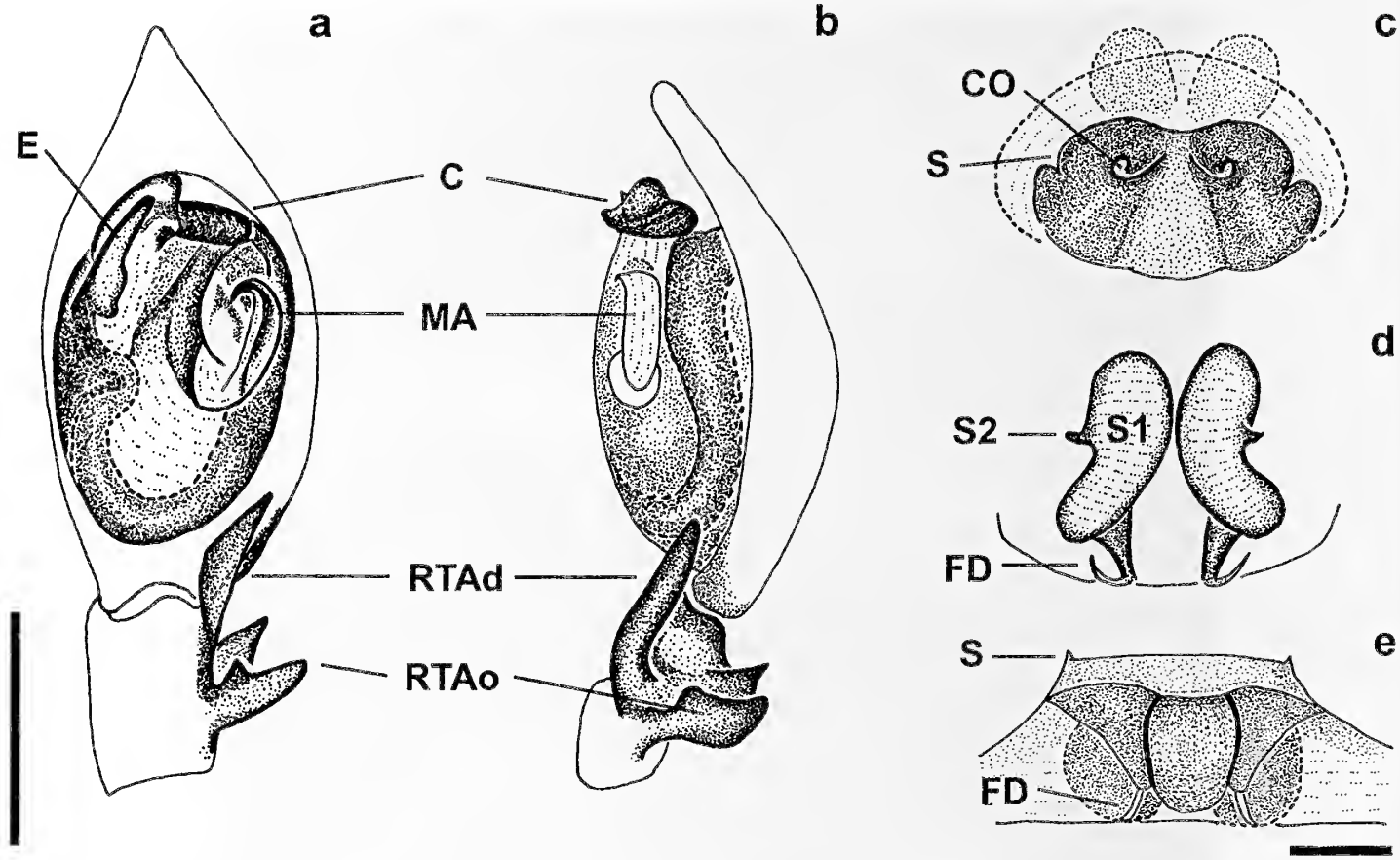

Figure 14.—*Cabolena kosatli* sp. nov., genitalia. a, b. Male pedipalp. c–e. Epigynum. a, c. Ventral view. b. Retrolateral view. d. Dorsal view. e. Posterior view. Abbreviations: C, conductor; CO, copulatory openings; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S, spurs; S1, primary spermathecae; S2, secondary spermathecae. Scale bars: a = 0.5 mm; e = 0.25 mm.

Legs: Length: I- femur 2.46/ patella-tibia 3.23/ metatarsus 2.31/ tarsus 1.46; II- 2.31/ 2.92/ 2.15/ 1.15; III- 2.3/ 2.92/ 2.46/ 1.15; IV- 3.08/ 3.77/ 3.46/ 1.69.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 1-1-0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-1-0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0; II- 0-0-1/ 2-2-2/ 0-1-1/ 0-1-0; III- 3-1-2/ 1-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 5, II- 6, III- 5, IV- 5.

Pedipalp: Dorsal spines on femur: 3. Prolateral spines on tibia: 1-2.

Epigynum: Plate length 0.67, width 0.85. Median plate strongly sclerotized. In posterior view, median plate uniformly wide. Copulatory ducts visible in dorsal view. Primary spermathecae uniformly wide and separated by their width (Figs. 11b, d, f, 12c–e).

Male (CARCIB 1903): *Coloration:* Similar to female, opisthosoma light brown with anterior brown spots and lateral white spots (Fig. 1c).

Habitus: Total length 5. Carapace length 2.38, width 1.88, cephalic region width 0.91, ocular region width 0.55. Eye diameter: AME and PME 0.1, ALE 0.12, PLE 0.13. Distance between eyes: AME-AME 0.04, AME-ALE 0.04, AME-PME 0.12, ALE-PLE 0.06, ALE-ALE 0.23, PME-PME 0.06, PME-PLE 0.1. Clypeus height 0.1. Chelicerae with three retromarginal teeth; basal segment length 0.91, fang length 0.39. Labium wider than long (0.36/0.27). Endites strongly convergent (distance at their base compared to their tips 0.36/0.06). Sternum longer than wide (1.52/1.1). Opisthosoma longer than wide (2.5/1.75). ALS separated by their basal diameter (0.21/ 0.21), PLS with distal segment as long as basal segment (0.3/ 0.3).

Legs: Length: I- femur 2.25/ patella-tibia 2.75/ metatarsus 1.88/ tarsus 1.5; II- 2.25/ 2.5/ 1.88/ 1.38; III- 1.88/ 2.25/ 2.25/ 1.13; IV- 2.5/ 3.13/ 3/ 1.5.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-0-0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0-1-1; II- 0/ 2-2-2/ 0-1-1/ 0-1-0; III- 2-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 6, II- 5, III- 5, IV- 6.

Pedipalp: Number of dorsal spines: femur 3, tibia 3. Cymbium length 0.88, width 0.55. Embolus uniformly slender. Conductor with ventral projection larger than dorsal one. One coil visible through the tegulum on mesal margin. RTA with dorsal projection flattened (Figs. 11a, c, e, 12a, b).

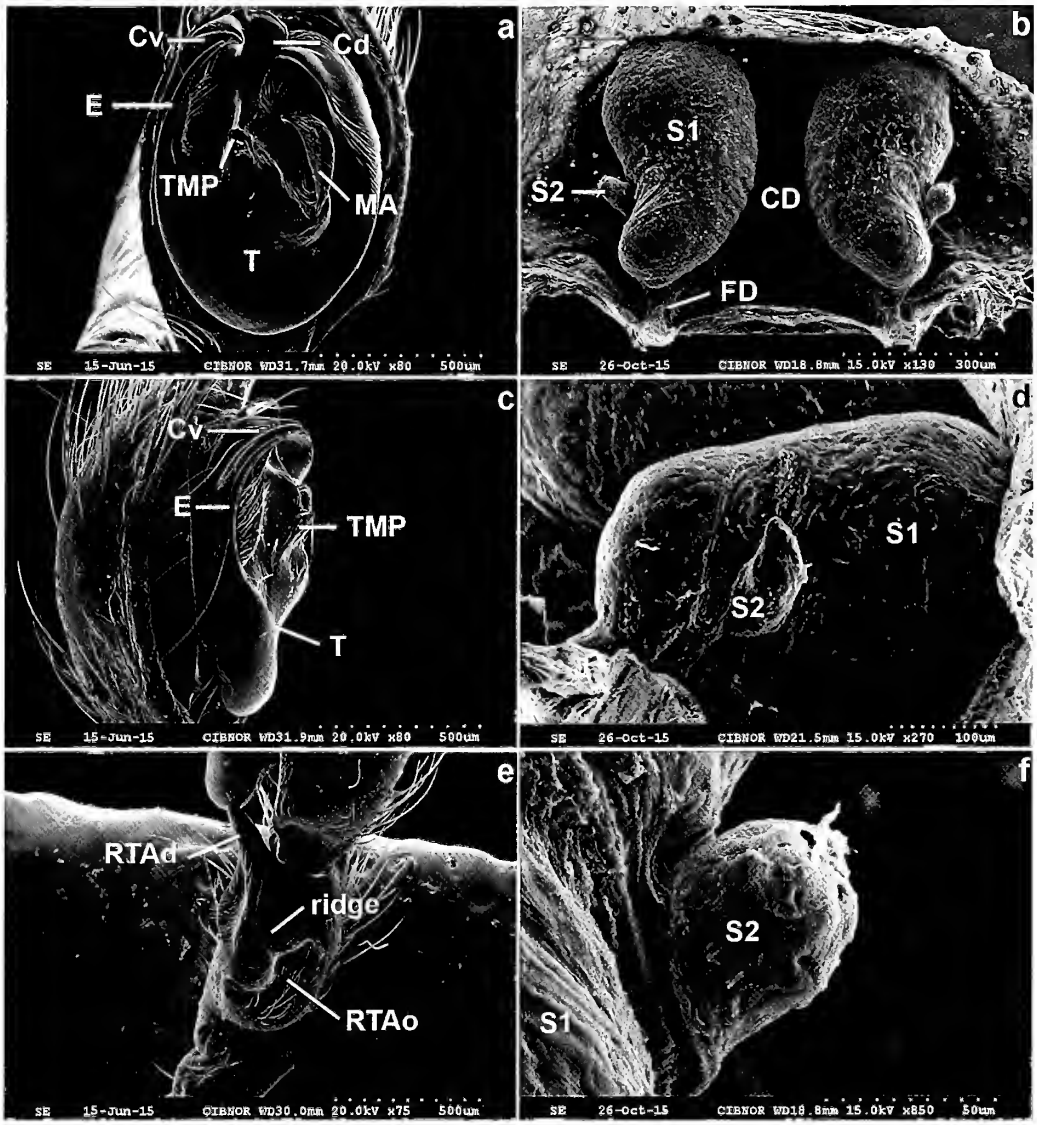

Figure 15.—*Cabolena sotol* sp. nov., genitalia (SEM). a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: CD, copulatory ducts; Cd, dorsal projection of conductor; Cv, ventral projection of conductor; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum; TMP, tegular median process.

Variation.—Total body length in males varies between 4.63 and 5.75 ($n = 4$) and in females between 4.88 and 7 ($n = 12$). Carapace length in males varies between 2.38 and 2.88 ($n = 4$) and in females between 2.5 and 3.38 ($n = 12$). Patella-tibia I length in males varies between 2.75 and 3.25 ($n = 4$) and in females between 2.38 and 3.25 ($n = 12$). One female paratype with four retromarignal teeth on chelicerae.

Natural history.—Seven adult females and two immature males from Punta San Pedro were kept under laboratory conditions for five months. Each female laid one to seven egg sacs. The males died two to three months after their last molt. As reported for *Agelenopsis aperta* (Gertsch, 1934) (Gering 1953; Becker et al. 2005), the male induces the female to a state of quiescence before they mate. In one mating observation, the male held the female with four legs on the same side of the pedipalp used to copulate (Fig. 1e). The pedipalp was constantly lubricated. The other pedipalp moved from top to bottom during lubrication. Fourteen minutes later, the pedipalp (and side) was changed. After 38 minutes of mating, the female recovered from the state of quiescence and the male and female separated quickly.

Habitat.—The specimens from Sierra La Laguna (1748–1818 m) were found in the understory and on the ground of the pine-oak forest dominated by *Pinus lagunae*, *Quercus tuberculata*, *Arbutus peninsularis*, and *Mimosa xanti* (Wiggins 1980; Rebman & Roberts 2012). The webs of spiders from the Punta San Pedro Oasis (6 m) were sighted from 0.5 to 4 m above the ground (Fig. 1a). The oasis is dominated by *Washingtonia robusta* and *Phoenix dactylifera* and is fed by a spring and separated from the sea by a broad beach and sand dunes (Llinas & Jiménez 2004).

Distribution.—Baja California Sur (Mexico) (Fig. 23b).

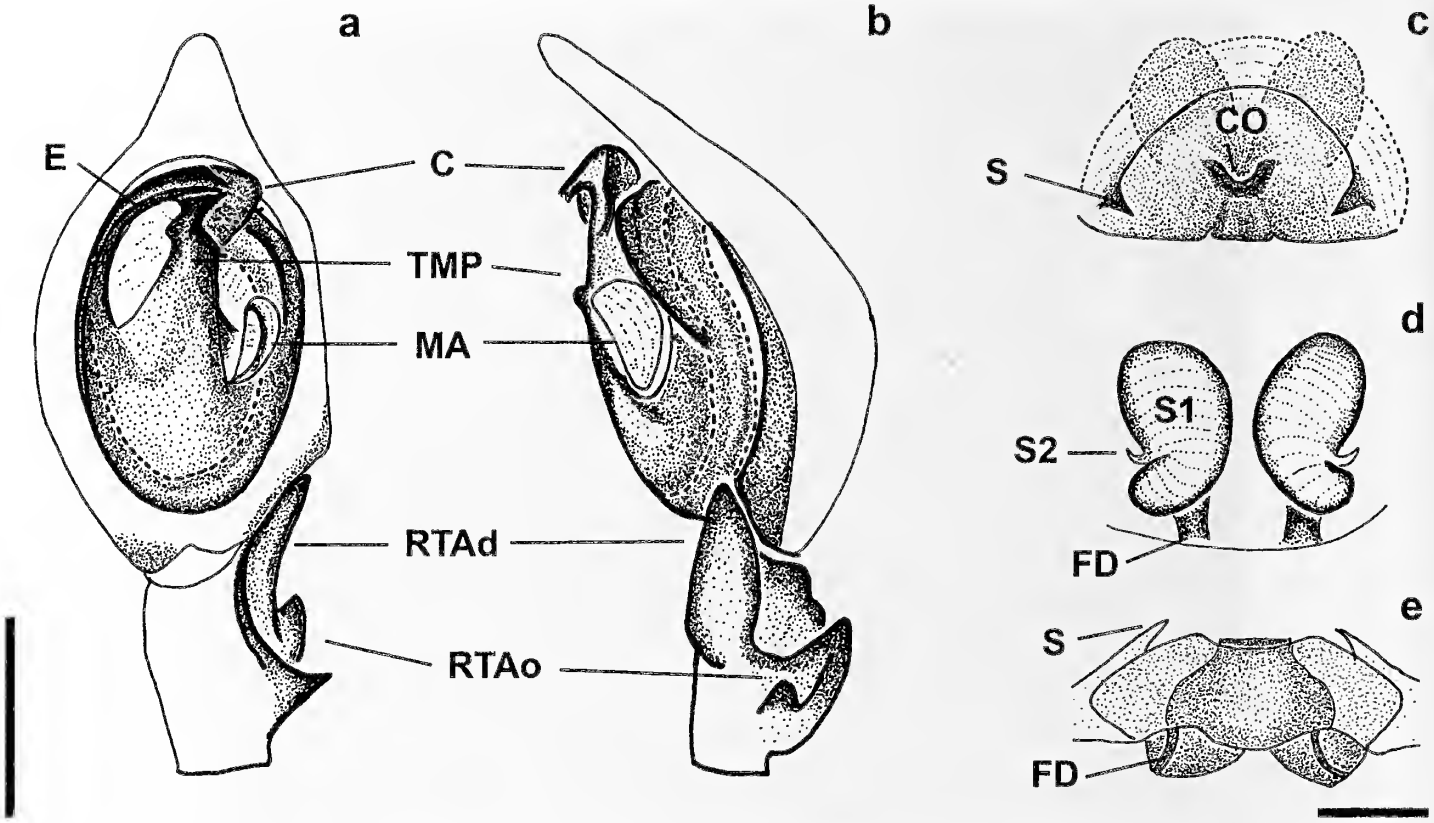

Figure 16.—*Cabolena sotol* sp. nov., genitalia. a, b. Male pedipalp. c–e. Epigynum. a, c. Ventral view. b. Retrolateral view. d. Dorsal view. e. Posterior view. Abbreviations: C, conductor; CO, copulatory openings; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S, spurs; S1, primary spermathecae; S2, secondary spermathecae; TMP, tegular median process. Scale bars: a = 0.5 mm; e = 0.35 mm.

Cabolena kosatli Maya-Morales, Jiménez & Palacios-Cardiel sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:217C9080-F457-4331-B393-2DC547BD3E33
(Figs. 13, 14, 23b)

Type material.—*Holotype female*: Municipality of La Paz, Biosphere Reserve Sierra La Laguna, road to Arroyo La Palma, Baja California Sur, Mexico, 23°33′22.6″N, 109°58′43.5″W, 1818 m, hand collecting on ground, 5 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1877). *Paratypes*: MEXICO: *Baja California Sur*: 1 ♀, same data as holotype except Cañón La Zorra, 1640 m, 3 July 1986, A. Cota (CARCIB 3); 1 ♂, 6 ♀, same data except 4 March 1986, F. & A. Cota (CARCIB 6); 1 ♂, 1 ♀, same data as holotype except Valle La Laguna, 1630 m, 30 September 1987, M.L. Jiménez (CARCIB 13); 1 ♂, same data except 19 April 1988 (CARCIB 17); 1 ♂, same data except 12 December 1986, F. Cota (CARCIB 3750); 1 ♂, same data except 25 February 1984 (CARCIB 3751); 1 ♀, same data except Mareh 1988 (CARCIB 3752); 1 ♀, same data as holotype except La Cieneguita, 23°33′06.7″N, 109°59′07.3″W, 1761 m, hand collecting on ground, 4 October 2011 (CARCIB 45); 1 ♂, same data (CARCIB 1878); 1 ♂, 1 ♀, same data except 1640 m, 1 November 1984, M.L. Jiménez (CARCIB 53); 2 ♂, 1 ♀, same data except 12 December 1986, A. Cota (CARCIB 1855); 1 ♀, same data as holotype except road to La Laguna, 23°33′06.8″N, 109°59′03.9″W, 1757 m, night collecting, 7 October 2011 (CARCIB 1874); 1 ♂, same data as holotype except Las Cascadas, 23°33′58″N, 109°58′05″W, 1748 m, hand collecting on ground, 3 November 2006, M. Correa (CARCIB 2520);

Other material examined.—MEXICO: *Baja California Sur*: 4 ♀, same data as holotype (CARCIB 46); 1 ♀, same data as holotype (CARCIB 1896); 1 ♀, same data as holotype except Cañón La Zorra, 1640 m, 28 September 1988, A. & F. Cota (CARCIB 1); 1 ♀, same data except M.L. Jiménez & A. Cota (CARCIB 2); 1 ♂, 2 ♀, same data except 13 January 1986, M.L. Jiménez (CARCIB 7); 1 ♀, same data except 25 February 1987, M. Acevedo & M.L. Jiménez (CARCIB 49); 1 ♂, same data except 19 August 1986, collectors unknown (CARCIB 1867); 4 ♀, same data as holotype except Valle La Laguna, 20 April 1988, M.L. Jiménez & S. Guzmán (CARCIB 8); 1 ♀, same data except 20 April 1988, M.L. Jiménez (CARCIB 12); 12 ♀, same data exeept 1630 m, 16 January 1988, V. Roth & M.L. Jiménez (CARCIB 14); 1 ♀, same data (CARCIB 3343); 1 ♂, same data except M.L. Jiménez (CARCIB 55); 2 ♀, same data except 12 December 1986, A. Cota (CARCIB 1852); 1 ♀, same data except 10 May 1985 (CARCIB 1853); 2 ♀, same data as holotype except Cañón La Burrera, 11 December 1986, M. Aeevedo (CARCIB 18); 1 ♀, same data (CARCIB 20); 1♀, same data as holotype except Palo Extraño, 21 April 1988, M.L. Jiménez & D. Domínguez

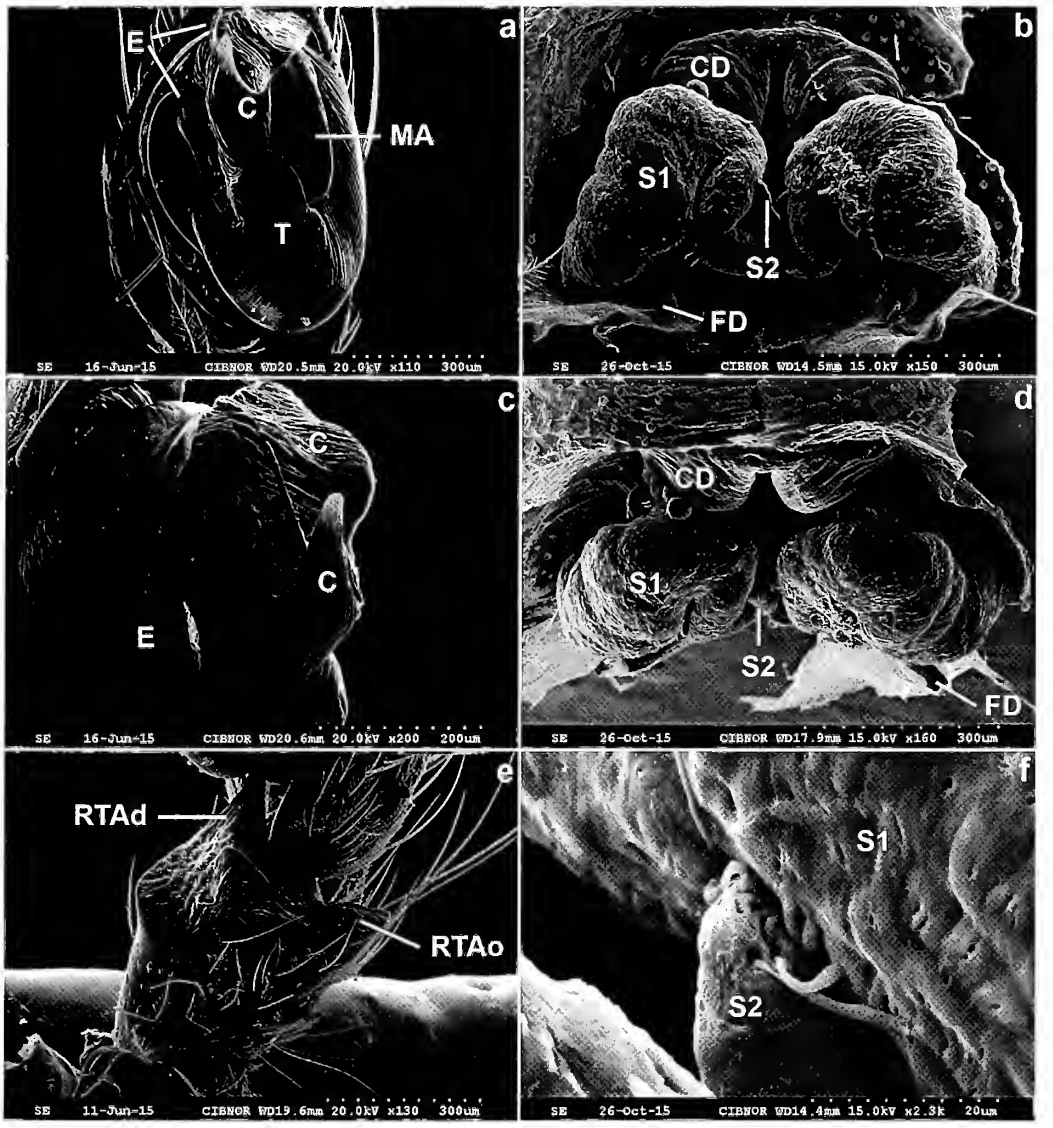

Figure 17.—*Callidalena quintin* sp. nov., genitalia (SEM). a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: CD, copulatory ducts; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum.

(CARCIB 52); 4 ♀, same data except 14 May 1986, F. Cota (CARCIB 11); 2 ♀, same data as holotype exeept Las Cascadas, 23°32′56.9″N, 109°58′07.6″W, 1734 m, 8 October 2011 (CARCIB 1879); 1 ♀, same data as holotype except Arroyo La Cieneguita, 23°33′02″N, 109°56′26.8″W, 1758 m, 7 October 2011 (CARCIB 1888); 2 ♀, same data except 19 April 1988, M.L. Jiménez (CARCIB 16); 1 ♀, same data as holotype except Arroyo La Palma, 23°34′24.8″N, 109°58′27″W, 1798 m, 6 October 2011 (CARCIB 1890).

Etymology.—The specific name is the Náhuatl word "kosatli" which means "vixen" ("zorra" in Spanish, the name of the canyon in the Sierra La Laguna where the species was found).

Diagnosis.—Females of *C. kosatli* differ from *C. huiztocatl* and *C. sotol* by having the copulatory openings easily distinguishable (Fig. 14c). Males differ from *C. huiztocatl* by having a conductor with the projections of similar size (Fig. 13a) and from *C. sotol* by having one spermophore coil visible through the tegulum (Fig. 14a).

Description.—Female (holotype): *Coloration:* Carapace yellow. Chelicerae brown. Condyles light brown. Endites orange with white tips. Labium light brown with white tip. Sternum yellow with black lateral lines. Femur yellow, patella-tarsus light brown. Three rings on femur, one on patella, and two on tibia. Opisthosoma brown, anterior reddish spot, two lateral white lines, four arrowhead shaped spots, several pairs of black spots, and one pair of white spots next to anal tubercle. Spinnerets yellow, basal segment of PLS with black spots.

Habitus: Total length 5.88. Carapace length 2.75, width 1.88, cephalic region width 1.12, ocular region width 0.61. Eye diameter: AME 0.1, ALE, PME and PLE 0.13. Distance between eyes: AME-AME 0.04, AME-ALE 0.06, AME-PME 0.13, ALE-PLE 0.04, ALE-ALE 0.23, PME-PME 0.08, PME-PLE 0.06. Clypeus height 0.19. Chelicerae with three retro-

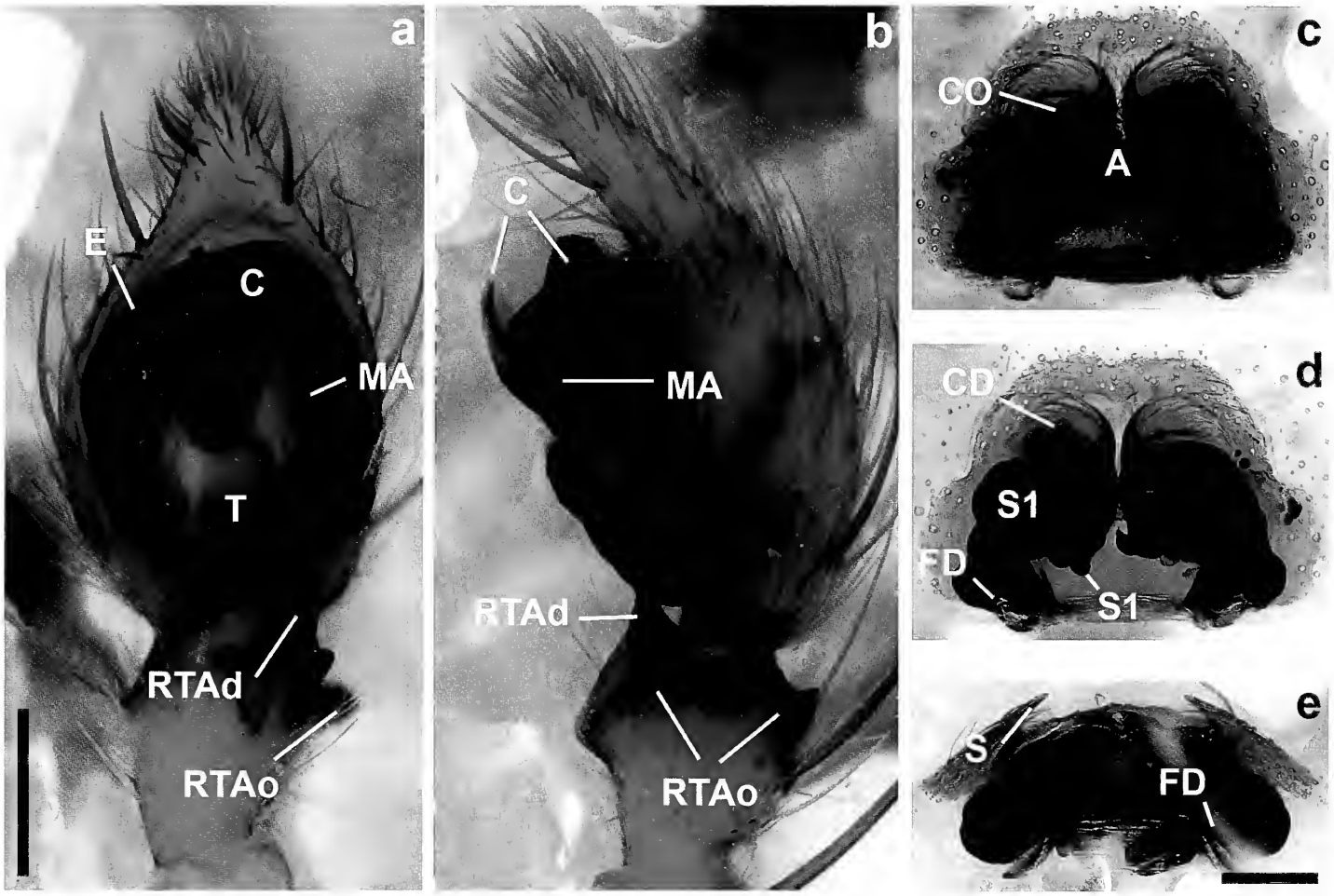

Figure 18.—*Callidalena quintin* sp. nov., genitalia. a, b. Male pedipalp. c–e. Epigynum. a, c. Ventral view; b. Retrolateral view. d. Dorsal view. e. Posterior view. Abbreviations: C, conductor; CO, copulatory openings; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S, spurs; S1, primary spermathecae; S2, secondary spermathecae. Scale bars: a = 0.25 mm; e = 0.2 mm.

marginal teeth; basal segment length 1.1, fang length 0.45. Labium wider than long (0.45/0.36). Endites slightly convergent (distance at their base compared to their tips 0.45/0.3). Sternum longer than wide (1.45/1.18). Opisthosoma longer than wide (3.13/2.25). ALS separated by less than their basal diameter (0.21/0.27), PLS with distal segment slightly longer than basal segment (0.52/0.48).

Legs: Length: I- femur 2.38/ patella-tibia 3.13/ metatarsus 2.13/ tarsus 1.5; II- 2.25/ 2.63/ 2/ 1.38; III- 2.25/ 2.75/ 2.38/ 1.25; IV- 2.88/ 3.75/ 3.13/ 1.63.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-0-0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-1-1-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0-0-1; II- 0/ 2-2-2/ 0-1-0/ 0-1-1; III- 2-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 2-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 6, II- 5, III- 5, IV- 6.

Pedipalp: Dorsal spines on femur: 3. Prolateral spines on tibia: 1-2.

Epigynum: Plate length 0.61, width 0.88. In posterior view, median plate uniformly wide. Copulatory openings separated by less than their width. L-shaped primary spermathecae separated by less than their width (Figs. 13b, d, f, 14c–d).

Male (paratype) (CARCIB 6): *Coloration:* Yellow, opisthosoma with several light brown spots.

Habitus: Total length 6.88. Carapace length 3.38, width 2.5, cephalic region width 1.21, ocular region width 0.67. Eye diameter: AME, PME and PLE 0.12, ALE 0.13. Distance between eyes: AME-AME 0.04, AME-ALE 0.08, AME-PME 0.19, ALE-PLE 0.06, ALE-ALE 0.25, PME-PME 0.1, PME-PLE 0.1. Clypeus height 0.23. Chelicerae with three retromarginal teeth; basal segment length 1.3, fang length 0.55. Labium wider than long (0.45/0.39). Endites slightly convergent (distance at their base compared to their tips 0.45/0.33). Sternum longer than wide (1.67/1.42). Opisthosoma longer than wide (3.5/1.88). ALS separated by less than their basal diameter (0.21/0.27), PLS with distal segment as long as basal segment (0.45/0.45).

Legs: Length: I- femur 3.13/ patella-tibia 3.75/ metatarsus 3.13/ tarsus 2.13; II- 3.13/ 3.63/ 3.63/ 1.75; III- 3.13/ 3.75/ 3.63/ 1.88; IV- 3.75/ 4.25/ 4.88/ 2.25.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/

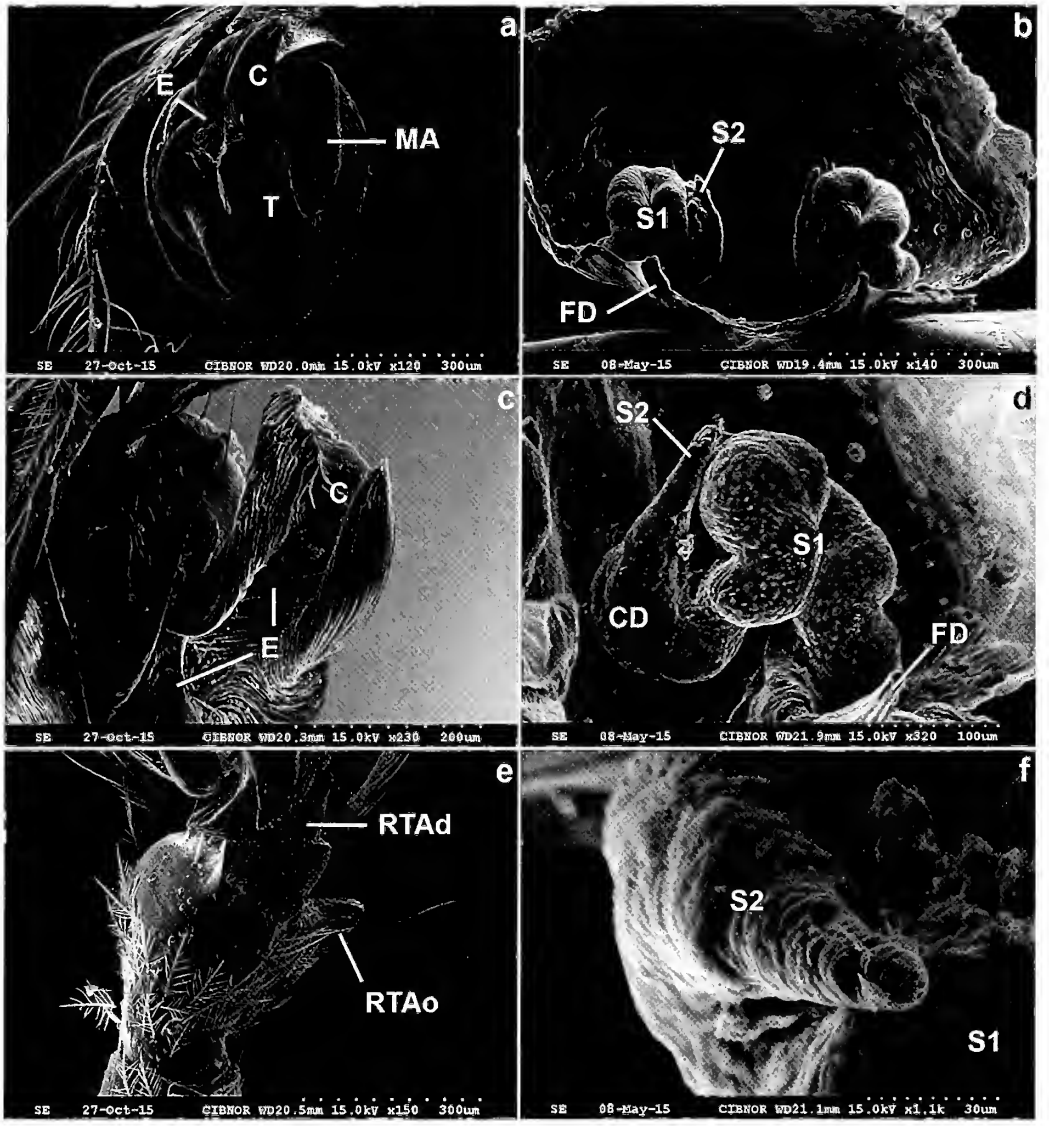

Figure 19.—*Callidalena tijuana* sp. nov., genitalia (SEM). a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: CD, copulatory ducts; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; T, tegulum.

0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 1-1-0; II- 0/ 1-2-2/ 1-1-0/ 1-1-0; III- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-1-1-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-0/ 0-1-1; II- 1-2-0/ 2-2-2/ 0-1-0/ 0-1-1; III- 3-2-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 2-1-2-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 6, II- 6, III- 6, IV- 5.

Pedipalp: Number of dorsal spines: femur 3, tibia 3. Cymbium length 1.24, width 0.7. Embolus with stout base. Conductor with projections of similar size. One coil visible through the tegulum on mesal margin. RTA with two subprocesses on dorsal projection (Figs. 13a, c, e, 14a, b).

Variation.—Total body length in males varies between 5.63 and 6.88 ($n = 8$) and in females between 5.38 and 8.75 ($n = 18$). Carapace length in males varies between 2.75 and 4 ($n = 9$) and in females between 2.63 and 4.38 ($n = 18$). Patella-tibia I length in males varies between 3.38 and 4.38 ($n = 9$) and in females between 2.5 and 4.25 ($n = 18$). Specimens with a central band and three pairs of yellow spots on sternum.

Distribution.—Baja California Sur (Mexico) (Fig. 23b).

Cabolena sotol Maya-Morales, Jiménez & Palacios-Cardiel sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:A1962DE3-F6A0-46B9-9D72-AB7D35AA16FC
(Figs. 15, 16, 23b)

Type material.—*Holotype female*: Municipality of La Paz, Biosphere Reserve Sierra La Laguna, Cañón La Zorra, Baja California Sur, Mexico, 1640 m, 13 January 1988, V. Roth (CARCIB 36). *Paratypes*: MEXICO: *Baja California Sur*: 3 ♀, same data as holotype (CARCIB 22); 1 ♀, same data as holotype (CARCIB 3755); 3 ♂, same data as holotype except 10 May 1986, M.L. Jiménez (CARCIB 5); 1 ♂, same data except 12 February 1986 (CARCIB 1860); 1 ♂, same data

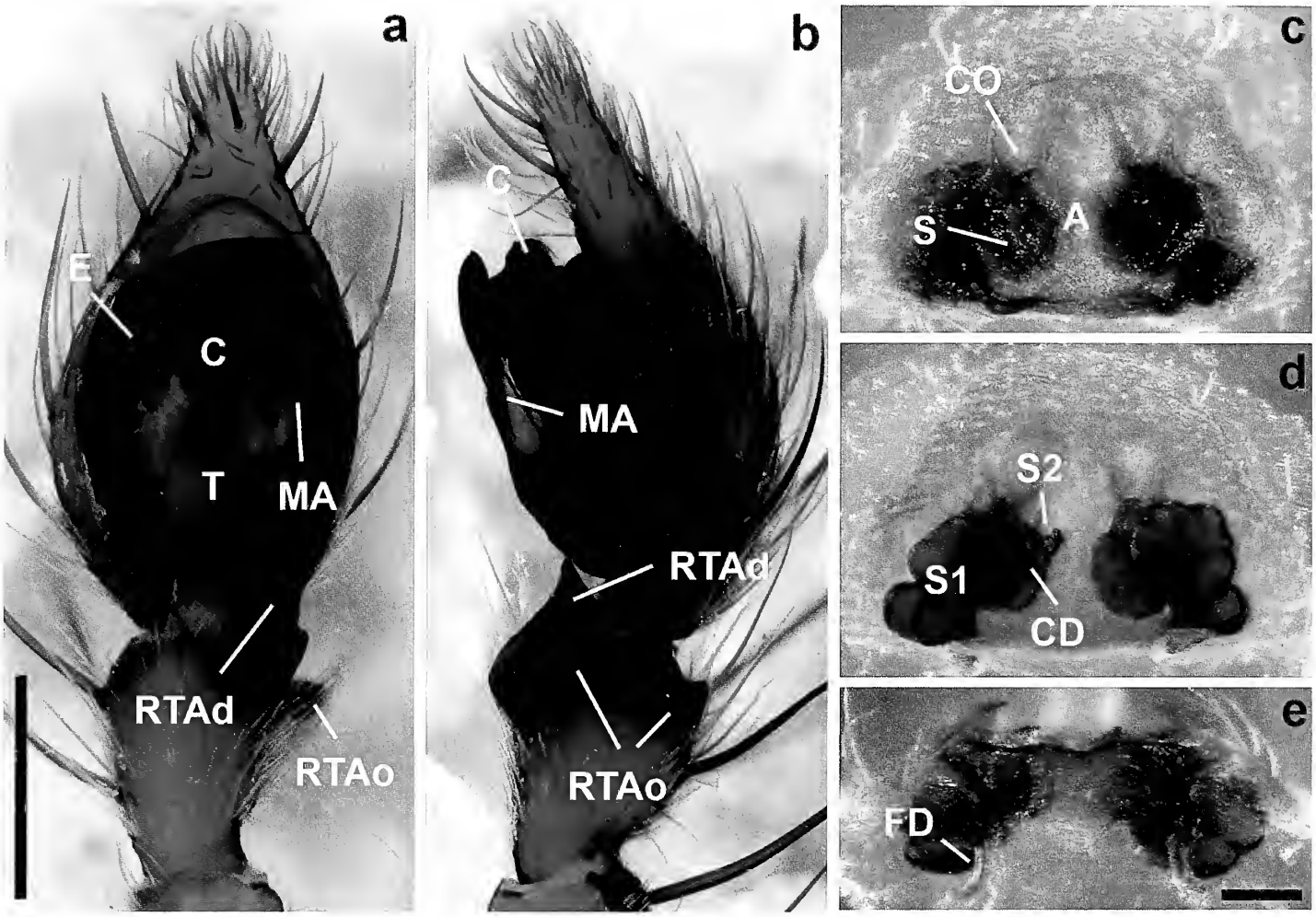

Figure 20.—*Callidalena tijuana* sp. nov., genitalia. a, b. Male pedipalp. c–e. Epigynum. a, c. Ventral view. b. Retrolateral view. d. Dorsal view. e. Posterior view. Abbreviations: C, conductor; CO, copulatory openings; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S, spurs; S1, primary spermathecae; S2, secondary spermathecae. Scale bars: a = 0.5 mm; e = 0.15 mm.

except F. Cota (CARCIB 3753); 1 ♂, same data as holotype except 15 January 1988, V. Roth & M.L. Jiménez (CARCIB 23); 1 ♂, 2 ♀, same data as holotype except 25 February 1984, F. Cota & M.L. Jiménez (CARCIB 38); 1 ♂, same data except F. Cota (CARCIB 3754);1♂, same data as holotype except 12 December 1986, M. Acevedo (CARCIB 1862); 1 ♀, same data as holotype except Valle La Laguna, 1830 m, 20 April 1988, M.L. Jiménez & R. Domínguez (CARCIB 1868); 1 ♀, same data as holotype except Las Cascadas, 23°32′56.9″N, 109°58′07.6″W, 1734 m, hand collecting on ground, 8 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1881); 1 ♀, same data as holotype except Arroyo La Palma, 23°34′24.8″N, 109°58′27″W, 1798 m, hand collecting on ground, 6 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1883); 3 ♂, same data as holotype except Palo Extraño, 14 April 1986, A. & F. Cota (CARCIB 25).

Other material examined.—MEXICO: *Baja California Sur*: 2 ♀, same data as holotype except 12 December 1986, A. Acevedo (CARCIB 26); 1 ♀, same data except 4 March 1986, F. & A. Cota (CARCIB 30); 1 ♀, same data except 12 April 1986, M.L. Jiménez (CARCIB 33); 1 ♀, same data except 3 July 1986, A. Cota (CARCIB 35); 2 ♀, same data as holotype except Palo Extraño, 1840 m, 13 January 1988, F. Cota (CARCIB 10); 1 ♀, same data except 21 March 1988, A. & F. Cota (CARCIB 31); 1 ♂, 3 ♀, same data except 1640 m, 13 January 1988, V. Roth (CARCIB 37); 2 ♂, 1 ♀, same data as holotype except Paso La Golondrina, 13 January 1987, V. Roth & M.L. Jiménez (CARCIB 15); 2 ♀, same data as holotype except Valle La Laguna, 6 June 1988, A. Cota (CARCIB 21); 1 ♀, same data except 27 September 1987, F. Cota (CARCIB 1856); 3 ♀, same data except 13 January 1984, V. Roth (CARCIB 1857); 1 ♀, same data except 1630 m, 29 September 1987, A. Cota & M.L. Jiménez (CARCIB 29); 1 ♀, same data as holotype except Arroyo La Palma, 1640 m, 11 December 1986, A. Acevedo (CARCIB 1866); 1 ♀, same data as holotype except road to La Palma, 23°33′22.6″N, 109°58′43.5″W, 1818 m, beat sheet, 5 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1884); 1 ♀, same data (CARCIB 1902); 1 ♀, same data (CARCIB 1910); 1 ♀, same data as holotype except Cerro Madroñito, 23°32′58″N, 109°58′05″W, 1812 m, 3 November 2006, C. Palacios (CARCIB 2521).

Etymology.—The specific name refers to the "sotol" plant (*Nolina beldingii*), where the species was found.

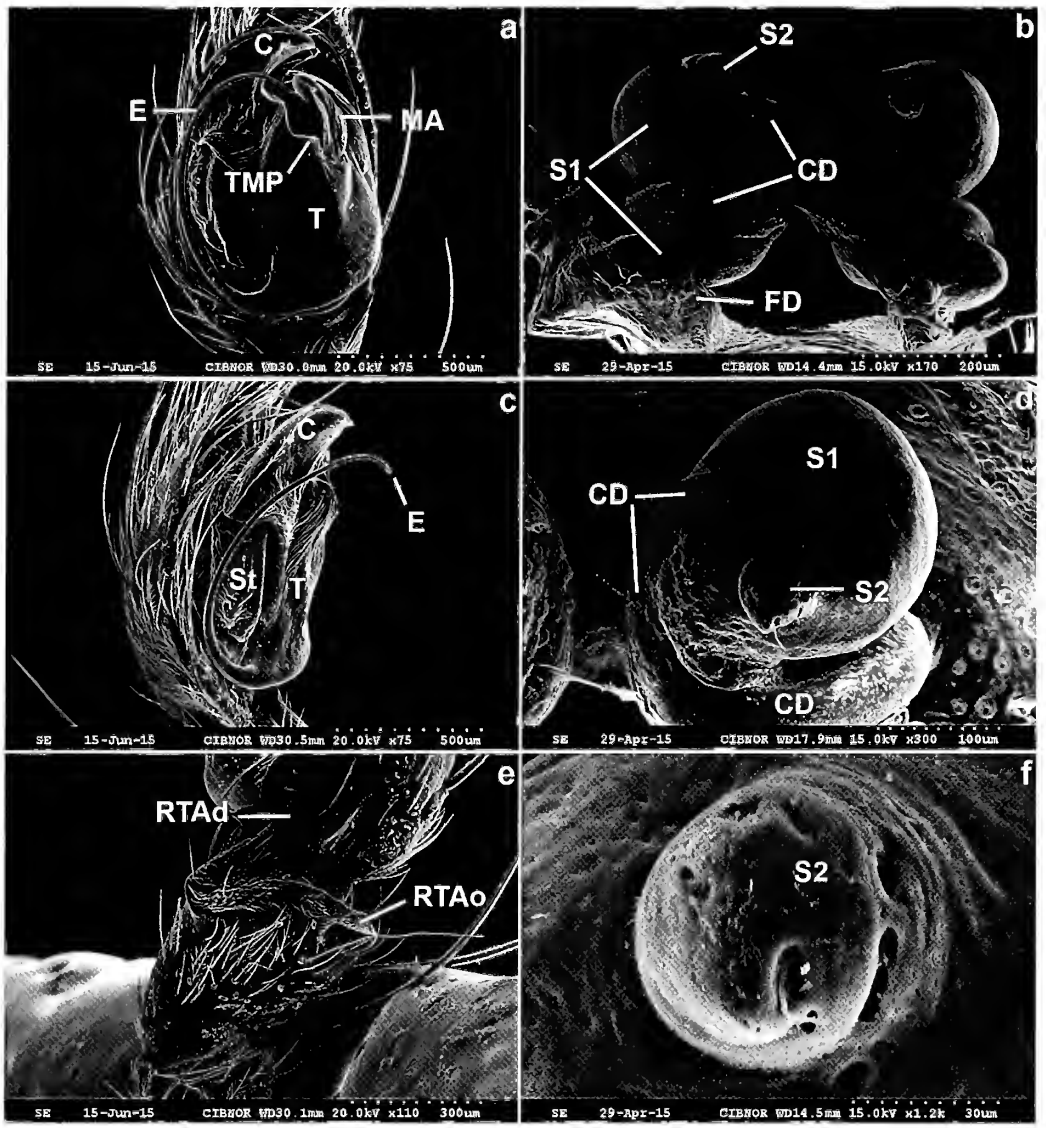

Figure 21.—*Lagunella guaycura* sp. nov., genitalia (SEM). a, c, e. Male pedipalp. b, d, f. Epigynum. Abbreviations: C, conductor; CD, copulatory ducts; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S1, primary spermathecae; S2, secondary spermathecae; St, subtegulum; T, tegulum; TMP, tegular median process.

Diagnosis.—Females of this species differ from *C. huiztocatl* by having the median plate of the epigynum wider and less sclerotized (Fig. 16c); and from *C. kosatli* by having smaller copulatory openings which are not visible in ventral view (Fig. 16c) and bean-shaped primary spermathecae with the anterior part wider than the posterior part (Fig. 16d). Males differ from *C. huiztocatl* and *C. kosatli* by the absence of any visible spermophore coils through the tegulum (Fig. 16a).

Description.—Female (holotype): *Coloration:* Carapace yellow, cephalic region brown, with white feathery scale-like setae. Chelicerae dark brown. Condyles orange. Endites and labium brown with white tips. Sternum yellow. Legs yellow, tibia-metatarsus I–II brown. Opisthosoma light brown with an anterior reddish spot and several lateral brown spots. Spinnerets yellow.

Habitus: Total length 10. Carapace length 4.5, width 3.63, cephalic region width 1.86, ocular region width 0.81. Eye diameter: AME 0.15, ALE 0.19, PME 0.13, PLE 0.17. Distance between eyes: AME-AME 0.08, AME-ALE 0.08, AME-PME 0.19, ALE-PLE 0.06, ALE-ALE 0.33, PME-PME 0.12, PME-PLE 0.13. Clypeus height 0.27. Chelicerae with three retromarginal teeth; basal segment length 1.67, fang length 0.62. Labium as long as wide (0.62/0.62). Endites slightly convergent (distance at their base compared to their tips 0.62/0.38). Sternum longer than wide (2.14/1.81). Opisthosoma longer than wide (5/3.13). ALS separated by less than their basal diameter (0.27/0.36), PLS with distal segment as long as basal segment (0.36/0.36).

Legs: Length: I- femur 3.5/ patella-tibia 4.38/ metatarsus 3.25/ tarsus 2.13; II- 3.38/ 4.13/ 3.13/ 1.88; III- 3.38/ 4.13/ 3.5/ 1.5; IV- 4.13/ 5.38/ 5/ 2.13.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 0/ 2-2-2/ 1-1-0/ 1-0-0; III- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0;

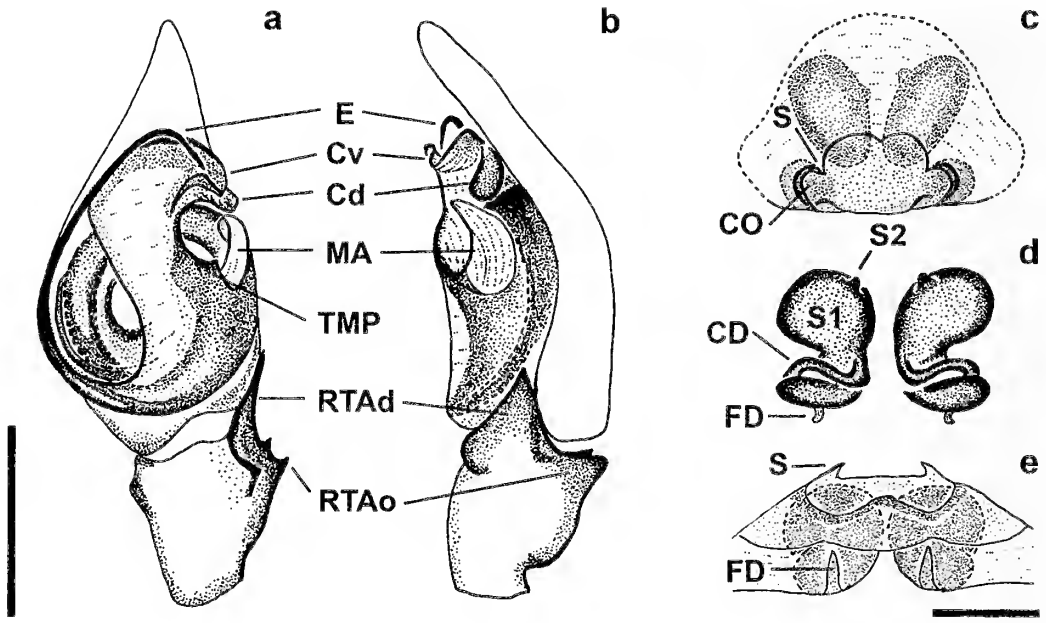

Figure 22.—*Lagunella guaycura* sp. nov., genitalia. a, b. Male pedipalp. c–e. Epigynum. a, c. Ventral view. b. Retrolateral view. d. Dorsal view. e. Posterior view. Abbreviations: CD, copulatory ducts; Cd, dorsal projection of conductor; CO, copulatory openings; Cv, ventral projection of conductor; E, embolus; FD, fertilization ducts; MA, median apophysis; RTAd, distal projection of RTA; RTAo, dorsal projection of RTA; S, spurs; S1, primary spermathecae; S2, secondary spermathecae; TMP, tegular median process. Scale bars: a = 0.5 mm; e = 0.35 mm.

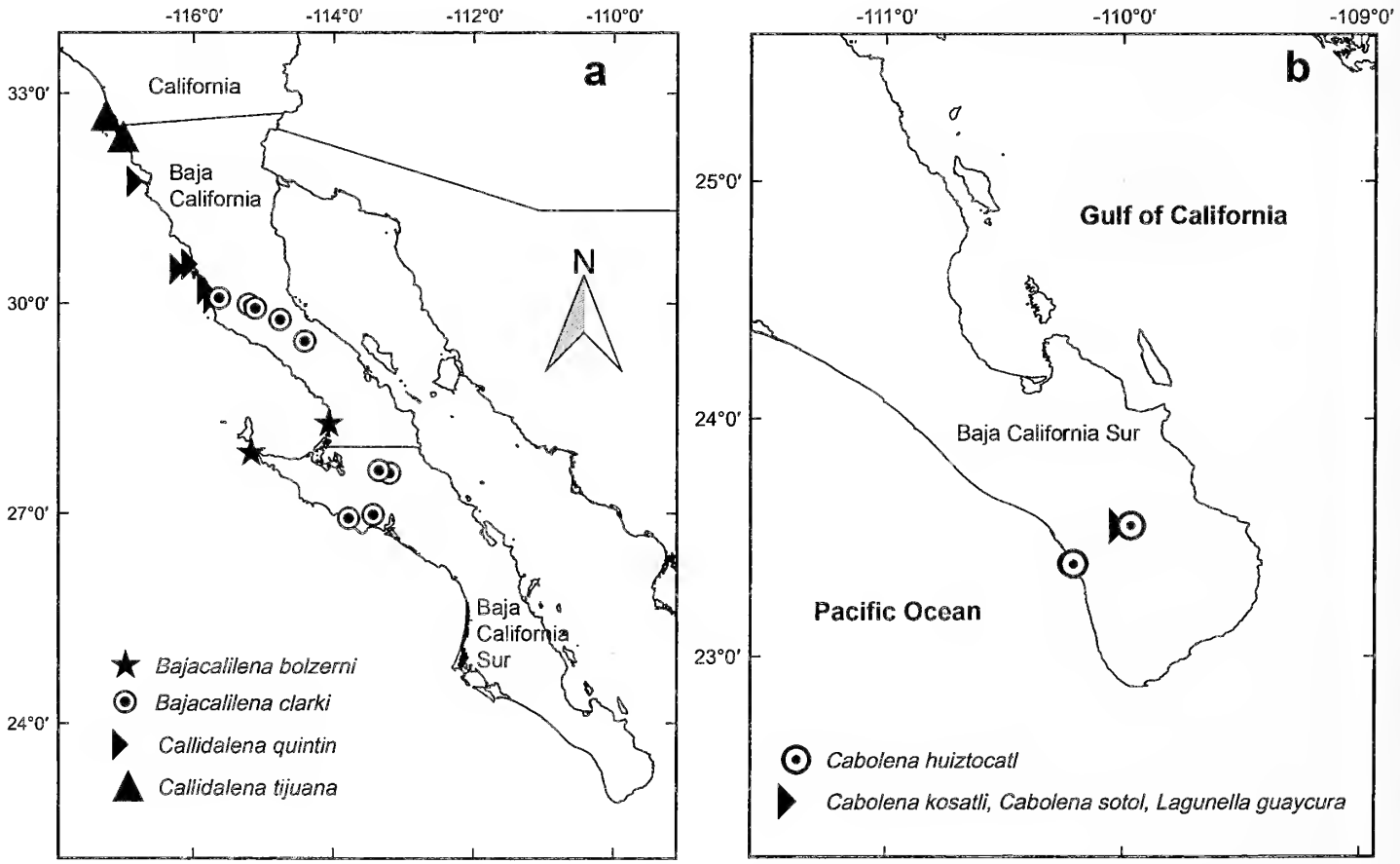

Figure 23.—a. Map showing distribution of *Bajacalilena bolzerni* sp. nov., *B. clarki* sp. nov., *Callidalena quintin* sp. nov. and *C. tijuana* sp. nov. b. Map showing distribution of *Cabolena huiztocatl* sp. nov., *C. kosatli* sp. nov., *C. sotol* sp. nov. and *Lagunella guaycura* sp. nov.

metatarsus I- 0/ 2-2-2/ 0-1-0/ 0-0-1; II- 0/ 2-2-2/ 0-1-1/ 0-1-1; III- 3-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-2-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 7, II- 7, III- 7, IV- 7.

Pedipalp: Dorsal spines on femur: 3. Prolateral spines on tibia: 1-2.

Epigynum: Plate length 0.67, width 1.09. In posterior view, median plate narrower toward ventral margin. Copulatory openings as small holes visible in anterior view. Bean-shaped primary spermathecae, wider at anterior part, and separated by less than their width (Figs. 15b, d, f, 16c–e).

Male (paratype from holotype locality) (CARCIB 5): *Coloration:* Carapace yellow, cephalic region brown. Chelicerae brown. Condyles orange. Endites and labium light brown with white tips. Sternum yellow. Femur yellow, patella-tarsus orange. Opisthosoma similar to female, spots darker. Spinnerets yellow, basal segment of PLS with black spots.

Habitus: Total length 7.38. Carapace length 4.25, width 2.5, cephalic region width 1.27, ocular region width 0.76. Eye diameter: AME 0.13, ALE 0.21, PME and PLE 0.19. Distance between eyes: AME-AME 0.06, AME-ALE 0.06, AME-PME 0.17, ALE-PLE 0.04, ALE-ALE 0.31, PME-PME 0.08, PME-PLE 0.08. Clypeus height 0.25. Chelicerae with three retromarginal teeth; basal segment length 1.42, fang length 0.64. Labium slightly longer than wide (0.52/0.48). Endites slightly convergent (distance at their base compared to their tips 0.48/0.29). Sternum longer than wide (2/1.48). Opisthosoma longer than wide (3.75/2). ALS separated by their basal diameter (0.24/0.24), PLS with distal segment slightly shorter than basal segment (0.42/0.45).

Legs: Length: I- femur 3.5/ patella-tibia 4.38/ metatarsus 3.5/ tarsus 2.5; II- 3.5/ 3.88/ 3.5/ 2.13; III- 3.5/ 4.25/ 3.63/ 2.25; IV- 4.38/ 5.38/ 5.5/ 2.5.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0-1-1; II- 0/ 1-2-2/ 1-1-0/ 1-1-0; III- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0-1-1; II- 0/ 2-2-2/ 0-1-1/ 0-1-1; III- 3-2-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-2-2/ 2-1-1-2/ 0-1-1/ 0-0-1. Number of trichobothria on tarsus: I- 6, II- 6, III- 5, IV- 5.

Pedipalp: Number of dorsal spines: femur 3, tibia 4. Cymbium length 1.33, width 0.76. Embolus uniformly slender. Conductor with dorsal projection slightly longer than ventral one. Tegular median process present. RTA with two subprocesses on dorsal projection (Figs. 15a, c, e, 16a, b).

Variation.—Total body length in males varies between 6.63 and 8.75 ($n = 10$) and in females between 7.5 and 12.13 ($n = 10$). Carapace length in males varies between 3.13 and 4.5 ($n = 10$) and in females between 3.38 and 5.13 ($n = 10$). Patella-tibia I length in males varies between 3.88 and 5.38 ($n = 10$) and in females between 3.63 and 5.13 ($n = 10$). Some paratypes with four retromarginal teeth on chelicerae.

Distribution.—Baja California Sur (Mexico) (Fig. 23b).

Callidalena Maya-Morales & Jiménez gen. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:BDD8A68E-C793-4169-AA0B-28DE3332BCB1

Type species.—*Callidalena quintin* sp. nov.

Etymology.—The generic name is derived from Latin "*Callida*" which means "hot" and is part of the origin of the word California. The gender is feminine.

Diagnosis.—*Callidalena* gen. nov. is diagnosed by the following characters in combination: male pedipalp with the embolus sinuous and supported by a folded conductor which has a deep ventral notch (Figs. 18a, 20a); and RTA confined to the distal part of the tibia and composed of two projections, one distal and one lateral across the tibia (Figs. 17e, 20b). Epigynum with an inverse T-shaped appearance in ventral view (Fig. 18c); spurs in a lateral position (Fig. 20c); copulatory openings at anterior position of plate (Fig. 20c); copulatory ducts short (Fig. 19d) and ventrally position relative to the folded primary spermathecae (Figs. 17b, 19b); and secondary spermathecae in diverticula (Figs. 17f, 19d).

Callidalena gen. nov. differs from *Eratigena* and *Tegenaria* by having strongly procurved eye rows in frontal view; from *Agelenopsis*, *Barronopsis*, *Melpomene* and *Tortolena* by having the embolus slightly curved and by the absence of a tegular lateral process; from *Hoffmannilena* by having the RTA on the distal part of the tibia and the epigynum poorly sclerotized; from *Novalena* by having a ridge on the dorsal projection of the RTA and by the folded primary spermathecae; from *Calilena* by the absence of both a fulcrum at the base of the embolus and a scape on the epigynum; from *Hololena* by having the embolus supported by the conductor only and by the shape of the epigynum, which has an inverse T-shaped appearance in ventral view; from *Rothilena* by having the embolus sinuous and supported by a folded conductor with a deep ventral notch and by the absence of hoods on the epigynal atrium; from *Bajacalilena* gen. nov. by having the embolus sinuous and the primary spermathecae folded; from *Cabolena* by having the RTA on the distal part of the tibia and by the shape of the epigynum, which has an inverse T-shaped appearance in ventral view; and from *Rualena* by the absence of both a membranous fulcrum and a thickened ridge on the posterior margin of the epigynal atrium.

Description.—Medium sized spiders, 4–9 mm in total length. Both eye rows strongly procurved in frontal view. Feathery scale-like setae present on carapace, opisthosoma, pedipalps, and legs. Carapace with two longitudinal symmetrical dark bands intensified by feathery setae, a black band around the border of thoracic region, and a clear median band wider on cephalic region. Chelicerae with three promarginal teeth and two retromarginal teeth. Sternum longer than wide. Pedipalp femur usually with two dorsal spines. Legs with spines and longer in males than in females. Leg IV the longest. Rings present on femur, patella and tibia. Patella-tibia I usually longer than carapace in males and shorter than carapace in females. Patella I and II with two dorsal spines and one prolateral spine, patella III and VI with two dorsal spines, one prolateral spine, and one retrolateral spine. Leg tarsi with five to six trichobothria. Capsulate tarsal organ in distal position of trichobothrial row. Opisthosoma oval with dorsal foliate pattern and/or posterior chevrons. Colulus divided, represented by few hairs. PLS longest with distal segment as long as or slightly longer than basal. Male pedipalp with folded conductor (Fig. 19c) with a deep ventral notch, forming two projections, the ectal one the longest (Fig. 18a). Median apophysis an elongated, spoon-shaped membrane (Fig. 19a).

RTA with a distal projection and a lateral projection across the tibia (Fig. 18b). Tibia with prolaterodorsal protuberance. Epigynal plate wider than long with an inverse T-shaped appearance in ventral view (Fig. 18c). Lateral hyaline spurs present (Fig. 20c). Copulatory openings in anterior position (Fig. 18c). Copulatory ducts short, in ventral position in relation to primary spermathecae (Fig. 17b). Primary spermathecae folded (Figs. 18d, 20d). Secondary spermathecae in diverticula (Figs. 17d, 19f). Fertilization ducts short (Fig. 19b).

Distribution.—*Callidalena* gen. nov. is distributed in the USA in the State of California and in Mexico in the State of Baja California (Fig. 23a).

Included taxa.—Two species: *C. quintin* sp. nov. and *C. tijuana* sp. nov.

Callidalena quintin Maya-Morales & Jiménez sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:0350041E-8FBC-418C-8043-0311A4A5A73A
(Figs. 17, 18, 23a)

Type material.—*Holotype male*: Municipality of Ensenada, San Quintín, Baja California, Mexico, 24 November 1962, P.R. Craig & D.L. Dailey (CASENT 9048919). *Paratypes*: MEXICO: *Baja California*: 2 ♀, same data as holotype (CASENT 9048919); 1 ♀, same data as holotype (CASENT 9048917); 2 ♀, same data as holotype (CASENT 9048918); 1 ♂, 2 ♀, same data as holotype except 23 November 1962 (CASENT 9048912); 1 ♂, same data (CASENT 9048914); 1 ♂, same data (CASENT 9048915); 1 ♀, Punta Banda, 2 December 1973, S.C. Williams & C.L. Mullinex (CASENT 9048921); 1 ♂, Isla San Martín, 30 June 1983, V.F. Lee (CASENT 9048922); 1 ♂, 2 ♀, 17.2 km N. of El Rosario, 25 November 1962, P.R. Craig & D.L. Dailey (CASENT 9048924); 1 ♂, 11.7 km E. of El Rosario, 30°04′30″N, 115°37′55″W, 180 m, pitfall trap, 7 January 1984 – 2 March 1986, W.H. Clark (CIDA 98,372); 1 ♂, same data except 3 January – 27 August 1989 (CIDA 99,732); 2 ♂, same data except 7 February 1984 – 2 April 1985, W.H. Clark & P.E. Blom (CIDA 107,417); 1 ♂, same data (CIDA 107,454); 3 ♂, same data (OJSMNH); 1 ♂, 10.7 km E. of El Rosario, 30°04′35″N, 115°38′25″W, 160 m, pitfall trap, 7 February 1984 – 2 April 1985, W.H. Clark (CIDA 107,432).

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—Males of this species differ from *C. tijuana* by having the ventral notch of the conductor deeper and wider (Fig. 18a) and by the more pronounced curves of the embolus (Fig. 17c). Females differ from *C. tijuana* by having copulatory openings occupying two-thirds of the anterior part of the epigynal plate (Fig. 18c) and primary spermathecae with a single pronounced curve (Fig. 17b).

Description.—Male (holotype): *Coloration:* Carapace yellow, black spot between AME. Chelicerae and condyles yellow. Endites and labium yellow with white tips. Sternum yellow with greyish border. Legs yellow, distal part of metatarsus brown. Opisthosoma greyish, brown anterior spot, lateral white spots, white foliage, and five pairs of lateral dark brown spots. Spinnerets yellow, basal segment of PLS with diffuse spots.

Habitus: Total length 4.63. Carapace length 2.5, width 1.38, cephalic region width 1.21, ocular region width 0.52. Eye diameter: AME, ALE, PME and PLE 0.1. Distance between eyes: AME-AME 0.06, AME-ALE 0.04, AME-PME 0.1, ALE-PLE 0.04, ALE-ALE 0.23, PME-PME 0.08, PME-PLE 0.08. Clypeus height 0.13. Chelicerae: basal segment length 0.91, fang length 0.45. Labium wider than long (0.39/0.24). Endites slightly convergent (distance at their base compared to their tips 0.39/0.33). Sternum longer than wide (1.1/0.95). Opisthosoma longer than wide (2.1/1.05). ALS separated by their basal diameter (0.19/0.19), PLS with distal segment slightly longer than basal segment (0.48/0.42).

Legs: Length: I- femur 1.92/ patella-tibia 2.31/ metatarsus 1.77/ tarsus 1.54; II- 2.08/ 2.46/ 2.23/ 1.62; III- 2.15/ 2.62/ 2.38/ 1.38; IV- 2.85/ 3.54/ 3.62/ 1.92.

Spination: Femur dorsal I- 1-1-2/ II- 1-3-2/ III- 1-3-2/ IV- 1-2-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 1-1-0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-1-0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-1-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 1-0-0/ 0-1-1; II- 0-0-1/ 2-2-2/ 0-1-1/ 0-1-0; III- 3-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 5, II- 5, III- 5, IV- 5.

Pedipalp: Number of dorsal spines: femur 2, tibia 4. Cymbium length 0.77, width 0.48. Embolus sinuous with a strong curve, exceeding distally the conductor ventral notch. The notch is deep extending two-thirds the conductor length (Figs. 17a, c, e, 18a, b).

Female (paratype from holotype locality) (CASENT 9048919): *Coloration:* Carapace yellow. Chelicerae light brown. Condyles orange. Endites and labium orange with white tips and small brown spots. Sternum yellow with brown border. Femur yellow, patella-tarsus light brown. Opisthosoma light brown with an anterior brown spots, several pairs of groups of white spots, and four pairs of lateral dark brown spots. Spinnerets orange.

Habitus: Total length 8.75. Carapace length 3.75, width 2.38, cephalic region width 1.36, ocular region width 0.76. Eye diameter: AME 0.13, ALE and PLE 0.15, PME 0.17. Distance between eyes: AME-AME 0.08, AME-ALE 0.06, AME-PME 0.17, ALE-PLE 0.06, ALE-ALE 0.33, PME-PME 0.1, PME-PLE 0.1. Clypeus height 0.21. Chelicerae: basal segment length 1.57, fang length 0.67. Labium wider than long (0.55/0.39). Endites slightly convergent (distance at their base compared to their tips 0.55/0.33). Sternum longer than wide (1.76/1.43). Opisthosoma longer than wide (4.75/2.88). ALS separated by less than their basal diameter (0.24/0.3), PLS with distal segment as long as basal segment (0.39/0.39).

Legs: Length: I- femur 3/ patella-tibia 3.38/ metatarsus 2.38/ tarsus 1.75; II- 2.88/ 3.13/ 2.5/ 1.75; III- 2.5/ 3.38/ 2.75/ 1.5; IV- 3.75/ 4.38/ 4.13/ 1.88.

Spination: Femur dorsal I- 1-1-2/ II- 1-3-2/ III- 1-3-2/ IV- 1-1-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 1-1-0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-1-0/ 2-2-2/ 1-1-0/ 0; III- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0; II- 0/ 2-2-2/ 0-1-1/ 0; III- 3-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 5, II- 5, III- 5, IV- 5.

Pedipalp: Dorsal spines on femur: 1. Prolateral spines on tibia: 1-2.

Epigynum: Plate length 0.58, width 0.91. Copulatory openings rounded separated by less than their width. Copulatory ducts less sclerotized than spermathecae. Primary spermathecae with one pronounced curve at anterior part where the copulatory ducts are connected. Primary spermathecae separated by less than their width (Figs. 17b, d, f, 18c–d).

Variation.—Total body length in males varies between 4.63 and 6.75 ($n = 15$) and in females between 5.38 and 8.75 ($n = 10$). Carapace length in males varies between 2.38 and 3.75 ($n = 15$) and in females between 2.63 and 3.75 ($n = 10$). Patella-tibia I length in males varies between 2.31 and 4 ($n = 13$) and in females between 2.38 and 3.38 ($n = 10$). Paratypes with three to four pairs of brown spots on sternum.

Distribution.—Baja California (Mexico) (Fig. 23a).

Callidalena tijuana Maya-Morales & Jiménez sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:324FFC1A-1015-4DE5-AFD6-5AA17834FE92
(Figs. 19, 20, 23a)

Type material.—*Holotype male*: Highway #1 km 47, Baja California, Mexico, 20 November 1962, P.R. Craig & D.L. Dailey (CASENT 9048909). *Paratypes*: MEXICO: *Baja California*: 1 ♀, same data as holotype (CASENT 9048909); 2 ♀, 3.4 km S. of Tijuana, Highway #1 km 35, 10 November 1962, P.R. Craig & D.L. Dailey (CASENT 9048908); 1 ♀, same data except 4 km S. of Tijuana, under stone, 21 November 1962, (CASENT 9048910); 1 ♀, same data (CASENT 9048911). USA: *California*: 1 ♂, San Diego Co., Naval Base Point Loma, 32°41′22.45″N, 117°14′30.52″W, pitfall trap, 10 August 2009, Naval Base Point Loma team (SDNHM a000797); 1 ♀, same data except 26 May 2009 (SDNHM a000842); 1 ♀, same data except 32°41′35.95″N, 117°15′09.17″W, 30 March 2009 (SDNHM a000808); 1 ♀, same data except 11 May 2009 (SDNHM a000858); 1 ♂, same data except 32°42′35.64″N, 117°15′09.13″W, 27 February 2009 (SDNHM a000811); 1 ♂, same data except 32°41′45.74″N, 117°14′36.24″W, 21 December 2009 (SDNHM a000843); 1 ♂, same data except 32°41′28.83″N, 117°14′55.01″W, 13 July 2009 (SDNHM a000860); 1 ♀, same data except 32°41′50.24″N, 117°14′42.07″W, 15 June 2000 (SDNHM a000872); 1 ♂, same data except 32°41′27.85″N, 117°14′55.11″W, 29 June 2009 (SDNHM a000862); 1 ♂, same data except 32°41′35.64″N, 117°15′09.13″W, 18 February 2010 (SDNHM a000868); 1 ♂, same data except 30 March 2009 (SDNHM a000859); 1 ♀, same data except 32°41′28.05″N, 117°15′14.68″W, 18 February 2010 (SDNHM a000861); 1 ♂, same data except 32°41′52.45″N, 117°14′59.26″W, 19 October 2009 (SDNHM a000856); 1 ♂, same data except 32°41′02.49″N, 117°14′49.14″W, 27 April 2009 (SDNHM a000867).

Other material examined.—USA: *California*: San Diego Co., Naval Base Point Loma, 32°41′49.88″N, 117°14′41.57″W, pitfall trap, 24 August 2009, Naval Base Point Loma team, 2 ♂ (SDNHM a000859); 1 ♂, same data except 32°41′28.99″N, 117°14′55.25″W, 10 August 2009 (SDNHM a000793); 1 ♂, same data except 32°41′28.22″N, 117°14′55.09″W (SDNHM a000794); 2 ♂, same data except 27 July 2009 (SDNHM a000801); 1 ♂, same data except 32°41′24.41″N, 117°15′19.45″W, 10 August 2009 (SDNHM a000795); 1 ♂, same data except 32°41′09.28″N, 117°14′28.43″W (SDNHM a000796); 1 ♂, same data except 32°42′13.44″N, 117°15′11.15″W, 16 March 2009 (SDNHM a000803); 1 ♂, same data except 32°42′35.82″N, 117°15′08.9″W, 6 April 2009 (SDNHM a000805); 1 ♀, same data except 32°42′35.64″N, 117°15′09.13″W, 16 March 2009 (SDNHM a000804); 1 ♂, same data except 32°42′36.23″N, 117°15′09.05″W, 27 July 2009 (SDNHM a000802); 1 ♂, same data except 30 March 2009 (SDNHM a000874); 1 ♂, same data except 32°41′03.06″N, 117°14′49.35″W, 16 March 2009 (SDNHM a000807); 1 ♂, same data except 32°41′43.74″N, 117°15′09.19″W, 27 February 2009 (SDNHM a000810); 1 ♂, same data except 32°41′02.49″N, 117°14′49.14″W, 30 March 2009 (SDNHM a000809); 1 ♂, same data except 11 May 2009 (SDNHM a000866); 1 ♂, same data except 32°41′52.78″N, 117°14′59.26″W, 27 February 2009 (SDNHM a000813); 1 ♀, same data except 32°42′36.45″N, 117°15′08.85″W (SDNHM a000812); 1 ♂, same data except 26 May 2009 (SDNHM a000841); 1 ♀, same data except 32°42′28.05″N, 117°15′14.68″W (SDNHM a000839); 1 ♀, same data except 32°41′03.36″N, 117°14′52.75″W, 11 May 2009 (SDNHM a000838); 1 ♂, same data except 32°41′28.99″N, 117°14′55.25″W, 21 December 2009 (SDNHM a000834); 1 ♂, same data except 32°39′34.27″N, 117°14′36.67″W, 18 February 2010 (SDNHM a000875); 2 ♂, same data except 32°42′35.45″N, 117°15′08.8″W, 13 July 2009 (SDNHM a000869); 2 ♂, same data except 32°41′45.74″N, 117°14′36.24″W, 18 February 2010 (SDNHM a000857); 1 ♂, same data except 32°39′34.42″N, 117°14′36.38″W (SDNHM a000863); 1 ♂, same data except 32°41′50.39″N, 117°14′42.43″W, 11 May 2009 (SDNHM a000865).

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—Males of this species differ from *C. quintin* by having the ventral notch of the conductor shallower and narrower (Fig. 20a); and by the embolus, which has less pronounced curves (Fig. 19c). Females differ from *C. quintin* by having copulatory openings, which are less conspicuous (Fig. 20c); and by the primary spermathecae, which have two pronounced curves (Fig. 19b).

Description.—Male (holotype): *Coloration:* Carapace yellow. Chelicerae brown. Condyles yellow. Endites yellow with white tips. Labium light brown with white tip. Sternum yellow with brown border. Legs yellow, tibia-metatarsus brown. Three rings on femur, one on patella, and two on tibia. Opisthosoma light brown, several dark brown spots, two pairs of anterior white spots, and a couple of white spots next to anal tubercle. Spinnerets yellow, basal segment of PLS with black borders.

Habitus: Total length 6.5. Carapace length 3.25, width 2.38, cephalic region width 1.21, ocular region width 0.67. Eye diameter: AME and PME 0.12, ALE and PLE 0.13. Distance between eyes: AME-AME 0.04, AME-ALE 0.04, AME-PME 0.13, ALE-PLE 0.04, ALE-ALE 0.29, PME-PME 0.1, PME-PLE 0.06. Clypeus height 0.17. Chelicerae: basal segment length 1.12, fang length 0.61. Labium wider than long (0.45/0.3). Endites slightly convergent (distance at their base compared to their tips 0.45/0.3). Sternum longer than wide (1.52/1.29). Opisthosoma longer than wide (3.38/1.88). ALS

separated by more than their basal diameter (0.27/0.23), PLS with distal segment as long as basal segment (0.42/0.42).

Legs: Length: I- femur 2.88/ patella-tibia 3.38/ metatarsus 2.5/ tarsus 2; II- 2.75/ 3.38/ 2.63/ 1.88; III- 3/ 3.25/ 3.25/ 1.75; IV- 3.63/ 4.38/ 4.5/ 2.25.

Spination: Femur dorsal I- 1-2-2/ II- 1-3-2/ III- 1-3-2/ IV- 1-1-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 1-2-1-2/ prolateral 0-1-2/ retrolateral 0; II- 1-1-0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-1-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-2-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 1-0-1/ 0; II- 0-0-1/ 2-2-2/ 0-1-1/ 0-1-1; III- 2-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 5, II- 5, III- 5, IV- 5.

Pedipalp: Number of dorsal spines: femur 2, tibia 4. Cymbium length 1.03, width 0.55. Embolus sinuous no exceeding distally the conductor ventral notch. The notch extends half the conductor length (Figs. 19a, c, e, 20a, b).

Female (paratype) (CASENT 9048908): *Coloration:* Carapace yellow, black spot between AME. Chelicerae and condyles brown. Endites and labium light brown with white tips. Sternum yellow with three pairs of brown spots. Femur yellow, patella-tarsus brown. Opisthosoma light brown with anterior brown spot, yellow foliage, and lateral brown spots. Spinnerets yellow, basal segment of PLS with black borders.

Habitus: Total length 7.88. Carapace length 3.13, width 1.88, cephalic region width 1.12, ocular region width 0.61. Eye diameter: AME and PME 0.12, ALE and PLE 0.15. Distance between eyes: AME-AME 0.04, AME-ALE 0.04, AME-PME 0.17, ALE-PLE 0.04, ALE-ALE 0.29, PME-PME 0.08, PME-PLE 0.1. Clypeus height 0.17. Chelicerae: basal segment length 1.29, fang length 0.67. Labium wider than long (0.45/0.36). Endites slightly convergent (distance at their base compared to their tips 0.45/0.3). Sternum longer than wide (1.57/1.19). Opisthosoma longer than wide (4.5/2.5). ALS separated by their basal diameter (0.27/0.27), PLS with distal segment slightly longer than basal segment (0.52/0.48).

Legs: Length: I- femur 2.38/ patella-tibia 2.85/ metatarsus 2/ tarsus 1.54; II- 2.23/ 2.54/ 2/ 1.46; III- 2.31/ 2.69/ 2.31/ 1.38; IV- 2.85/ 3.54/ 3.08/ 1.62.

Spination: Femur dorsal I- 1-2-2/ II- 1-3-2/ III- 1-3-2/ IV- 1-2-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 0/ 2-2-2/ 1-1-0/ 0; III- 1-1-0/ 1-1-2/ 1-1-0/ 1-1-0; IV- 1-1-0/ 1-1-2/ 1-1-0/ 1-1-0; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0; II- 0-0-1/ 2-2-2/ 0-1-1/ 0-0-1; III- 2-1-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 3-1-2/ 1-1-1-2-2/ 0-1-1/ 0-1-1. Number of trichobothria on tarsus: I- 5, II- 5, III- 5, IV- 6.

Pedipalp: Dorsal spines on femur: 2. Prolateral spines on tibia: 1-2.

Epigynum: Plate length 0.52, width 0.82. Copulatory openings separated by their width. Copulatory ducts as sclerotized as spermathecae. Primary spermathecae with two pronounced curves, one at anterior part where the copulatory ducts are connected, and one at posterior part. Primary spermathecae separated by their width (Figs. 19b, d, f, 20c–e).

Variation.—Total body length in males varies between 4.38 and 6.5 ($n = 10$) and in females between 5 and 7.88 ($n = 10$). Carapace length in males varies between 2.25 and 3.25 ($n = 10$) and in females between 2.63 and 3.38 ($n = 10$). Patella-tibia I length in males varies between 2.5 and 3.5 ($n = 10$) and in females between 2.25 and 3 ($n = 10$).

Distribution.—California (USA) and Baja California (Mexico) (Fig. 23a).

Lagunella Maya-Morales & Jiménez gen. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:F45F3431-312D-4ED5-8A3C-EC6DC3398752

Type species.—*Lagunella guaycura* sp. nov.

Etymology.—The generic name is derived from the Biosphere Reserve Sierra La Laguna, which is unique because it has the largest pine-oak forest on the BCP. The gender is feminine.

Diagnosis.—*Lagunella* gen. nov. is diagnosed by the following characters in combination: male pedipalp with a whip-shaped embolus originating on the basal part of the tegulum (Fig. 21c); conductor with two projections (Fig. 22b); tegulum with ventral part mostly membranous; tegular median process sclerotized (Fig. 22a); and RTA with distal and dorsal projections (Fig. 21e). Epigynum with atrium wider than long; copulatory openings in lateral position; anterolateral hyaline spurs present (Fig. 22c); copulatory ducts long tubes surrounding the primary spermathecae dorsally (Fig. 22d); primary spermathecae longer than wide and curved (Fig. 21b); secondary spermathecae in short and rounded diverticula (Fig. 21f) at the junction of the copulatory ducts and the primary spermathecae (Fig. 21d); and fertilization ducts short (Fig. 22d).

Lagunella gen. nov. differs from *Eratigena* and *Tegenaria* by having strongly procurved eye rows in frontal view. It differs from *Agelenopsis*, *Barronopsis*, *Melpomene* and *Tortolena* by the absence of a tegular lateral process; from *Calilena* by the absence of both a fulcrum on the male pedipalp and a scape on the epigynum; from *Hololena* by having the embolus supported by the conductor only and by the shape of the primary spermathecae, which are longer than wide; from *Rualena* by the absence of both a membranous fulcrum and a posterior ridge on the posterior margin of the epigynal atrium; from *Rothilena* by having two projections on the conductor and no hoods on the epigynal atrium; from *Callidalena* gen. nov. by having the embolus originating from the basal part of tegulum and by the shape of the epigynal atrium, which has as a deep posterior cavity; and from *Bajacalilena* gen. nov. by having the embolus with a simple curve and the primary spermathecae longer than wide. *Lagunella* gen. nov. also differs from *Calilena*, *Hololena*, *Rualena*, *Rothilena*, *Callidalena* gen. nov. and *Bajacalilena* gen. nov. by having three to four retromarginal teeth on the chelicerae. Males of *Lagunella* gen. nov. differ from *Hoffmannilena*, *Novalena*, and *Cabolena* gen. nov. by having the embolus originating from the basal part of the tegulum and the RTA on the distal part of the tibia. Females of *Lagunella* gen. nov. differ from *Hoffmannilena* by the absence of a strongly sclerotized epigynal plate, and from *Novalena* and *Cabolena* gen. nov. by having the copulatory ducts of the epigynum connected anteriorly to the primary spermathecae.

Description.—Medium-sized spiders, 6–12 mm total length. Both eye rows strongly procurved in frontal view. Carapace with two longitudinal symmetrical dark bands intensified by feathery scale-like setae, a black band around the border of

thoracic region, and a clear median band wider on cephalic region. Chelicerae with three promarginal teeth and three to four retromarginal teeth. Sternum longer than wide. Pedipalp femur with three dorsal spines. Legs with spines, longer in males than in females. Leg IV the longest. Rings present on femur, patella and tibia. Patella-tibia I shorter than carapace. Patella I and II with two dorsal spines and one prolateral spine, patella III and VI with two dorsal spines, one prolateral spine, and one retrolateral spine. Leg tarsi with seven to nine trichobothria. Capsulate tarsal organ in distal position of trichobothrial row. Opisthosoma oval with dorsal foliate pattern and/or posterior chevrons. Colulus divided, represented by few hairs. PLS longest with distal segment usually as long as basal. Embolus a long whip originating on basal part of tegulum (Fig. 21a). Conductor with ventral and dorsal projections of similar size. Membranous part covering two-thirds the ventral surface of tegulum (Fig. 22a). Tegular median process present (Fig. 21a). RTA on distal part of tibia and with distal and dorsal projections (Fig. 22b). Dorsal projection with one spine. Epigynal plate and atrium wider than long. Copulatory openings in lateral position. Anterolateral hyaline spurs present (Fig. 22c). Copulatory ducts long and surrounding dorsally the primary spermathecae and connected anteriorly (Fig 21b). Primary spermathecae longer than wide and curved (Fig. 22d). Secondary spermathecae in short and rounded diverticula on union of copulatory ducts and primary spermathecae (Fig. 21d). Fertilization ducts short (Fig. 22d).

Distribution.—*Lagunella* gen. nov. is distributed in Mexico in the State of Baja California Sur (Fig. 23b).

Included taxa.—One species: *L. guaycura* sp. nov.

Lagunella guaycura Maya-Morales, Jiménez & Palacios-Cardiel sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:D9FBAD42-9823-4EC6-B6E8-5D287860AC5E
(Figs. 21, 22, 23b)

Type material.—*Holotype male*: Municipality of La Paz, Biosphere Reserve Sierra La Laguna, La Cieneguita, Baja California Sur, Mexico, 23°33′02″N, 109°56′26.8″W, 1758 m, 7 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 3749). *Paratypes*: MEXICO: *Baja California Sur*: 1 ♂, same data as holotype (CARCIB 1887); 1 ♀, same data as holotype (CARCIB 1911); 4 ♂, 4 ♀, same data as holotype (CARCIB 1912); 1 ♀, same data as holotype (CARCIB 3749); 1 ♀, same data as holotype except Valle La Laguna, 1630 m, 29 September 1987, A. Cota & M.L. Jiménez (CARCIB 54); 1 ♂, same data as holotype except Cañón La Burrera, Arroyo La Palma, 11 December 1986, A. Acevedo (CARCIB 24); 1 ♀, same data except 19 April 1988, M.L. Jiménez (CARCIB 1859); 1 ♀, same data as holotype except Cañón La Zorra, 1640 m, 4 November 1986, F. & A. Cota (CARCIB 48); 1 ♂, same data except 12 February 1988, M.L. Jiménez (CARCIB 1863); 2 ♀, same data as holotype except Las Cascadas, 23°33′56.9″N, 109°58′07.6″W, 1734 m, hand collecting on ground, 8 October 2011 (CARCIB 1880); 1 ♂, same data as holotype except road to La Palma, 23°33′22.6″N, 109°58′43.9″W, 1818 m, hand collecting on ground, 5 October 2011 (CARCIB 1889); 1 ♀, same data (CARCIB 1913); 4 ♂, 1 ♀, same data (CARCIB 1914); 1 ♂, same data as holotype except La Ventana, 21 April 1988, M.L. Jiménez (CARCIB 3746); 1 ♀, same data (CARCIB 3748); 1 ♂, same data as holotype except Valle La Laguna, 21 September 1987, F. Cota (CARCIB 3747); 1 ♂, same locality as holotype, 4 December 1944, M. Correa (AMNH).

Other material examined.—MEXICO: *Baja California Sur*: 2 ♀, same data as holotype except Cañón La Zorra, 1640 m, 1 November 1984, M.L. Jiménez (CARCIB 4); 5 ♀, same data except 25 February 1987, M. Acevedo & M.L. Jiménez (CARCIB 19); 9 ♀, same data (CARCIB 39); 1 ♀, same data except 19 August 1986, F. Cota & M.L. Jiménez (CARCIB 34); 7 ♂, same data (CARCIB 42); 1 ♀, same data except 28 September 1986, A. & F. Cota (CARCIB 43); 1 ♀, same data except date unknown, M.L. Jiménez & A. Cota (CARCIB 51); 3 ♂, same data except 13 January 1988, M.L. Jiménez (CARCIB 1864); 3 ♀, same data as holotype except Valle La Laguna, 1830 m, 20 April 1988, M.L. Jiménez & R. Domínguez (CARCIB 27); 7 ♂, same data except 1630 m, 29 September 1987, A. Cota & M.L. Jiménez (CARCIB 28); 8 ♀, same data except 4 June 1988, A. Cota (CARCIB 50); 5 ♀, same data except 16 January 1988, V. Roth & M.L. Jiménez (CARCIB 1851); 3 ♂, same data except 27 September 1987, F. Cota (CARCIB 1854); 1 ♀, same data as holotype except road to La Laguna, 23°33′06.8″N, 109°59′03.9″W, 1757 m, night collecting, 7 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1875); 8 ♂, same data as holotype except La Cieneguita, 20 April 1988, M.L. Jiménez & S. Guzmán (CARCIB 40); 1 ♀, same data except 19 April 1988, M.L. Jiménez (CARCIB 1848); 1 ♀, same data as holotype except La Ventana, 21 April 1988, M.L. Jiménez (CARCIB 1858); 1 ♂, same locality as holotype, 12 December 1986, A. Cota (CARCIB 1861); 1 ♂, same data as holotype except Paso La Golondrina, 1640 m, 13 January 1988, V. Roth (CARCIB 1865); 1 ♀, same data as holotype except Arroyo La Palma, 23°34′24.8″N, 109°58′27″W, 1798 m, hand collecting on ground, 6 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1882); 4 ♂, 3 ♀, same data (CARCIB 3826); 1 ♂, same data except beat sheet, A. Orozco (CARCIB 1891); 1 ♀, same data except 23°33′22.6″N, 109°58′43.5″W, 1818 m, 5 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1885); 1 ♂, same data as holotype except Las Cascadas, 23°32′57.7″N, 109°58′06.2″W, 1739 m, beat sheet, 8 October 2011, C. Palacios, J. Maya & J. Villarreal (CARCIB 1892).

Etymology.—The specific name is a noun in apposition and refers to the now extinct native tribe "Guaycura" that occupied the southern part of the BCP.

Diagnosis.—By the characters of the genus.

Description.—Male (holotype): *Coloration:* Carapace yellow with white feathery scale-like setae. Chelicerae and condyles brown. Endites yellow with white tips. Labium light brown with white tip. Sternum orange with a diffuse pattern of black spots. Femur yellow, patella and tarsus orange, metatarsus brown. Three rings on femur, black spots on metatarsus. Opisthosoma reddish with lateral black bands, four arrowhead shaped spots. Spinnerets orange, PLS with basal segment black.

Habitus: Total length 7.25. Carapace length 4, width 2.38, cephalic region width 1.27, ocular region width 0.7. Eye diameter: AME 0.12, ALE 0.19, PME 0.15, PLE 0.13. Distance between eyes: AME-AME 0.06, AME-ALE 0.04, AME-PME 0.13, ALE-PLE 0.04, ALE-ALE 0.29, PME-PME

0.08, PME-PLE 0.12. Clypeus height 0.23. Chelicerae with four retromarginal teeth; basal segment length 1.36, fang length 0.58. Labium slightly wider than long (0.52/0.48). Endites slightly convergent (distance at their base compared to their tips 0.52/0.24). Sternum longer than wide (1.9/1.38). Opisthosoma longer than wide (3.75/2). ALS separated by less than their basal diameter (0.13/0.25), PLS with distal segment slightly shorter than basal segment (0.42/0.44).

Legs: Length: I- femur 2.63/ patella-tibia 3.25/ metatarsus 2.38/ tarsus 1.75; II- 2.5/ 3.13/ 2.5/ 1.63; III- 3.13/ 3.38/ 2.88/ 1.5; IV- 3.13/ 4/ 3.75/ 1.75.

Spination: Femur dorsal I- 1-2-3/ II- 1-3-3/ III- 1-3-3/ IV- 1-2-2; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 0/ 1-2-2/ 1-1-0/ 0; III- 1-1-0/ 2-2-2/ 1-1-0/ 1-1-0; IV- 1-2-0/ 1-1-2-2/ 1-1-0/ 1-1-1; metatarsus I- 0/ 2-2-2/ 0-1-1/ 0; II- 0/ 2-2-2/ 0-1-1/ 0; III- 3-2-2/ 1-2-2/ 0-0-1/ 0-0-1; IV- 6-0-2/ 2-2-2/ 1-1-1/ 0-0-1. Number of trichobothria on tarsus: I- 8, II- 7, III- 9, IV- 7.

Pedipalp: Number of dorsal spines: femur 3, tibia 7. Cymbium length 1.12, width 0.58.

Female (paratype from holotype locality) (CARCIB 3749): *Coloration:* Carapace yellow. Chelicerae dark brown and condyles orange. Endites and labium orange with white tips. Sternum brown with a central yellow band. Femur-patella yellow, tibia-metatarsus brown, tarsus light brown. Opisthosoma as in male but with five arrowhead shaped spots. ALS orange, PLS with basal segment black, distal segment yellow.

Habitus: Total length 10.63. Carapace length 4.88, width 2.88, cephalic region width 1.67, ocular region width 0.88. Eye diameter: AME and PME 0.19, ALE and PLE 0.21. Distance between eyes: AME-AME 0.04, AME-ALE 0.08, AME-PME 0.19, ALE-PLE 0.06, ALE-ALE 0.37, PME-PME 0.1, PME-PLE 0.15. Clypeus height 0.29. Chelicerae with three retromarginal teeth; basal segment length 1.64, fang length 0.76. Labium slightly wider than long (0.57/0.52). Endites slightly convergent (distance at their base compared to their tips 0.57/0.43). Sternum longer than wide (2.05/1.67). Opisthosoma longer than wide (5/3.25). ALS separated by less than their basal diameter (0.24/0.36), PLS with distal segment slightly longer than basal segment (0.52/0.45).

Legs: Length: I- femur 3/ patella-tibia 3.88/ metatarsus 2.5/ tarsus 1.88; II- 2.88/ 3.75/ 2.63/ 1.63; III- 2.75/ 3.75/ 3/ 1.5; IV- 3.5/ 4.63/ 4.25/ 1.75.

Spination: Femur dorsal I- 1-2-3/ II- 2-3-3/ III- 1-3-3/ IV- 1-2-3; patella I- dorsal 1-1/ prolateral 1/ retrolateral 0; II- 1-1/ 1/ 0; III- 1-1/ 1/ 1; IV- 1-1/ 1/ 1; tibia I- dorsal 0/ ventral 2-2-2/ prolateral 1-1-0/ retrolateral 0; II- 1-1-0/ 1-2-2/ 1-1-1/ 0; III- 1-2-1-0/ 2-2-2/ 0-1-0/ 0-0-1; IV- 1-2-1-0/ 1-2-2/ 1-1-0/ 0-1-0; metatarsus I- 0/ 2-1-2-2/ 0/ 0-0-1; II- 0/ 2-2-1/ 0-1-1/ 0-0-1; III- 2-2-2/ 2-2-2/ 0-1-1/ 0-1-1; IV- 2-1-2/ 1-1-1-1-2/ 0-1-1/ 1-0-1. Number of trichobothria on tarsus: I- 7, II- 7, III- 7, IV- 7.

Pedipalp: Dorsal spines on femur: 3. Prolateral spines on tibia: 1-2.

Epigynum: Plate length 0.64, width 0.94.

Variation.—Total body length in males varies between 6.25 and 8.5 ($n = 16$) and in females between 7.88 and 11.25 ($n = 14$). Carapace length in males varies between 3.5 and 4.25 ($n = 16$) and in females between 3.38 and 5 ($n = 14$). Patella-tibia I length in males varies between 3.25 and 3.75 ($n = 15$) and in females between 3.13 and 4.38 ($n = 14$).

Distribution.—Baja California Sur (Mexico) (Fig. 23b).

RESULTS

Molecular data.—We obtained 48 COI sequences from 11 species of Ageleninae, including five of the seven new species described in this study that are found on the BCP and in California. Sequence lengths ranged from 632 to 647 bp. For each species, we obtained one to five unique haplotypes (Table 2), and all 28 haplotypes were used in the molecular analysis. Five haplotypes in a single species were found in *Rothilena cochimi* from three localities and three unique haplotypes in *Cabolena kosatli* sp. nov. from one locality (Table 3). High intraspecific pairwise sequence divergence was found in *Bajacalilena clarki* sp. nov. (2.2%) while *Rothilena cochimi* and *R. pilar* showed the smallest interspecific divergence (1.4%) (Table 3). Genetic divergences between genera ranged from 7.5% (between *Cabolena* gen. nov. and *Lagunella* gen. nov.) to 13.8% (between *Bajacalilena* gen. nov. and *Calilena*, and between *Cabolena* gen. nov. and *Hololena*). Bayesian phylogenetic analysis showed *Bajacalilena* gen. nov. and *Rothilena* as sister-taxa with a posterior probability of 99%; this clade was sister to *Callidalena* gen. nov. with a posterior probability of 97% (Fig. 24). *Hololena* formed a monophyletic group with all three genera (posterior probability of 95%). The other two new genera, *Cabolena* and *Lagunella* were sister-taxa with a posterior probability of 100% (Fig. 24).

DISCUSSION

In the Western Hemisphere, the subfamily Ageleninae is now composed of 17 genera: *Agelenopsis*, *Barronopsis*, *Calilena*, *Eratigena*, *Hoffmannilena*, *Hololena*, *Melpomene*, *Neotegenaria*, *Novalena*, *Rothilena*, *Rualena*, *Tegenaria*, *Tortolena*, and the four new genera proposed in this study. With the exception of *Eratigena* and *Tegenaria*, the genera are restricted to the Americas and their distribution is mostly limited to North and Central America.

Three of the four new genera are presumably endemic to the BCP and the fourth, *Callidalena* gen. nov., is also present in southern California (Fig. 23). The richness of agelenine genera on the BCP is greater in the northern part (State of Baja California) with the presence of North America genera such as *Agelenopsis*, *Calilena*, *Hololena* and *Rualena*. The richness of genera and species is lower in the central part of the BCP, with only *Bajacalilena* gen. nov. and *Rualena* (Maya-Morales & Jiménez 2016). The number of species increases in the southern part of the BCP (State of Baja California Sur), where *Rothilena*, *Cabolena* gen. nov. and *Lagunella* gen. nov. are found. The last two genera are present in the Biosphere Reserve Sierra La Laguna above 1600 m. *Cabolena huiztocatl* is also present along the Pacific coast (Fig. 23b).

At the genus level, we found substantial sequence divergence (7.4–13.8%) among the seven genera analyzed in this study (Table 3). Comparison of these with other genera of agelenids from other regions of the world (data not shown here) further confirmed that the new genera described in this study are indeed distinct. However, genetic distance information showed two species of *Cabolena* gen. nov., *Cabolena*

Table 2.—Haplotype data of included COI sequences of agelenids from the Baja California Peninsula and California.

Species	Haplotype	No.	Locality
Bajacalilena clarki	Bc-H1	1♂	Mexico, Baja California Sur, SE. of Mesa El Tecolote, 26°59′N, 113°26′W
Bajacalilena clarki	Bc-H2	1♂	Mexico, Baja California Sur, Arroyo San Lorenzo, 26°56′N, 113°47′W
		1♀	Mexico, Baja California, 9 km NW. of Rancho Santa Inés, 26°46′N, 114°46′W
Bajacalilena clarki	Bc-H3	1♂	Mexico, Baja California, 11.7 km E. of El Rosario, 30°04′30″N, 115°37′55″W
Cabolena huiztocatl	Ch-H1	1♂	Mexico, Baja California Sur, Sierra La Laguna, 23°33′22.6″N, 109°58′43.5″W
Cabolena huiztocatl	Ch-H2	1♀	Mexico, Baja California Sur, Punta San Pedro, 23°23′22.4″N, 110°12′30.2″W
Cabolena huiztocatl	Ch-H3	2♀	Mexico, Baja California Sur, Punta San Pedro, 23°23′22.4″N, 110°12′30.2″W
Cabolena huiztocatl	Ch-H4	1♀	Mexico, Baja California Sur, Sierra La Laguna, 23°33′06.7″N, 109°59′07.3″W
Cabolena kosatli	Ck-H1	1♀	Mexico, Baja California Sur, Sierra La Laguna, 23°33′06.8″N, 109°59′03.9″W
Cabolena kosatli	Ck-H2	1♂	Mexico, Baja California Sur, Sierra La Laguna, 23°33′06.7″N, 109°59′07.3″W
Cabolena kosatli	Ck-H3	1♀	Mexico, Baja California Sur, Sierra La Laguna, 23°33′22.6″N, 109°58′43.5″W
Cabolena sotol	Cs-H1	2♀	Mexico, Baja California Sur, Sierra La Laguna, 23°33′22.6″N, 109°58′43.5″W
Calilena angelena	Ca-H1	1♀	Mexico, Baja California, Highway Ensenada-Tijuana km 14, 31°54′24″N, 116°43′59″W
Calilena angelena	Ca-H2	1♂	Mexico, Baja California, 8 km NW. of Santo Tomás, 31°37′N, 116°27′W
Calilena angelena	Ca-H3	2♂, 1♀	Mexico, Baja California, 8 km NW. of Santo Tomás, 31°37′N, 116°27′W
Callidalena tijuana	Ct-H1	1♂	USA, California, San Diego, Naval Base Point Loma, 32°41′28.22″N, 117°14′55.09″W
Callidalena tijuana	Ct-H2	3♂, 3♀	USA, California, San Diego, Naval Base Point Loma
Hololena septata	Hs-H1	1♂	USA, California, San Diego, Naval Base Point Loma, 32°42′44.06″N, 117°15′09.04″W
Hololena septata	Hs-H2	1♂	USA, California, Lemon Grove
Hololena septata	Hs-H3	1♀	USA, California, Balboa Park East
Lagunella guaycura	Lg-H1	4♂, 5♀	Mexico, Baja California Sur, Sierra La Laguna
Rothilena cochimi	Rc-H1	1♀	Mexico, Baja California Sur, San José de Comondú, 23°06′34″N, 111°49′13″W
Rothilena cochimi	Rc-H2	1♂	Mexico, Baja California Sur, San Javier, 25°52′16.4″N, 111°32′46.4″W
Rothilena cochimi	Rc-H3	1 ♂	Mexico, Baja California Sur, San Javier, 25°52′16.4″N, 111°32′46.4″W
Rothilena cochimi	Rc-H4	1♂	Mexico, Baja California Sur, San Javier, 25°52′16.4″N, 111°32′46.4″W
Rothilena cochimi	Rc-H5	1♀	Mexico, Baja California Sur, Cuevas Pintas, 25°58′41.4″N, 111°27′54.6″W
Rothilena pilar	Rp-H1	1♀	Mexico, Baja California Sur, El Pilar, 24°28′19.9″N, 111°00′10.2″W
		2♂	Mexico, Baja California Sur, Rancho El Camarón, 24°19′11.6″N, 110°40′06.9″W
Rothilena pilar	Rp-H2	1♀	Mexico, Baja California Sur, Rancho El Camarón, 24°19′11.6″N, 110°40′06.9″W
Rothilena sudcalifornienses	Rs-H1	1♀	Mexico, Baja California Sur, Sierra Las Cacachilas, 23°48′15.7″N, 110°06′43.7″W

huiztocatl sp. nov. and *C. kosatli* sp. nov. closer to *Lagunella guaycura* sp. nov. (7.8% and 7.5% variation, respectively) compared to the congeneric species *C. sotol* sp. nov. (9.8% and 9.1% variation, respectively). Because of the genetic distances and the same distribution of *Cabolena* gen. nov. and *Lagunella* gen. nov., these two taxa could be considered as only one genus with high variability. According to Griswold (2001), some genera are necessarily monotypic because they are the sister groups of well defined clades with multiple species, and to define genera more broadly to eliminate monotypy would mean that these more inclusive groups become extremely difficult to diagnose (Griswold 2001). In this case, *Lagunella* gen. nov. and *Cabonela* gen. nov. have morphological characters that are useful for diagnosing them as separate genera (see above). Even though *Lagunella* gen. nov. appears to be monotypic, we think that the two groups will form separate clades when more species of *Lagunella* gen. nov. are discovered and included in the analysis.

Among the 11 species we studied, except for the three species from the genus *Rothilena*, all showed inter-specific genetic divergences greater than 3%. The ABGD analysis also showed evidence for nine groups (species) instead of 11. *Bajacalilena clarki* sp. nov., *Calilena angelena*, *Callidalena tijuana* sp. nov., *Cabolena huiztocatl* sp. nov., *Cabolena kosatli*

Table 3.—Kimura 2-parameter distance matrix for mitochondrial COI gene among 11 species of Agelenidae from the Baja California Peninsula and California. Distances within species in diagonal.

	Species	1	2	3	4	5	6	7	8	9	10	11
1	*Bajacalilena clarki*	0.022										
2	*Cabolena huiztocatl*	0.127	0.004									
3	*Cabolena kosatli*	0.120	0.061	0.009								
4	*Cabolena sotol*	0.141	0.098	0.091	-							
5	*Calilena angelena*	0.138	0.118	0.113	0.126	0.010						
6	*Callidalena tijuana*	0.112	0.136	0.127	0.137	0.132	0.002					
7	*Hololena septata*	0.115	0.122	0.108	0.138	0.105	0.115	0.004				
8	*Lagunella guaycura*	0.123	0.078	0.075	0.099	0.113	0.116	0.125	-			
9	*Rothilena cochimi*	0.089	0.134	0.129	0.142	0.137	0.104	0.125	0.114	0.004		
10	*Rothilena pilar*	0.091	0.129	0.126	0.137	0.131	0.103	0.121	0.106	0.014	0.002	
11	*Rothilena sudcalifornienses*	0.084	0.137	0.123	0.144	0.136	0.106	0.126	0.115	0.024	0.025	-

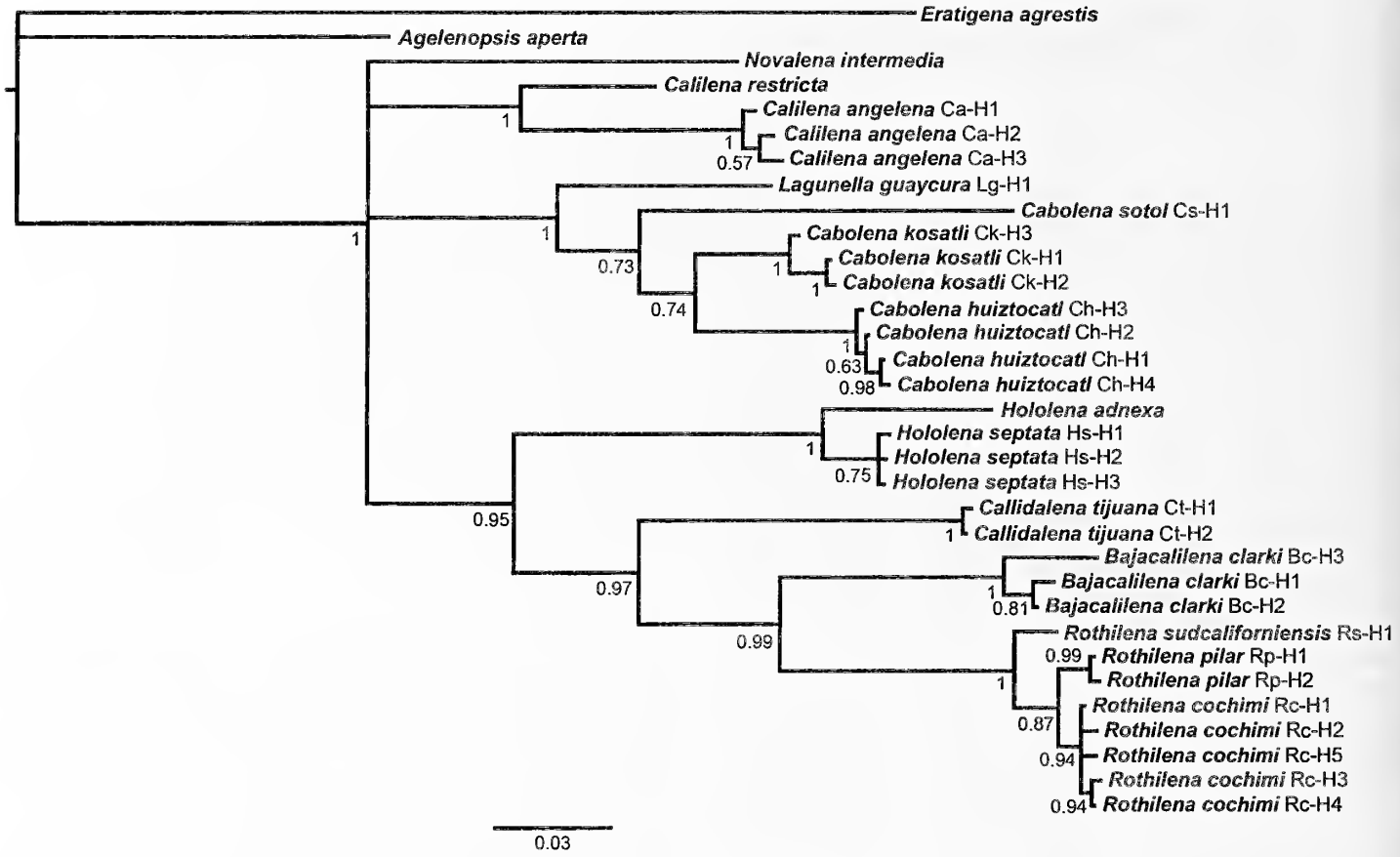

Figure 24.—Phylogenetic tree of sequenced Agelenidae, based on Bayesian analysis of cytochrome c oxidase subunit I (COI). Species names are followed by their haplotype information. Numbers at the nodes represent posterior probabilities.

sp. nov., *Cabolena sotol* sp. nov., *Hololena septata*, and *Lagunella guaycura* sp. nov. were recovered as different species. Yet the group composed of *Rothilena cochimi*, *R. pilar* and *R. sudcaliforniensis* showed genetic divergences of 1.1–2.5%. However, there is some evidence showing inconsistencies between morphological and molecular data, including: (a) species are not discernible on the basis of mtDNA sequences according to a barcode gap; (b) species do not form distinguishable molecular clades; and (c) specimens from different species present a continuum of genital morphologies that may represent a single and highly variable species (Paquin & Hedin 2004; Bolzern et al. 2013). According to genetic distances, the species of *Rothilena* are not discernible, suggesting that COI may not be a suitable gene to separate these species, compared to other agelenids (Croucher et al. 2004). It is also possible that congeneric species, showing low genetic divergence, can be attributed to their recent origin (Heber et al. 2003). Nonetheless, the Bayesian analysis showed the three species as three different groups (*R. sudcaliforniensis* is only represented by one sequence) (Fig. 24), and morphologically, the three species are recognized by the particular shape of the conductor and the RTA in the male pedipalp and the shape of the hoods on the epigynum. It is important to note that, although the distribution of the genus is limited (Maya-Morales & Jiménez 2013: fig. 7), we have not found more than one species of *Rothilena* in each locality.

The phylogenetic tree showed that *Bajacalilena* gen. nov., *Rothilena* and *Callidalena* gen. nov. are likely closely related. Also, *Cabolena* gen. nov. and *Lagunella* gen. nov. were grouped together as sister-taxa (Fig. 24). The first clade (*Bajacalilena* gen. nov., *Callidalena* gen. nov. and *Rothilena*) is distributed in arid habitats (desert shrubland and deciduous lowland forest). The second clade (*Cabolena* gen. nov. and *Lagunella* gen. nov.) is present in the higher pine-oak forest. Similar relationships were observed with maximum likelihood tree analysis, using PhyML software (Guindon et al. 2010) with nearest neighbor interchange and subtree pruning and a regrafting tree search option with 5,000 pseudoreplicates (not shown here). While the use of multiple genes is the most effective method for studying phylogenetic relationships, the geographic distribution of the genera and the analysis of a COI gene fragment nonetheless indicate a relationship with the vicariant events hypothesized for the BCP (Riddle et al. 2000; Crews & Hedin 2006). The agelenids of the BCP are thus a useful group of spiders and an interesting model for future studies on the biogeography and evolution of the biota of this region.

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Taxonomic revision of the genus *Crassicrus* Reichling & West, 1996 (Araneae: Theraphosidae: Theraphosinae), with the description of additional keels on the embolus

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Abstract. Since its original description, the theraphosid spider genus *Crassicrus* Reichling & West, 1996 has not been revised and no new species have been described. While reviewing material deposited in the Mexican National Collection of Arachnids (National Autonomous University of Mexico, Mexico City) and the American Museum of Natural History (New York, USA), we encountered specimens corresponding to four new species of *Crassicrus* from Mexico. In this revision, we include a redescription of the genus and its type species, *C. lamanai* Reichling & West, 1996, and describe four new species: *C. bidxigui*, *C. tochtli*, *C. cocona*, and *C. yumkimil*. Species habitat data are provided, as well as identification keys for males and females. In addition, new keels on the male embolus were identified and are described. In the Theraphosinae, the presence of one retrolateral keel has been reported, but in *Crassicrus*, there are two or three retrolateral keels, and a new taxonomical nomenclature for these keels is proposed. The genus *Crassicrus* is recorded from Mexico for the first time, increasing the number of known theraphine genera in the country to 16.

Keywords: Taxonomy, embolus keels, spermatic pore, morphology, new species

http://zoobank.org/?lsid=urn:lsid:zoobank.org:pub:76D547C2-07FA-4998-A673-582B7F4DF028

The morphology of the genitalia in Theraphosidae, and in Mygalomorphae more generally, has not been studied in detail, although genitalia provide important features used in the classification and identification of species (Bücherl 1957; Schiapelli & Gerschman 1962; Gerschman & Schiapelli 1970; Goloboff 1993; Ortiz & Francke 2014). The most diverse subfamily of the Theraphosidae is the Theraphosinae Thorell, endemic to the Americas. The structure of the male palpal bulb has been analyzed for some genera of this subfamily and some primary homology hypotheses for the keels on the bulb have been established (Pérez-Miles et al. 1996; Bertani 2000). According to Bertani (2000), in theraphosine palpal bulbs there are four major groups of keels: (1) the prolateral keels (superior and inferior); (2) the apical keel; (3) the subapical keel; and (4) the retrolateral keel. The taxonomy of Theraphosinae is problematic and most genera lack revisions or are diagnosed based on relatively few characters (Raven, 1985, 1990; Smith 1995; Pérez-Miles et al. 1996; Prentice 1997; Fukushima et al. 2008; Yamamoto et al. 2012). Some factors that contribute to this problematic taxonomy are the morphological uniformity among members of this group, the small number of traditional taxonomists working on Theraphosinae, and the subfamily's broad geographic distribution (Schiapelli & Gerschman 1979; Valerio 1980; Raven 1985, 1990; Goloboff 1993; Pérez-Miles et al. 1996; Bertani 2000, 2001). The revision of genitalic features as well as of other structures is important in order to increase our knowledge and understanding of this group, and to propose homologies among characters for the numerous theraphosine genera (Bücherl 1957; Schiapelli & Gerschman 1962; Bertani 2000; Ortiz 2008). This is especially so as the number of revisions and taxonomic works involving theraphosids has increased over the last decade. However, in North America there have been relatively few studies in comparison to the known diversity of the region. Mexico is the second most diverse country in terms of known tarantula species worldwide and this number has been increasing annually, with new descriptions displaying the growing importance and diversity of North American theraphosid species (Locht 2007; World Spider Catalog 2016). The only North American genera that have been revised, or partially revised to date are *Aphonopelma* Pocock, 1901, *Hemirrhagus* Simon, 1903, *Bonnetina* Vol, 2000, and *Brachypelma* Simon, 1891 (see Hamilton et al. 2011, 2016; Mendoza 2012; Mendoza 2014; Ortiz & Francke 2014; Ortiz & Mendoza, pers. comm.).

With respect to Belize and southeastern Mexico, the theraphosid fauna has not been studied in detail. According to Reichling (2003) and the World Spider Catalog (2016), there are only nine species reported from Belize and eight from southeastern Mexico. One of the genera reported for Belize is *Crassicrus* Reichling & West, 1996, which is a monotypic genus with *C. lamanai* Reichling & West, 1996. With the revision of biological material deposited in the Mexican National Collection of Arachnids (CNAN) (National Autonomous University of Mexico, Mexico City; UNAM) and the American Museum of Natural History (New York, USA; AMNH), we found specimens corresponding to four undescribed species of Mexican *Crassicrus*.

In this contribution, we present the first revision of the genus *Crassicrus*, including a redescription of the type species *C. lamanai*, a redescription and comparative diagnosis of the genus, and descriptions of four new species. This is the first record for the genus in Mexico. In addition, we found embolic keels on the males of *Crassicrus* that have not been reported before, and we describe these and report other features of the male genitalia that were not widely reported previously. The purpose of this work, in addition to the generic revision, is to contribute to the knowledge of Theraphosidae and provide new characters for future studies on the systematics of the family.

METHODS

The general description format follows Bertani et al. (2011). A Nikon SMZ 625 stereomicroscope was used for the observation of specimens and structures; urticating setae were examined with a Nikon Eclipse E100 compound microscope. Digital images were taken with a Nikon Coolpix S10 VR digital camera, with an adapter for the stereomicroscope. Male palpal bulbs and small sections of exuviae were dissected, critical-point dried, gold coated, and examined at low vacuum in Hitachi S-2460N and SU1510 scanning electron microscopes (SEM) at UNAM. Measurements are given in millimeters (mm), except SEM measurements which are in micrometers (μm); all measurements were taken along the central axis of the structures, in smaller structures with an ocular micrometer attached to the microscope, and in larger ones with a digital caliper with an error of 0.1 mm. Size ranges are given in millimeters (mm). Total body length was measured excluding the chelicerae and spinnerets. The leg span was measured with the legs fully extended, and was measured from the apex of tarsus I to the apex of tarsus IV of the side where the legs would be least damaged. Leg and pedipalp measurements were taken from the left appendages, except in the case of absence or damage. The width of all segments was measured laterally at the midpoint of each segment; specific leg segments having a considerably greater width in comparison with the same segment on different appendages were considered and described as thickened. See Appendix 1 for comparative material examined as part of this study.

Spination and setae.—Spination descriptions follow Bertani (2001). The classification of urticating setae follows Bertani & Guadanucci (2013). The description of the lateral scopulae follows Mendoza (2014), adding the presence of thin plumose setae. The metatarsal scopulae are described in percentages, considering the proportion of the segment length that is covered with scopulae. For leg spination, only the surfaces with spines are mentioned.

Pedipalp.—The terminology of the male palpal bulb keels follows Bertani (2000) with the following modifications: in *Crassicrus* there are two or three keels on the retrolateral face of the embolus; for comparisons of these keels between the different species, every keel was named; for the keels of the spermatic pore, we follow Ortiz & Francke (2014).

Mapping.—The distribution map was created using gvSIG version 2.1.0, using geographical and political division layers downloaded from Natural Earth (2015). The geographical coordinates were obtained in the field with an Etrex GPS. For localities that were not directly sampled or those that only had distance data, Google Earth version 7.1.2.2041 was used for the geo-referencing of localities and to estimate distances based on label landmarks.

Abbreviations.—Abbreviations follow Bertani (2000) and Ortiz & Francke (2014) for male palpal bulb keels; Coyle (1995) for spermathecae; Raven (1985) for somatic characters; Bertani & Guadanucci (2013: fig. 2) for the abdominal region; and Mendoza (2014) for tibial apophyses, as follows: a, apical; A, apical keel; ALE, anterior lateral eyes; AME, anterior median eyes; d, dorsal; MA, median anterior region of abdomen; MM, median region of abdomen; p, prolateral; Pap, prolateral branch of leg I tibial apophysis; PI, prolateral inferior keel; PLE, posterior lateral eyes; PME, posterior median eyes; PLS, posterior lateral spinnerets; PMS, posterior median spinnerets; PS, prolateral superior keel; r, retrolateral; Rap, retrolateral branch of leg I tibial apophysis; RI, retrolateral inferior keel; RM, retrolateral median keel; RS, retrolateral superior keel; SA, subapical keel; SB, spermathecae bulb; SP, spermatic pore keel; SS, spermathecal stalk; v, ventral.

SYSTEMATICS

Family Theraphosidae Thorell, 1870
Subfamily Theraphosinae Thorell, 1870
Genus *Crassicrus* Reichling & West, 1996

Crassicrus Reichling & West, 1996: 254.

Type species.—*Crassicrus lamanai* Reichling & West, 1996, by original designation.

Diagnosis (emended).—Males and females of *Crassicrus* can be distinguished from all other genera of Theraphosinae except *Aphonopelma*, *Citharacanthus* Pocock, 1901, *Cyrtopholis* Simon, 1892, *Lasiodora* C. L. Koch, 1850, *Megaphobema* Pocock, 1901, *Sphaerobothria* Karsch, 1879, *Stichoplastoris* Rudloff, 1997 and *Vitalius* Lucas, Silva & Bertani, 1993 by the presence of only urticating setae type I on the dorsal surface of the abdomen (Cooke et al., 1972) (Fig. 1). Males and females can be distinguished from these genera by presenting cuneiform thorn-like setae on the prolateral face of coxae I–IV, which are thicker near the ventral region (Figs. 1E, 7F, 8G, 11G, 13E, 14H, 16F, 17G), and by having the labio-sternal mounds semicircular and well separated (Figs. 5B, 7B, 8B, 10B, 11B, 13B, 14B, 16B, 17B). Males are further distinguished by having the following combination of characters: palpal bulb with the proximal region of the tegulum rounded (Figs. 6B, 9B, 12B, 15B, 18B); tibia with two apophyses which do not originate from a common base (Figs. 5G & H, 8H, 11H, 14G, 17H); and palpal bulb with proventral face of subapical region of embolus (between the PI and SA keels) convex (Figs. 6A, 9A, 12A, 15A, 18A). In other Theraphosinae species, e.g., *Aphonopelma anitahoffmannae* Locht, Medina, Rojo & Vázquez, 2005, this subapical region is flat, and in species like *Eupalaestrus weijenberghi* (Thorell, 1894) and *Vitalius sorocabae* (Mello-Leitão, 1923), it is slightly concave. Females are distinguished for the presence of spiniform setae on the ventral and proventral surfaces of femora II–IV (Figs. 7G, 10G, 13I, 16I), and two spermathecae partially fused by a heavily sclerotized median region, with the SB as wide as or wider than long (Figs. 7I & J, 10H, 13J, 16H).

Description.—Total length: males 28–37 mm; females 35–49 mm.

Prosoma: Female carapace dark brown; male carapace dark brown to black with coppery and violet iridescent setae. Cephalic region slightly darker than pars thoracica. Carapace widest at level of coxae II–III. Caput slightly elevated. Fovea variable: straight (Figs. 10A, 13A), slightly recurved (Figs. 5A, 11A, 14A, 17A), or slightly procurved (Fig. 16A). Anterior eye row straight or procurved; posterior eye row recurved. Clypeus very narrow. Cheliceral prolateral furrow with 11 to 16 teeth. Labium wider than long; anterior region with 24 to 122 cuspules. Labio-sternal mounds semicircular, separated from each other by less than half of their width. Maxillae

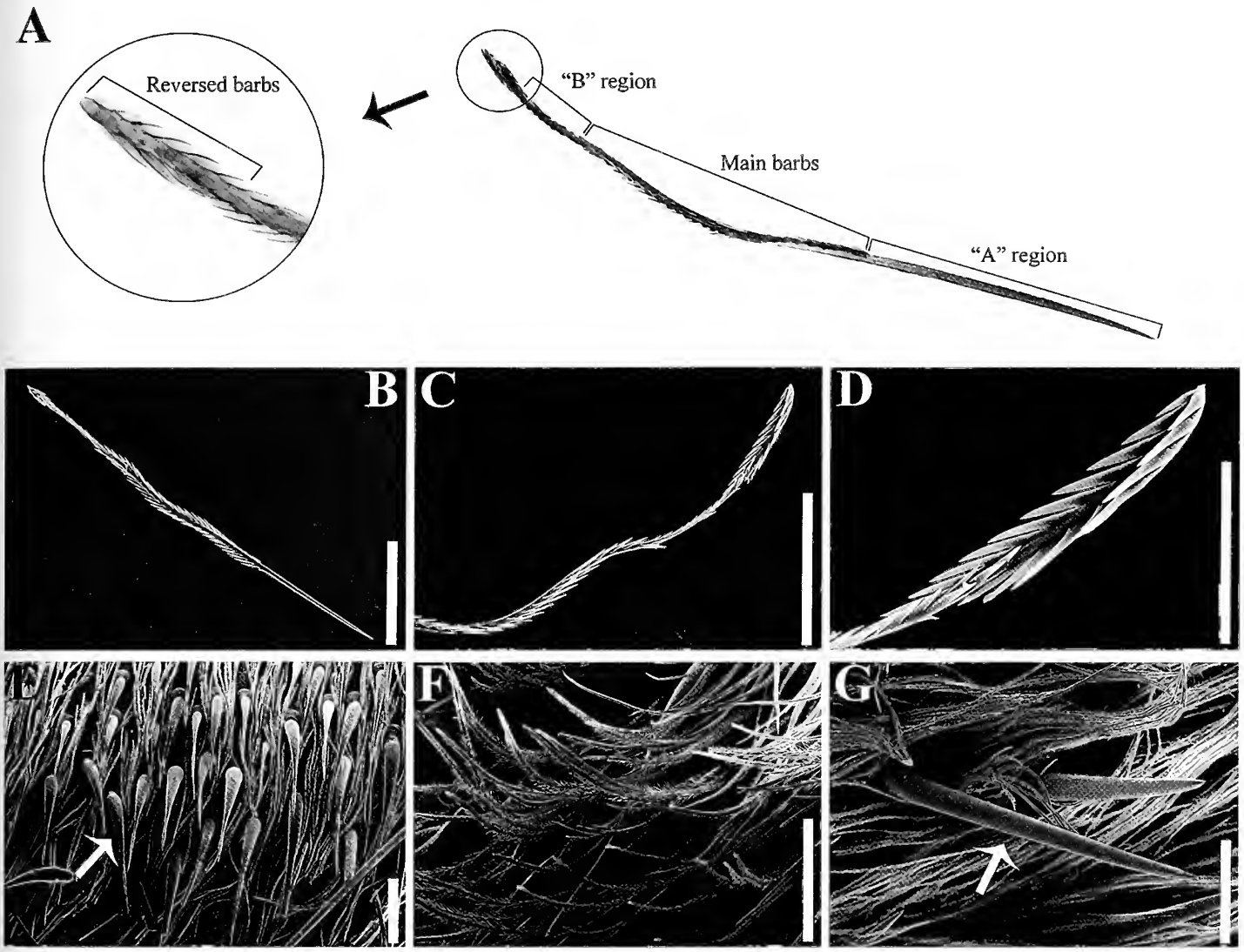

Figure 1.—Important morphological features found in *Crassicrus*. A. Modified urticating setae type I of median region of abdomen of *C. cocona* sp. nov. B–D. Urticating setae type I of median region of abdomen of *C. yumkimil* sp. nov.: B. Urticating setae type I with region "A" longer than "B". C. Detail of main barbs, "B" region, and reversed barbs. D. Detail of reversed barbs. E. Conical spiniform setae (arrow) on prolateral face of coxa I of male *C. cocona* sp. nov. F. Thin plumose setae on prolateral face of femur I of male *C. cocona* sp. nov. G, Elongated spiniform setae (arrow) on prolatero-ventral face of femur III of female of *Crassicrus* sp. Scale bars: 40 μm (D), 100 μm (B–C), 200 μm (E–G).

longer than wide, with 124 to 290 cuspules on baso-prolateral region. Sternum longer than wide; posterior margin not extending between coxae IV. Sternum convex (Figs. 8B, 11B, 14B) or flat (Figs. 5B, 17B); sigilla present (Figs. 5B, 17B) or absent (Figs. 10B, 13B); if present, they are close to basal retrolateral region of coxae I–III, and the third pair is the largest (Figs. 5B, 14B, 17B).

Legs: Leg formula: IV, I, II, III. In females and juveniles, the patellae, tibiae, metatarsi, and tarsi of the pedipalps and legs I–II are light brown, whereas on legs III and IV these segments are dark brown to black (Fig. 4B, C, E, G); the femora of the pedipalps and legs are black. In males, the legs are uniformly black, and can have violet iridescent setae on dorsal regions of the coxae, trochanters and femora (Fig. 4A, D, F). Retrolateral surface of palpal trochanter, prolateral surfaces of trochanter I and femur I, and prolateral surfaces of trochanter II and femur II are covered with long, thin, plumose setae (Fig. 1F). Prolateral surfaces of coxae I–IV are covered with short, cuneiform thorn-like setae that are thicker near the ventral region (Figs. 1E, 7F, 8G, 10F, 11G, 13E, 14H, 16F, 17G). Retrolateral surfaces of maxillae and coxae I–III sparsely covered by very short spiniform setae (Figs. 8F, 13G, 17I). Females present long spiniform setae on the proventral surfaces of femora II–IV (Figs. 1G, 7G, 10G, 13I, 16I). Tibiae IV can be slightly to very incrassate (Fig. 7H) or not at all. Male metatarsus I straight; when flexed, it touches the lateral external face of the retrolateral branch of leg I tibial apophysis. Tarsal scopulae undivided, in some species the tarsal scopulae of leg IV can be divided by a longitudinal row of longer setae.

Tibial apophyses: Male tibia I bears two branches, with separated bases: the prolateral (Pap) is digitiform, and in some species thickened (Fig. 11H); the retrolateral (Rap) is longer than Pap and slightly curved distally towards the Pap (Figs. 5G, 8H, 11H, 14G, 17H).

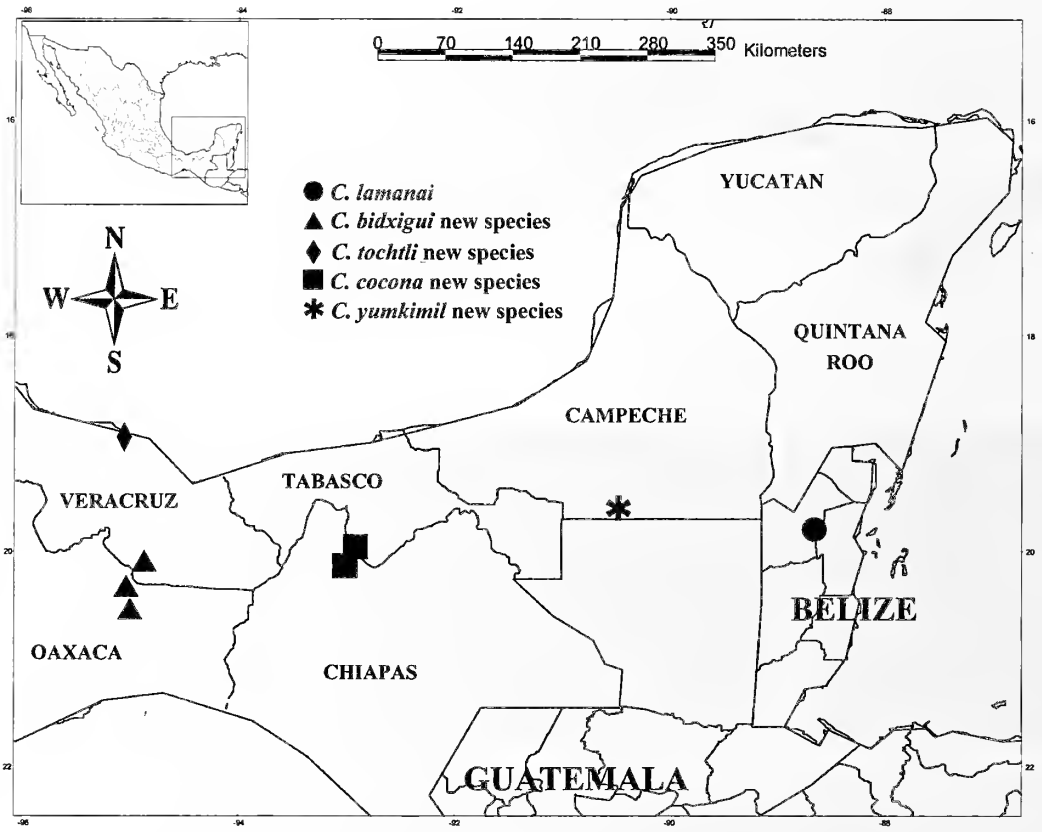

Figure 2.—Distribution map of the species of the genus *Crassicrus*.

Opisthosoma: Abdomen with dorsal surface covered with short dark setae, giving it a velvety appearance, interspersed with longer yellow to orange setae (Figs. 7C, 10C, 13C, 16C). Under the short setae, there is coppery brown pubescence corresponding to the urticating setae patch and extending posteriorly to two-thirds the length of the abdomen. Ventral region covered by numerous short black setae.

Urticating setae: Type I (Fig. 1), with region "A" larger than "B" (Fig. 1B). In most species, the males have considerably longer urticating setae on area MM in comparison to those of area MA (Figs. 1C, 1D); with region "A" very long (Fig. 1B). In some species, the urticating setae type I are modified and the region with reversed barbs is very short (Fig. 1A).

Male pedipalpal bulb: Embolus short, subapical dorsal region concave. In some species, the median ventral region is flat and, in others, it presents a shallow depression (Figs. 6A, 18A). Some species present striations on the prolateral upper face (Figs. 9A, 15A, 18A) or on the ventral region near the embolus (Fig. 12F). The embolus presents eight or nine keels, including: an apical keel (A), which is very reduced (Figs. 6E, 9F, 12E, 15E, 18E); a subapical keel (SA), which is serrated, and distally curves towards the retrolateral face of the embolus (Figs. 6B, 9D, 12D, 15B, 18D); and two prolateral keels (PI and PS) (Figs. 6A, 9A, 12A, 15A, 18A). Some species have two keels on the retrolateral face of the embolus: a retrolateral median (RM) keel, and a retrolateral inferior (RI) keel (Figs. 9B, 12B, 15B, 18D). The retrolateral median keel is located on the medial portion of the retrolateral face of the embolus; in some species, this keel is distally connected to the prolateral keels, forming the embolus tip. The retrolateral inferior keel is located on the inferior half of the retrolateral face of the embolus, between the retrolateral median and subapical keels, and it is weakly sclerotized distally. Other species, in addition to having the RM and RI keels, have a third retrolateral keel (Fig. 6B). The retrolateral superior (RS) keel shapes the dorsal edge of the embolus and is generally heavily sclerotized on its median portion; in some species, this keel is distally connected to the prolateral superior keel, and together they form the tip of embolus. Finally, two curved keels surround the spermatic pore (Figs. 6E, 9F, 12E, 15E, 18E).

Spermathecae: Female genitalia consisting of two receptacles partially fused by a heavily sclerotized median region. In some species, the median region is wider and slightly curved on its upper portion (Figs. 10H, 13J), whereas in others the median region has the same width throughout (Figs. 7J, 16H). The SB are as wide as or wider than long.

Composition.—*Crassicrus lamanai*, *C. bidxigui* sp. nov., *C. tochtli* sp. nov., *C. cocona* sp. nov., and *C. yumkimil* sp. nov.

Distribution.—*Crassicrus* is known from only five localities situated between latitudes 19° N and 21° N, from western Oaxaca (Isthmus of Tehuantepec) and southern Veracruz in Mexico, east to northern Belize (Fig. 2).

Natural history.—Spiders of the genus *Crassicrus* are known from locations with a tropical climate and elevations below 250 m. Their typical habitat is open areas, where native vegetation (mainly tropical rainforest and deciduous forest) has been replaced by roads, agricultural fields and pastures (Fig. 3A, C, D, F). Despite intensive collection efforts, specimens of *Crassicrus* were not found in highly preserved areas as Reichling & West (1996) mentioned; this could be due

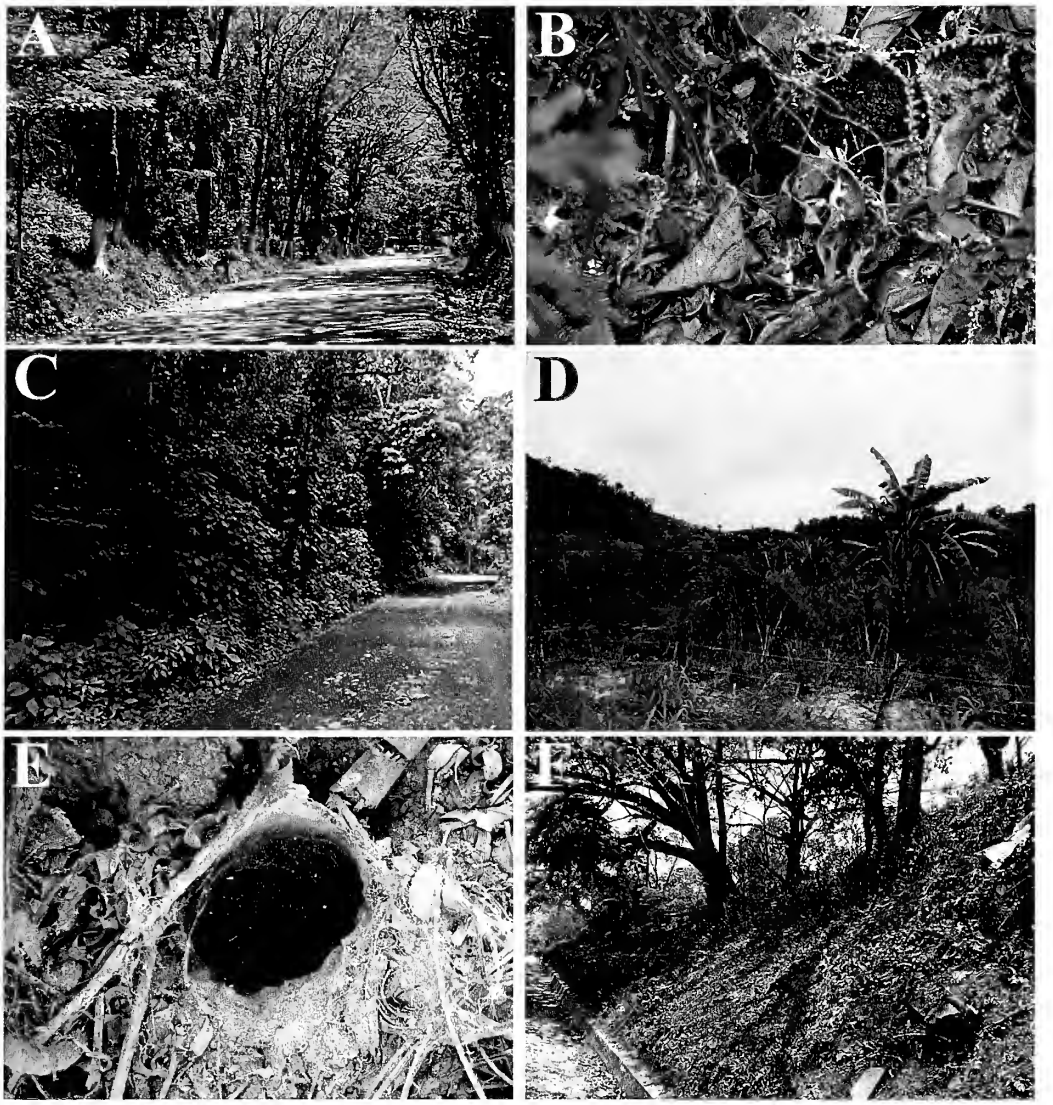

Figure 3.—*Crassicrus* species, habitats and burrows: A. Rainforest on road to Grutas de Coconá, Tabasco, Mexico, type locality of *C. cocona* sp. nov. B. Burrow of *C. cocona* sp. nov. C. Rainforest close to Los Tuxtlas Biological Station Veracruz, Mexico, type locality of *C. tochtli* sp. nov. D. Deciduous forest 1 km W. of El Pañuelo, Campeche, Mexico, type locality of *C. yumkimil* sp. nov. E. Burrow of *C. bidxigui* sp. nov. F. Deciduous forest at Piedra Blanca, San Juan Guichicovi, Oaxaca, Mexico, locality of *C. bidxigui* sp. nov.

to their preference for exposed sunny terrains over shadowy areas with dense vegetation. Most of the specimens of *Crassicrus* were found in burrows located along the borders of crop fields; the burrows are about 30 to 40 cm deep, with a circular entrance and sparsely covered with a layer of silk (Fig. 3B, E). It is worth noting that only adult females and juvenile males were obtained from burrows, and in some cases, juveniles were obtained by searching under rocks. Juvenile males were raised in captivity until they became sexually mature, usually in the rainy season from July to September. Considering the material deposited in collections, the reproductive season seems to occur from August to January, because adult males were collected during those months wandering near roadsides. All of the species of *Crassicrus* from known localities are sympatric with species of *Brachypelma* whose individuals are also burrowers, and clearly more abundant (pers. obs.) than those of *Crassicrus*. In Los Tuxtlas (Veracruz, Mexico) *Crassicrus* was also found to be sympatric with a non-digging tarantula species tentatively assigned to the contentious genus *Citharacanthus*.

KEYS TO THE KNOWN SPECIES OF *CRASSICRUS*

MALES

1. Sternum flat (Figs. 5B, 17B); ventral region of bulb with a shallow depression (Figs. 6A, 18A)..... **2**
– Sternum convex (Figs. 8B, 11B, 14B); ventral region of bulb without a shallow depression (Figs. 9A, 12A, 15A)..... **3**

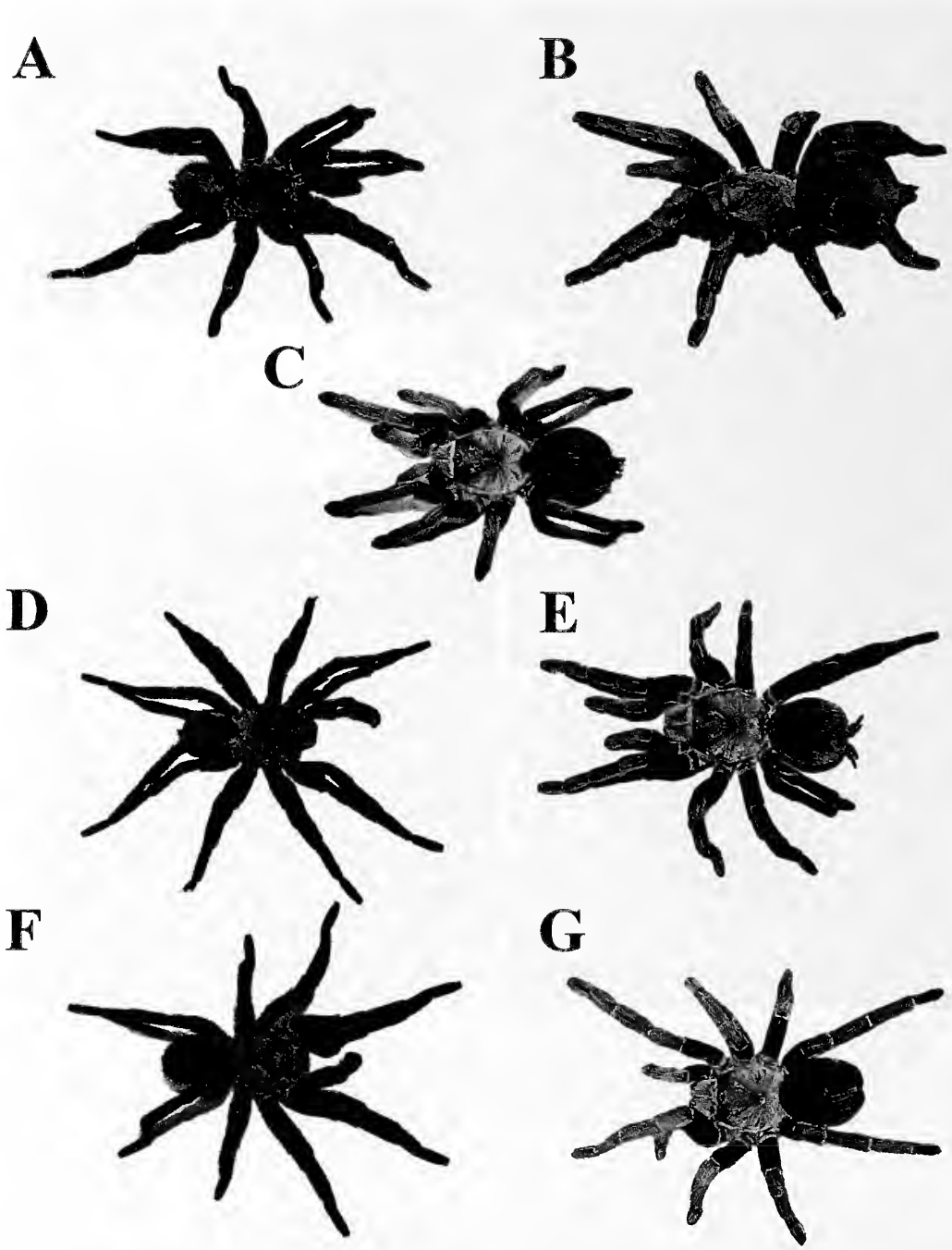

Figure 4.—*Crassicrus* species, habitus images. A–B. *Crassicrus lamanai*: A. Male. B. Female from 0.5 km W. of New River Lagoon, Indian Church Village, near Lamanai Forest Reserve, Orange Walk District, Belize. C. *Crassicrus bidxigui* sp. nov. female from Tolosa Donají, Matías Romero Avendaño, Oaxaca, Mexico. D–E. *Crassicrus tochtli* sp. nov.: D. Male (CNAN-T0898). E. Female from Biological Station "Los Tuxtlas", San Andrés Tuxtla, Veracruz, Mexico. F–G. *Crassicrus cocona* sp. nov.: F. Male (CNAN-T0894). G. Female (CNAN-T0895) from road to Grutas de Coconá, Teapa, Tabasco, Mexico. Photos A & B by Rick C. West.

2. Palpal bulb's prolateral face with striations (Fig. 18A); retrolateral face with two parallel keels (RM and RI) (Fig. 18D) ..... ***C. yumkimil*** sp. nov.

– Palpal bulb's prolateral face without striations (Fig. 6A); retrolateral face with three parallel keels (RS, RM and RI) (Fig. 6B) ..... ***C. lamanai***

3. Urticating setae type I modified, with the region of the reversed barbs very reduced (Fig. 14J); RI keel of palpal bulb bearing denticles on the proximal region (Fig. 15F) ..... ***C. cocona*** sp. nov.

– Urticating setae type I not modified, with the region of the reversed barbs not reduced (Fig. 1D); RI keel of palpal bulb without denticles on proximal region **4**

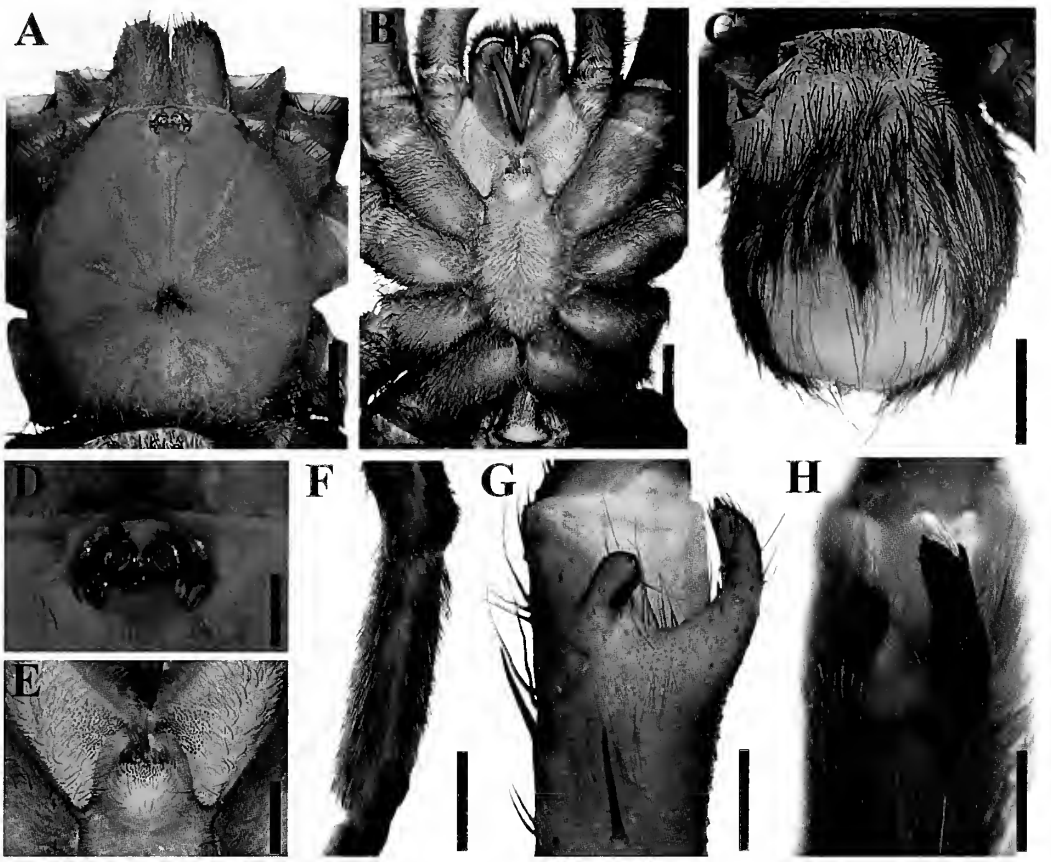

Figure 5.—*Crassicrus lamanai* male morphology. A–G. Holotype: A. Carapace. B. Prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Labium, maxillae, and labio-sternal mounds. F. Tibia IV, dorsal view. G. Tibial apophyses, ventro-prolateral view. H. Paratype, tibial apophyses, ventral view. Scale bars: 1 mm (D), 2 mm (G–H), 2.5 mm (E), 5 mm (A–C, F).

4. Coxae with basal spiniform setae on prolateral faces, these setae longer and wider on coxae III and IV; palpal bulb with striations on prolateral face (Fig. 9A), without striations on ventral surface; leg I tibial apophyses with Pap not thickened ..... ***C. bidxigui*** sp. nov.
– Spiniform setae fully covering prolateral faces of coxae, these setae slightly shorter and thinner on coxae III and IV; palpal bulb without striations on prolateral face, with striations on ventral surface near the embolus (Fig. 12F); leg I tibial apophyses with Pap thickened (Fig. 11H) ..... ***C. tochtli*** sp. nov.

FEMALES

NB. Females of *C. yumkimil* sp. nov. are unknown

1. Tibia IV thickened with respect to other leg segments (Fig. 7H); sternum flat (Fig. 7B) ..... ***C. lamanai***
– Tibia IV not thickened with respect to other leg segments; sternum convex (Figs. 10B, 13B, 16B) **2**
2. Spermathecae without broad upper edge on median region (Fig. 16H) ..... ***C. cocona*** sp. nov.
– Spermathecae with broad upper edge on median region (Figs. 10H, 13J) **4**
4. Coxae with basal spiniform setae on prolateral faces, these setae longer and wider on coxae III and IV; femur IV longer than metatarsus IV ..... ***C. bidxigui*** sp. nov.
– Spiniform setae fully covering prolateral faces of coxae, these setae slightly shorter and thinner on coxae III and IV; femur IV shorter than metatarsus IV ..... ***C. tochtli*** sp. nov.

Crassicrus lamanai Reichling & West, 1996
(Figs. 5–7)

Crassicrus lamanai Reichling & West, 1996: 254, figs. 1–9; Schmidt, 1997: 19, figs. 187–189; Vol, 1999: 11, fig. D; Schmidt, 2003: 136, figs. 198–200; Schmidt, 2007a: 8, figs. 1, 2; Schmidt, 2007b: 100, figs. 1, 2.

Type material.—*Holotype male.* BELIZE: *Orange Walk District*: 0.5 km W. of New River Lagoon, Indian Church Village, near Lamanai Forest Reserve, 6 January 1995, S.B. Reichling (AMNH).

Paratypes. BELIZE: *Orange Walk District*: 1 ♀, same data as holotype (AMNH); 1 ♂, same data except 7 January 1995 (AMNH; not examined); 2 ♂, same data except 3 September

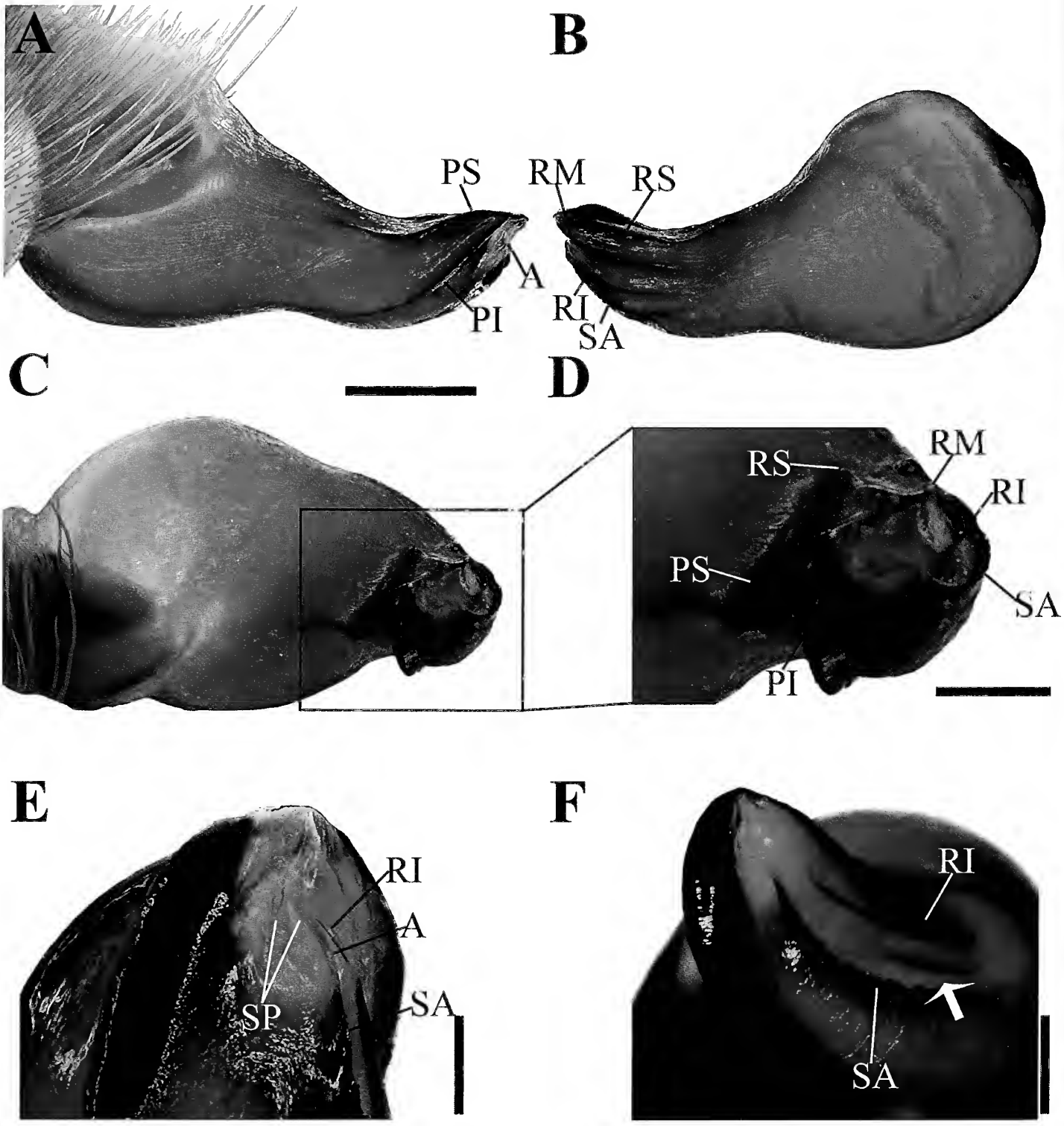

Figure 6.—Palpal bulb of male of *Crassicrus lamanai*. A–E. holotype: A. Prolateral view. B. Retrolateral view. C. Dorsal view. D. Detail of embolus in dorsal view. E. Apical region of embolus in ventro-prolateral view. F. Paratype, embolus in ventro-retrolateral view showing the variation of number of keels. Abbreviations: A = apical keel; PI = prolateral inferior keel; PS = prolateral superior keel; RI = retrolateral inferior keel; RM = retrolateral median keel; RS = retrolateral superior keel; SA = subapical keel; SP = spermatic pore keels. Scale bars: 0.25 (E, F), 0.5 mm (D), 1 mm (A–C).

1995 (AMNH); 4 ♀, same data except 9 January 1995 (AMNH).

Diagnosis.—*Crassicrus lamanai* can be distinguished from all other congeners except *C. yumkimil* sp. nov. by having tibia IV thickened. Males can be separated from those of *C. yumkimil* sp. nov. by the presence of three (rather than two) keels on the retrolateral face of the embolus. Females of *C. yumkimil* sp. nov. are unknown.

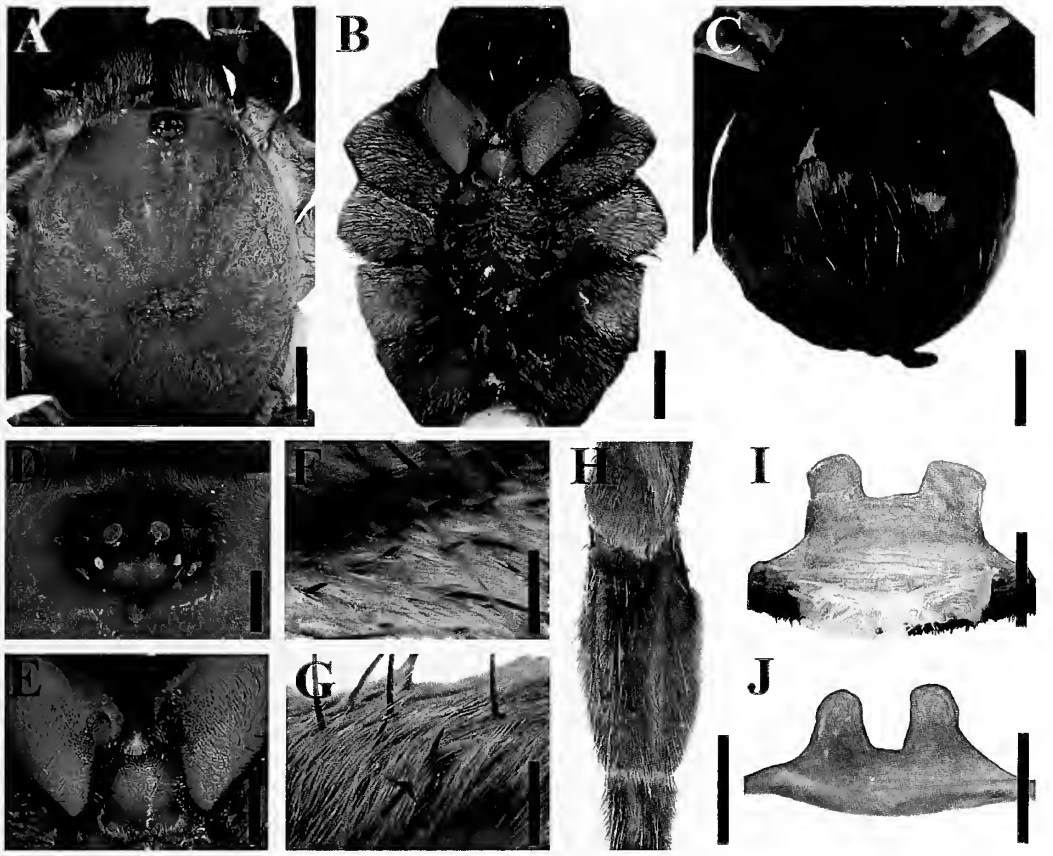

Figure 7.—*Crassicrus lamanai* female paratypes (AMNH): A. Carapace. B. Prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Labium and maxillae. F. Conical spiniform setae on prolatero-ventral region of coxa II. G. Spiniform setae (arrow) on prolatero-ventral region of femur III. H. Thickened tibia IV. I, J. Spermathecae variation of (I) female of redescription and (J) female of original description. Scale bars: 0.5 mm (F, G), 2 mm (D, I, J), 3 mm (E), 5 mm (A–C, H).

Description (male holotype).—*Prosoma:* Dorsal surface covered with short, fine setae, color jet-black in life (Reichling & West 1996), setae on carapace margin longer. Carapace semi-chordate, widest between coxae II and III (Fig. 5A). Caput slightly elevated (Fig. 5A). Fovea deep, recurved (Fig. 5A). Anterior eye row procurved; posterior eye row slightly recurved (Fig. 5D). AME rounded, ALE and PME oval, PLE subtriangular. Ocular tubercle wider than long; clypeus very narrow (Fig. 5D). Anterior margin of carapace covered with brown thin setae interspersed with longer and thicker setae (Fig. 5D). Chelicerae longer than wide, surface covered with coppery brown pubescence, and long thick brown setae. Prolateral furrow of chelicerae: left (damaged); right with 12 teeth (proximal to distal: 10–12 largest; 1, 3, 5, 7–9 medium-sized; 2, 4, 6 smallest). Labium wider than long, with 56 cuspules anteriorly (Fig. 5E). Labio-sternal mounds semicircular and separated (Fig. 5E). Maxillae longer than wide; left with 188 cuspules, right with 199 cuspules on baso-prolateral region (Fig. 5E). Sternum longer than wide, flat (Fig. 5B); surface covered with short, thin, grey setae, intermixed with brown setae that are longer laterally; with three pairs of oval sigilla located close to basal-retrolateral face of coxae I, II, and III; third pair largest (Fig. 5B).

Legs: All leg segments jet-black in life. Ventral surface of coxae covered with short, fine, grey setae, intermixed with brown longer setae. Coxae I–IV prolaterally covered with short cuneiform thorn-like setae, thicker ventrally. Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae. All other segments covered with coppery brown pubescence, intermixed with long brown setae. Femur III thickened with respect to femora I–II, IV. Tibia IV thickened with respect to tibiae I–III (Fig. 5F). Metatarsus IV longer than femur IV. Tarsal scopulae I–IV entire. Metatarsal scopulae I–III entire and IV divided by setae. Metatarsal scopulae extension: I complete, II 0.87, III 0.65, IV 0.18. Metatarsus I straight, when flexed touches lateral face of Rap.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa, trochanter). Leg II: p (coxa, trochanter, femur); r (coxa, trochanter). Leg III: p (coxa, trochanter); r (coxa). Leg IV: p (coxa); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (trochanter, baso-retrolateral face of femur). Leg I: p (trochanter, femur). Leg II: p (trochanter, femur).

Leg spination: Pedipalp: femur p0–0–2d, tibia p1–0–2a. Leg I: femur p0–0–1a, tibia v0–1–1a, p0–0–2, metatarsus v0–0–1a. Leg II: femur p0–0–1d, tibia v0–2–3a(1p), p0–1–1, metatarsus v1r–1–1ap, p0–0–1v. Leg III: femur d0–0–1p, patella r1, tibia v1–2–1, p0–1–1, r0–1–1, metatarsus v1–2–3a(1p, 1r), p1–1–1, r0–1–1. Leg IV: tibia v1–2–3a, p–1–1–0, r0–1–1, metatarsus v13(3a), p1–1–1, r1–1–1d.

Leg I tibial apophyses: Tibia I with two branches that do not originate from a common base (Fig. 5G, H). Prolateral branch (Pap) short, straight, digitiform, retrolateral face with a megaspine that does not protrude apically (Fig. 5G, H). Retrolateral branch (Rap) longer than Pap and curved towards it. Subapical region straight and median region slightly narrower; retroventral surface with a subapical megaspine that protrudes apically (Fig. 5G, H).

Opisthosoma: Dorsal surface covered with short jet-black setae in life (Reichling & West, 1996), intermixed with long setae (Fig. 5C). Under the short jet-black setae, there is located coppery brown pubescence, which corresponds to the urticating setae.

Urticating setae: Type I, with region "A" long and "B" short.

Pedipalpal bulb: Median ventral area with a shallow depression (Fig. 6A). Embolus short, slightly curved towards retrolateral face, with dorsal median region slightly concave and distally flat (Fig. 6A, C). Embolus with nine keels (Fig. 6D, E): (1) apical keel (A) very reduced and semitransparent (Fig. 6E); (2) subapical (SA) fully serrated, extending for more than half of embolus length and retrolaterally curved distally (Fig. 6B); (3–4) prolateral inferior (PI) and prolateral superior (PS) sharp and thin, extending for more than half of embolus length, PS thin and not extending beyond the dorsal plane of embolus (Fig. 6A); (5) retrolateral superior (RS) forming dorsal edge of embolus, sharp, and heavily sclerotized only on its median portion (Fig. 6B); (6) retrolateral median (RM) thin, extending for more than half of embolus length, distally fused with PS and PI and together form the tip of embolus (Fig. 6B); (7) retrolateral inferior (RI) thicker on its median portion (Fig. 6B), distally semitransparent (Fig. 6E); (8–9) spermatic pore keels (SP) semitransparent, surrounding the seminal duct opening; the retrolateral is longer than the prolateral, curved, parallel to A keel, and it extends to the distal region of SA (Fig. 6E).

Measurements: Total length (prosoma + opisthosoma): 32.66. Leg span (measured from apex of right tarsus I to apex of right tarsus IV): 130.38. Carapace: length 15.62, width 13.89, carapace width/length 0.89. Ocular tubercle: height 0.78, length 1.48, width 1.90. Eye sizes and interocular distances: AME 0.42; ALE 0.26 × 0.50; PME 0.17 × 0.25; PLE 0.34 × 0.49; AME–AME 0.27; AME–ALE 0.10; AME–PME 0.13, ALE–ALE 1.15, ALE–PME 0.21, PME–PME 0.98; PME–PLE 0.05; PLE–PLE 1.35; PLE–AME 0.30, PLE–ALE 0.24. Fovea: width 1.79. Labium: length 2.10, width 2.45. Chelicerae: length 7.43, width 5.36. Sternum: length 7.21, width 5.60. Leg lengths (femur, patella, tibia, metatarsus, tarsus, total): I: 15.78, 7.80, 12.66, 13.32, 8.59, 58.15; II: 14.10, 6.37, 10.67, 11.19, 8.03, 50.36; III: 12.28, 6.24, 9.21, 12.66, 7.87, 48.26; IV: 15.32, 6.29, 13.19, 18.34, 9.23, 62.37. Pedipalp: 8.72, 5.17, 8.15, –, 3.29, 25.33. Leg formula IV, I, II, III. Leg widths: femora I–IV: 3.28, 3.05, 3.86, 3.15, pedipalp 2.44; patellae I–IV: 3.14, 2.90, 2.95, 3.07, pedipalp 2.54; tibiae I–IV: 2.33, 2.55, 2.55, 2.81, pedipalp 2.68; metatarsi I–IV 1.73, 1.66, 1.81, 1.99; tarsi I–IV: 1.90, 1.66, 1.61, 1.44, pedipalp 2.51. Abdomen: length 17.04, width 13.43. Spinnerets: PMS: length 1.75, width 0.80; PMS–PMS: – (the spinnerets are detached from abdomen); PLS: basal 2.52, median 2.58, distal 3.01; width: 1.07, 0.99, and 0.78 respectively. Palpal bulb: length 3.88; tegulum length 1.94, height 2.02; embolus length 1.94, width 0.80.

Description (female paratype).—*Prosoma:* Carapace light brown in life (Reichling & West 1996); surface covered with short, fine, yellow setae, slightly longer marginally (Fig. 7A). Carapace shape as for holotype; caput slightly elevated (Fig. 7A). Fovea slightly recurved (Fig. 7A). Anterior eye row procurved; posterior eye row slightly recurved (Fig. 7D). Ocular tubercle wider than long; clypeus very narrow (Fig. 7D). Chelicerae longer than wide. Prolateral furrow of chelicerae: left with 13 teeth (proximal to distal: 11, 12 largest; 1, third, 3, 6, 8–10, 13 medium-sized; 2, 4, 7 smallest); right with 13 teeth (proximal to distal: 11, 12 largest; 1, 3, 5, 7–10, 13 medium-sized; 2, 4, 6 smallest). Labium wider than long, with 108 cuspules anteriorly (Fig. 7E). Labio-sternal mounds as for holotype (Fig. 7E). Maxillae longer than wide; left maxilla with 231 cuspules, right with 236 cuspules on baso-prolateral region (Fig. 7E). Sternum as for holotype; with three pairs of oval sigilla located close to basal-retrolateral region of coxae I–III; third sigilla largest (Fig. 7B).

Legs: Coxae, trochanters, patellae, tibiae, metatarsi, and tarsi of legs I–IV and pedipalp light brown in life; femora of legs I–II and pedipalp dark brown; patellae, tibiae, metatarsi, and tarsi of legs III and IV dark brown, femora black (Reichling & West 1996). Coxae ventrally covered with short, fine, grey setae interspersed with long brown setae. Coxae I–IV prolaterally covered with cuneiform thorn-like setae, which on coxae II–IV are extended ventrally (Fig. 7F). Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae. Proventral surfaces of femora II–IV with elongated spiniform setae (Fig. 7G). All other segments are covered with small, yellow setae interspersed with longer brown setae. Femur III thickened with respect to femora I–II, IV. Tibia III slightly thickened, tibia IV strongly thickened with respect to tibiae I–II (Fig. 7H). Femur IV slightly longer than metatarsus IV. Tarsal scopulae I–IV entire. Metatarsal scopulae I–III entire, IV divided by setae. Metatarsal scopulae extension: I complete; II 0.87; III 0.57; IV 0.12.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa). Leg II: p (coxa, trochanter, femur); r (coxa). Leg III: p (coxa, trochanter); r (coxa). Leg IV: p (coxa); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (trochanter, baso-retrolateral face of femur). Leg I: p (trochanter, femur). Leg II: p (trochanter, femur).

Leg spination: Pedipalp: femur p0–0–1d, tibia v0–1p–1a, p0–1–2. Leg I: metatarsus v0–0–1a. Leg II: tibia v0–0–1ap, metatarsus v1–0–2a(1p). Leg III: tibia v0–1p–2a, p0–1–1, r0–1–1, metatarsus v2–0–2a(1p, 1r), p1–1–1, r0–1–1. Leg IV: femur d0–0–1r, tibia v0–1–2a, r1–1–1, metatarsus v15(5a), p0–1–1, r0–1–1.

Opisthosoma: Dorsal surface covered with short thin, brown setae, interspersed with long orange setae (Fig. 7C). Under the short brown setae, there is located dark brown pubescence, which corresponds to the urticating setae. Ventrally covered with short and long black setae.

Urticating setae: Type I, with region "A" long and "B" short.

Genitalia: Spermathecae composed of two seminal receptacles partially fused by a heavily sclerotized median region (Fig.

Table 1.—Variation in the type specimens of *Crassicrus lamanai* Reichling & West, 1996.

Measurement	♂ Holotype, 2 ♂ Paratype	5 ♀ Paratypes
Total length	30.24–33.39	39.38–48.90
Carapace length	15.65–17.66	15.23–21.79
Carapace width	13.89–15.75	13.51–18.75
Carapace width/length	0.89–0.97	0.81–0.89
Cheliceral teeth	11–12	12–14
Labial cuspules	24–64	82–122
Maxillary cuspules	134–199	202–290
Palpal bulb length	3.88–3.96	–
Embolus width/length	0.51–0.61	–
Spermathecal bulbs width/length	–	0.94–0.98
Spermathecal base width/length	–	2.17–2.29

7I, J); each SB subquadrate, slightly wider than long (Fig. 7I, J); SS as wide as SB.

Measurements: Total length (prosoma + opisthosoma): 45.37. Leg span (measured from apex of left tarsus I to apex of left tarsus IV): 120.17. Carapace: length 21.79, width 18.75, carapace width/length 0.83. Ocular tubercle: height 1.03, length 1.84, width 2.28. Eye sizes and interocular distances: AME 0.51; ALE 0.27 × 0.51; PME 0.29; PLE 0.28 × 0.47; AME–AME 0.32; AME–ALE 0.29; AME–PME 0.38, ALE–ALE 1.80, ALE–PME 0.53, PME–PME 1.19; PME–PLE 0.17; PLE–PLE 1.53; PLE–AME 0.49, PLE–ALE 0.38. Fovea: width 3.33. Labium: length 2.38, width 3.58. Chelicerae: length 9.64, width 8.24. Sternum: length 10.42, width 8.40. Leg lengths (femur, patella, tibia, metatarsus, tarsus, total): I: 14.69, 9.20, 10.26, 9.91, 6.86, 50.92; II: 13.92, 8.34, 8.54, 9.26, 6.89, 46.95; III: 12.52, 7.62, 7.93, 10.33, 6.44, 44.84; IV: 15.94, 8.52, 11.40, 15.31, 7.13, 58.30. Pedipalp: 10.87, 6.71, 7.97, –, 7.53, 33.08. Leg widths: femora I–IV: 3.62, 3.71, 4.09, 3.83, pedipalp 2.94; patellae I–IV: 3.72, 3.80, 3.77, 4.11, pedipalp 3.03; tibiae I–IV: 3.04, 2.82, 3.46, 5.32, pedipalp 2.93; metatarsi I–IV: 2.45, 2.29, 2.02, 2.55; tarsi I–IV: 1.95, 2.13, 2.00, 2.04, pedipalp 2.45. Abdomen: length 23.22, width 19.51. Spermatheca: Base: length 1.62, width 3.67; SB: length 1.09, width 1.11; SS: width 1.13; SB–SB: 1.23. Spinnerets: PMS: length 2.45, width 1.22; PMS–PMS: 0.98; PLS: basal 3.64, median 2.52, distal 3.50; width: 1.85, 1.64, 1.05 respectively.

Distribution.—Known only from Belize, in the Orange Walk District (near Lamanai Forest Reserve) and Cayo District (Hummingbird Highway) (Reichling & West 1996) (Fig. 2).

Natural history.—According to Reichling & West (1996), this species prefers open areas such as corn and banana plantations. The burrows they found were straight and almost perpendicular to the surface. The mature males started appearing during the last days of June and were abundant in September. The females built egg sacs with approximately 350–400 eggs in March. *Crassicrus lamanai* is often sympatric with *Brachypelma vagans* (Ausserer, 1875).

Variation.—In the male paratypes the shape of the embolus and tegulum is constant, but there is variation in the number of keels present on the retrolateral face of the embolus, which can be three, as on the holotype, or four, having one underdeveloped and weakly sclerotized keel between RI and SA keels (Fig. 6F). We did not assign a name to this structure because there is no evidence of any other equivalent keel to assume primary homology. Also, because its presence is not constant in the male specimens of this species, and its low structural complexity, this keel could be a characteristic unique to certain individuals. See Tables 1–3 for details of size variation in different characters.

Crassicrus bidxigui sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:C6888BAF-89FB-419A-924F-2C8605903144
(Figs. 8–10)

Type material.—*Holotype male.* MEXICO: *Oaxaca*: Tolosa Donají, Matías Romero Avendaño municipality, 1–12 September 1947, B. Malkin (AMNH).

Table 2.—Variation in the lengths and widths of appendage segments for three adult males of the type series of *Crassicrus lamanai* Reichling & West, 1996. Segments with the data in bold were considered as thickened.

Segment	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Length					
Femur	8.72–9.57	15.78–16.57	14.10–15.03	12.28–13.01	15.32–16.65
Patella	5.17–5.80	7.80–8.41	6.37–7.72	6.24–6.86	6.29–7.68
Tibia	8.15–8.54	12.37–13.05	10.67–11.39	9.63–9.71	13.19–13.80
Metatarsus	–	12.83–13.41	11.19–12.81	12.66–13.24	18.34–19.74
Tarsus	3.29–3.99	8.59–9.20	8.03–8.95	7.87–8.35	9.23–9–90
Total	25.33–27.67	58.15–60.64	50.36–55.90	48.26–51.17	62.37–67.77
Width					
Femur	2.44–2.96	3.28–3.93	3.05–3.86	**3.86–4.16**	3.15–3.99
Tibia	2.68–3.12	2.33–2.97	2.50–2.62	2.55–2.99	**3.46–3.77**

Table 3.—Variation in the lengths and widths of appendage segments for five adult females of the type series of *Crassicrus lamanai* Reichling & West, 1996. Segments with the data in bold were considered as thickened.

Segment	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Length					
Femur	8.72–10.19	11.73–14.69	10.24–13.92	9.59–12.52	12.50–15.94
Patella	5.31–6.71	6.63–9.20	6.00–8.34	5.55–7.62	5.99–8.71
Tibia	5.51–7.97	8.00–10.26	7.11–8.54	6.20–7.89	9.53–11.68
Metatarsus	–	7.76–9.92	7.84–9.47	8.14–10.33	11.62–15.32
Tarsus	6.26–7.53	4.69–6.86	4.66–6.89	5.61–6.25	5.73–7.13
Total	25.94–33.08	38.81–49.17	35.85–46.95	34.09–44.84	45.37–58.30
Width					
Segment	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Femur	2.38–3.40	3.18–4.03	3.09–3.87	**3.57–4.38**	3.45–4.29
Tibia	2.16–3.11	2.78–3.14	2.27–3.02	2.45–3.29	**4.09–5.48**

Paratypes. MEXICO: *Oaxaca*: 1 ♂, same data as holotype except 23–20 August 1947, B. Malkin (AMNH); 3 ♀, Palomares, Matías Romero Avendaño municipality, July–August 1909, A. Petrunkevitch (AMNH); 1 ♀, same data except 23 July 1909, A. Petrunkevitch (AMNH); 1 ♀, outside Escuela Técnica Secundaria 104, Tolosa Donají, Matías Romero Avendaño municipality, 17.2299°N, 95.05808°W, 71 m, 05 April 2014, C. Santibáñez, J. Cruz, D. Candia, A. Guzmán, L. Gómez (CNAN–T1094); 1 ♀, Piedra Blanca, San Juan Guichicovi municipality, 16.98883°N, 95.01451°W, 123 m, 11 December 2010, S. Longhorn, J. Mendoza, E. Goyer, E. Hijmensen (CNAN–T1005). 1 ♀, same data except (CNAN–T1006). *Veracruz*: 1 ♂, Hacienda La Oaxaqueña, 30 km SW

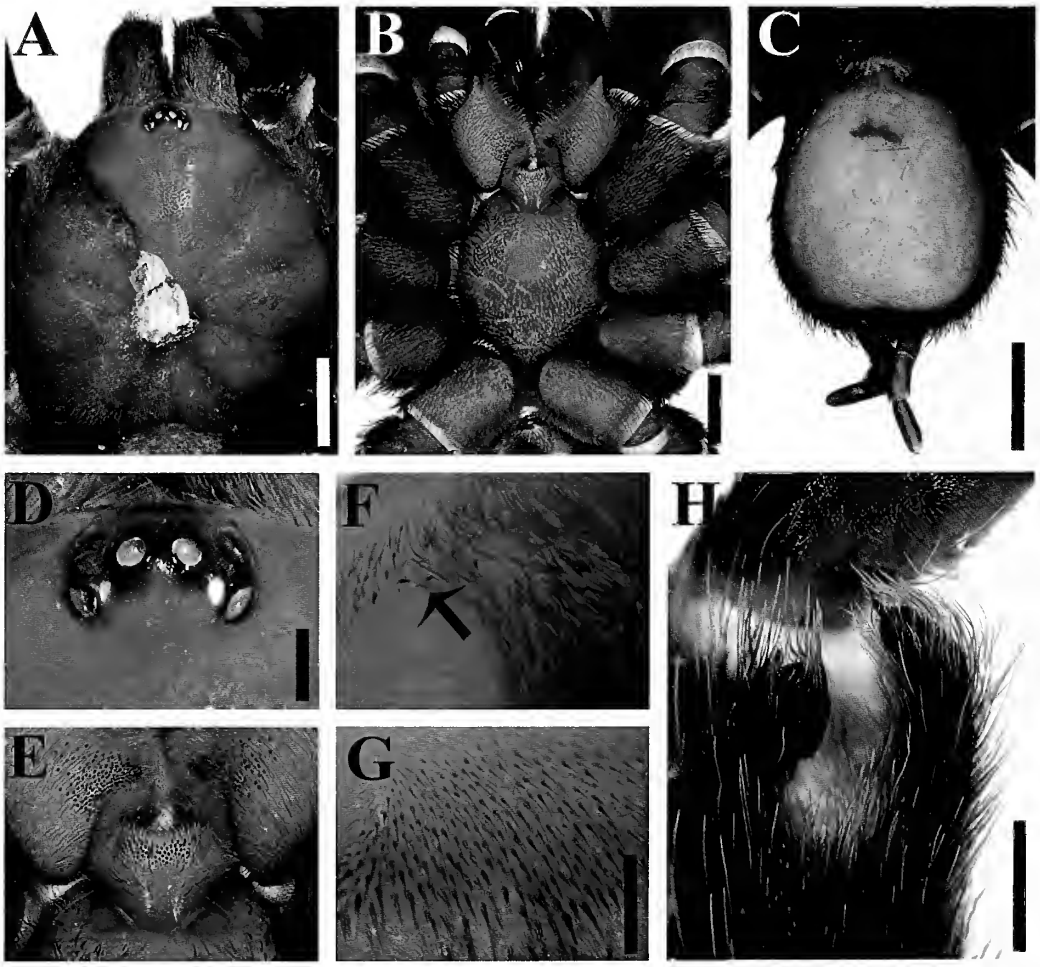

Figure 8.—*Crassicrus bidxigui* sp. nov. male holotype: A. Carapace. B. Prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Labium, maxillae, and labio-sternal mounds. F. Spiniform setae (arrow) on retrolateral superior region of coxa I. G. Conical spiniform setae on prolateral face of coxa I. H. Tibial apophyses, ventral view. Scale bars: 0.5 mm (F–G), 2 mm (D, H), 3 mm (E), 5 mm (A–C).

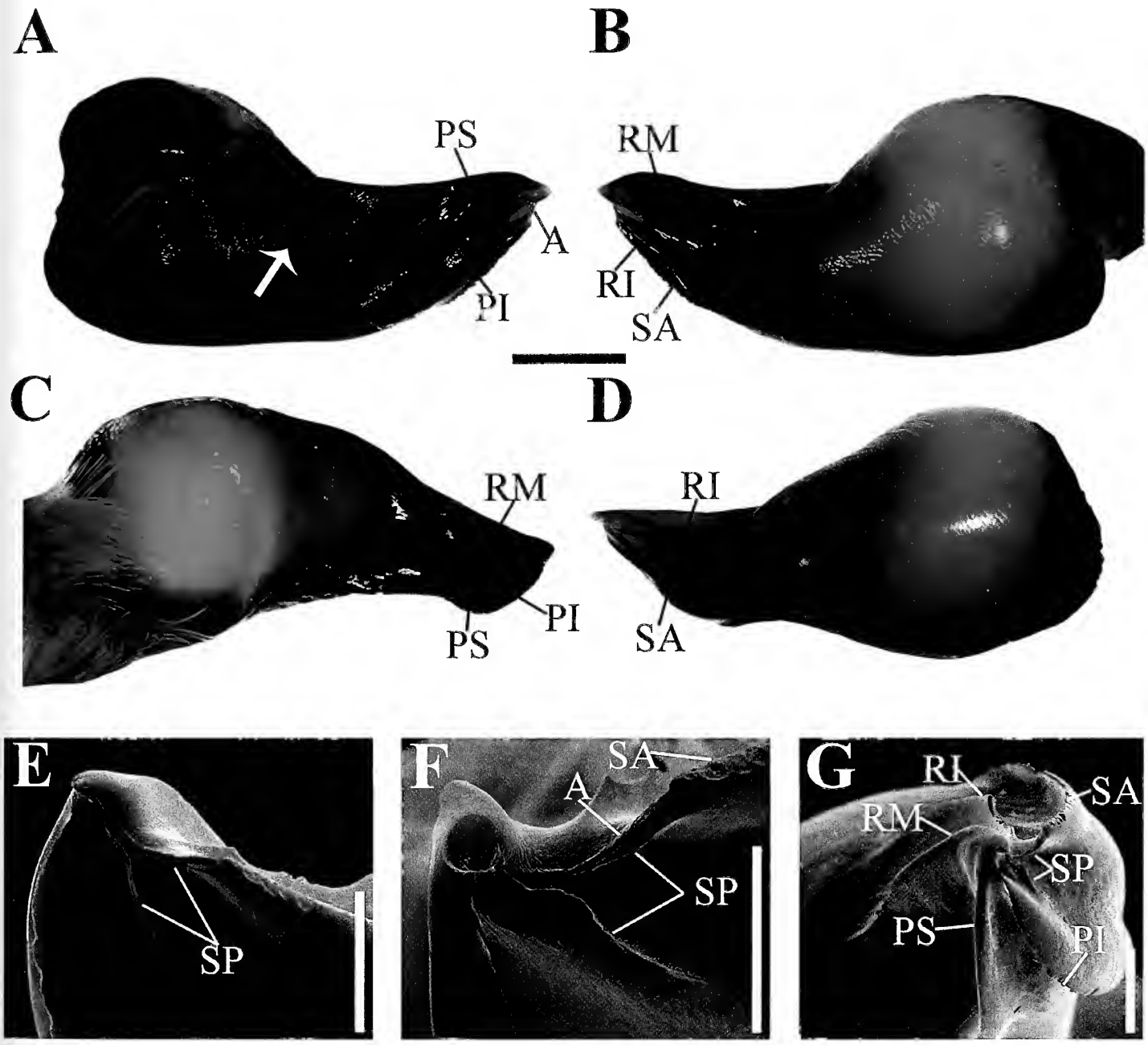

Figure 9.—Palpal bulb of males of *Crassicrus bidxigui* sp. nov. A–D. Holotype: A. Prolateral view. B. Retrolateral view. C. Dorsal view. D. Ventral view. E–G. Apical region of embolus of male from Tolosa Donají, Matías Romero Avendaño, Oaxaca: E. prolatero-ventral view. F. Detail of spermatic pore keels. G. Antero-dorsal region. Arrows point to striations on prolateral face of the bulb. Abbreviations: A = apical keel; PI = prolateral inferior keel; PS = prolateral superior keel; RI = retrolateral inferior keel; RM = retrolateral median keel; SP = spermatic pore keels. Scales: 100 μm (F), 250 μm (E, G), 1 mm (A–D).

from Jesús Carranza, Coatzacoalcos river, Jesús Carranza municipality, 15 October 1939, C. M. Bogert (AMNH).

Other material examined.—MEXICO: *Oaxaca*: 1 ♂, Tolosa Donají, Matías Romero Avendaño municipality, 1–12 September 1947, B. Malkin (AMNH); 1 juvenile, Piedra Blanca, San Juan Guichicovi municipality, 16.98883°N, 95.01451°W, 123 m, 5 April 2014, D. Candia, J. Cruz, L. Gómez, A. Guzmán, C. Santibáñez (CNAN–Ar010116).

Etymology.—The specific name is a noun in apposition in Zapotec, one of the many languages spoken in the Isthmus of Tehuantepec region, where this species was collected. "Bidxiguí" means spider in Zapotec.

Diagnosis.—*Crassicrus bidxigui* sp. nov. can be distinguished from all other congeners except *C. tochtli* sp. nov. and *C. cocona* sp. nov. by having a convex sternum (Figs. 8B, 10B). It is distinguished from *C. cocona* sp. nov. by lacking visible sternal sigilla, and by having proportionately shorter coxae I (Figs. 8B, 10B). It is distinguished from *C. tochtli* sp. nov. by having the coxal spiniform setae only on the baso-prolateral face of the segment, and these setae are larger on coxae III and IV. The males can be further distinguished from

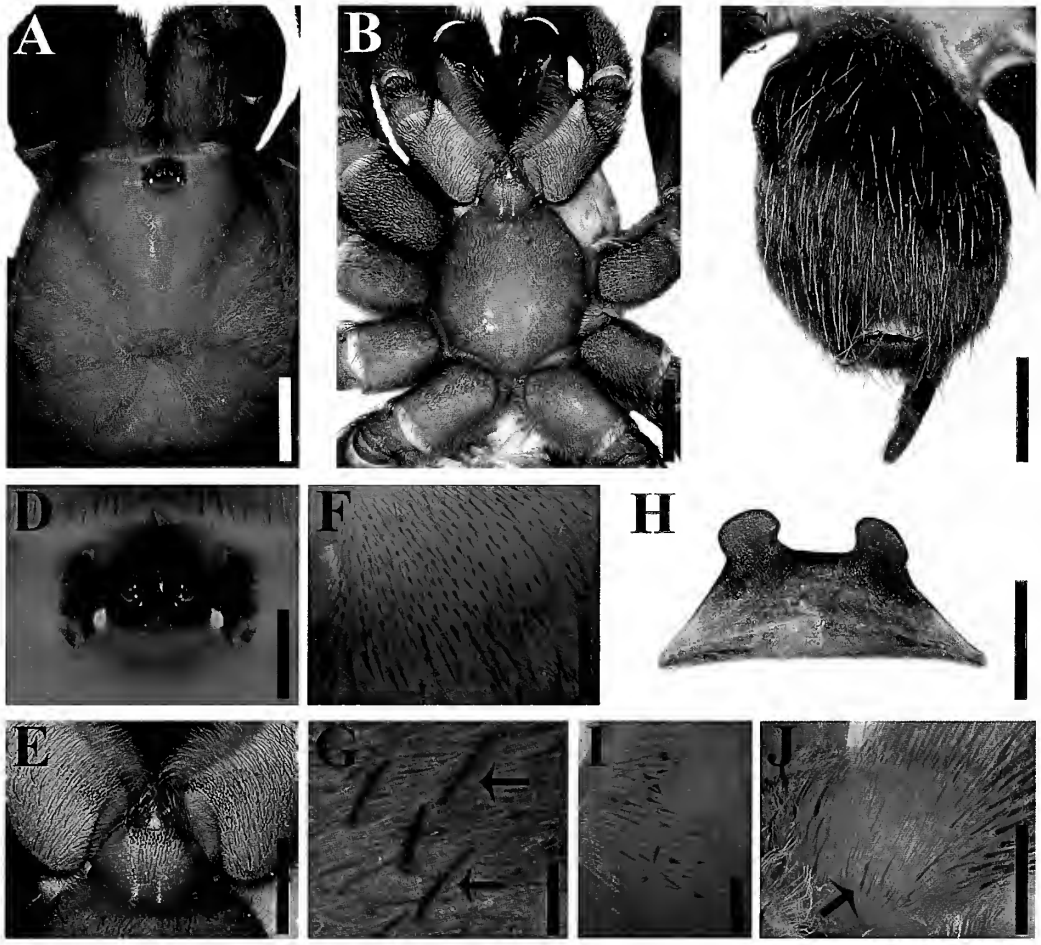

Figure 10.—*Crassicrus bidxigui* sp. nov. female paratype: A. Carapace. B. Prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Labium, maxillae, and labio-sternal mounds. F. Spiniform setae on prolateral face of coxa I. G. Spiniform setae (arrows) on prolatero-ventral face of femur III. H. Spermathecae, dorsal view. I. Spiniform setae on retrolateral superior region of coxa I. J. Spiniform setae (arrow) protruding from the thin plumose setae on prolateral face of trochanter I. Scale bars: 0.25 mm (G), 0.5 mm (I), 1 mm (D, F, J), 2 mm (H), 3 mm (E), 5 mm (A–C).

those of *C. tochtli* sp. nov. by the presence of striations on the prolateral face of the palpal bulb, and by having the PS keel wide and extending proximally beyond the dorsal body of the embolus (Fig. 9A). The females can be further distinguished from those of *C. tochtli* sp. nov. by having a more curved edge on the median upper region of the spermathecae (Fig. 10H), by having thinner spiniform setae on the pro-ventral faces of femora II–IV, and by having femur IV longer than metatarsus IV.

Description (male holotype).—*Prosoma:* Dorsal surface covered with short grey setae, interspersed with thicker brown setae (Fig. 8A). Carapace semi-chordate, without pronounced boss. Caput slightly elevated (Fig. 8A). Fovea damaged. Anterior eye row procurved, posterior eye row slightly recurved (Fig. 8D). AME rounded, ALE, PME and PLE oval (Fig. 8D). Ocular tubercle wider than long; clypeus very narrow (Fig. 8D). Anterior margin of carapace covered with fine white setae interspersed with thicker yellow setae (Fig. 8D). Chelicerae longer than wide, surface covered with fine grey setae interspersed with long brown setae. Prolateral furrow of chelicerae: left: with 12 teeth (proximal to distal: 1, 3, 10, 11 largest; 5, 7–9, 12 medium-sized; 2, 4, 6 smallest); right with 13 teeth (proximal to distal: 3, 10–12 largest; 1, 5, 7–9, 13 medium-sized; 2, 4, 5 smallest). Labium wider than long, with 60 cuspules anteriorly (Fig. 8E). Labio-sternal mounds semicircular and separated (Fig. 8E). Maxillae longer than wide; left with 134 cuspules, right with 154 cuspules on baso-prolateral region (Fig. 8E). Sternum slightly longer than wide, convex; surface covered with short and long black setae; sigilla not visible (Fig. 8B).

Legs: Ventral surface of coxae covered with small fine grey setae, intermixed with short and long brown setae. Prolatero-basal surface of coxae I–IV covered with cuneiform thorn-like setae, thicker ventrally; these setae are noticeably larger on coxae III and IV (Fig. 8G). Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae (Fig. 8F). All other segments are covered with short fine grey setae and long brown setae. Femur III

thickened with respect to femora I–II, IV. Tibia IV not thickened. Metatarsus IV longer than femur IV. Tarsal scopulae I–IV entire. Metatarsal scopulae I–III entire, IV divided by long setae. Metatarsal scopulae extension: I complete, II: 0.82; III: 0.62; IV: 0.29. Metatarsus I straight; when flexed it touches the retrolateral face of Rap.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg I: p: (coxa, trochanter, femur); r (coxa, trochanter). Leg II: p (coxa, trochanter, femur); r (coxa, trochanter). Leg III: p (coxa, trochanter); r (coxa). Leg IV: p (coxa, trochanter); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur). Leg II: p (coxa, trochanter, femur).

Leg spination: Pedipalp: femur p0–0–2d, patella p1, tibia v0–1–2a(1p), p1–3–8(4a, 1d). Leg I: femur p0–0–1, tibia v0–1–1a, p0–1–1, metatarsus v0–0–1a. Leg II: femur p0–0–1d, tibia v0–1–2a, p1–1–1, metatarsus v0–0–1a, p0–0–1. Leg III: femur d0–0–2, patella r1, tibia v1–1–1, p2–3–3(2a), r1–1–1, metatarsus v2–3–1a, p1–1–1v, r1v–1–1d. Leg IV: femur d0–0–1r, tibia v2–3–3(2ap), p1–4–3(2a), r1–1–1, metatarsus v29(6a), p0–1–1, r1–2–1.

Leg I tibial apophyses: Tibia I with two branches that do not originate from a common base (Fig. 8H). Prolateral branch (Pap) short, slightly curved to the retrolateral branch (Rap); retrolateral face with a megaspine that does not protrude apically (Fig. 8H). Rap longer than Pap and curved towards it. Median region of Rap slightly narrower (Fig. 8H); ventro-retrolateral surface with a subapical megaspine that protrudes apically (Fig. 8H).

Opisthosoma: Laterally covered with thin brown setae, interspersed with long, thick, yellow setae (Fig. 8C). Dorsal median region with few setae on the area where the urticating setae patch should be located; not unexpected given the age of the museum specimen (Fig. 8C).

Urticating setae: Type I, with region "A" very long and "B" short.

Pedipalpal bulb: Bulb with striations on prolateral face of tegulum (Fig. 9A); ventral region flat. Embolus short, slightly curved towards retrolateral face (Fig. 9E), with dorsal median region concave and distally flat (Fig. 9A–C). Embolus with eight keels (Fig. 9G): (1) apical keel (A) very reduced and semitransparent (Fig. 9D); (2) subapical (SA) fully serrated; extending for more than half of embolus length and distally is retrolaterally curved (Fig. 9A, B); (3–4) prolateral inferior (PI) and prolateral superior (PS) keels sharp and wide, extending for more than half of embolus length (Fig. 9A); PS extending beyond the dorsal plane of embolus; (5–6) retrolateral inferior (RI) and retrolateral median (RM) keels sharp and wide, extending for more than half of embolus length (Fig. 9B). RM more developed than RI; distally fused with PS and together form the tip of embolus; (7, 8) spermatic pore keels (SP) semitransparent, surrounding the seminal duct opening (Fig. 9D, E); the retrolateral keel is longer than the prolateral, curved, parallel to A, and it extends to the distal region of SA (Fig. 9D–F).

Measurements: Total length (prosoma + opisthosoma): 32.79. Leg span (measured from apex of right tarsus I to apex of right tarsus IV): 126.23. Carapace: length 17.82, width 16.36, carapace width/length 0.92. Ocular tubercle: height 0.90, length 1.89, width 2.4. Eyes sizes and interocular distances: AME 0.32; ALE 0.40 × 0.65; PME 0.22 × 0.36; PLE 0.30 × 0.46; AME–AME 0.22; AME–ALE 0.14; AME–PME 0.22, ALE–ALE 1.40, ALE–PME 0.43, PME–PME 1.18; PME–PLE 0.03; PLE–PLE 1.53, PLE–AME 0.48, PLE–ALE 0.23. Labium: length 2.16, width 3.6. Chelicerae: length 7.24, width 5.95. Sternum: length 9.0, width 8.45. Legs length (femur, patella, tibia, metatarsus, tarsus, total): I: 15.78, 8.72, 11.84, 12.24, 8.27, 56.85; II: 14.83, 7.23, 10.82, 11.14, 8.05, 52.07; III: 13.08, 6.62, 9.05, 12.56, 7.33, 48.64; IV: 15.98, 7.27, 12.79, 17.9, 8.78, 62.72. Pedipalp: 9.7, 5.4, 8.33, –, 4.16, 27.59. Leg formula: IV, I, II, III. Leg widths: femora I–IV: 3.75, 3.72, 4.2, 3.69, pedipalp: 2.91; patellae I–IV: 3.15, 2.97, 3.03, 3.26, pedipalp: 2.74; tibiae I–IV: 3.43, 3.24, 3.14, 3.07, pedipalp: 3.2; metatarsi I–IV 2.27, 2.23, 2.22, 2.05; tarsi I–IV: 2.18, 1.98, 1.83, 1.87, pedipalp: 2.31. Abdomen: length 15.24. Spinnerets: PMS: length 2.13, width 0.93; PMS–PMS: 1.17; PLS: basal 3.2, median 2.05, distal 3.65; width: 1.1, 0.5, and 0.85 respectively. Palpal bulb: length 4.50; tegulum: length 2.24, height: 2.26; embolus: length: 2.26, width: 1.30.

Description (female paratype).—*Prosoma:* Dorsal surface covered with short white setae; marginally intermixed with longer setae (Fig. 10A). Carapace shape as for holotype; caput slightly elevated (Fig. 10A). Fovea not very deep, straight. Anterior eye row procurved; posterior eye row slightly recurved (Fig. 10D). Ocular tubercle wider than long; clypeus very narrow (Fig. 10D). Chelicerae longer than wide. Prolateral furrow of chelicerae: left with 14 teeth (proximal to distal: 2, 4, 11–14 largest; 5–6, 8–10 medium-sized; 1, 3, 7 smallest); right with 14 teeth (proximal to distal: 1, 3, 11–14 largest; 4, 6, 8–10, 13 medium-sized; 2, 5, 7 smallest). Labium wider than long, with 61 cuspules anteriorly (Fig. 10E). Labiosternal mounds as for holotype (Fig. 10E). Maxillae longer than wide; left with 124 cuspules, right with 128 cuspules on baso-prolateral region (Fig. 10E). Sternum as for holotype, surface covered with short grey setae and long brown setae; sigilla not visible (Fig. 10B).

Legs: Ventral surface of coxae covered with short fine white setae and brown long setae. Prolateral surface of coxae I–IV covered with cuneiform thorn-like setae, thicker ventrally (Fig. 10F). Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae (Fig. 10I). Prolateral and prolatero-dorsal surfaces of coxae and trochanters I–IV with long spiniform setae (Fig. 10J). Prolatero-ventral surface of femora II–IV covered with elongated sharp spiniform setae (Fig. 10G). All other segments are covered with short yellow setae and long brown setae. Femur III thickened with respect to femora I–II, IV. Tibia IV not thickened. Femur IV longer than metatarsus IV. Tarsal scopulae I–III entire, IV with a row of setae. Metatarsal scopulae I–III entire, IV divided by setae. Metatarsal scopulae extension: I: complete; II: 0.96; III: 0.66; IV: 0.19.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa, trochanter). Leg II: p (coxa, trochanter, femur); r (coxa, trochanter). Leg III: p (coxa, trochanter; r (coxa). Leg IV: p (coxa, trochanter); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (trochanter). Leg I: p (trochanter, femur). Leg II: p (trochanter, femur).

Table 4.—Variation in the type specimens of *Crassicrus bidxigui* sp. nov.

	Crassicrus bidxigui	
Specimens	♂ Holotype and 2 ♂ Paratypes	6 ♀ Paratypes
Total length	32.01–33.06	29.47–40.20
Carapace length	16.25–17.82	14.68–19.88
Carapace width	15.01–16.36	12.46–16.65
Carapace width/length	0.85–0.92	0.83–0.94
Sternum length	9.00–9.45	8.10–9.45
Sternum width	8.40–8.45	7.95–9.50
Sternum width/length	0.89–0.93	0.93–0.98
Chelicerae teeth	12–13	11–14
Labial cuspules	60–74	49–127
Maxillary cuspules	124–158	112–181
Bulb length	4.30–4.50	–
Embolus width/length	0.53–0.62	–
Spermathecae bulbs width/length	–	1.20–1.47
Spermathecae base width/length	–	2.44–3.38

Leg spination: Pedipalp: femur d0–0–2, tibia v0–0–3a(1p, 2r), p0–2–2. Leg I: femur p0–0–1ad, metatarsus v0–0–1a. Leg II: tibia v1–0–2a(1p), p0–1–0, metatarsus v1–0–2a(1p). Leg III: femur d0–0–1r, tibia v0–0–2a, p0–2–2, r0–1–0, metatarsus v0–1–3a(1p, 2r), p1–1–1, r0–1–1. Leg IV: femur d0–0–1r, tibia v0–0–2a, p0–2–0, r1–1–1, metatarsus v15(6a), p0–1–1, r0–1–1.

Opisthosoma: Dorsal surface covered with short coppery brown setae, interspersed with long yellow setae (Fig. 10C). Under the coppery brown short setae, there is located dark brown pubescence, which corresponds to the urticating setae.

Urticating setae: Type I, with region "A" long and "B" short.

Genitalia: Spermathecae composed of two seminal receptacles partially fused by a heavily sclerotized median region with a wide, slightly curved superior border (Fig. 10H). SB wider than long; SS slightly narrower than SB.

Measurements: Total length (prosoma + opisthosoma): 37.03. Leg span (measured from apex of right tarsus I to apex of right tarsus IV): 103.81. Carapace: length 17.94, width 15.06, carapace width/length 0.84. Ocular tubercle: height 0.83, length 1.70, width 2.35. Eye sizes and interocular distances: AME 0.34; ALE 0.30 × 0.52; PME 0.16 × 0.25; PLE 0.32 × 0.36; AME–AME 0.38; AME–ALE 0.34; AME–PME 0.28, ALE–ALE 1.46, ALE–PME 0.43, PME–PME 1.24; PME–PLE 0.14; PLE–PLE 1.80; PLE–AME 0.62, PLE–ALE 0.38. Fovea: width 2.60. Labium: length 2.75, width 3.65. Chelicerae: length 9.38, width 6.73. Sternum: length 9.45, width 9.50. Legs length (femur, patella, tibia, metatarsus, tarsus, total): I: 12.44, 7.22, 8.91, 7.71, 5.8, 42.08; II: 11.35, 6.68, 7.56, 7.03, 5.76, 38.38; III: 10.64, 6.30, 7.27, 8.30, 5.54, 38.05; IV: 13.25, 6.63, 10.21, 12.59, 6.23, 48.91. Pedipalp: 8.95, 5.40, 6.32, –, 6.64, 27.31. Leg formula: IV, I, II, III. Leg widths: femora I–IV: 3.08, 3.02, 3.23, 3.06, pedipalp: 2.72; patellae I–IV: 2.96, 2.79, 2.86, 2.81, pedipalp: 2.65; tibiae I–IV: 2.71, 2.25, 2.54, 2.50, pedipalp: 2.64; metatarsi I–IV: 2.24, 1.94, 2.49, 2.92; tarsi I–IV: 2.32, 2.12, 2.22, 2.32, pedipalp: 2.07. Abdomen: length 19.09. Spermathecae: Base: length 1.53, width 4.75; SB: length 0.74, width 0.82; SS: width 0.74; SB–SB: 1.20 Spinnerets: PMS: length 1.97, width 1.00; PMS–PMS: 1.35; PLS: basal 3.22, median 2.40, distal 3.48; width: 1.55, 1.20, and 0.92 respectively.

Distribution.—This species is found in the north-western region of the Isthmus of Tehuantepec in Oaxaca and in southern Veracruz, near the border with Oaxaca (Fig. 2).

Natural history.—Adult males were collected in August, September, and October, so the reproductive season of this species includes the rainy season. The localities where this species was found are lower than 150 m in elevation, and contained disturbed vegetation. Some females and juveniles were excavated from straight burrows, approximately 20 cm deep, and surrounded by sparse silk. In the localities where this species was found, individuals of *Brachypelma* sp. were also found and were more abundant.

Variation.—The number of keels is constant in all the male palpal bulbs examined ($n = 6$); however, there is variation in the general morphology of the bulbs, the development of the keels, and the depth of the striations. The width of the PS and RI keels is highly variable. In the spermathecae, the length and the width of the base are variable; however, the shape of the receptacles and BS are constant. See Tables 4–6 for details of size variation in different characters.

Crassicrus tochtli sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:447A8D7F-47F4-45AF-9E9C-36F258398F7E
(Figs 11–13)

Type material.—*Holotype male.* MEXICO: *Veracruz*: Biological Station "Los Tuxtlas", San Andrés Tuxtla municipality, 18.58500° N, 95.0710° W, 139 m, 28 July 2014, D. Candia (CNAN–T0898).

Paratypes. MEXICO: *Veracruz*: 1 ♀, same data as holotype except 08 June 2009, J. Mendoza (CNAN–T0899). 1 ♀ same data except 28 July 2014, D. Candia (CNAN–T1090).

Other material examined.—*MEXICO*: *Veracruz*: 1 ♀, 2 juveniles, same data as holotype except 29 January 2001, C. Durán (CNAN–Ar003662); 1 ♀, "Castle Ranch", Coyame, Catemaco municipality, 30 January 2001, C. Durán (CNAN–Ar003643)

Etymology.—The specific name is a noun in apposition from Nahuatl, which is the language where the name of the type

Table 5.—Variation in the lengths and widths of appendage segments for three adult males of the type series (including the holotype) of *Crassicrus bidxigui* sp. nov. The segment with the data in bold was considered as thickened.

Segment	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Length					
Femur	9.05–9.70	14.90–15.78	13.79–15.00	12.24–13.54	15.06–16.51
Patella	4.91–5.40	7.44–8.72	6.82–7.25	6.17–6.66	6.43–7.27
Tibia	7.27–8.33	11.33–12.58	9.96–10.91	9.05–10.32	12.28–13.51
Metatarsus	–	11.23–12.24	10.69–11.70	11.11–12.70	15.43–17.92
Tarsus	3.30–4.16	7.63–8.27	7.33–8.16	6.91–7.33	7.78–8.78
Total	24.53–36.99	52.53–66.90	48.59–62.96	45.84–59.99	56.98–74.53
Width					
Femur	2.74–2.96	3.52–3.75	3.50–3.72	**4.09–4.20**	1.90–2.22
Tibia	2.93–3.20	2.96–3.43	2.99–3.24	2.90–3.14	2.97–3.26

locality of "Los Tuxtlas" has its origin. The word "tochtli" means rabbit.

Diagnosis.—*Crassicrus tochtli* sp. nov. can be distinguished from all other congeners except *C. bidxigui* and *C. cocona* sp. nov. by the presence of a convex sternum (Figs. 11B, 13B). It is distinguished from *C. cocona* sp. nov. by the absence of visible sigilla on the sternum and by having coxae I relatively shorter (Figs. 11B, 13B). It is distinguished from *C. bidxigui* by the presence of spiniform setae fully covering the prolateral faces of coxae I–IV, which are slightly thinner and shorter on coxae III and IV. The males can be further distinguished from *C. bidxigui* by the presence of thick spiniform setae on the carapace, close to the margin (Fig. 11F), and by the presence of deep striations on the ventral region of the palpal bulb, near the embolus (Fig. 12F). The females can be further distinguished by the presence of a wide, curved superior border medially on the spermathecae (Fig. 13J), and by having metatarsus IV longer than femur IV.

Description (male holotype).—*Prosoma:* carapace dark brown in life. Dorsal surface covered with short black setae (Fig. 11A). Carapace margin covered with grey setae that near the outer region are interspersed with violet setae and with thick spiniform setae, more abundant distally (Fig. 11F). Carapace semi-chordate; without pronounced boss; caput slightly elevated (Fig. 11A). Fovea deep, recurved (Fig. 11A). Anterior eye row slightly procurved; posterior eye row recurved (Fig. 11D). AME rounded, ALE and PME oval, PLE subtriangular. Ocular tubercle wider than long; clypeus very narrow (Fig. 11D). Anterior margin of carapace covered with fine, thick black setae. Chelicerae longer than wide, surface covered with grey setae; dorso-prolateral region covered with fine thin coppery setae, interspersed with thicker blue setae. Prolateral furrow of chelicerae: left with 15 teeth (proximal to distal: 13–14 largest; 1, 3, 5–6, 9–12, 15 medium-sized; 2, 4, 7–8 smallest); right with 14 teeth (proximal to distal: 3, 11–13 largest; 1, 4–5, 8–10, 14 medium-sized; 2, 6–7 smallest). Labium wider than long, surface covered with short and long dark brown setae; with 58 cuspules anteriorly (Fig. 11E). Labio-sternal mounds semicircular and separated (Fig. 11E). Maxillae longer than wide; left with 171 cuspules, right with 148 cuspules on baso-prolateral region (Fig. 11E). Sternum longer than wide, convex; surface covered with short and long black setae; sigilla not visible (Fig. 11B).

Legs: Prolateral surface of coxae I–IV covered with short cuneiform thorn-like setae, thicker ventrally (Fig. 11G). Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae. Coxae and trochanters with scattered violet setae dorsally. Patellae and tibiae with two longitudinal bald stripes dorsally. All other segments covered with short fine, and long black setae. Femur III thickened with respect to femora I–II, IV. Tibia IV not thickened. Metatarsus IV longer than femur IV. Tarsal scopulae I–III entire, IV with a median row of setae. Metatarsal scopulae I–III entire and IV divided by setae. Metatarsal scopulae extension: I complete, II 0.91, III 0.61, IV 0.17. Metatarsus I straight, when flexed touches the lateral face of Rap.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa). Leg II: p (coxa, trochanter,

Table 6.—Variation in the lengths and widths of appendage segments for five adult females of the type series of *Crassicrus bidxigui* sp. nov. The segment with the data in bold was considered as thickened.

Segment	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Length					
Femur	7.95–9.77	10.90–13.90	9.94–12.35	9.31–11.17	11.63–14.44
Patella	4.99–5.53	6.29–7.99	5.58–7.04	5.19–6.59	5.92–6.98
Tibia	5.72–6.42	8.30–9.71	6.93–8.65	6.50–8.01	8.91–10.61
Metatarsus	–	6.42–8.28	6.31–8.54	7.34–9.64	11.04–14.23
Tarsus	5.99–7.04	5.30–6.20	4.87–5.97	5.20–6.50	5.78–7.65
Total	24.85–28.76	37.21–46.08	33.63–42.55	33.61–41.91	43.28–53.87
Width					
Femur	2.18–2.96	2.59–3.08	2.73–3.09	**3.05–3.61**	2.73–2.89
Tibia	2.07–2.76	2.11–2.76	2.03–2.66	2.19–2.83	2.24–2.87

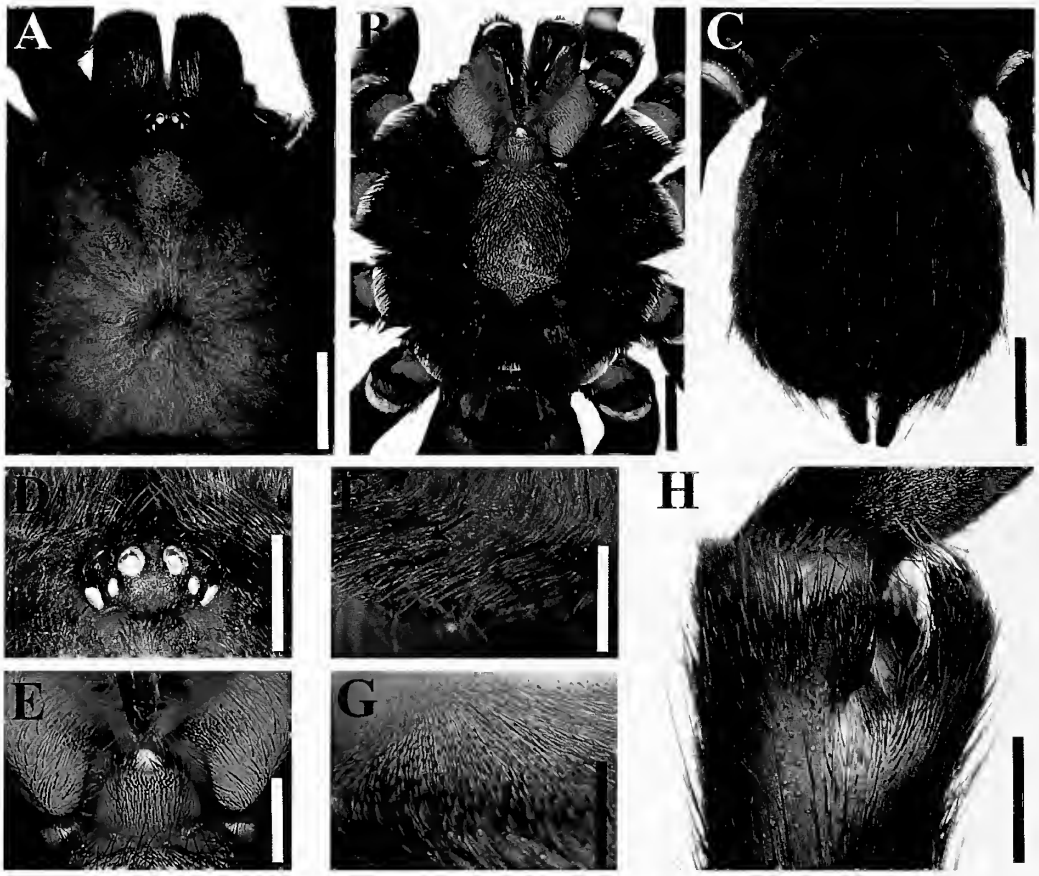

Figure 11.—*Crassicrus tochtli* sp. nov. male holotype: A. Carapace. B. Prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Labium, maxillae, and labio-sternal mounds. F. Spiniform setae (arrow) on carapace border. G. Conical spiniform setae on prolateral face of coxa I. H. Tibial apophysis, ventral view. Scale bars: 0.5 mm (F–G), 2 mm (D, H), 3 mm (E), 5 mm (A–C).

femur); r (coxa). Leg III: p (coxa, trochanter); r (coxa). Leg IV: p (coxa, trochanter); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa). Leg II: p (coxae, trochanter, femur); r (coxa).

Leg spination: Pedipalp: femur p0–0–1d, tibia p2–4–3. Leg I: femur p0–0–1, tibia v0–3(1p)–1a, p1–0–1, metatarsus v0–0–1a. Leg II: femur p0–0–1d, tibia v0–1–3a(1p) p1–1–0, metatarsus v1–0–1a. Leg III: femur p0–0–1d, r0–0–1d, tibia v2(1p)–2–4(2a), p1–1–1, r1–1–0, metatarsus v3–2–3a(1p, 1r), p1–1–1a, r0–1–1. Leg IV: femur r0–0–1d, patella r1, tibia v3–4–3a, p1–1–0, r1–1–1–1a, metatarsus v19(5a), p0–1–1, r1–1–1–1a.

Leg I tibial apophyses: Tibia I with two branches that do not originate from a common base (Fig. 11H). Prolateral branch (Pap) short, thick, and straight; retrolateral face with a megaspine that does not protrude apically (Fig. 11H). Retrolateral branch (Rap) slightly longer than Pap, slightly curved towards it. Base conical, and distally digitiform; ventro-retrolateral face with a subapical megaspine that protrudes apically (Fig. 11H).

Opisthosoma: Dorsally covered with short, thin black setae interspersed with long, thick, brown setae (Fig. 11C). Ventrally with short and long black setae. Under the black short setae there is located coppery brown pubescence, which corresponds to the urticating setae.

Urticating setae: Type I, with region "A" long, and "B" short.

Pedipalpal bulb: Bulb with striations on ventral face of tegulum, close to PI keel (Fig. 12A, D, F), ventral region flat (Fig. 12A, B). Embolus short, slightly curved towards retrolateral face, with dorsal median region concave and distally flat (Fig. 12A, C). Embolus with eight keels: (1) apical keel (A) very short and semitransparent (Fig. 12E); (2) subapical (SA) fully serrated, extending for more than half of embolus length and distally is retrolaterally curved (Fig. 12A, D). (3–4) prolateral inferior (PI) and prolateral superior (PS) sharp and wide, extending for more than half of embolus length (Fig. 12A); the distal half of PS is wide and extends beyond the dorsal plane of embolus (Fig. 12A). (5–6) retrolateral median (RM) and retrolateral inferior (RI) keels strong, slightly wider distally (Fig. 12B); extending for less than half of embolus length; RM distally fused with PS and together form the tip of embolus (Fig. 12B). (7–8) spermatic pore keels (SP) semi-transparent, surrounding the seminal duct opening; the retrolateral longer than prolateral, curved, parallel to A, and it extends to distal region of SA (Fig. 12E).

Measurements: Total length (prosoma + opisthosoma): 35.50. Leg span (measured from apex of left tarsus I to apex of left tarsus IV): 127.48. Carapace: length 18.07, width 15.69, carapace width/length 0.87. Ocular tubercle: height 1.04, length 1.63, width 2.45. Eye sizes and interocular distances: AME 0.48; ALE 0.33 × 0.63; PME 0.18 × 0.31; PLE 0.36 × 0.47; AME–AME 0.32; AME–ALE 0.32; AME–PME 0.14, ALE–ALE 1.42, ALE–PME 0.40, PME–PME 1.23; PME–

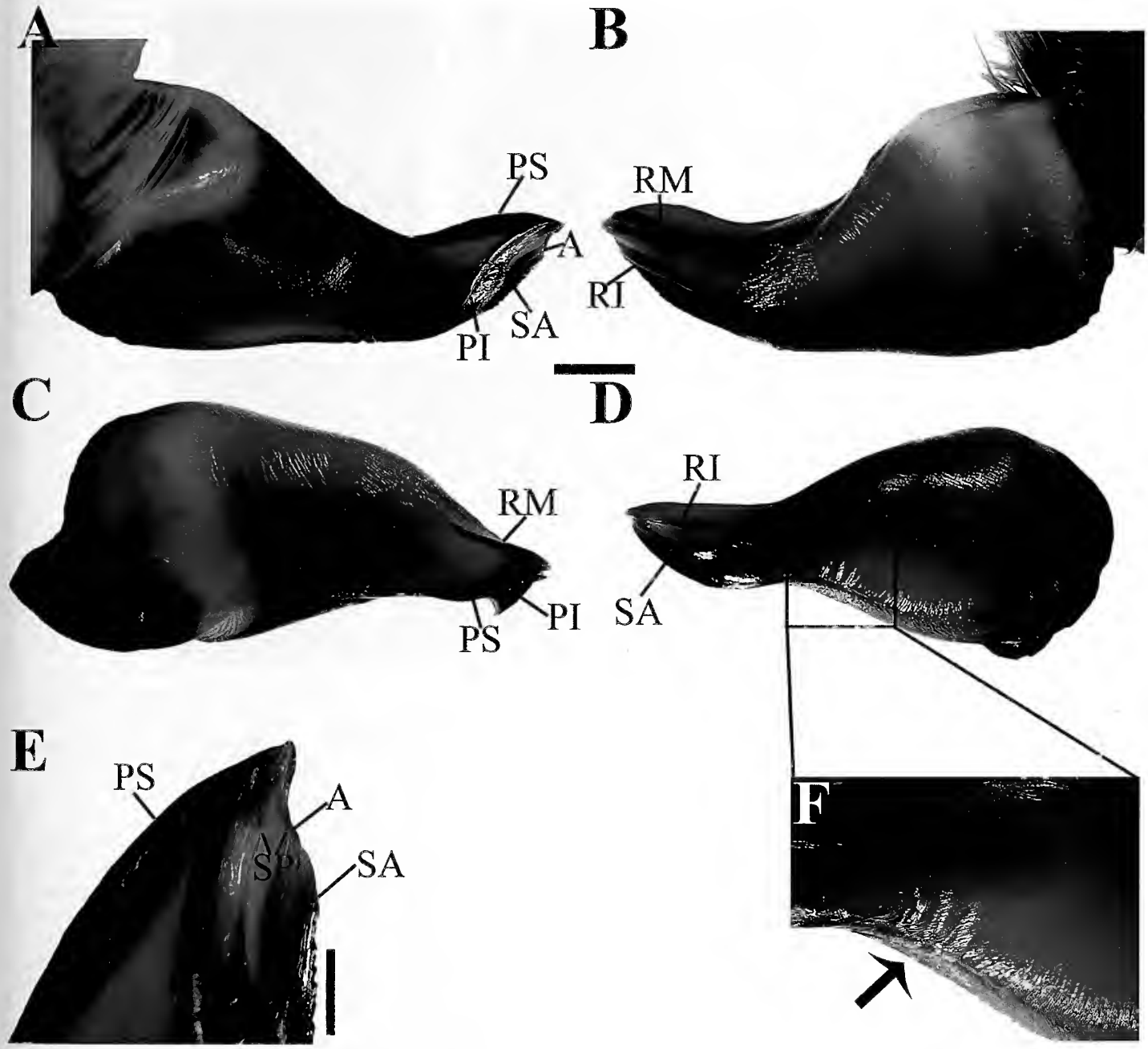

Figure 12.—Palpal bulb of male holotype of *Crassicrus tochtli* sp. nov.: A. Prolateral view; B, Retrolateral view. C. Dorsal view. D. Ventral view. E. Embolus apical region on prolatero-ventral view. F. Median ventral region of bulb. Arrows point to striations on ventral face of bulb. Abbreviations: A = apical keel; PI = prolateral inferior keel; PS = prolateral superior keel; RI = retrolateral inferior keel; RM = retrolateral median keel: SP = spermatic pore keel. Scale bars: 0.25 mm (E), 0.50 mm (F), 1 mm (A–D).

PLE 0.14; PLE–PLE 1.66, PLE–AME 0.48, PLE–ALE 0.24. Fovea: width 2.40. Labium: length 2.67, width 3.35. Chelicerae: length 7.42, width 5.79. Sternum: length 9.50, width 8.25. Leg length (femur, patella, tibia, metatarsus, tarsus, total): I: 15.01, 8.00, 11.88, 12.04, 8.15, 55.08; II: 13.82, 7.56, 10.09, 11.52, 7.73, 50.72; III: 12.97, 6.58, 9.27, 12.12, 6.89, 47.83; IV: 15.63, 6.77, 12.88, 17.85, 8.78, 61.91. Pedipalp: 9.79, 5.47, 8.62, –, 4.17, 27.59. Leg formula: IV, I, II, III. Width: femora I–IV: 3.57, 3.50, 3.96, 3.63, pedipalp: 2.71; patellae I–IV: 3.46, 3.25, 3.01, 3.06, pedipalp: 2.70; tibiae I–V: 3.12, 2.90, 2.65, 3.10, pedipalp: 3.34; metatarsi I–IV 2.09, 2.23, 1.95, 2.07; tarsi I–IV: 1.95, 1.84, 1.72, 1.58, pedipalp: 2.09. Abdomen: length 17.43. Spinnerets: PMS: length 1.96, width 0.84; PMS–PMS: 1.18; PLS: basal 2.80, median 1.55, distal 3.0.5; width: 1.30, 1.17, 0.87 respectively. Palpal bulb: length 4.65; tegulum: length 2.30, height 2.35; embolus: length 2.35, width 1.57.

Description (female paratype CNAN-T0899).—*Prosoma:* Dorsal surface covered with short yellow setae, marginally intermixed with longer setae. Carapace shape same as on holotype; caput slightly elevated (Fig, 13A). Fovea not very deep, straight (Fig. 13A). Anterior eye row procurved; posterior eye row recurved (Fig. 13D). Ocular tubercle wider

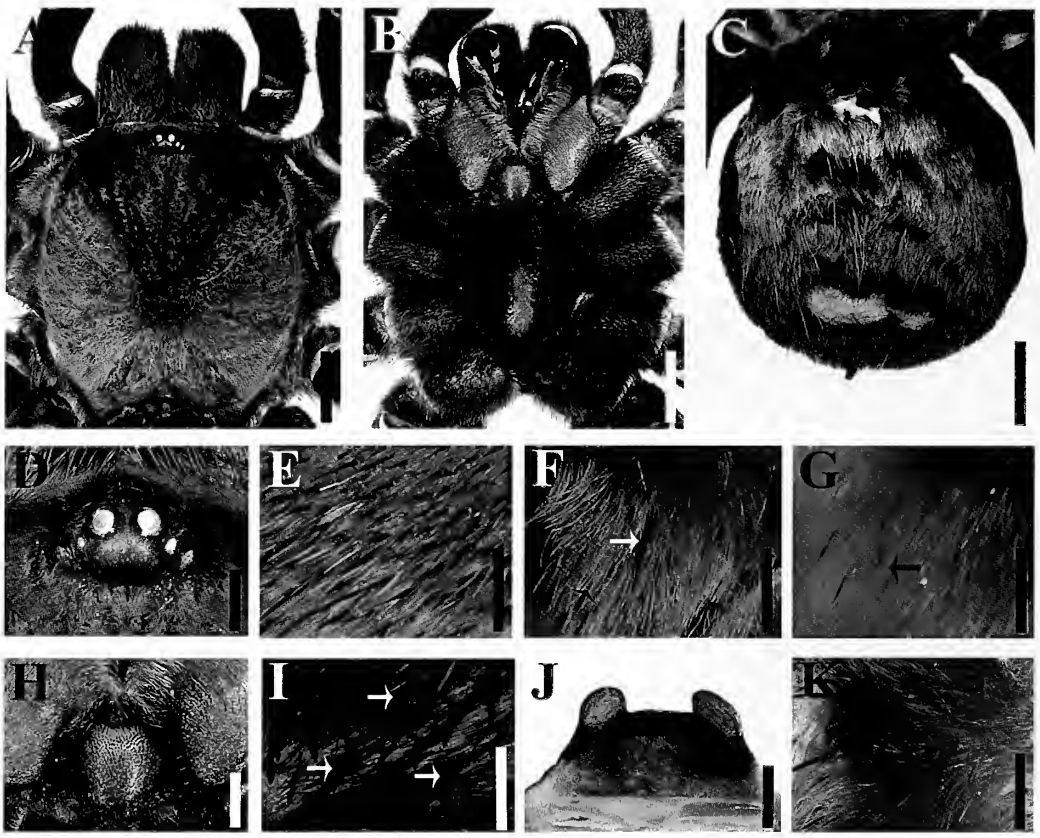

Figure 13.—*Crassicrus tochtli* sp. nov. female paratype: A. Carapace. B. prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Conical spiniform setae on prolateral face of coxa I. F. Spiniform setae (white arrow) protruding the thin plumose setae (black arrow) on prolatero-dorsal surface of trochanter I. G. Spiniform setae (arrow) on retrolateral face of coxa III. H. Labium, maxillae, and labio-sternal mounds. I. Elongated spiniform setae (arrows) on ventral face of femur III. J. Spermathecae, dorsal view. K. Spiniform setae (arrow) on dorsal face of palpal trochanter. Scale bars: 0.5 mm (E–G, I, K), 1 mm (D, J), 2 mm (H), 5 mm (A–C).

than long; clypeus very narrow (Fig. 13D). Chelicerae longer than wide. Prolateral furrow of chelicerae: left with 14 teeth (proximal to distal: 12–14 largest; 1, 3, 5, 9, 11 medium-sized; 2, 4, 6–8, 10 smallest); right with 15 teeth (proximal to distal: 13–14 largest; 1, 3–4, 6, 10–12 medium-sized; 2, 5, 7–9, 15 smallest). Labium wider than long, with 88 cuspules anteriorly (Fig. 13H). Labio-sternal mounds as for holotype (Fig. 13H). Maxillae longer than wide; left maxilla with 220 cuspules, right with 209 cuspules on baso-prolateral region (Fig. 13H). Sternum as for holotype, surface covered with short light-brown setae and long dark-brown setae; sigilla not visible (Fig. 13B).

Legs: Coloration in life: coxae and trochanters I–IV brown. Patellae, tibiae, metatarsi and tarsi of legs I and II light brown with long brown setae on dorsal surfaces; patellae, tibiae, metatarsi and tarsi of legs III and IV dark brown with long reddish setae dorsally. All femora are black. Coxae I–IV prolaterally covered with cuneiform thorn-like setae, longer and slightly thicker ventrally (Fig. 13E). Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae, longer on coxae II and III (Fig. 13G). Dorsal surface of palpal trochanter sparsely covered with elongated spiniform setae (Fig. 13K). Prolateral and prolatero-dorsal surfaces of coxae and trochanters I–IV with thick spiniform setae (Fig. 13F). Ventro-basal surface of femora I–IV with elongated sharp spiniform setae, more abundant on III and IV (Fig. 13I). All other segments covered with short brown setae intermixed with long and thick setae, basally brown and distally yellow. Femur III slightly thickened with respect to femora I–II, IV. Tibia IV not thickened. Metatarsus IV longer than femur IV. Tarsal scopulae I–III entire, IV with a row of setae. Metatarsal scopulae I–III entire, IV divided by setae: I: complete, II: 0.93, III: 0.65, IV: 0.23.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa). Leg II: p (coxa, trochanter, femur); r (coxa). Leg III: p (coxa, trochanter); r (coxa). Leg IV: p (coxa, trochanter); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa, trochanter). Leg II: p (coxa, trochanter, femur).

Leg spination: Pedipalp: femur p0–0–1d, tibia v0–1–3(1r), p1–2–2. Leg I: femur p0–0–1d, tibia v0–0–2(1p), metatarsus v0–0–1a. Leg II: femur p0–0–1d, tibia p0–0–3(1p), metatarsus v0–0–2(1p). Leg III: femur d0–0–2, patella 1r, tibia v2–1–3(1p), p3–1–1, r1–1–0, metatarsus v3–1–3(1p, 1r), p1–1–1, r0–1–1. Leg IV: tibia v2–3–3(1p), p1–1–0, r0–2–1, metatarsus v17, p0–1–0, r0–1–0.

Opisthosoma: Dorsal surface covered with short dark brown setae, interspersed with long, thick yellow setae (Fig. 13C). Under the short brown setae, there is located dark pubescence, which corresponds to the urticating setae (Fig. 13C). Ventrally covered with short and long black setae.

Table 7.—Variation in material examined for *Crassicrus tochtli* sp. nov.

	Crassicrus tochtli		
Specimens	♂ Holotype	2 ♀ Paratypes	2♀
Total length	35.50	41.09, 48.87	35.75, 34.29
Carapace length	18.07	20.30, 21.16	16.97, 17.70
Carapace width	15.69	17.30, 19.88	14.49, 15.45
Carapace width/length	0.87	0.85, 0.94	0.85, 0.87
Sternum length	9.50	11.00, 12.00	9.30, 10.75
Sternum width	8.25	8.90, 9.00	8.45, 8.75
Sternum width/length	0.87	0.81, 0.94	0.91, 0.81
Chelicerae teeth	14–15	13–15	13–14
Labial cuspules	58	88, 91	87, 81
Maxillary cuspules	148–171	208–220	149–217
Bulb length	4.65	–	–
Embolus length/width	1.50	–	–
Spermathecae bulbs width/length		1.73, 1.36	1.10, 1.00
Spermathecae base width/length		2.54, 2.58	2.53, 2.34

Urticating setae: Type I, with region "A" long and "B" short.

Genitalia: Spermathecae composed by two seminal reeeptacles partially fused by a heavily sclerotized median region with a wide, curved superior border (Fig. 13J); SB wider than long; SS slightly narrower than SB. (Fig. 13J).

Measurements: Total length (prosoma + opisthosoma): 41.09. Leg span (measured from apex of left tarsus I to apex of left tarsus IV): 111.37. Carapace: length 20.30, width 17:30, carapace width/length 0.85. Clypeus: 0.20. Ocular tubercle: height 1.05, length 1.80, width 2.73. Eye sizes and interocular distances: AME 0.50; ALE 0.34 × 0.52; PME 0.20 × 0.30; PLE 0.40 × 0.42; AME–AME 0.22; AME–ALE 0.32; AME–PME 0.20, ALE–ALE 1.62, ALE–PME 034, PME–PME 1.52; PME–PLE 0.19; PLE–PLE 2.00; PLE–AME 0.59, PLE–ALE 0.29. Fovea: width 3.30. Labium: length 2.90, width 4.35. Chelicerae: length 8.52, width 6.34. Legs length (femur, patella, tibia, metatarsus, tarsus, total): I: 14.45, 8.41, 10.51, 9.84, 7.01, 50.22; II: 12.43, 7.66, 9.20, 9.45, 6.92, 45.66; III: 11.76, 7.13, 8.30, 10.44, 6.95, 44.58; IV: 14.74, 7.39, 11.76, 15.37, 7.52, 56.78. Pedipalp: 10.12, 6.10, 7.96, –, 8.37, 32.55. Leg formula: IV, I, II, III. Leg widths: femora I–IV: 3.45, 3.45, 3.72, 3.57, pedipalp: 3.04; patellae I–IV: 3.23, 3.22, 3.00, 2.96, pedipalp: 2.74; tibiae I–IV: 2.53, 2.53, 2.60, 2.53, pedipalp: 2.59; metatarsi I–IV: 2.16, 2.05, 2.02, 1.94; tarsi I–IV: 1.96, 1.94, 2.02, 2.01, pedipalp: 2.31. Abdomen: length 20.79. Spermathecae: Base: length 1.40, width 3.55; SB: length 0.56, width 0.97; SS width 0.97; SB–SB: 1.17. Spinnerets: PMS: length 2.00, width 1.00; PMS–PMS: 1.50; PLS: basal 3.1, median 1.75, distal; width: 1.20, 1.10, 0.65 respectively.

Distribution.—This species is found in Veracruz, Mexico, and is known from only two localities in the municipalities of Catemaco and San Andrés Tuxtla, which are located in the central south-east of the state of Veracruz (Fig. 2).

Natural history.—The holotype male was collected as an immature; it was excavated from a perpendicular burrow approximately 25 cm deep and the entrance was covered with a layer of silk. It was collected in the month of July and its final molt was in mid-August, during the rainy season. The locality where the specimens were collected is in a well-conserved rainforest, in a protected area. *Crassicrus tochtli* is sympatric with species of the genera *Brachypelma* and *Citharacanthus*, and the arboreal species *Psalmopoeus victori* Mendoza, 2014.

Variation.—See Tables 7–8 for details of size variation in different characters.

Crassicrus cocona sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:FA144E4E-8ECD-4FCB-B250-C2F10C3BEC3D
(Figs. 14–16)

Type material.—*Holotype male.* MEXICO: *Tabasco*: road to Grutas de Coconá, Teapa municipality, 17.563728° N, 92.929281° W, 37 m, 13 April 2014, D. Candia, B. Ramírez (CNAN–T0894).

Paratypes. MEXICO: *Tabasco*: 1 ♀, same data as holotype except (CNAN–T0895). 1 ♀, same data except (CNAN–T0896). 1 ♀, same data as holotype except (CNAN–T0897). 1 ♀, pastures behind San Felipe Cemetery, Teapa municipality, 17.54218° N, 92.95899° W, 53 m, 26 December 2011, J. Mendoza, G. Contreras, E. Goyer, E. Hijmensen (CNAN–T01015). *Chiapas*: 1 ♀, community La Carretera, La Unión, Solosuchiapan municipality, 17.38889° N, 93.02342° W, 231 msnm, 19 December 2011, J. Mendoza, G. Contreras, E. Hijmensen, E. Goyer (CNAN–T01016). 1 ♀, same data except (IBSP 166991).

Other material examined.—MEXICO: *Chiapas*: 1 ♂ subadult, community La Carretera, La Unión, Solosuchiapan municipality, 17.38889° N, 93.02342° W, 231 msnm, 19 December 2011, J. Mendoza, G. Contreras, E. Hijmensen, E. Goyer (CNAN–Ar004153).

Etymology.—The specific name is a noun in apposition from the Zoque language, where the name of Cocona Caves has its origin. The word "coconá" means "deep water".

Diagnosis.—*Crassicrus cocona* sp. nov. can be distinguished from all other congeners except *C. bidxigui* and *C. tochtli* by the presence of a convex sternum (Figs. 14B, 16B). It is distinguished from *C. bidxigui* and *C. tochtli* by the presence of relatively longer coxae, and poorly developed spiniform setae prolaterally on coxae III–IV (Fig. 16G). The males can be further distinguished from *C. tochtli* by the presence of

Table 8.—Variation in the lengths and widths of appendage segments for four adult females of *Crassicrus tochtli* sp. nov. (including paratypes). The segment with the data in bold was considered as thickened.

Segment	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Length					
Femur	8.97–10.81	12.60–15.34	11.44–14.03	10.45–13.35	13.25–16.98
Patella	5.12–6.99	7.91–9.17	6.40–8.66	5.73–8.05	6.13–8.14
Tibia	6.90–7.96	9.21–11.33	8.33–9.89	7.95–8.98	10.39–12.80
Metatarsus	–	7.89–10.33	7.54–10.31	8.99–11.65	13.46–17.35
Tarsus	6.99–9.11	6.36–8.48	5.90–7.94	5.67–7.37	6.71–8.71
Total	27.98–34.86	43.97–54.65	39.61–50.83	38.79–49.40	49.94–63.98
Width					
Femur	2.53–3.04	3.16–3.51	3.17–3.45	**3.34–3.75**	3.24–3.57
Tibia	2.53–2.83	2.53–2.87	2.27–2.84	2.44–2.96	2.46–2.91

striations on the prolateral face of the palpal bulb (Fig. 15A); and from *C. bidxigui* by having the region above RM very concave and wide (Fig. 15B), and by having tiny denticles on the proximal region of RI (Fig. 15F). Females can be further distinguished from *C. tochtli* and *C. bidxigui* by the presence of longer and thieker spiniform setae on proventral faces of femora II–IV (Fig. 16I).

Description (male holotype).—*Prosoma:* Carapace brown in life, with iridescent coppery brown setae on ocular tubercle; cephalic region darker. Dorsal surface covered with short grey setae and black thin setae; the grooves on thoracic region covered with coppery brown setae. Carapace margins covered with black and coppery brown setae, interspersed with violet setae on outer region; close to border are long, thin, sharp spiniform setae. Carapace semi-chordate; without pronounced boss. Caput slightly elevated (Fig. 14A). Fovea deep and slightly recurved (Fig. 14A). Anterior eye row procurved; posterior eye row recurved (Fig. 14D). AME rounded, ALE and PME oval, PLE subtriangular. Ocular tubercle wider than long; clypeus very narrow (Fig. 14D). Anterior margin of carapace covered with thin yellow setae and with thick setae basally black and distally yellow. Chelicerae longer than wide, surfaee covered with white setae, interspersed with iridescent coppery brown and black setae; dorso-prolateral region covered with long setae basally brown and distally yellow. Prolateral furrow of chelicerae: left with 14 teeth (proximal to distal: 4, 11–13 largest; 1, 6, 8–10, 14 medium-sized; 2, 3, 5, 7 smallest); right with 15 teeth (proximal to distal: 3, 12–14 largest; 1, 7, 9–11, 15 medium-sized; 2, 4–6, 8 smallest). Labium wider than long, surface covered with short and long brown setae; with 53 cuspules anteriorly (Fig. 14E). Labio-sternal semicircular and separated (Fig. 14E). Maxillae longer than wide; left with 162 cuspules, right with 175 cuspules on baso-prolateral region (Fig. 14E). Sternum longer than wide, convex; surface covered with short and long black setae; with three pairs of oval sigilla located close to baso-retrolateral face of coxae I–III; third pair largest and located close to sternum edge (Fig. 14B).

Legs: Dorsal surface of coxae and trochanters covered with dark brown and violet setae. Coxae I–IV prolaterally covered with cuneiform thorn-like setae, thicker ventrally (Fig. 14H). Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae. Femora covered with fine black tiny setae and violet setae. All other segments are covered by short and long fine black setae. Femur III thickened with respect to femora I–II, IV. Tibia IV not thickened. Metatarsus IV longer than femur IV. Tarsal scopulae I–IV entire. Metatarsal scopulae I–III entire, IV divided by long setae. Metatarsal scopulae extension: I complete, II complete, III 0.65, IV 0.18. Metatarsus I straight, when flexed touches the lateral face of Rap.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg. I: p (coxa, trochanter, femur); r (coxa, trochanter). Leg II: p (coxa, trochanter, femur); r (coxa). Leg III: p (coxa); r (coxa, trochanter). Leg IV: p (coxa); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa, trochanter). Leg II: p (coxa, trochanter, femur); r (coxa, trochanter).

Leg spination: Pedipalp: femur p0–0–1, tibia v0–0–2(1ap), p0–2–2. Leg I: femur p0–0–1, tibia v0–0–1a, p1–1–0, metatarsus v0–0–1a. Leg II: femur p0–0–1d, tibia v0–1–3a(1p), p1–1–1, metatarsus v0–1–2a, p1–1–0. Leg III: femur d0–0–2, patella 1r, tibia v2–3–3a(1p), p1–1–1, r1–1–1, metatarsus v2–0–2a(1p), p1–2–1, r1–0–1. Leg IV: femur d0–0–1r, patella r1, tibia v1–1–2–1, p1–1–0, r1–1–1–1, metatarsus v30(6a), p1–1–1–1, r1–1–0–0.

Leg I tibial apophyses: Tibia I with two branehes that do not originate from a common base (Fig. 14G). Prolateral branch (Pap) elongated, slightly curved towards the retrolateral branch (Rap), retrolateral face with a megaspine that does not protrude apieally. Rap slightly longer than Pap, almost straight, on its apieal portion is curved towards Pap (Fig. 14G). Base subconical; ventro-retrolateral region with a subapical megaspine that protrudes apically.

Opisthosoma: Dorsal surface covered with short, thin black setae interspersed with long, thick orange setae (Fig. 14C). Under the short black setae, there is located dark pubescence, which corresponds to the urticating setae. Ventrally covered with short and long black setae.

Urticating setae: Type I, with region "A" long and "B" short (Fig. 14F). The urticating setae on MM region are modified, retaining the helicoidally main barbs (Fig. 14I), but with region "A" very elongated and "B" reduced (Fig. 14F); region of reversible barbs very reduced (Fig. 14J), difficult to observe and can give the setae an appearance of urticating setae type III.

Pedipalpal bulb: Bulb with striations on prolateral face of tegulum; ventral region flat (Fig. 15A). Embolus short, slightly curved towards retrolateral face, with dorsal median region concave and distally flat (Fig. 15A, C). Embolus with eight

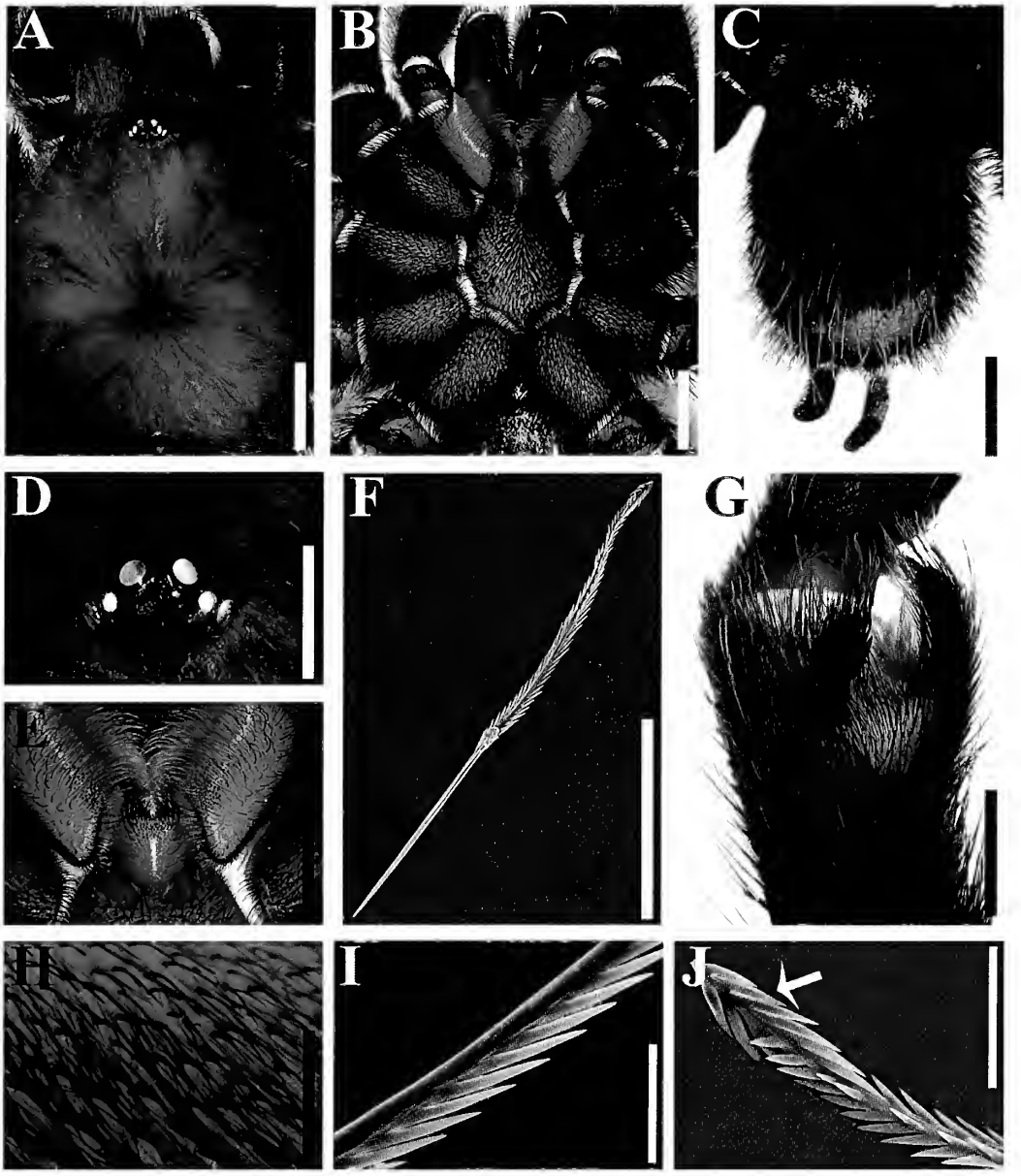

Figure 14.—*Crassicrus cocona* sp. nov. male holotype: A. Carapace. B. Prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Labium, maxillae, and labio-sternal mounds. F. Urticating setae type I. G. Tibial apophysis, ventral view. H. Conical spiniform setae on prolateral face of coxae. I, J. Modified urticating setae type I on median region of abdomen showing (I) detail of main barbs and (J) detail of reversed barbs (arrow). Scale bars: 20 μm (I), 30 μm (J), 200 μm (F), 0.25 (H), 2 mm (D–E), 5 mm (A–C, G).

keels: (1) apical keel (A) very reduced and semitransparent (Fig. 15E); (2) subapical keel (SA) fully serrated, extending for more than half of embolus length, distally is retrolaterally curved (Fig. 15B, D); (3–4) prolateral inferior (PI) and prolateral superior (PS) keels sharp and wide, extending for more than half of embolus length (Fig. 15A), PS pronounced and extending beyond dorsal plane of embolus (Fig. 15A); (5–6) retrolateral inferior (RI) and retrolateral median (RM) strong, extending for less than half of embolus length (Fig. 15B), RM distally fused with PS and together form the tip of embolus, RI with small denticles on proximal region (Fig. 15F); (7–8) spermatic pore keels (SP) semitransparent, surrounding the seminal duct opening; the retrolateral is two times longer than prolateral, curved, parallel to A, and it extends to the distal region of SA (Fig. 15E).

Measurements: Total length (prosoma + opisthosoma): 36.60. Leg span (measured from apex of left tarsus I to apex of left tarsus IV): 144.34. Carapace: length 18.62, width 17.23, carapace width/length 0.93. Ocular tubercle: height 1.12, length 1.83, width 2.40. Eye sizes and interocular distances: AME 0.58; ALE 0.42 × 0.50; PME 0.25 × 0.36; PLE 0.31 × 0.46; AME–AME 0.34; AME–ALE 0.22; AME–PME 0.10, ALE–ALE 1.54, ALE–PME 0.44, PME–PME 1.20; PME–PLE 0.07; PLE–PLE 1.66, PLE–AME 0.42, PLE–ALE 0.38. Fovea: width 2.40. Labium: length 2.10, width 3.10. Chelicerae: length 9.16, width 6.73. Sternum: length 8.20, width 7.30. Legs length (femur, patella, tibia, metatarsus, tarsus, total): I:

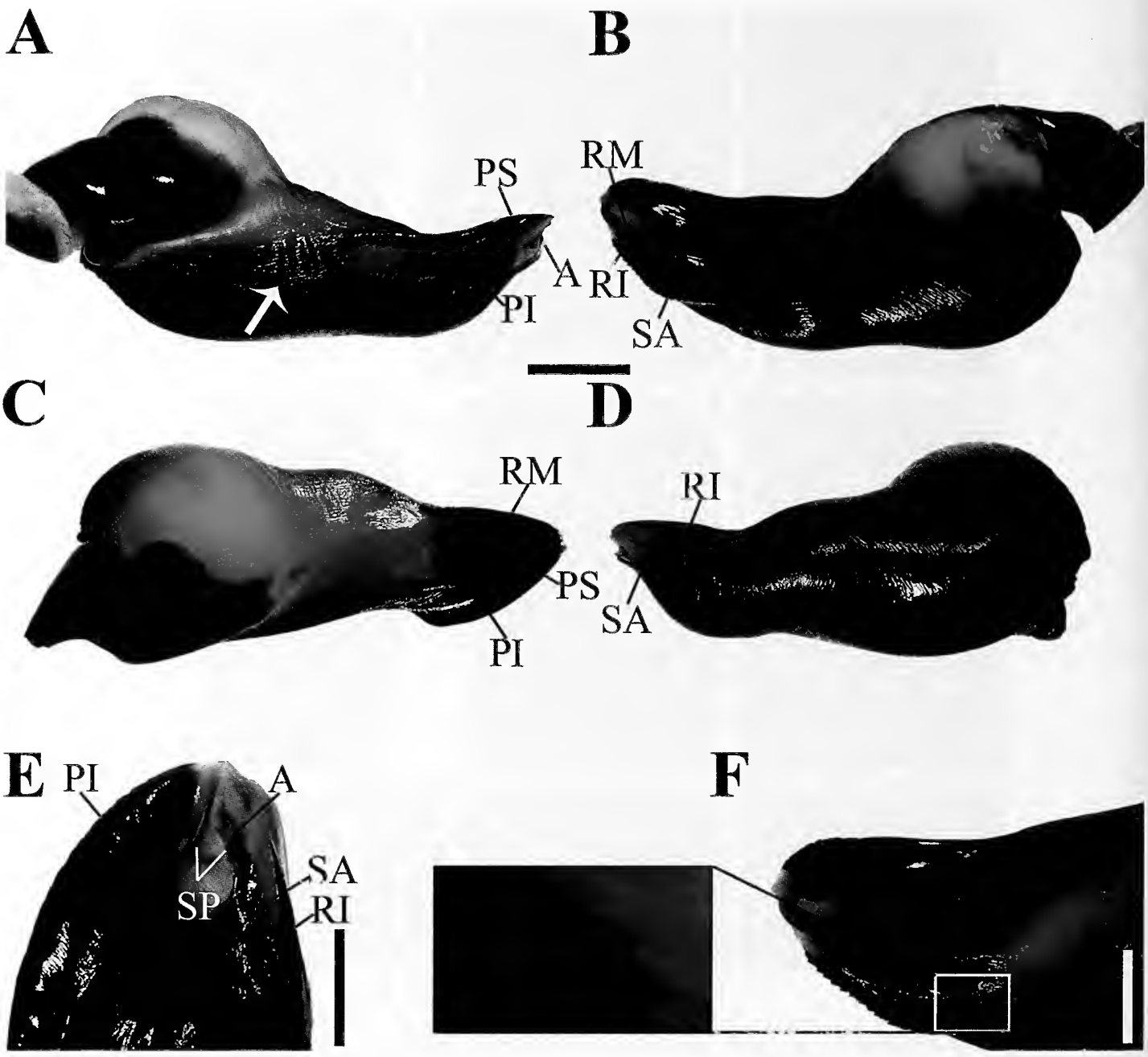

Figure 15.—Palpal bulb of male holotype of *Crassicrus cocona* sp. nov.: A. Prolateral view. B. Retrolateral view. C. Dorsal view. D. Ventral view. E. Embolus apical region on prolatero-ventral view. F. Detail of retrolateral keels. White arrow points to striations on prolateral face of bulb; black arrow points to denticles on posterior portion of retrolateral inferior keel. Abbreviations: A = apical keel; PI = prolateral inferior keel; PS = prolateral superior keel; RI = retrolateral inferior keel; RM = retrolateral median keel. SP: spermatic pore keels. Scale bars: 0.5 mm (E–F), 1 mm (A–D).

17.78, 9.62, 14.55, 14.48, 10.45, 66.88; II: 16.81, 9.06, 12.91, 13.85, 10.44, 63.07; III: 15.11, 7.70, 11.38, 14.83, 9.72, 58.74; IV: 18.40, 8.53, 15.21, 21.39, 9.85, 73.38. Pedipalp: 10.57, 6.71, 9.43 –, 4.41, 31.12. Leg formula: IV, I, II, III. Leg widths: femora I–IV: 4.03, 3.99, 4.68, 3.92, pedipalp: 3.34; patellae I–IV: 3.62, 3.54, 3.51, 3.49, pedipalp: 2.70; tibiae I–IV: 3.32, 3.17, 3.09, 3.38, pedipalp: 3.40; metatarsi I–IV: 2.21, 2.50, 2.33, 2.27; tarsi I–IV: 1.91, 1.70, 1.77, 1.70, pedipalp: 2.71. Abdomen: length 18.04. Spinnerets: PMS: length 2.15, width 0.90; PMS–PMS: 1.00; PLS: basal 3.55, median 3.05, distal 4.35; width: 1.42, 1.25, and 0.90 respectively. Palpal bulb: length 4.65; tegulum length 2.30, height 2.35; embolus length 2.35, width 1.23.

Description (female paratype CNAN-T0895).—*Prosoma:* Carapace brown in life, cephalic region darker. Dorsal surface covered with short and long thin yellow setae (Fig. 16A). Anterior margin of carapace covered with long brown setae, intermixed with long reddish setae. Carapace shape as for holotype; caput slightly elevated (Fig. 16A). Fovea not very deep, slightly procurved (Fig. 16A). Anterior eye row

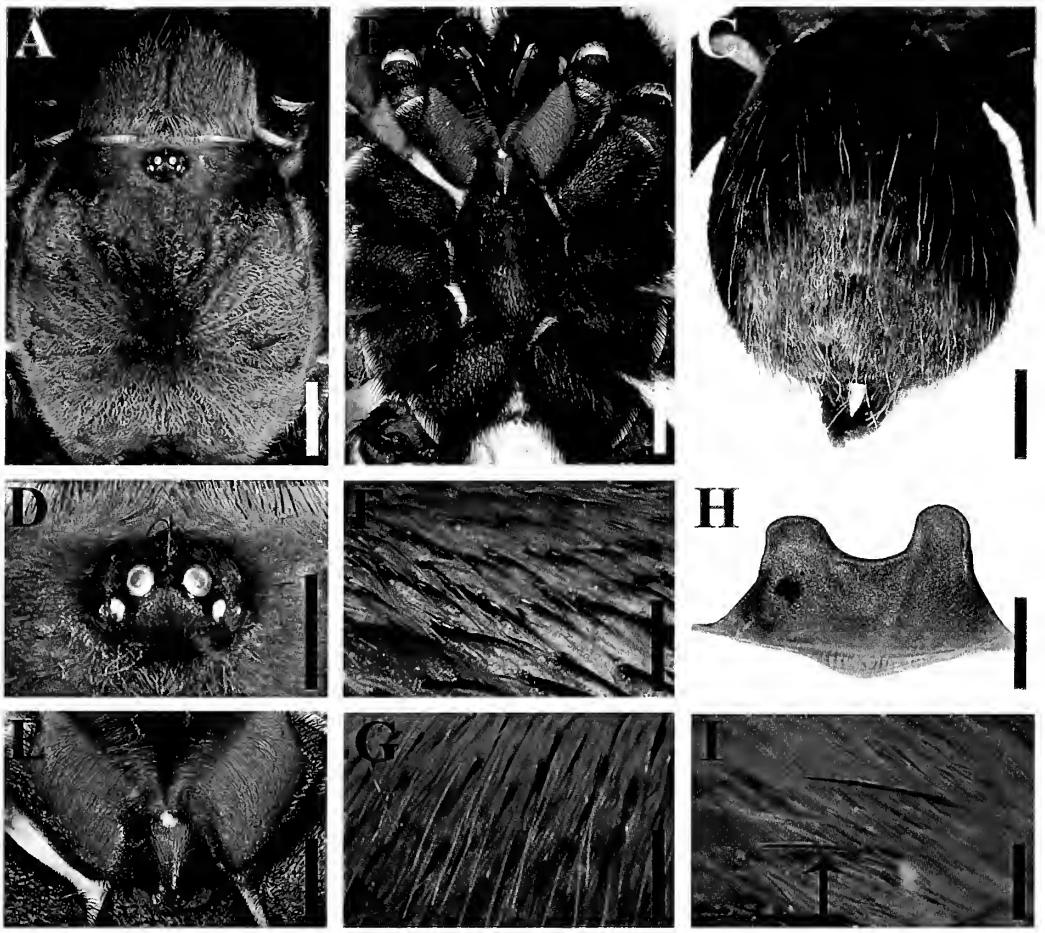

Figure 16.—*Crassicrus cocona* sp. nov. female paratype: A. Carapace. B. Prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Labium, maxillae, and labio-sternal mounds. F. Spiniform setae on prolateral face of coxa I. G. Spiniform setae on prolateral face of coxa IV. H. Spermathecae, dorsal view. I. Spiniform setae (arrow) on ventro-prolateral face of femur III. Scale bars: 0.5 mm (F–G, I), 2 mm (D, H), 4 mm (E), 5 mm (A–C).

procurved; posterior eye row recurved (Fig. 16D). AME rounded, ALE and PME oval, PLE subtriangular. Ocular tubercle wider than long, with long setae on anterior and posterior regions (Fig. 16D); clypeus very narrow. Chelicerae longer than wide, surface covered with short coppery brown setae intermixed with long brown setae; dorsally with small iridescent setae and long white setae; dorso-prolateral region with very long setae that are basally brown and distally yellow. Prolateral furrow of chelicerae: left with 13 teeth (proximal to distal: 4, 11–13 largest; 1, 6, 9–10 medium-sized; 2, 3, 5, 7, 8 smallest); right with 16 teeth (proximal to distal: 4, 13–15 largest; 1, 7, 10–12, 16 medium-sized; 2, 3, 5, 6, 8, 9 smallest). Labium wider than long, with 36 cuspules anteriorly (Fig. 16E). Labio-sternal mounds as for holotype (Fig. 16E). Maxillae longer than wide; left with 234 cuspules, right with 250 cuspules on baso-prolateral region (Fig. 16E). Sternum as for holotype, surface covered with short grey setae and long black setae; sigilla not visible (Fig. 16B).

Legs: In live specimens, all segments are brown except for black femora. Ventral surface of coxae covered with short grey setae intermixed with short and long black setae. Coxae I–IV prolaterally covered with cuneiform thorn-like setae, slightly thicker ventrally, on coxae I–II larger ventrally (Fig. 16F), on coxae III–IV are weakly developed (Fig. 16G). Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae. Prolateral and prolatero-dorsal surfaces of trochanters I–IV with elongated spiniform setae. Prolatero-ventral surface of femora I–IV with elongated spiniform setae (Fig. 16I). Patellae and tibiae with two bald, longitudinal stripes dorsally. Metatarsi I–III with a bald longitudinal stripe on dorsal face. All other segments are covered with short grey setae, and long setae that are basally brown and distally yellow. Femur III slightly thickened with respect to femora I–II, IV. Tibia IV not thickened. Femur IV longer than metatarsus IV. Tarsal scopulae I–IV entire. Metatarsal scopulae I–III entire, IV divided by setae. Metatarsal scopulae extension: I complete; II 0.91; III 0.68; IV 0.24.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa, trochanter). Leg II: p (coxa, trochanter, femur); r (coxa). Leg III: p (coxa, trochanter); r (coxa). Leg IV: p (coxa, trochanter); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa, trochanter). Leg II: p (coxa, trochanter, femur).

Leg spination: Pedipalp: femur p0–0–1d, tibia v0–0–4a(2p, 2r), p0–3–2. Leg I: tibia v0–0–1ap, p1–1–0, metatarsus v0–0–

Table 9.—Variation in material examined for *Crassicrus cocona* sp. nov.

	Crassicrus cocona		
Specimens	♂ Holotype	6 ♀ Paratypes	1 ♂ Subadult
Total length	36.66	33.88–44.19	39.79
Carapace length	18.62	17.36–21.43	18.76
Carapace width	17.23	15.06–19.32	16.14
Carapace width/length	0.92	0.87–0.92	0.86
Sternum length	9.70	6.80–10.50	8.8
Sternum width	8.30	6.20–9.12	7.75
Sternum width/length	0.86	0.85–0.95	0.88
Bulb length	4.65	–	–
Embolus width/length	0.52	–	–
Seminal receptacles width/length	–	1.04–1.34	–
Spermathecae base width/length	–	2.07–3.10	–
Chelicerae teeth	14–15	12–16	13–16
Labial cuspules	53	36–71	41
Maxillary cuspules	162–175	163–250	131–140

1a. Leg II: patella p1, tibia v0–0–3a(1p), p1–1–1, metatarsus v1–0–2a(1p). Leg III: femur d1–1–1r, patella p1, tibia v0–2–3a(1p, 1r), p1–1–1, r1–1–1, metatarsus v0–2–4a(1p, 2r), p1–1–1, r0–1–1. Leg IV: femur d1–1–1r, tibia v2–2–3a(2p, 1r), p1–1–1, r1–1–1–1, metatarsus v22(5a), p1–1–1, r1–1–1.

Opisthosoma: Dorsal surface covered with short brown setae, interspersed with long yellow setae (Fig. 16C). Under the short brown setae, there is black pubescence, which corresponds to urticating setae.Ventrally covered with short and long black setae.

Urticating setae: Type I, with region "A" long and "B" short.

Genitalia: Spermathecae composed of two seminal receptacles partially fused by a heavily sclerotized median region with the median superior border slightly concave; each SB subquadrate, slightly wider than long (Fig. 16H); SS slightly wider than SB (Fig. 16H).

Measurements: Total length (prosoma + opisthosoma): 42.44. Leg span (measured from apex of left tarsus I to apex of left tarsus IV): 135.11. Carapace: length 21.43, width 19.32, carapace width/length 0.90. Clypeus: 0.42. Ocular tubercle: height 1.27, length 2.10, width 2.77. Eye sizes and interocular distances: AME 0.55; ALE 0.34 × 0.52; PME 0.27 × 0.42; PLE 0.29 × 0.44; AME–AME 0.28; AME–ALE 0.26; AME–PME 0.20, ALE–ALE 1.90, ALE–PME 0.34, PME–PME 1.49; PME–PLE 0.14; PLE–PLE 1.68; PLE–AME 0.55, PLE–ALE 0.38. Fovea: width 3.37. Labium: length 3.25, width 4.35. Chelicerae: length 10.74, width 8.56. Sternum: length 10.19, width 9.12. Legs length (femur, patella, tibia, metatarsus, tarsus, total): I: 16.74, 9.73, 12.80, 11.00, 8.37, 58.64; II: 15.50, 8.87, 10.65, 10.71, 7.85, 53.58; III: 14.30, 8.13, 9.86, 11.72, 7.47, 38.79, 51.38; IV: 18.57, 8.67, 12.86, 16.95, 8.49, 65.54. Pedipalp: 11.95, 7.03, 8.67, –, 9.56, 37.21. Leg formula IV, I, II, III. Leg widths: femora I–IV: 4.44, 4.39, 4.80, 4.43, pedipalp: 3.85; patellae I–IV: 3.99, 3.93, 3.84, 3.93, pedipalp: 3.40; tibiae I–IV: 3.20, 3.14, 3.26, 3.49, pedipalp: 3.08; metatarsi I–IV: 2.56, 2.47, 2.64, 2.53; tarsi I–IV: 2.11, 2.23, 2.37, 2.05, pedipalp: 2.57. Abdomen: length 21.01. Spermathecae: Base: length 2.04, width 4.25; SB: length 0.94, width 1.03; SS: width 1.40; SB–SB: 1.50. Spinnerets: PMS: length 2.50, width 1.25; PMS–PMS: 1.70; PLS: basal 4.45, median 2.65, distal 4.30; width: 2.03, 1.70, 1.30 respectively.

Distribution.—This species has been reported from southern Tabasco (in Teapa municipality) to northern Chiapas, near to the border with Tabasco (in Solosuchiapan municipality) (Fig. 2).

Natural history.—The specimens were found in straight burrows, approximately 30 cm deep. Two burrows were parallel and another two were perpendicular to the ground. The burrows had circular entrances and the vegetation surrounding them was covered with a thin layer of silk (Fig. 2B). The specimens were collected in April and the females did not have egg sacs. The holotype male was collected as an immature and its final molt in captivity was in early September. The locality where the specimens were collected was slightly disturbed, and it was between an area of very well conserved rainforest and cattle pastures.

Variation.—The number of visible sigilla is variable. In the holotype male, there are three pairs of sigilla, and, in female paratypes, there are from none to three pairs; if sigilla are visible, they are oval and small, with the third pair the largest. See Tables 7 & 8 for details of size variation in different characters. See Tables 9 &10 for details of size variation in different characters.

Crassicrus yumkimil sp. nov.
http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:72B512D8-39C9-4468-B534-A9418244E761
(Figs. 17, 18)

Type material.—*Holotype male.* MEXICO: *Campeche*: 1 km West from El Pañuelo (Miguel de la Madrid), Candelaria municipality, 17.92422° N, 90.48160° W, 124 m, 16 October 2011, O. Francke, A. Valdez, G. Montiel, D. Candia, D. Barrales (CNAN–T0938).

Etymology.—The specific name is a noun in apposition from the Mayan language. "Yum Kimil" is the Mayan god of death and it means "lord of the dead".

Diagnosis.—*Crassicrus yumkimil* sp. nov. can be distinguished from all other congeners except *C. lamanai* by having tibia IV thickened with respect to tibiae I–III. It is

Table 10.—Variation in the lengths and widths of appendage segments for six adult females of the type series of *Crassicrus cocona* sp. nov. The segment with the data in bold was considered as thickened.

Segment	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Length					
Femur	10.68–11.95	15.05–16.74	13.56–15.58	12.54–14.37	16.00–18.57
Patella	6.30–7.03	8.63–9.73	7.51–8.87	7.11–8.13	7.64–8.67
Tibia	7.85–8.67	11.23–12.80	9.83–10.65	9.09–9.86	12.10–12.86
Metatarsus	–	9.38–11.00	9.03–10.71	10.59–11.72	15.43–16.95
Tarsus	8.53–9.56	7.47–8.37	7.11–7.85	7.16–7.47	8.14–8.49
Total	33.36–37.21	51.76–58.64	47.04–53.58	46.72–51.48	59.31–65.54
Width					
Femur	3.23–3.85	3.65–4.44	3.65–4.39	**3.94–4.80**	3.70–4.43
Tibia	2.83–3.08	3.01–3.20	2.95–3.14	3.02–3.51	3.04–3.49

distinguished from *C. lamanai* by having the tibia IV slightly thickened, and by the presence of cuneiform, thorn-like setae on the retrolateral inferior faces of the maxillae and coxa I (Fig. 17F). The males can be further distinguished from *C. lamanai* by the presence of two keels (RM and RI) on the retrolateral face of the embolus (Fig. 18B), and by having striations on the prolateral face of the palpal bulb (Fig. 18A). Females are unknown.

Description (male holotype).—*Prosoma:* Dorsal surface covered with short, thin black setae; cephalic region with some coppery brown setae (Fig. 17A). Carapace margins covered with short grey setae and sharp spiniform brown setae. Posterior region of carapace covered with long, thick brown setae and long, soft white setae. Carapace semi-chordate, without pronounced boss. Caput slightly elevated (Fig. 17A). Fovea deep, recurved (Fig. 17A). Anterior eye row slightly procurved; posterior eye row recurved (Fig. 17D).

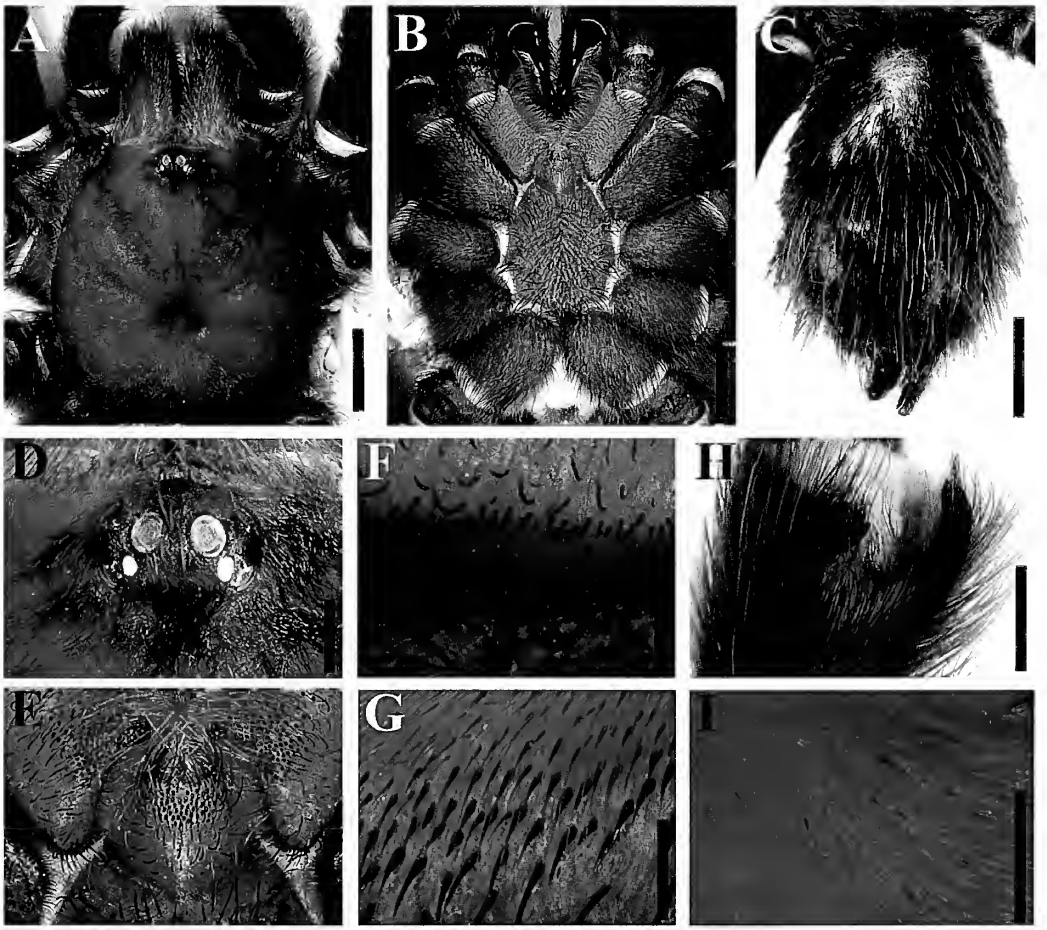

Figure 17.—*Crassicrus yumkimil* sp. nov. male holotype: A. Carapace. B. Prosoma, ventral view. C. Abdomen, dorsal view. D. Ocular tubercle. E. Labium, maxillae, and labio-sternal mounds. F, G. Spiniform setae on prolateral face of coxa I, (F) ventral view, (G) prolateral view. H. Tibia IV, dorsal view. I. Tibial apophysis, ventral view. J. Spiniform setae on retrolateral face of coxa I. Scale bars: 0.25 (G), 0.5 mm (F), 1 mm (I), 2 mm (D, E), 5 mm (A–C, H).

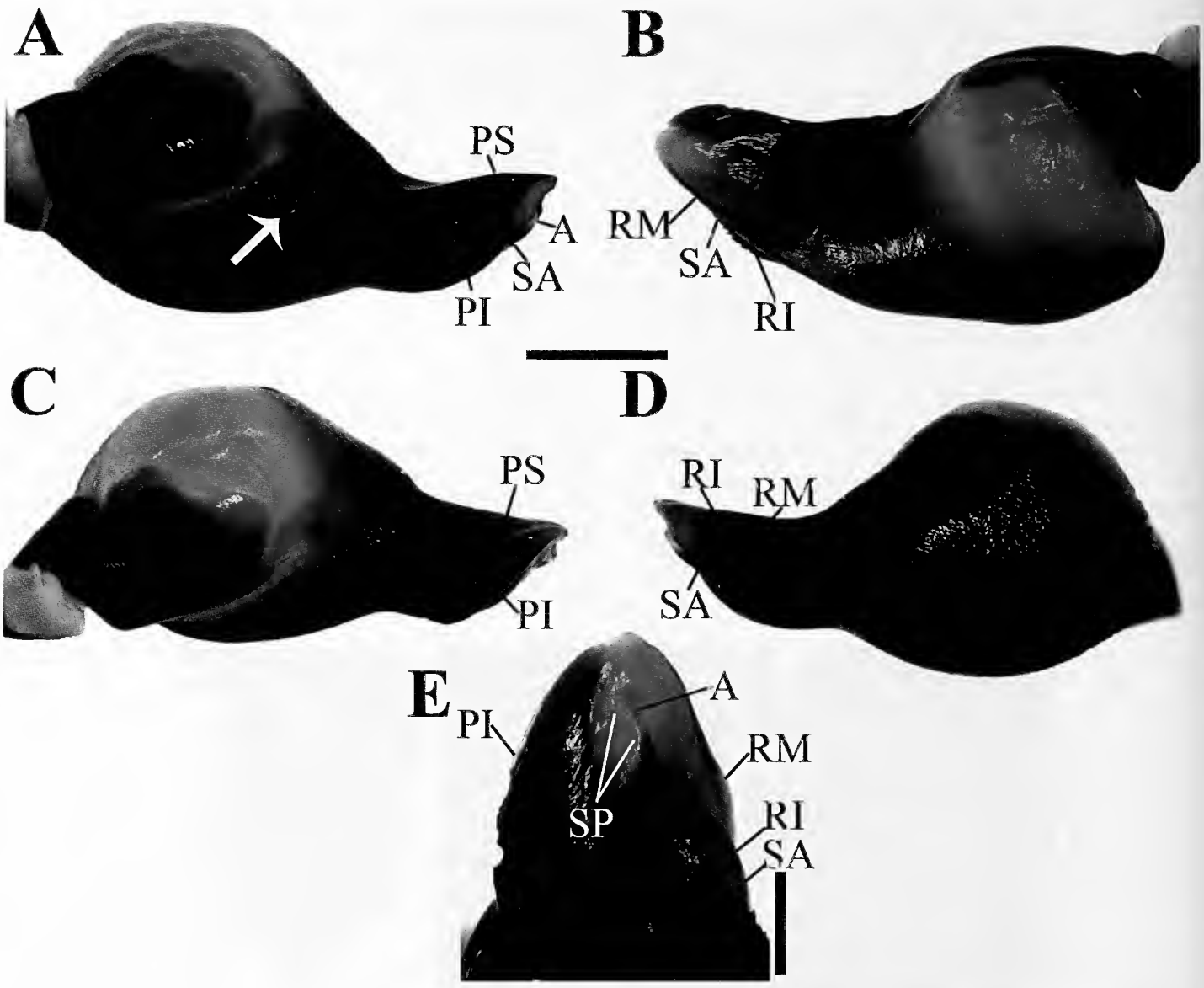

Figure 18.—Palpal bulb of male holotype of *Crassicrus yumkimil* sp. nov.: A. Prolateral view. B. Retrolateral view. C. Dorsal view. D. Ventral view. E. Embolus apical region, prolatero-ventral view. Abbreviations: A = apical keel; SP = spermatic pore keels; PI = prolateral inferior keel; PS = prolateral superior keel; RI = retrolateral inferior keel; RM = retrolateral median keel. Scale bars: 0.25 mm (E), 1 mm (A–D).

AME rounded, ALE and PME oval, PLE subtriangular. Ocular tubercle wider than long; clypeus very narrow (Fig. 17D). Anterior margin of carapace covered with long, thin, black setae intermixed with thicker setae. Chelicerae longer than wide, surface covered with fine grey setae; dorso-prolateral region covered with fine coppery brown setae interspersed with long brown setae. Prolateral furrow of chelicerae: left with 13 teeth (proximal to distal: 1, 3, 11–13 largest; 6, 8–10 medium-sized; 2, 4, 5, and 7 smallest); right with 16 teeth (proximal to distal: 1, 3, 12, 14–16 largest; 4, 6, 9–11 medium-sized; 2, 5, 7, 8, and 13 smallest). Labium wider than long, surface covered with long dark brown setae; with 62 cuspules anteriorly (Fig. 17E). Labio-sternal mounds semicircular and separated (Fig. 17E). Maxillae longer than wide; left with 173 cuspules, right with 158 cuspules on baso-prolateral region (Fig. 17E). Sternum longer than wide, flat (Fig. 17B); surface covered with fine grey setae intermixed with short and long dark setae; with three pairs of oval sigilla located close to baso-retrolateral face of coxae I, II, and III; third pair is the largest and located close to sternum edge (Fig. 17B).

Legs: Ventral surface of coxae covered with short and long black setae. Coxae I–IV prolaterally covered with short cuneiform thorn-like setae, thicker ventrally; in this species these spiniform setae are less abundant than in other congeners and are mainly basally distributed, near ventral edge (Fig. 17G, F). Retrolateral superior surface of maxillae and coxae I–III sparsely covered with very short spiniform setae (Fig. 17I). Coxae, trochanters, and femora covered with violet setae on dorsal face. Femur III thickened with respect to femora I–II, IV. Tibia IV slightly thickened with respect to tibiae I–III. Metatarsus IV longer than femur IV. Tarsal scopulae I–IV entire, IV divided with long setae. Metatarsal scopulae extension: I: complete, II: 0.90, III: 0.60, IV: 0.25.

Metatarsus I straight, when flexed touches the lateral face of Rap.

Leg lateral scopulae: Pedipalp: r (coxa, trochanter). Leg I: p (coxa, trochanter, femur); r (coxa). Leg II: p (coxa, trochanter, femur); r (coxa). Leg III: p (coxa); r (coxa). Leg IV: p (coxa); r (coxa, trochanter, femur).

Leg thin plumose setae: Pedipalp: r (trochanter, femur). Leg I: p (trochanter, femur). Leg II: p (trochanter, femur).

*Leg spination:*Pedipalp: femur d0–0–1p, tibia v0–0–1, p2–7–3. Leg I: femur d0–0–1p, tibia v2–2–1a, p1–2–0, metatarsus v0–0–1a. Leg II: femur d0–0–1p, tibia v2–1–3a(1p), p1–1–1, metatarsus v1–0–2a, p1–0–0. Leg III: femur d0–0–2(1, 1r), p1–1–1, r0–1–1. Leg IV: femur d0–0–1r, tibia v1–4(1p)–3a(1p), p1–0–1–0, r1–1–1–1, metatarsus v14, p1–1–0–1, r0–1–1–2.

Leg I tibial apophyses: Tibia I with two branches that do not originate from a common base (Fig. 17H). Prolateral branch (Pap) short, longer than wide, retrolateral face with a megaspine that does not protrude apically (Fig. 17H). Retrolateral branch (Rap) almost two times longer than Pap, slightly curved towards it. Base subconical and distally digitiform; retroventral surface with a subapical megaspine that protrudes apically.

Opisthosoma: Dorsal surface covered with short thin dark brown setae intermixed with long setae (Fig. 17C). Under the short brown setae, there is coppery brown pubescence, which corresponds to the urticating setae. Ventral surface covered with short and long black setae.

Urticating setae: Type I, with region "A" long and "B" short.

Pedipalpal bulb: Bulb with striations on prolateral face of tegulum; ventral region with a shallow depression (Fig. 18A). Embolus short, slightly curved towards retrolateral face, with dorsal median region slightly concave and distally flat (Fig. 18A, C). Embolus with eight keels: (1) apical keel (A) very reduced and semitransparent (Fig. 18E); (2) subapical keel (SA) fully serrated, extending for more than half of embolus length and retrolaterally curved distally (Fig. 18B, D); (3, 4) prolateral inferior (PI) and prolateral superior (PS) keels sharp and wide, extending for more than half of embolus length (Fig. 18A); PS thin and not extending beyond the dorsal plane of embolus (Fig. 18A); (5, 6) retrolateral median (RM) and retrolateral inferior (RI) keels strong, slightly wider on their distal portion (Fig. 18B); extending for more than half of embolus length; RM distally fused with PS and together form the tip of embolus (Fig. 18B); (7, 8) Spermatic Pore keels (SP) semitransparent, surrounding the seminal duct opening, curved outside; the retrolateral is longer than the prolateral, curved, parallel to A and it extends to the distal region of SA (Fig. 18E).

Measurements: Total length (prosoma + opisthosoma): 28.43. Leg span (measured from apex of left tarsus I to apex of left tarsus IV): 127.48. Carapace: length 14.21, width 12.59, carapace width/length 0.89. Ocular tubercle: height 0.90, length 1.50, width 2.05. Eye sizes and interocular distances: AME 0.42; ALE 0.35 × 0.48; PME 0.18 × 0.26; OLP 0.30 × 0.32; AME–AME 0.26; AME–ALE 0.22; AME–PME 0.08, ALE–ALE 1.30, ALE–PME 0.42, PME–PME 0.96; PME–PLE 0.12; PLE–PLE 1.40, PLE–AME 0.36, PLE–ALE 0.32. Fovea: width 1.50. Labium: length 1.75, width 2.55. Chelicerae: length 7.16, width 4.54. Sternum: length 6.80, width 6.00. Legs length (femur, patella, tibia, metatarsus, tarsus, total): I: 13.78, 7.30, 11.25, 10.61, 7.39, 50.33; II: 12.45, 6.62, 9.47, 9.82, 7.18, 45.54; III: 11.01, 5.03, 8.74, 11.06, 7.16, 43.00; IV: 13.70, 5.91, 11.48, 15.87, 8.64. Pedipalp: 8.22, 4.65, 7.52, –, 3.17, 23.56. Leg formula: IV, I, II, III. Leg widths: femora I–IV: 2.88, 2.83, 3.40, 2.87, pedipalp: 2.44; patellae I–IV: 2.62, 2.63, 2.71, 2.65, pedipalp: 2.20; tibiae I–IV: 2.09, 1.90, 2.17, 2.36, pedipalp: 2.55; metatarsi I–IV 1.91, 1.57, 1.54, 1.60; tarsi I–IV: 1.31, 1.44, 1.22, 1.13, pedipalp: 1.91. Abdomen: length 14.22. Spinnerets: PMS: length 1.63, width 0.67; PMS–PMS: 0.47; PLS: basal 2.57, median 1.55, distal 2.67; width: 1.05, 0.95, 0.67 respectively. Palpal bulb: length 3.65; tegulum: length 2.05, height 1.85; embolus: length 1.60, width 0.82.

Distribution.—Known only from the type locality, in Campeche, México (Fig. 3).

Natural history.—The holotype male was collected in July, during the rainy season, when it was already adult. It was found wandering on the surface near roadsides.

DISCUSSION

In the description of *Crassicrus,* Reichling & West (1996) proposed diagnostic characters to distinguish the genus based only on the morphology of the type species *C. lamanai.* With the revision of new species, we observed that some of these characters are not diagnostic for an expanded *Crassicrus.* The thickening of tibia IV is only shared by *C. lamanai* and *C. yumkimil,* and, in *C. yumkimil,* it is only slightly thickened. According to Bertani (2001) and Bertani et al. (2011), this character state appears several times in the phylogeny of Theraphosinae, and the only genus thus far where it is uniformly present is *Eupalaestrus* Pocock, 1901. To date, *Crassicrus* has not been included in any phylogenetic analysis and the relationships between this genus and other Theraphosinae genera remain unclear. Similarly, the relationship between *Crassicrus* and *Eupalaestrus,* based on the incrassate tibia IV, is weakly supported since this character state occurs in some other genera; furthermore, it is possible that the widening of posterior leg segments in Theraphosidae in general is due to convergence related to the fossorial habitus.

Reichling & West (1996) also proposed the presence of fine plumose setae as being diagnostic for *Crassicrus.* However, these setae can be found sparsely distributed or in patches on the retrolateral face of the palpal trochanter and femur, the prolateral surfaces of coxa I, trochanter I and femur I, the retrolateral surfaces of coxa I and trochanter I, and on the prolateral surfaces of trochanter II and femur II, as indicated in the new species descriptions above. Furthermore, *Crassicrus* is not the only genus with these setae. In the description of *Citharacanthus meermani* Reichling & West, 2000, the authors mentioned that *C. livingstoni* Schmidt & Weinmann, 1996 and *C. meermani* have fine plumose setae on femora I and II (Reichling & West 2000). By comparing SEM images of the fine plumose setae on the femur I of *Cr. cocona* (Fig. 1F) with those of the description of *Ci. meermani,* we found that the plumose setae have similar morphologies. In addition, material of the South American genera *Lasiodora* C. L. Koch, 1850 and *Nhandu* Lucas, 1983 were examined and also found to possess fine plumose setae on the lateral faces of the legs and pedipalps. According to Pérez-Miles et al. (2005), these setae can occur along with stridulatory setae as spines and

claviform setae; however, because of the weak structure of the plumose setae, they seem to be unrelated to stridulation.

Other features that have been proposed as diagnostic for *Crassicrus* include the spiniform setae present on the prolateral surfaces of the leg coxae and on the ventral and proventral surfaces of femora II–IV (Reichling & West 1996). These two kinds of setae are morphologically distinct. On the coxae, the spiniform setae are small, cuneiform, and are slightly larger and thicker close to the ventral region in both males and females. These spiniform coxal setae ean also be found in species of other genera, such as *Aphonopelma*, *Citharacanthus* and *Vitalius* Lucas, Silva & Bertani, 1993 (Hamilton et al. 2016; pers. obs.). However, these setae are usually thinner, longer and are not thick close to the ventral region as in other genera, or if they are, the spiniform setae are only present on coxae I–II. The second kind of spiniform setae are elongated and sharp, and are only present on the ventral and proventral surfaces of the leg femora of females. These two kinds of setae are present in virtually all *Crassicrus* species known (except the female of *C. yumkimil*). Therefore, we can confirm that these two charaeters are diagnostic for *Crassicrus*.

According to the revision of Theraphosinae palpal bulbs made by Bertani (2001), the male palpal bulb of *C. lamanai* has five keels: PS, PI, R, and probably two A keels, one of them dented. Our revision of the bulb of *C. lamanai* indicates that this species really has nine keels; and comparing it with the palpal bulbs of *Eupalaestrus weijenberghi* (Thorell, 1894), *Nhandu coloratovillosus* (Schmidt, 1998), *Vitalius sorocabae* (Mello-Leitão, 1923) and *Lasiodora* sp., we observed that the dented keel positioned on the ventral surface of the embolus of *C. lamanai* shares the same position and form as the SA keel found in the other species (both keels are positioned behind A keel, extend for more than half of the embolus length and both have small denticles). However, the homology of these two structures among the genera examined should be tested using a phylogenetic analysis.

In addition, we found that in *Crassicrus,* there are two or three retrolateral keels positioned on the inferior, median, and superior regions, respectively. Comparing the bulbs of *Crassicrus* with those of *E. weijenberghi, N. coloratovillosus, V. sorocabae* and *Lasiodora* sp., it is difficult to establish which of the three retrolateral keels found in the species of *Crassicrus* could be homologous to the single retrolateral keel found in the other genera. However, the revision of the bulbs of *Citharacanthus meermani*, which also has two retrolateral keels, indicates that the retrolateral inferior keel is very similar (morphologically and by position) to the keel present on the other genera. Currently, *Crassicrus* is the first genus where the presence of more than one retrolateral keel is constant; however, because this feature also appears in the species *C. meermani*, it cannot be considered diagnostic for the genus.

Ortiz & Francke (2014) described for the first time the spermatic pore keels (SP) found on the ventral apex of the embolus of *Bonnetina* Vol, 2000, as two structures surrounding the spermatic pore. These two keels have not been reported in other genera; however, in *Crassicrus*, they are present in all species. These keels are shorter and heavily sclerotized, whereas in the two species of *Bonnetina* for which the keels have been described, they are straight and almost parallel. In *Crassicrus*, the prolateral SP keel is shorter, and the retrolateral SP is curved, parallel to A keel, and extends to the apical region of the SA keel. The revision of specimens of other genera, such as *Eupalaestrus* and *Lasiodora*, indicates that these genera also have the SP keels, but that they are morphologically different from those observed in *Crassicrus* and *Bonnetina*; therefore, we recommend that these structures should be studied in further detail because they can provide potentially useful taxonomic information on the relationships among Theraphosinae.

Bertani and Guadanucci (2013) reported the different usage of the urticating setae types I and III in males and females, and the variation in the length of urticating setae across the abdominal area. Our examination of the urticating setae of males of *Crassicrus* revealed that in *C. cocona*, there are modified urticating type I setae on the median region of the abdomen of the male. According to Bertani and Guadanucci (2013), towards the median and posterior regions of abdomen, the length of the urticating setae increases. This elongation seems to be related to the more effieient use of these setae toward predator deterrence. In *C. cocona* the urticating type I setae on MM of the abdomen are more elongated than those of MA region, and have the region of the reversed barbs very reduced. The type III urticating setae seem to be more effective for defense against predators because they can be thrown easily; however, the type I urticating setae, due to the reversed barbs, get stuck to each other and cannot be thrown effectively. Therefore, the reduction of the reversed barbs in *Crassicrus cocona* could be an adaptation for the urticating setae to be thrown more efficiently (J. Guadanucci, pers. com.).

Considering the taxonomic revisions by Bertani (2000, 2001) and Bertani et al. (2011), we infer that the genus *Crassicrus* is probably phylogenetically related to the genera *Lasiodora, Vitalius, Nhandu, Eupalaestrus, Proshapalopus* Mello-Leitão, 1923, and *Pterinopelma* Poeock, 1901. These genera share the presence of R keel (in *Crassicrus* it is our RI keel), and share the slightly concave retrolateral face of the embolus above and below the retrolateral keel(s) (Bertani 2001). Additionally, *Crassicrus* females have spermathecae consisting of two receptacles partially fused by a heavily sclerotized median region, as do the females of *Vitalius* and *Nhandu*. However, we cannot test the placement of *Crassicrus* with these genera until performing a more thorough phylogenetic analysis.

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APPENDIX 1

The following material was examined for comparative taxonomic purposes. Specimens are deposited in the CNAN, IBSP and MNHN.

TAXONOMY

Family Theraphosidae Thorell, 1870
Subfamily Theraphosinae Thorell, 1870
Eupalaestrus weijenberghi (Thorell, 1894)

Material examined.—URUGUAY: *Dto. Canelones*: 1 ♂, Salinas Norte, R39, Municipio Canelones, 2–3 March 2013, F.G. Costa (FCE-MV 1190). *Dto. Montevideo*: 1 ♀, Melilla, 9 March 2004, F.G. Costa, F. Pérez-Miles, Postiglioni (FCE-MV 1192).

***Lasiodora* sp.**

Material examined.—BRAZIL: *Minas Gerais*: 1 ♀, Juiz de Fora, December, 1980, S. Lucas (IBSP 4588); 1 ♀, same data except no collector (IBSP 3991). *São Paulo*: 1 ♂, Serra de Taubaté, J. L. Bagetto (IBSP 6375); 1 ♂, Taubaté, C. Bombeiros (IBSP 6395).

Nhandu coloratovillosus (Schmidth, 1998).

Material examined.—BRAZIL: *Maranhão*: 1 ♂, Usina Hidroelétrica Estreito, Estreito municipality, 02 March 2011, M. Lima (CNAN–Ar010129) ; 1 ♀ same data except 28 March 2011, J. Carneiro (CNAN–Ar010130).

Vitalius sorocabae (Mello-Leitão, 1923).

Material examined.—BRAZIL: *São Paulo*: 1 ♂, Iperó, M. A. Pepeira (CNAN–Ar010128). 1 ♀ without data (CNAN–Ar010127); 1 ♀, Caucaia (CNAN–Ar010126).

Citharacanthus meermani Reichling & West, 2000.

Material examined.—MEXICO: *Quintana Roo*: 1 ♂, Akumal, Tulum municipality, 20.39782°N, 87.31426°W, 4 m, 24 November 2010, P. Bryant (CNAN–Ar004154).

2017. Journal of Arachnology 45:99–111

The morphological phylogeny of the family Protoschizomidae revisited (Arachnida: Schizomida): setal characters, fossil and paraphyletic genera

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Abstract. The schizomid family Protoschizomidae, endemic to North America, is represented by two genera and 15 species. While most of the species are distributed in caves in the Sierra Madre Oriental system in Mexico; other species are found in caves in the Sierra Madre Occidental system. Recently, a new species of this family was described from a cave in the Mexican Trans-Volcanic Belt, representing the linking bridge between both Sierras. In the present contribution, we propose a new nomenclature of the pedipalp setae of the protoschizomids. We revise the phylogenetic status of Protoschizomidae using 137 morphological characters (including the proposed pedipalp setae) and 7 outgroup taxa using parsimony criteria. Based on our results, Protoschizomidae was recovered as monophyletic, but the monophyly of *Protoschizomus* Rowland, 1975 was not recovered because of the inclusion of *Agastoschizomus* Rowland, 1971 and the fossil *Onychothelphynous bonneri* Pierce, 1951. Therefore, we transfer the genus *Onychothelyphonus* Pierce, 1951 and species *O. bonneri* to this family, but other taxonomical changes were not considered.

Keywords: Pedipalp setae, parsimony, fossil

The family Protoschizomidae Rowland, 1975, a relatively small, distinctive group of schizomids (Fig. 1), is currently represented by two genera and 15 species mainly distributed in Mexico (Harvey 2003; Prendini 2011; Monjaraz-Ruedas 2013; Monjaraz-Ruedas et al. 2016a; listed in Table 1), with some specimens reported from Texas (Cokendolpher & Reddell 1992; Reddell & Cokendolpher 1995; Monjaraz-Ruedas et al. 2016a). The family was originally described by Rowland (1975) to accommodate the newly created genus *Protoschizomus* Rowland, 1975, and to transfer the genus *Agastoschizomus* Rowland, 1971, previously assigned to the subfamily Megaschizominae Rowland, 1973 (see Cokendolpher & Reddell 1992). *Protoschizomus* currently contains four troglobitic species and three epigean species, whereas *Agastoschizomus* is represented by eight strictly troglobitic species (Monjaraz-Ruedas 2013; Monjaraz-Ruedas et al. 2016a).

The distribution of both genera is quite interesting. Even though most of the species are found in cave systems in the Sierra Madre Oriental, they don't follow the same pattern of distribution as other arachnids found in the same mountain system (in the Mexican states of Hidalgo, San Luis Potosí, Oaxaca, Tamaulipas and Veracruz), such as species of scorpion genus *Typhlochactas* Mitchell, 1971 (Vignoli & Prendini 2009); species of several opilionid genera such as *Karos* Goodnight & Goodnight, 1944 and *Chapulobunus* Goodnight & Goodnight, 1946 (Cruz-López & Francke 2015); or pseudoscorpion species in the genus *Typhloroncus* Muchmore, 1979 [although this genus is also represented by a species in the Virgin Islands (Harvey & Muchmore 2013)]. So far there are no reports of species of protoschizomids in the Sierra Madre Oriental, south of the Mexican Trans-Volcanic Belt in the states of Oaxaca, Puebla and Veracruz. However, there are three species of protoschizomids in the Sierra Madre Occidental in Guerrero and Colima (Montaño-Moreno & Francke 2009; Monjaraz-Ruedas 2013; see Fig. 2); and recently our team described a new species of *Agastoschizomus* from Estado de México, which represents a biogeographic bridge in the Mexican Trans-Volcanic Belt (Morrone 2005) joining the distribution of these species in those two branches of the Sierra Madre (Monjaraz-Ruedas et al. 2016a).

Previous phylogenetic analyses.—Cokendolpher & Reddell (1992) tested the monophyly of the family using a cladistic analysis of morphological traits. Their analysis, based on 14 taxa and 43 characters, had two purposes: first to investigate the relationship of the orders Thelyphonida and Schizomida; and second, the relationships of the members of the family Protoschizomidae. The monophyly of the family was supported by five synapomorphies: (1) a pair of setae at the base of the anterior process; (2) the pedipalps without sexual dimorphism; (3) female flagellum without annuli; (4) flagellar setal pattern different in both sexes; and (5) the male flagellum without distinct stalk (Cokendolpher & Reddell 1992). *Agastoschizomus* was supported by five synapomorphies and *Protoschizomus* was supported by three (see fig. 2 in Cokendolpher & Reddell 1992).

In the same contribution, Cokendolpher & Reddell (1992) proposed two species groups within *Protoschizomus*: the "*pachypalpus*" group (*P. pachypalpus* (Rowland, 1973), *P. rowlandi* Cokendolpher & Reddell, 1992 and *P. occidentalis* Roland, 1975) and the "*sprousei*" group (*P. sprousei* Cokendolpher & Reddell, 1992 and *P. purificacion* Cokendolpher & Reddell, 1992). The "*pachypalpus*" group was supported by four characters (two anteriorly placed setae pairs present in the dorsal propeltidiam; the male pedipalps longer than the body length; the tergite III with four setae and the

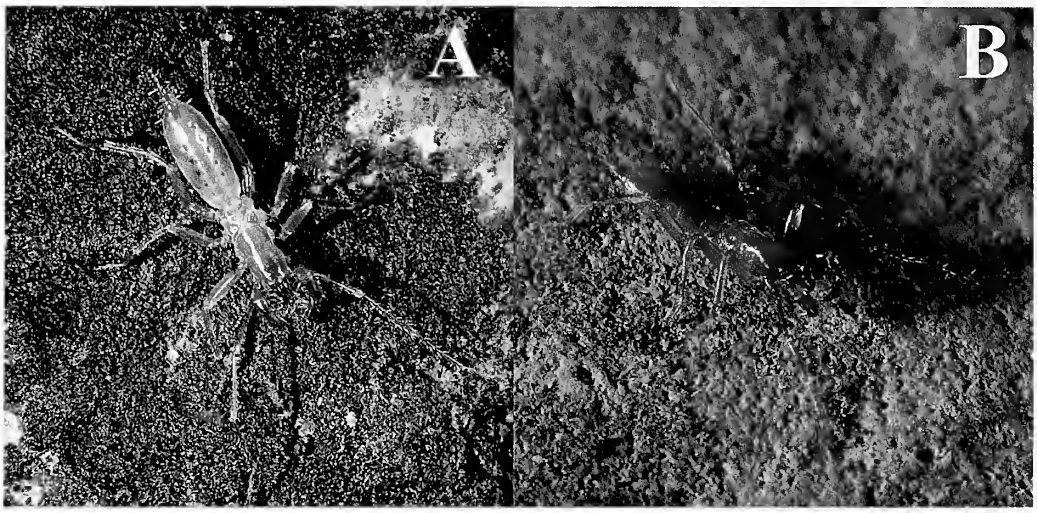

Figure 1.—Species representatives of the family Protoschizomidae. A. *Protoschizomus tenebris*. B. *Agastoschizomus texanus*, photo by Jean Krejca.

receptaculum margins smooth with pits, see Cokendolpher & Reddell 1992); whereas the "*sprousei*" group was supported only by two characters (the pedipalp trochanter slightly produced, and the absence of *Dm4* seta on the female flagellum). Also, *Agastoschizomus* was recovered as monophyletic as an unresolved polytomy (Cokendolpher & Reddell 1992; their fig. 2).

In a recent contribution, Monjaraz-Ruedas et al. (2016b) revised the ancestral state of the schizomid female flagellum annuli, and the homology of the flagellum setae across Protoschizomidae and Hubbardiidae. The monophyly of Protoschizomidae was not recovered using only those characters proposed by Cokendolpher & Reddell (1992). However, new observations on the pedipalp setae (Monjaraz-Ruedas, unpublished data; this contribution) provided additional characters to explore this problem in the systematics of Protoschizomidae.

The status of *Onychothelyphonus bonneri*.—Arachnid fossils are abundant and all of the extant orders are represented by fossil species. Several schizomid fossils are known: (a) the family Calcitronidae Petrunkevitch, 1945 contains one genus and two fossil species, one from the U.S.A. (Pliocene) and one from China (Oligocene), (b) and two monotypic genera assigned to the family Hubbardiidae, subfamily uncertain, *Calcoschizomus* Pierce, 1951 (Pliocene, U.S.A.) and *Onychothelyphonus* Pierce, 1951 (Pliocene, U.S.A.) (Harvey 2003). Published illustrations of *Onychothelyphonus bonneri* Pierce, 1951 (Pierce 1951; Petrunkevitch 1955; Dunlop & Penney 2012) suggest that this fossil actually belongs in the family Protoschizomidae and, for that reason, we included it in the phylogenetic analyses below.

In the present contribution, we propose a nomenclature for the setae found on the pedipalp femur, patella and tibia of protoschizomids; and we include those characters in a

Table 1.—Listed species currently recognized in family Protoschizomidae. *Indicates fossil taxa

Genus	Distribution	Habitat
***Agastoschizomus* Rowland, 1971**		
A. huitzmolotitlensis Rowland, 1975	San Luis Potosi, Mexico	Hypogean
A. juxtlahuacensis Montaño-Moreno & Francke, 2009	Guerrero, Mexico	Hypogean
A. lucifer Rowland, 1971	San Luis Potosi, Mexico	Hypogean
A. patei Cokendolpher & Reddell, 1992	Tamaulipas, Mexico	Hypogean
A. stygius Cokendolpher & Reddell, 1992	Hidalgo, Mexico	Hypogean
A. tamaulipensis Monjaraz-Ruedas, Francke & Cokendolpher, 2016	Tamaulipas, Mexico	Hypogean
A. tenebris Monjaraz-Ruedas, Francke & Cokendolpher, 2016	Tamaulipas, Mexico	Hypogean
A. texanus Monjaraz-Ruedas, Francke & Cokendolpher, 2016	Texas, United States	Hypogean
Onychothelyphonus* Pierce, 1950		
O. bonneri Pierce, 1950*	Arizona, United States	Unknown
***Protoschizomus* Rowland, 1975**		
P. franckei Monjaraz-Ruedas, 2013	Guerrero, Mexico	Hypogean
P. gertschi Cokendolpher & Reddell, 1992	Tamaulipas, Mexico	Hypogean
P. occidentalis Rowland, 1975	Colima, Mexico	Epigean
P. pachypalpus (Rowland, 1973)	Tamaulipas, Mexico	Epigean
P. purificacion Cokendolpher & Reddell, 1992	Tamaulipas, Mexico	Hypogean
P. rowlandi Cokendolpher & Reddell, 1992	San Luis Potosi, Mexico	Epigean
P. sprousei Cokendolpher & Reddell, 1992	Tamaulipas, Mexico	Hypogean

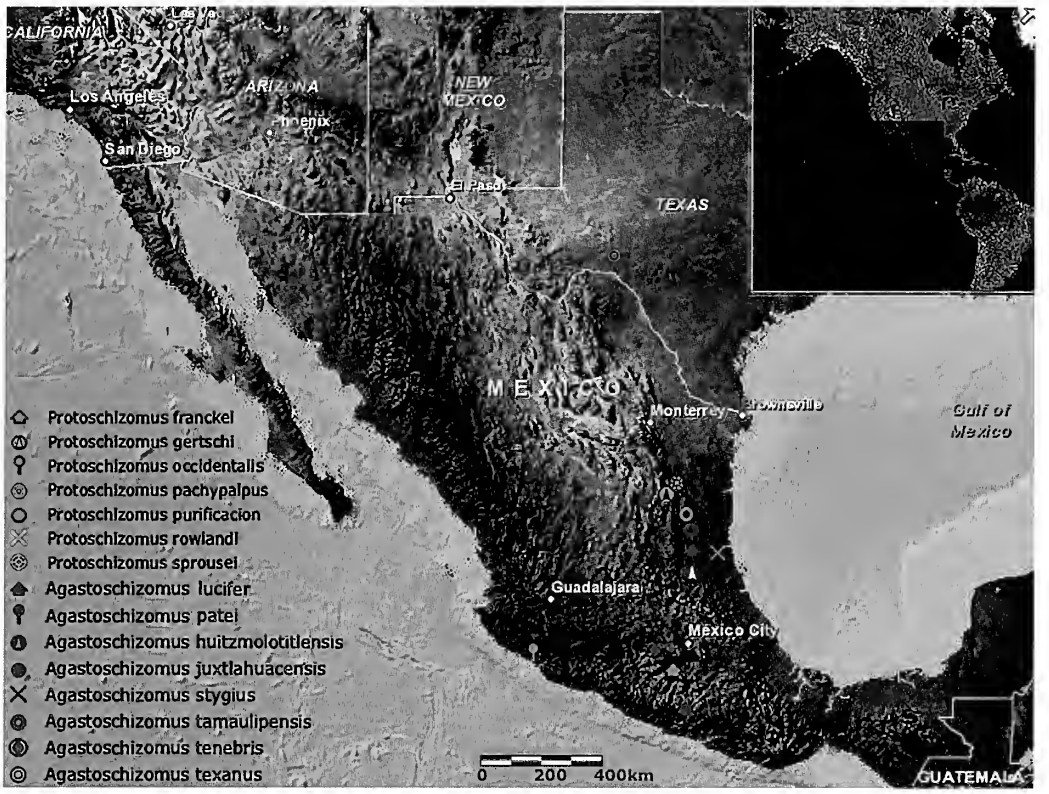

Figure 2.—Distribution map of the extant species of the family Protoschizomidae.

phylogenetic analysis using 15 species of the family Protoschizomidae as the in-group: seven species of genus *Protoschizomus* (*Protoschizomus treacyae* Cokendolpher & Reddell, 1992 represents a junior synonym of *P. purificacion*, **new synonymy**; see below), and the eight described species of genus *Agastoschizomus*. As out-groups, we included the fossil *O. bonneri* and seven exemplar species, representing five genera of the subfamily Hubbardiinae (Hubbardiidae), and *Megaschizomus mossambicus* (Lawrence, 1958) of the subfamily Megaschizominae (Hubbardiidae) to root our topologies. The matrix contains 137 morphological characters: 65 characters from pedipalp setae, 25 characters from males, and 30 characters from females only. Analyses were conducted with parsimony under equal and three implied weighting regimes. Unfortunately, efforts to collect fresh tissues of these animals to obtain molecular data have been unsuccessful in the past 10 years. This is not rare because until today, only one schizomid molecular phylogeny has been published (Harvey et al. 2008). Until this becomes possible, the branch support values here reported were not considered significant enough to make the necessary taxonomical changes.

METHODS

Taxa.—Material examined is deposited in the following collections: American Museum of Natural History, New York (AMNH), and in the Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (CNAN), and it is listed in Appendix 1.

Observations were made using Nikon SMZ-800 and SMZ-1500 stereomicroscopes, and a Nikon Eclipse E100 optical microscope. Measurements (mm) follow Cokendolpher & Reddell (1992), and were obtained with an ocular micrometer calibrated at 10x. Morphological terminology follows Cokendolpher & Reddell (1992), except for cheliceral setae (Lawrence 1969), flagellar setae terminology (Monjaraz-Ruedas et al. 2016b) and pedipalp setae terminology (see below).

Drawings were copied from digital images taken under visible light with a Nikon Coolpix S10 VR camera attached to a Nikon SMZ-800 microscope. The focal planes of image stacks were fused with CombinedZM (Hadley 2008), composite images were edited with Adobe Photoshop CS6, and drawings edited with Adobe Illustrator CS6.

Pedipalp setal nomenclature.—There are four kinds of setae (Figs. 3, 4): (a) acuminate setae, present on most of the genera of the family Hubbardiidae (Fig. 3A–D); (b) macrosetae (Fig. 3E, F), that are present only in the family Protoschizomidae, and are the equivalent of acuminate setae of hubbardiids but longer and wider than said acuminate setae; (c) feathered setae, present primarily on the pedipalp tibia (Fig. 4); (d) spiniform setae, which are dark, thickened setae with an evident socket and strongly sclerotized, and that are very common in genus *Hubbardia* Cook, 1899 and on Protoschizomidae (Fig. 4).

Setal patterns and setal forms were examined on all segments of the pedipalp in search of phylogenetically informative characters. In this contribution, we consider and describe: (a) the setae present on ectal and mesal surfaces of the femur, (b) the setae present on the ventral surface of the patella, and (c) the setae present on the ventro-mesal surface of the tibia. Seta numbering on each surface is performed from basal to distal position of the segment.

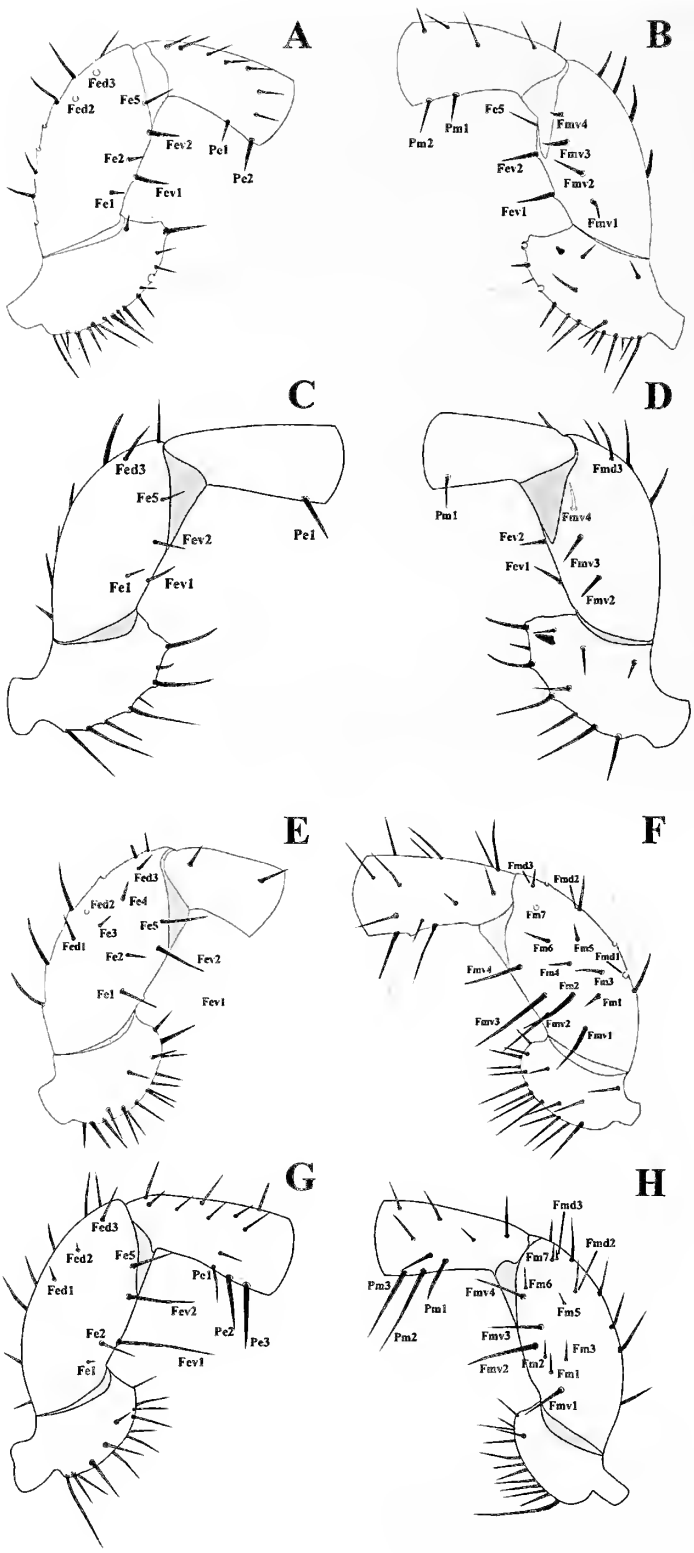

Figure 3.—Setal pattern of the pedipalp femur of Schizomida. *Hubbardia pentapeltis*: A. Femur ectal view. B. Femur mesal view. *Stenochrus pecki*: C. Femur ectal view. D. Femur mesal view. *Agastoschizomus juxtlahuacensis*: E. Femur ectal view. F. Femur mesal view. *Protoschizonus franckei*: G. Femur ectal view. H. Femur mesal view.

Setae are named based on position (Segment and surface of the pedipalp), with capital letters indicating the different segments of the pedipalp and lower case letters indicating surface or position: ***Fe*** = femur ectal, ***Fed*** = femur ectal dorsal, ***Fev*** = femur ectal ventral, ***Fm*** = femur mesal, ***Fmd*** = femur mesal dorsal ***Fmv*** = femur mesal ventral; ***Pe*** = patella ectal, ***Pm*** = patella mesal, ***Pmm*** = patella medial mesal, ***Pme*** = patella medial ectal and ***Ter*** = tibia external row, ***Tmr*** = tibia medial row, ***Tir*** = tibia internal row, ***Tm*** = tibia medial.

The pedipalp femur of protoschizomids, in general presents more setae than the femur of hubbardiids: protoschizomids (Fig. 3A, C) possess on ectal faee 1-3 ecto-dorsal setae (*Fed*), more than three ectal setae (*Fe*) and one pair of ecto-ventral setae (*Fev*), whereas hubbardiids (Fig. 3E, G) present only two ecto-dorsal setae, three ectal setae and one pair of ecto-ventral setae. On the mesal surface of the pedipalp femur, hubbardiids (Fig. 3F, H) possess only a meso-ventral row of three or four setae (*Fmv*), whereas protoschizomids (Fig. 3B, D) possess dorsal (*Fmd*), mesal (*Fm*), and meso-ventral setae (*Fmv*), the number of setae in each group varies among species and is phylogenetically informative within the family (see Appendix 2).

The patella possesses two ill-defined rows of setae (Fig. 4): one on the ventro-ectal margin (*Pe*) and one on ventro-mesal margin (*Pm*); hubbardiids usually have only acuminate setae on the patella (Fig. 4E–H), whereas protoschizomids tend to have macrosetae (Fig. 5A–D). Setae *Pmm* and *Pme* vary among species of Protoschizomidae, however, in Hubbardiidae, the setae *Pme1* and *Pmm3* are always present (see Fig. 5C, E).

The tibia possesses three distinct rows of setae on the ventral and the ventro-mesal surface on both families: the external row (*Te*) usually possesses three setae on hubbardiids and seven setae on protoschizomids; the medial and internal rows possess four setae on hubbardiids and five on protoschizomids, which also present an extra pair of setae *Tm*, located medially, near medial row and distal margin (Fig. 4). The number of setae and the shape of the setae (acuminate, feathered or spiniform) of all segments is diagnostic to species level and of phylogenetic importance at the generic level.

Data matrix.—One hundred and thirty-seven qualitative characters of adult morphology (Appendix 2) were scored (Appendix 3) for the 23 terminal taxa in the analysis using museum material. Forty-seven characters were multistate and 90 binary. Twenty-five characters were scored only for males, and 30 were scored only for females. Adult females are unknown in *Agastoschizomus huitzmolotitlensis* Rowland, 1975 and *Agastoschizomus juxtlahuacensis* Montaño-Moreno & Francke, 2009; whereas adult males are unknown in *P. gertschi* Cokendolpher & Reddell, 1992, *P. purificacion* (sub adult male), *A. stygius* Cokendolpher & Reddell, 1992 and *A. texanus* Monjaraz-Ruedas, Francke & Cokendolpher, 2016. *Onychothelyphonus bonneri* was coded from the literature (Pierce 1950; Petrunkevitch 1955; Dunlop & Penney 2012).

Sixty-five characters were seored from setal patterns in the pedipalp trochanter, femur, patella and tibia; and forty-three characters are coded from the flagellum. Seven characters were uninformative and deactivated in all parsimony analyses († in Appendix 2).

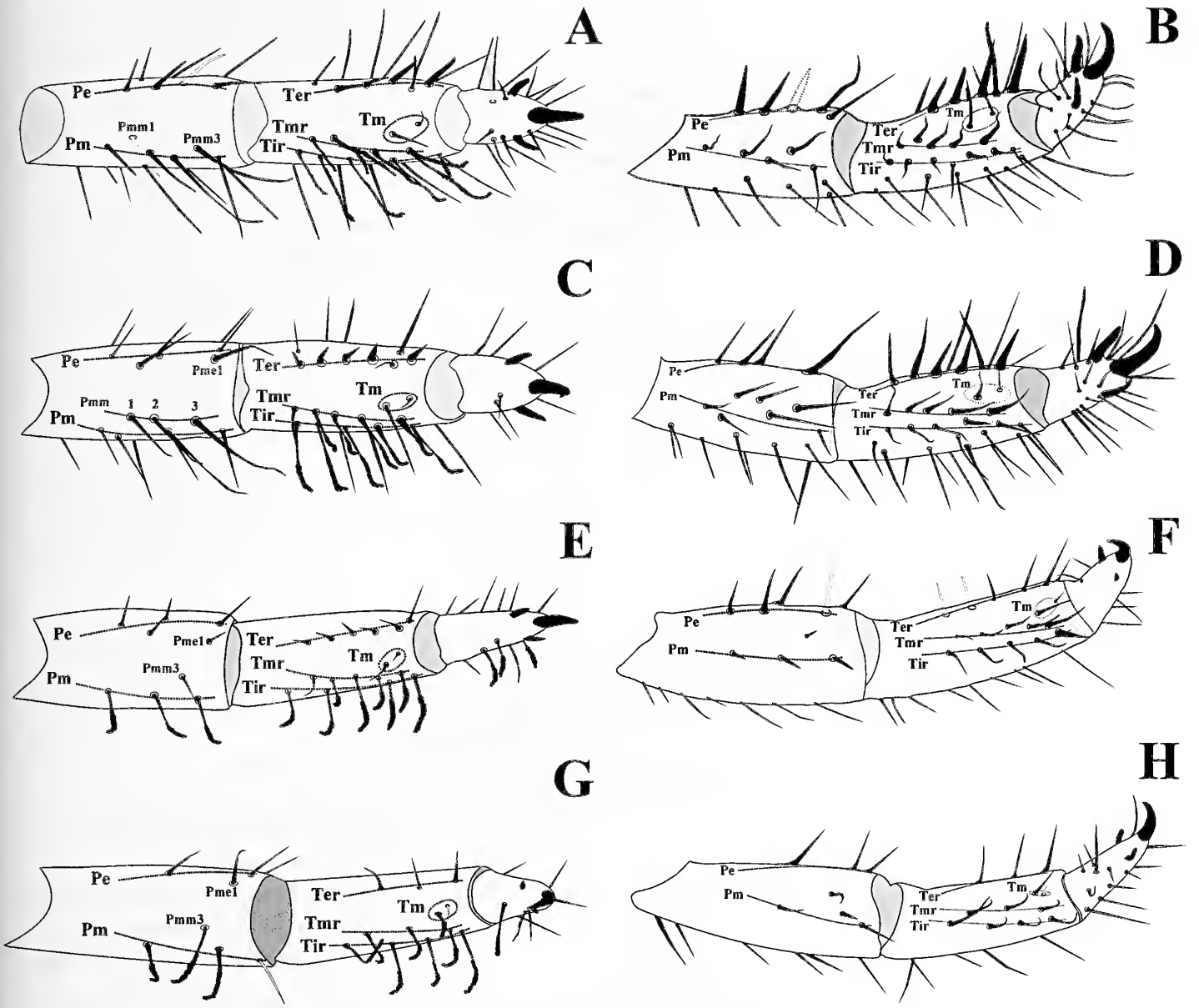

Figure 4.—Setal patterns of the pedipalp patela and tibia of Schizomida. *Agastoschizomus juxtlahuacensis*: A. ventral view. B. Mesal view. *Protoschizomus franckei*: C. Ventral view. D. Mesal view. *Hubbardia pentapeltis*: E. Ventral view. F. Mesal view. *Stenochrus pecki*: G. Ventral view. H. Mesal view. Feathered setae = Tibia internal and medial rows (**Tir** and **Tmr**); spiniform setae = Tibia external row (**Ter**).

Parsimony phylogenetic analyses.—A driven search of the 130 informative characters was conducted in TNT (Goloboff et al. 2003a,b, 2008) combining three of the new technology algorithms (Goloboff 1999; Nixon 1999) executed using a script file modified from Dimitrov et al. (2013) and Santibáez-López et al. (2014): *hold 100000; rseed1; xm: noverb nokeep; rat: it 0 up 4 down 4 au 0 num 36 give 99 equa; dri: it 10 fit 1.00 rfi 0.20 aut 0 num 36 give 99 xfa 3.00 equa; sec: mins 45 maxs 45 self 43 incr 75 minf 10 god 75 drift 6 glob 5 dglob 10 rou 3 xss 10- 14+2 noxev noeq; tf: rou 5 minf 3 best ke nochoo swap; xm : level 10 nochk rep 50 fuse 3 dri 10 rss css noxss mult nodump conse 5 conf 75 nogive notarg upda autoc 3 xmix; xm; xmult:;*. Analyses were carried out with equal weighting and implied weighting using three values of the concavity constant ($k = 1$, 3, 10), to assess the effect of weighting against homoplastic characters. The relative support for each node on the preferred hypothesis was calculated with Bremer support (Bremer 1994) and jackknife resampling (Farris et al. 1996). Bremer support was calculated in TNT by searching for suboptimal trees 10 steps longer, and holding 1000 trees per replication, using the command *bremer*;. Jackknife support was estimated with heuristic searches of 1000 pseudoreplicates, using the commands *resample jak repl*;. Cladograms were generated with WinClada (Nixon 2002) and edited with Adobe Illustrator C6.

RESULTS

Based on the revision of the holotypes of *Protoschizomus treacyae* and *P. purificacion* (both females), we concluded that in the original description by Cokendolpher & Reddell (1992), the diagnostic characters were not correctly observed. These

Figure 5.—The single most parsimonious tree obtained from the cladistic analysis of 137 morphological characters scored from 23 species in 9 schizomid genera with implied weighting and k value = 3. Unambiguous synapomorphies optimized on branches: black squares indicate apomorphic states, while white squares indicate either parallel derivations of apomorphic characters or reversal to plesiomorphic states; numbers above squares indicate characters, numbers below indicate states. Jackknife values greater than 65% indicated above branches. Bremer support values indicated below branches. A. Monophyly of Protoschizomidae. B. Internal relationships within Protoschizomidae.

authors differentiated *P. treacye* from *P. purificacion* as follows: *Dm2* on female's flagellum is absent in *P. treacye*, but it is present in *P. purificacion*; the segment/article 5 in female's flagellum is present in *P. treacye*, but absent in *P. purificacion*. However, seta *Dm2* is also absent in *P. purificacion*; and recently, Monjaraz-Ruedas et al. (2016b) proposed new terminology for the segments/articles in schizomids ("flagellomere" and "annuli"); therefore, both species have the flagellomere 5. In addition to this, we compared the spermathecae of both species and they are similar. Therefore, *P. treacyea* is now considered a synonymy of *P. purificacion* **(new synonym)**.

Phylogenetic analyses of family Protoschizomidae.—The analysis with equal weighting and with implied weighting using three values of k (1, 3, 10) recovered the monophyly of family Protoschizomidae. Our preferred topology was the one obtained from the analysis with implied weighting and k value = 3 because of its tree statistics (Table 2) and the branch support values for the clades recovered (Jackknife and Bremer). In this topology, the family Protoschizomidae was supported by 29 synapomorphies (22 from pedipalp setae characters, Figs. 5, 6) and five homoplastic characters; and with high support values of jackknife and Bremer values (Fig. 5). Despite the great number of synapomorphies supporting the family, the relationships within Protoschizomidae were not resolved.

The genus *Protoschizomus* was never recovered as monophyletic due to the terminal placement of *Agastoschizomus*, which was recovered monophyletic (but with low branch support values); and due to the inclusion of the fossil

Table 2.—Tree statistics from the most parsimonious trees or the consensus trees (*) obtained from cladistic analyses of 23 species in 9 schizomid genera. MP = Most parsimonious trees, L= Length, CI= Consistency Index, RI= Retention index, FIT= Fit, AH= Adjusted Homoplasy, EW= Equal weighting, IW= Implied weighting.

		MP	L	CI	RI	FIT	AH
EW		6	378*	0.487*	0.711*	97.04*	——
IW	k=10	1	371	0.496	0.721	115.54	14.46
IW	k=3	1	371	0.496	0.721	97.09	32.91
IW	k=1	1	374	0.492	0.717	75.97	54.03

Onychothelyphonus bonneri. The phylogenetic position of *Onychothelyphonus bonneri* (supported by the absence of the mesal spur in the pedipalp trochanter; the absence of the annulus 'b' in the female's flagellum and the position of the seta *Dl3* in relation to *V12*) suggests close relationships with extant protoschizomids, rather than being an extinct member of family Hubbardiidae (with which it shared only the size of the female's flagellum, char 105; see below).

The genus *Agastoschizomus* was recovered monophyletic supported by three synapomorphies (one seta on the anterior process of the propeltidium, the femur of leg IV more than 4.8 times longer than deep, and the male's flagellum seta *D13* anterior to *V12*) but with low jackknife support (70%). There was no internal resolution within *Agastoschizomus* because the species' relationships had no branch support values.

DISCUSSION

Phylogenetic position of *Onychothelyphonus bonneri*.—Scoring morphological traits for the fossil terminal for a matrix this size might have resulted in a dubious phylogenetic position. Wiens (2003) mentioned that the number of characters scored for terminals like this is critical for its

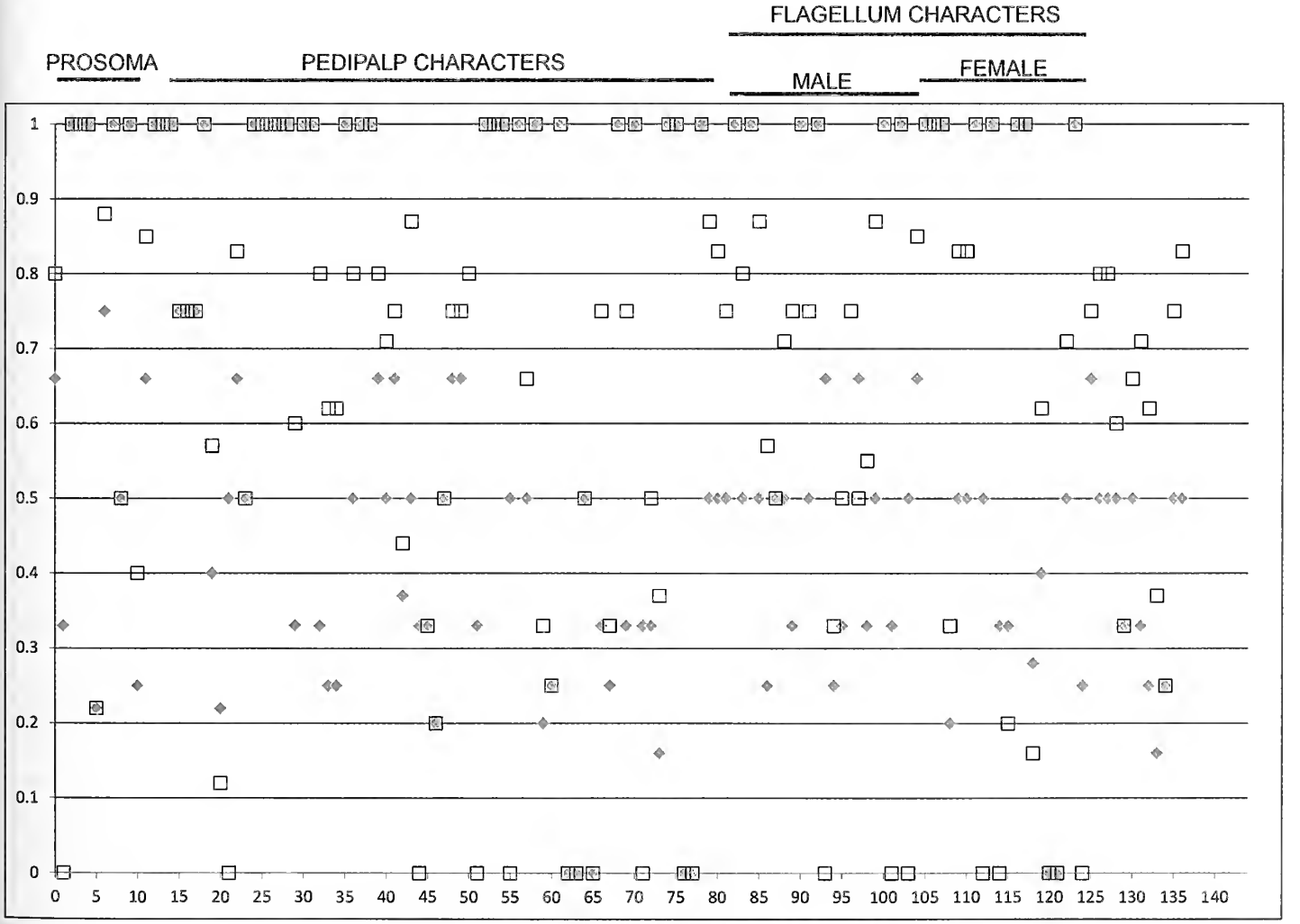

Figure 6.—Consistency indices (CI, gray diamonds) and retention indices (RI, white squares) of 137 morphological characters used in the cladistic analysis of 23 schizomid taxa, including all species of the family Protoschizomidae, the fossil *Onychothelyphonus bonneri* and several species of the family Hubbardiidae as outgroup.

"correct" phylogenetic position. He also mentioned that the insufficient sampling of characters in an incomplete taxon may lead to poor accuracy, both through incomplete resolution, and by increasing the chances that the taxon is spuriously placed on the tree by one or more homoplastic characters (Wiens 2003). However, how many characters are necessary to establish a fossil taxon's correct phylogenetic position? According to Wiens (2003), in theory only a single character may be necessary, but increasing the number of characters sampled increases the probability that such a key character will be found.

We consider it is possible to observe "those necessary characters" to include *Onychothelyphonus bonneri* in the family Protoschizomidae: (1) absence of mesal spur, (2) trochanter IV about ½ length of femur IV, (3) female flagellum with seta *Dm3*, (4) female flagellum with seta *Dl1*, (5) female flagellum seta *Dl3* at same level as *Vl2*, (6) female flagellum with four annuli.

The phylogenetic relationship of *O. bonneri* with the extant protoschizomids would certainly not represent a surprise, given the young age of the fossil deposits (Pliocene 1.8 to 5.3 my), as suggested by Dunlop and Penney (2012). However, in our current database, in which *O. bonneri* is missing 131 characters, we can't assure that this species represents an extinct species of genus *Protoschizomus*, or in any case, to put into synonymy this genus under *Onychothelyphonus* (by the principle of precedence); but it certainly represents a member of the family Protoschizomidae and not of Hubbardiidae where it is currently placed. Therefore, we transfer genus *Onychothelyphonus* and the species *O. bonneri* to family Protoschizomidae **(new familial assignment)**.

Interestingly, all analyses recovered the following clade: ((*P. purificacion* + (*P. gertschi* + *O. bonneri*)). This relationship was supported by three homoplastic characters (chars 19, 128, 130; see Fig. 5 and Appendix 2); but with low support values. This relationship has not been recovered before (i.e., Cokendolpher & Reddell 1992).

Status of the two genera within Protoschizomidae.—The genus *Protoschizomus* was not recovered monophyletic nor were the two species groups as in the analysis of Cokendolpher & Reddell (1992). Those authors recovered the monophyly of *Protoschizomus* supported by three characters: trochanter IV about ½ length of femur, sternite VI short, and the male's flagellum expanded distally (unknown in *P. gertschi, P. purificacion* (sub adult male), *A. stygius* and *A. texanus*). We modified their trochanter IV character into two characters: the ratio of trochanter length: width, and the ratio of trochanter length: propeltidium width (chars 79 & 80 respectively, see Appendix 2); both of which didn't support the monophyly of *Protoschizomus*. In our analyses, the "sternite VI short" character was recovered as a synapomorphy for the family Protoschizomidae, but with a reversal in *Agastoschizomus* (char 136 in Fig. 5). Finally, the "male flagellum expanded distally" character (our char 83) is the plesiomorphic condition (absent in *Agastoschizomus*), because it is present in all hubbardiids studied here, and in all but the two species of *Protoschizomus* for which the male is unknown.

In the analysis of Cokendolpher & Reddell (1992), *Agastoschizomus* was supported by five synapomorphies, but with no internal resolution. In our analyses, three of those five synapomorphies were recovered, whereas one character (our char 135) was recovered as a regression (because it was shared with the hubbardiids studied here), and the other character (our char 89) is a potential synapomorphy for the family (it is unknown in two *Protoschizomus* species and in *Onychothelyphonus bonneri*).

Traditionally, genus *Protoschizomus* is differentiated from *Agastoschizomus* based on the adult body size and by the presence of two setae in the anterior process of the propeltidium. Body size is no longer a good character because *A. texanus* is a small species. In our analysis, the presence of those setae was recovered as the plesiomorphic state (char 6 state 0) in *Protoschizomus* (shared with *Surazomus sturmi* (Kraus, 1957), *Rowlandius viridis* (Rowland & Reddell, 1969) and *Mayazomus infernalis* (Rowland, 1975)) and as a synapomorphy for *Agastoschizomus* (char 6 state 1). Therefore, this character remains as the most reliable to diagnose both genera as presently recognized. Unfortunately, molecular data are still missing for almost all protoschizomid species; and until this information becomes available to compare different phylogenetic hypotheses (which may provide better branch support values and better internal resolution), the necessary taxonomical arrangements should wait.

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Appendix 1. Terminal taxa used for the cladistics analyses of 15 schizomid species of the family Protoschizomidae, and seven species of Hubbardiidae and 141 morphological characters. Material examined is deposited in the following collections: American Museum of Natural History (AMNH), New York, U.S.A; Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México (CNAN), Mexico City, Mexico; Natural History Museum (NHM), London, England; Museum of Texas Tech University – Invertebrate Zoology (TTU-Z), Lubbock, U.S.A; and Texas Natural History Collections at the University of Texas at Austin (TMM). Coordinates in brackets are retrieved from Google Earth.

Outgroup

Megaschizomus mossambicus (Lawrence, 1958). MOZAMBIQUE: *Sofala*: Serra da Gorongosa (Mt Gorongoza), [18.4211°S, 34.1120°E 800 m.], September 1957, R. F. Lawrence. 1 female paratype (NHM).

***Bamazomus* sp.** MADAGASCAR: Mangabe Island: Antogil Bay [15.4944°S, 49.7677°E, 268 m.], 19 February 1977, W. L. Brown. 1 male (AMNH).

Hubbardia borregoensis (Briggs & Holm, 1966). U.S.A.: *California*: San Diego County: Borrego Palm Canyon [33.2500°N, 116.38333°W, 232 m.], 12 January 1971, J.M. Rowland, T. Moisi. Two males, one female (AMNH).

Hubbardia pentapeltis Cook, 1899. U.S.A.: *California*: Orange County: Dripping Springs, near Yail Lake [33.73333°N, 117.68333°W, 397 m.], 6 March 1971, J. M. Rowland. 3 males, 5 females (AMNH).

Mayazomus infernalis (Rowland, 1975). MEXICO: *Chiapas*: Municipio Palenque, 0.8 km north of Ruinas de Palenque, 1[17.483839°N, 92.045353°W 154 m.], 25 July 1973, R. Mitchell and J. Reddell. 1 male holotype, 1 female allotype, 1 male, 3 female paratypes (AMNH). Convention Center of Ruinas de Palenque (17.3200°N, 92.0215°W 57 m.), 31 July 2013, O. Francke, J. Mendoza, R. Monjaraz, C. Santibáñez A. Valdez, K. Zarate. 1 male and 1 female (CNAN-Sz000122).

Rowlandius viridis (Rowland & Reddell, 1979a). JAMAICA: *Manchester Parish*: Abey Cave, 4 km. south-west of Mandeville, [18.008°N, 77.528°W, 751 m.], 24 December 1973, S. and J. Peck. male holotype, female allotype, 1 female and 3 female paratypes (AMNH).

Surazomus sturmi (Kraus, 1957). COLOMBIA: *Cundinamarca*: Distrito Capital, 3 km east of Bogota, [4.60°N, 74.08333°W, 2500 m.], October, 1956, H. Sturm. One female paratype (AMNH).

Ingroup

Agastoschizomus huitzmolotitlensis Rowland, 1975. MEXICO: *San Luis Potosí:* Xilitla, Sótano de Huitzmolotitla, 1 km ESE of Tlamaya

(=2 km NNW Xilitla), [21.408320°N, 99.0018°W. 600 m; depth in the cave where it was collected is unknown], 24 January 1964, T. Raines, T. Phillips, male holotype (AMNH).

Agastoschizomus juxtlahuacensis Montaño-Moreno and Francke, 2009. MEXICO: *Guerrero*, Quechultenango, Grutas de Juxtlahuaca, [17.4387333 °N, 99.1595°W, 938? m.], 5 April 2007, H. Montaño, O. Francke, A. Valdez, C. Santibáñez, male holotype (CNAN-T0245), one adult male paratype (CNAN-T0246), one juvenile female paratype (CNAN-T0249).

Agastoschizomus lucifer Rowland, 1971. MEXICO: *San Luis Potosí*: Ciudad Valles, Sótano de la Tinaja, 10 km NNE of Ciudad Valles, [22.07597°N, 98.9778°W, 165.5 m.], 9 April 1966, J. Fish, D. McKenzie, male holotype, female paratype, 1 immature (AMNH). Ciudad Valles, Sótano de la Tinaja, 10 km NNE of Ciudad Valles, [22.07597°N, 98.9778°W, 165.5 m.], 11 May 2012, J.Cruz, J. Mendoza, G. Contreras, R. Monjaraz. One female (CNAN-Sz000136).

Agastoschizomus patei Cokendolpher and Reddell, 1992. MEXICO: *Tamaulipas*: Mainero, Cueva de la Llorona, 3.5 km SSE Yerbabuena, [24.4832°N, 99.599733°W, 1860 m.], 12-17 October 1986, P. Sprouse, male holotype (AMNH).

Agastoschizomus stygius Cokendolpher and Reddell, 1992. MEXICO: *Hidalgo*: Jacala, Sótano Hondo de Pinalito, Pinalito (a village located at kilometer post 105 on highway 85 north of Jacala), [21.01611°N, 99.164765°W, 1600 m.], 1 January 1976, C. Soileau, P. Strickland, female holotype (AMNH).

Agastoschizomus tamaulipensis Monjaraz-Ruedas, Francke & Cokendolpher, 2016. MEXICO: *Tamaulipas*: Municipio Ciudad Mante, Grutas de Quintero, 1.5 km S of Quintero (22.6499333°N, 99.041155°W, 452 m.), 27 November 2004, E. Fant, J. Fant holotype. Adult male (CNAN-T0983). Paratype: 1 subadult female (CNAN-T0984), 28 November 2004, same data as holotype.

Agastoschizomus tenebris Monjaraz-Ruedas, Francke & Cokendolpher, 2016. MEXICO: *Estado de México*: Valle de Bravo, Cueva del Diablo, Peña de Valle de Bravo (19.20069°N, 100.14148°W, 1885 m.), 27 August 2011, D. Barrales, J. Mendoza, E. Miranda, R. Monjaraz, A. Valdez, holotype. Adult female (CNAN-T0989). Paratype: 1 subadult female (CNAN-T0990), same data as holotype.

Agastoschizomus texanus Monjaraz-Ruedas, Francke & Cokendolpher, 2016. U.S.A.: *Texas*: Seminole Sink (= Seminole Canyon Cave), Seminole Canyon State Park, Val Verde County (415 m.), 20 February 2009, P. Paquin, M. Sanders, K. O'Connor, holotype adult female (TTU-Z_060311). Paratypes: 1 subadult male, (TTU-Z_060312), same data as holotype. 1 female and 1 subadult female (CNAN-T1002), same locality as holotype, 29 May 2015, P. Sprouse, B. Hutchins, and A. Scott.

Protoschizomus franckei Monjaraz-Ruedas, 2013. MEXICO: Guerrero: Taxco de Alarcón, Cueva de Boca del Diablo, Acuitlapán, [18.59916°N, 99.54579°W, 1594 m.], 21 April 2012, G. Contreras, J. Mendoza, R. Monjaraz, D. Ortiz, male holotype (CNAN-T0384), female paratype (CNAN-T0385).

Protoschizomus gertschi Cokendolpher and Reddell, 1992. MEXICO: *Tamaulipas*: Miquihuana, Sótano de Riachuelo, 6.5 km N. and 2 km E. of Miquihuana, [23.6333°N, 99.7819°W, 1850 m.], 16 February 1981, P. M. Jameson and R. Jameson. Female paratype (AMNH).

Protoschizomus occidentalis Rowland, 1975. MEXICO: *Colima*: 20.9 km SW Colima, [19.113469°N, 103.8571°W, 202 m.], 16 July 1972, A. Jung, male holotype (AMNH).

Protoschizomus pachypalpus (Rowland, 1973). MEXICO: *Tamaulipas*: Gómez Farías, Nacimiento del Río Frío, 3 miles S. of Gómez Farías, [23.070213°N, 99.147765°W, 450 m.], 12 March 1969, J. Reddell. Female holotype (AMNH).

Protoschizomus purificacion Cokendolpher and Reddell, 1992. MEXICO: *Tamaulipas*: Hidalgo, Cueva X, Conrado Castillo, [23.96311°N, 99.47554°W, 1950 m.], 27 December 1986, P. Sprouse, female holotype (AMNH); 15 April 1980, D. Pate, immature male paratype (TMM). *Protoschizomus treacyae* **[new synonymy]** - Cueva del Borrego, 0.5 km S of Conrado Castillo, [23.48333°N, 99.300°W, 1980 m.], 26 December 1986, Treacy Sprouse, female holotype (AMNH).

Protoschizomus rowlandi Cokendolpher and Reddell, 1992. MEXICO: San Luis Potosí: Ciudad Valles, 51.5 miles (82.9 km) E. of Ciudad Valles on Highway 70, [21.985355°N, 98.216481°W, 4 m.], 17 October 1972, B. Firstman, V. Roth. One male holotype and one female paratype (AMNH).

Protoschizomus sprousei Cokendolpher and Reddell, 1992. MEXICO: *Tamaulipas*: Güémez, Cueva del Tecolote, Los San Pedro, [23.959502°N, 99.474805°W, 1940 m.], 18 November 1984, P. Sprouse. One male holotype and one female paratype (AMNH).

Appendix 2. List of 138 morphological characters scored for the phylogenetic analyses of 15 protoschizomid species and seven outgroup hubardiids species. Characters from previous analyses that correspond partially or entirely to the present list (and in the matrix, Appendix 3) are indicated in brackets using the following abbreviations: C&R95 (Cokendolpher & Reddell, 1992) followed by the character number from the corresponding publication. Seven uninformative characters (excluded from all analyses) are indicated by †.

0. Chelicerae, mesal surface, setae G5, number: absent (0); ≤8 (1); ≥9 (2).
1. Chelicerae, mesal surface, movable finger, margin: smooth (0); with teeth (1).
2. Chelicerae, mesal surface, fixed finger, tooth, number: 2 (0); > 3 (1); 3 (2) [C&R95: 14].
3. Chelicerae, mesal surface, movable finger, serrula: rounded knobs (0); hyaline teeth (1) [C&R95: 15].
4. Cheliceral brush: absent (0); present (1) [C&R95: 16].
5. Propeltidium, size: small [1.06-1.26mm] (0); medium [1.36-1.52mm] (1); large [1.70-1.87mm] (2).
6. Propeltidium, anterior process, number of setae: one (0); row of two (1); 2+1 (2); without setae (3) [C&R95: 3].
7. Propeltidium, anterior process, pair of setae at the base: present (0); absent (1).
8. Propeltidium, pairs of dorsal setae: >2 (0); two anterior pairs (1); two separated pairs (2) [C&R95: 5]
9. Dorsoventral muscles, number: 8 (0); 7 (1) [C&R95: 29]
10. Metapeltidium, divided: absent (0); present (1).
11. Length of pedipalps compared to body length (♂): approximately same length (0); pedipalp longer than body (1); pedipalp shorter (2) [C&R95: 21].

12. Pedipalp, trochanter, mesal surface, number of setae near ventral margin: >4 (0); 3 (1).
13. Pedipalp, trochanter, mesal surface, setae: acuminate (0); spiniform (1).
14. Pedipalp, trochanter, mesal spur: absent (0); present (1).
15. Pedipalp, femur, ectal surface, seta Fev1: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
16. Pedipalp, femur, ectal surface, seta Fev2: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
17. Pedipalp, femur, ectal surface, seta Fe1: acuminate (0); spiniform (1); spiniform setiferous tubercle (2); macrosetae (3).
18. Pedipalp, femur, ectal surface, seta Fe2: acuminate (0); microseta (1); macrosetae (2).
19. Pedipalp, femur, ectal surface, seta Fe3: absent (0); present as acuminate (1); present as microseta (2).
20. Pedipalp, femur, ectal surface, seta Fe4: absent (0); present as acuminate (1); present as microseta (2).
21. Pedipalp, femur, ectal surface, seta Fe5, shape: acuminate (0); spiniform (1).
22. Pedipalp, femur, ectal surface, seta Fed1: absent (0); acuminate (1); microseta (2).
23. Pedipalp, femur, ectal surface, seta Fed2: absent (0); present, acuminate (1).
24. Pedipalp, femur, ectal surface, seta Fed3: acuminate (0); spiniform (1).
25. Pedipalp, femur, mesal surface, seta Fmv1: absent (0); present, macroseta (1); presente, spiniform (2).
26. Pedipalp, femur, mesal surface, seta Fmv2: spiniform (0); acuminate (1); macroseta (2).
27. Pedipalp, femur, mesal surface, seta Fmv3: spiniform (0); acuminate (1); macroseta (2).
28. Pedipalp, femur, mesal surface, seta Fmv4: spiniform (0); acuminate (1); macroseta (2).
29. Pedipalp, femur, mesal surface, seta Fm1: absent (0); spiniform (1).
30. Pedipalp, femur, mesal surface, seta Fm2: absent (0); spiniform (1).
31. Pedipalp, femur, mesal surface, seta Fm3: absent (0); spiniform (1).
32. Pedipalp, femur, mesal surface, seta Fm4: absent (0); spiniform (1).
33. Pedipalp, femur, mesal surface, seta Fm5: absent (0); spiniform (1).
34. Pedipalp, femur, mesal surface, seta Fm6: absent (0); spiniform (1).
35. Pedipalp, femur, mesal surface, seta Fm7: absent (0); acuminate (1).
36. Pedipalp, femur, mesal surface, seta Fmd1: absent (0); present, acuminate (1); present, spiniform (2).
37. Pedipalp, femur, mesal surface, seta Fmd2: macroseta (0); acuminate (1); spiniform (2).
38. Pedipalp, femur, mesal surface, seta Fmd3: absent (0); acuminate (1); spiniform (2), macrosetae (3).
39. Pedipalp, Patella, ventral surface, seta Pe4, shape: acuminate (0); spiniform (1); feathered (2).
40. Pedipalp, Patella, ventral surface, seta Pm5, shape: acuminate (0); spiniform (1); feathered (2).
41. Pedipalp, Patella, ventral surface, seta Pme1: absent (0); present as acuminate (1); present as spiniform (2).
42. Pedipalp, Patella, ventral surface, seta Pmm3: absent (0); present as acuminate (1); present as spiniform (2); present as feathered (3).
43. Pedipalp, Patella, ventral surface, seta Pmm2: absent (0); present (1).
44. Pedipalp, Patella, ventral surface, seta Pmm1: absent (0); present (1).
45. Pedipalp, Patella, ventral surface, seta Pe3, shape: acuminate (0); spiniform (1).
46. Pedipalp, Patella, ventral surface, seta Pe2, shape: acuminate (0); spiniform (1).
47. Pedipalp, Patella, ventral surface, seta Pe1: absent (0); present as acuminate (1); present as spiniform (2).
48. Pedipalp, Patella, ventral surface, seta Pm4, shape: acuminate (0); spiniform (1); feathered (2).
49. Pedipalp, Patella, ventral surface, seta Pm3, shape: acuminate (0); spiniform (1); feathered (2).
50. Pedipalp, Patella, ventral surface, seta Pm2: absent (0); present as acuminate (1); present as spiniform (2); present as feathered (3).
51. Pedipalp, Patella, ventral surface, seta Pm1: absent (0); present (1).
52. Pedipalp, Tibia, ventral surface, external row of setae, seta 1, shape: acuminate (0); spiniform (1).
53. Pedipalp, Tibia, ventral surface, external row of setae, seta 2, shape: acuminate (0); feathered (1).
54. Pedipalp, Tibia, ventral surface, external row of setae, seta 3, shape: acuminate (0); spiniform (1).
55. Pedipalp, Tibia, ventral surface, external row of setae, seta 4: absent (0); present (1).
56. Pedipalp, Tibia, ventral surface, external row of setae, seta 4, shape: acuminate (0); spiniform (1).
57. Pedipalp, Tibia, ventral surface, external row of setae, seta 5: absent (0); present (1).
58. Pedipalp, Tibia, ventral surface, external row of setae, seta 5, shape: acuminate (0); spiniform (1).
59. Pedipalp, Tibia, ventral surface, external row of setae, seta 6: absent (0); present as spiniform (1).
60. Pedipalp, Tibia, ventral surface, external row of setae, size: same size (0); distal enlargment (1).
61. Pedipalp, Tibia, ventral surface, internal row of setae, seta 1, shape: acuminate (0); feathered (1); spiniform (2).
62. Pedipalp, Tibia, ventral surface, internal row of setae, seta 3, shape: acuminate (0); feathered (1).
†63. Pedipalp, Tibia, ventral surface, internal row of setae, seta 4, shape: acuminate (0); feathered (1).
†64. Pedipalp, Tibia, ventral surface, internal row of setae, seta 5: absent (0); present (1).
65. Pedipalp, Tibia, ventral surface, internal row of setae, seta 5, shape: acuminate (0); feathered (1).
†66. Pedipalp, Tibia, ventral surface, internal row of setae, seta 6: absent (0); present (1).
67. Pedipalp, Tibia, ventral surface, internal row of setae, size: same size (0); distal enlargement (1); basal enlargement (2).
68. Pedipalp, Tibia, ventral surface, medial row of setae, seta 1, shape: spiniform (0); feathered (1).
69. Pedipalp, Tibia, ventral surface, medial row of setae, seta 2, shape: spiniform (0); feathered (1).
70. Pedipalp, Tibia, ventral surface, medial row of setae, seta 3, shape: spiniform (0); feathered (1).
71. Pedipalp, Tibia, ventral surface, medial row of setae, seta 4: absent (0); present (1).
72. Pedipalp, Tibia, ventral surface, medial row of setae, seta 4, shape: spiniform (0); feathered (1).
73. Pedipalp, Tibia, ventral surface, medial row of setae, seta 5: absent (0); present, feathered (1).
74. Pedipalp, Tibia, ventral surface, medial row of setae, size: same size (0); distal enlargement (1).
75. Pedipalp, Tibia, ventral surface, seta TM1, shape: acuminate (0); feathered (1).
76. Pedipalp, Tibia, ventral surface, seta TM2: absent (0); present (1).
†77. Pedipalp, Tibia, ventral surface, seta TM2, shape: spiniform (0); feathered (1).
†78. Pedipalp, Tarsus, spurs: symmetrical (0); asymmetrical (1).

79. Leg IV, Trochanter, length, in proportion with length of the femur: 1/2 (0); 1/3 (1) [C&R95: 25].
80. Leg IV, Femur, less than 4.8 times longer than high: less (0); more (1). [C&R92: 24]
81. Flagellum (♂), dorsoventrally compressed: not compressed (0); compressed (1).
82. Flagellum (♂), shape: bulbous (0); tubular (1); lanceolate (2).
83. Flagellum (♂), widened distally: absent (0); present (1). [C&R92: 37]
84. Flagellum (♂), stalks: present (0); absent (1). [C&R92: 38]
85. Flagellum (♂), ventro-lateral lobes: absent (0); present (1).
86. Flagellum (♂), ratio width/length: over 3x long as wide (0); less than 3x long as wide (1) [C&R92: 39].
87. Flagellum (♂), distal portion: rounded (0); pointed (1).
88. Flagellum (♂), seta Dm1, position respect to Vm1: anterior (0); posterior (1); at the same level (2).
89. Flagellum (♂), seta Dm2: present (0); absent (1) [C&R92: 34].
90. Flagellum (♂), seta Dm3: absent (0); present (1).
91. Flagellum (♂), seta Dm4, position respect to Dl2: anterior (0); posterior (1); at the same level (2).
92. Flagellum (♂), seta Dl1: absent (0); present (1).
93. Flagellum (♂), seta Dl1, position respect to Vm3: anterior (0); posterior (1); at the same level (2).
94. Flagellum (♂), seta Dl2, position respect to Vl1: at the same level (0); anterior (1); posterior (2).
95. Flagellum (♂), seta Dl3, position respect to Vl2: at the same level (0); posterior (1); anterior (2).
96. Flagellum (♂), seta Dl4: absent (0); present, macroseta (1); present, microseta (2).
97. Flagellum (♂), seta Dl4, position respect to Dl3: anterior (0); posterior (1); at the same level (2).
98. Flagellum (♂), seta Vm1, position respect to Vm2: at the same level (0); posterior (1); anterior (2).
99. Flagellum (♂), seta Vm4: present (0); absent (1) [C&R92: 35].
100. Flagellum (♂), seta Vm5: absent (0); present (1).
101. Flagellum (♂), seta Vm5, position respect to Vl1: at the same level (0); posterior (1).
102. Flagellum (♂), microsetae, dorso-anterior pair: absent (0); present (1).
103. Flagellum (♂), microsetae, antero-lateral pair: absent (0); present (1).
104. Flagellum (♀), annuli shape: wide (0); slender (1); absent (2).
105. Flagellum (♀), size: less than 2.9 (0); more than 3 (1).
106. Flagellum (♀), annuli a: absence (0); presence (1).
107. Flagellum (♀), annuli b: absence (0); presence (1).
108. Flagellum (♀), annuli c: absent (0); present (1).
109. Flagellum (♀), annuli d: absence (0); presence (1).
110. Flagellum (♀), annuli e: absence (0); presence (1).
111. Flagellum (♀), seta Dm1, position respect to Vm1: at the same level (0); posterior (1).
112. Flagellum (♀), seta Dm2: absent (0); present (1).
113. Flagellum (♀), seta Dm3: absent (0); present (1).
114. Flagellum (♀), seta Dm4: present (0); absent (1).
115. Flagellum (♀), seta Dm4, position respect to Dl2: anterior (0); posterior (1); at the same level (2).
116. Flagellum (♀), seta Dl1: absent (0); present (1).
117. Flagellum (♀), seta Dl1, position respect to Vm3: anterior (0); posterior (1); at the same level (2).
118. Flagellum (♀), seta Dl2, position respect to Vl1: at the same level (0); anterior (1); posterior (2).
119. Flagellum (♀), seta Dl3, position respect to Vl2: at the same level (0); posterior (1); anterior (2).
120. Flagellum (♀), seta Dl4, position respect to Dl3: anterior (0); posterior (1).
†121. Flagellum (♀), seta Vm2: absent (0); present (1).
†122. Flagellum (♀), seta Vm1, position respect to Vm2: at the same level (0); posterior (1); anterior (2).
123. Flagellum (♀), seta Vm4: absent (0); present (1).
124. Flagellum (♀), microsetae, number of pairs: 2 (0); 3 (1).
125. Spermathecae, number of lobes: 1 pair (0); 2 pairs (1); more than 2 pairs (2).
126. Spermathecae, Gonopod: absent (0); present (1).
127. Spermathecae, chitinized arch: absent (0); present (1).
128. Spermathecae, margins of the receptaculum: smooth with pits (0); lobed with pits (1); saw-toothed with pits (2) [C&R92: 43].
129. Spermathecae, Microtubulus: absent (0); present (1).
130. Spermathecae, bulbs: absent (0); present (1).
131. Spermathecae, symmetry between lobes: symmetrical (0); asymmetrical (1).
132. Spermathecae, lobes: straight (0); curved (1).
133. Spermathecae, lobes, size between lobes: same size (0); different size (1).
134. Terguite III, number of setae: 2 (0); 4 (1).
135. Sternites, setae patterns (♂): scattered or irregular rows (0); two distinct rows (1) [C&R92: 27].
136. Sternite VI, size: long (0); short (1) [C&R92: 28].

Appendix 3. Distribution of the 137 morphological characters (Appendix 2) among ingroup and outgroup taxa for the phylogenetic analysis of the schizomid family Protoschizomidae Rowland, 1975. Material examined is listed in Appendix 1. Character states are recorded as 0-3, unknown (?), or inapplicable (-).

Megaschizomus mossambicus
21211230010200111112212112000000011122200031101222311011111
11111111001111110111000010000110107010?0110110011111101 1-10-
10101101 1??0100010

Bamazomus sp.
21111121011010100010000100111000000001000100000100000000-0-
00100100111111010111101010010210 10-010-01111111110000000 10-
210100?211110101010

Hubbardia pentapeltis
20111221011101111110000102000000000000221122001121100000101 0
01211110100111110101101010000210 10-110-11111111111001000 10-
0101001211110101010

Hubbardia borregoensis
20111121011101111110110002000000000002210210011200100001010
01211110101111110111010100102101 0-110-11111111110010001 0-
010100?211110101010

Surazomus sturmi
10111111011110100010100000111000000001100100000000000001 00-
001110-00111110010-110101000021010-210-11101?1111000?00010-
??01?0?100111000010

Rowlandius viridis
11111011010110111110000000111000000001110210011000000000-0-
011110-021110-00111110001001021010-000-11111?1111100?00010-
0101000111111011010

Mayazomus infernalis
10111011210110122210000100000000000002201110000111200001010
001110?011110-01011110101001021010-100-01111111111000000 10-
0101000111110000010

Protoschizomus rowlandi
0000011010110003330010111122211111011032203001122210111111101111110100010010110000033300000111222011111100320001010222311111111111111111000101101101102011100010101222101111001011110100100001210?000100110101

Protoschizomus occidentalis
0000001010110003330010111122211111011032200001022210111111101111110000010010110000021110000101210202010110?010????????????1???000110110101

Protoschizomus sprousei
0000021000100003330000111122211110011032203011122211111111111111111110001001011000021110000010100010101111001011110111-12200121000001011100 1

Protoschizomus franckei
0000011000100003330000111122211111011032200001122210111111111111111000001111011000021110010101010202011110010111101011010012100001101010011

Protoschizomus pachypalpus
0000001010110003330000111122201110111032200001002210111110-01111110000111010110000011101101010002221117100101111010110100010100001101111 01

Protoschizomus gertschi
0000021000?000333011011112220111101103220000112221011111110111110100111100??????????????????????1010011111001000010100000111110?1

Protoschizomus purificacion
0000011000?000333011011112220111001103220000112221011111110111110100111100?010?111121000102011110010111101021020012110000111110?1

Agastoschizomus juxtlahuacensis
0000020000100003330110111122211111111032003111122301111111111111111000101101101102011101110101220101110001011110111111020121000?????010

Agastoschizomus lucifer
0000020000100003330000011122201111110032000101022231111111111111111000101101101102011100010101222101111001011110100112201010000000010010

Agastoschizomus huitzmolotitlensis
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Onychotelyphonus bonneri
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A modified definition of the genus *Haplochernes* (Pseudoscorpiones: Chernetidae), with a new species from Hainan Island

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Abstract. The pseudoscorpion genus *Haplochernes* Beier, 1932, is redescribed and restricted to those species of Chernetidae with only four setae on the cheliceral hand and a pair of moderately long, slender spermathecae. This new definition is shared by only two species: the type species *H. boncicus* (Karsch, 1881) from Japan and possibly Taiwan and *H. wuzhiensis* Gao and Zhang sp. nov. from Hainan Island, China. *Haplochernes madagascariensis* Beier, 1932 from Madagascar and *H. hagai* Morikawa, 1953 from Japan are treated as new synonyms of *H. boncicus*.

Keywords: taxonomy, morphology, Asia, Australasia

ZooBank: http://zoobank.org/References/4B621118-DAAB-478C-A82B-B49EE0E525ED

When initially described, the pseudoscorpion genus *Haplochernes* Beier, 1932 included 14 species from the Indo-Pacific region, with the most westerly species from Madagascar and the most easterly from Samoa. Some of the species originally included in the genus have since been removed to other genera, and several new species have been added including species from the Pacific region (Chamberlin 1938; Beier 1940, 1948; Morikawa 1953; Beier 1957, 1976b) and the island of Réunion, located in the south-western Indian Ocean (Mahnert 1975). There are currently 16 valid species of *Haplochernes* (Harvey 2013).

The type species *Chelifer boncicus* Karsch, 1881, originally described from Japan (Karsch 1881), was redescribed and comprehensively illustrated by Sato (1979b), in which the presence of only four setae on the eheliceral hand was noted and illustrated. This rather important difference suggested to us that most species of *Haplochernes*, which have five cheliceral setae, may be misplaced in the genus. Other major differences include the position of the internal series of trichobothria which extend to the distal half of the fixed chelal finger in *H. boncicus* and *H. madagascariensis* Beier, 1932 (Beier 1932; Sato 1979b), but are grouped basally in other species (e.g., Beier 1932, 1957, 1976b; Harvey 1988), and the position of trichobothrium *est* which is situated submedially in *H. boncicus* and *H. madagascariensis* (Beier 1932; Sato 1979b), but is located subbasally near trichobothrium *esb* in most other *Haplochernes* (e.g., Chamberlin 1938; Beier 1940, 1948, 1957, 1976b; Harvey 1988). To begin to unravel this conundrum, we present a redescription of *H. boncicus* based on the type specimens and other material from Japan, and describe a morphologically similar new species of *Haplochernes* from Hainan Island. In addition to the differences already noted above, we found that the spermathecae of *H. boncicus* are moderately long, curved and laek terminal bulbs, compared with the short spermathecae of other *Haplochernes* species which have enlarged round terminal bulbs (e.g., Harvey 1988). A new diagnosis of *Haplochernes* is presented, and the systematic position of the remaining species will be treated in a second paper (Harvey, unpublished data).

METHODS

This study is based on speeimens that are lodged in the Museum of Hebei University, Baoding City, China (MHBU), Western Australian Museum, Perth (WAM) and the Museum für Naturkunde, Berlin (ZMB). The specimens were studied using temporary slide mounts prepared by immersion of the specimen in lactic acid at room temperature for several hours to days, and mounting them on microscope slides with 10 or 12 mm coverslips supported by small sections of 0.25, 0.35 or 0.5 mm diameter nylon fishing line. After study, the speeimens were rinsed and returned to 75% ethanol with the dissected portions placed in 12 × 3 mm glass genitalia microvials (BioQuip Products, Inc.). Specimens were examined with either a Leica M165C and a Leica M205A stereomicroscope (ZZG, FZ), a Leica MZ–16A stereomicroseope (MSH), a Nikon YS100 (ZZG, FZ), an Olympus BH–2 or a Leiea DM2500 (MSH) compound microseope, the latter fitted with interference contrast. Illustrations were made with the aid of a drawing tube attaehed to the compound microscopes. Measurements were taken at the highest possible magnification using an ocular graticule.

Terminology and mensuration mostly follow Chamberlin (1931), with the exeeption of the nomenclature of the pedipalps, legs and with some minor modifications to the

terminology of the trichobothria (Harvey 1992), chelicera (Judson 2007) and faces of the appendages (Harvey et al. 2012). The following abbreviations are used in the text. Chelal trichobothria: *b* = basal; *sb* = subbasal; *st* = subterminal; *t* = terminal; *ib* = interior basal; *isb* = interior subbasal; *ist* = interior subterminal; *it* = interior terminal; *eb* = exterior basal; *esb* = exterior subbasal; *est* = exterior subterminal; *et* = exterior terminal. Cheliceral setae: *gls* = galeal seta; *es* = exterior seta; *is* = interior seta; *ls* = laminal seta; *bs* = basal seta.

SYSTEMATICS

Family Chernetidae Menge, 1855
Subfamily Chernetinae Menge, 1855
Genus *Haplochernes* Beier, 1932

Haplochernes Beier, 1932: 108.

Type species.—*Chelifer boncicus* Karsch, 1881, by original designation.

Diagnosis.—*Haplochernes* is distinguished from all other chernetid genera by the combined presence of only 4 setae on the cheliceral hand (Figs. 2B, 4A, 5A, 6B) and the slightly curved, paired spermathecae that lack terminal bulbs (Figs. 2J, 4G, 6D).

Description (adult).—*Setae:* moderately long, generally straight, and many slightly dentate.

Chelicera (Figs. 2B, 4A, 5A, 6B): hand with 4 setae, *sbs* absent; movable finger with 1 long subdistal seta; rallum of 3 blades (Figs. 2C, 4C, 5C), only the most distal blade serrate, others smooth; galea with distal rami (Figs. 2B, 4B, 5B); lamina exterior present.

Pedipalp: robust; fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Figs. 2E, 4E, 5E): trichobothria *eb*, *esb*, *ib* and *ist* subbasal; *est* medial, midway between *esb* and *et*; *et* subdistal; *isb* and *it* submedial; *b* and *sb* subbasal; *st* slightly closer to *sb* than to *t*. Venom apparatus only present in movable chelal finger, venom duct terminating in nodus ramosus slightly basal to *t* (Figs. 2E, 4E, 5E); marginal chelal teeth juxtadentate, with accessory chelal teeth on retrolateral and prolateral margins of both fingers.

Carapace: evenly granulate (Fig. 2A); without eye-spots or with 1 pair of faint eye-spots (Fig. 2A); furrows present or absent; posterior margin straight.

Coxal region: manducatory process with small sub-oral seta on medial edge; median maxillary lyrifissure rounded and situated submedially; posterior maxillary lyrifissure rounded.

Legs (Figs. 2H, 4H & I, 5F & G, 6E & F): junction between femora and patellae of legs I and II strongly oblique; suture line between femora and patellae of legs III and IV strongly oblique; femora of legs III and IV much smaller than patellae; patellae and tibiae of legs III and IV without pseudotactile setae; tarsi of legs III and IV with long tactile seta; legs with subterminal tarsal setae arcuate and acute; all tarsi with slit sensillum on raised mound; arolium undivided, slightly shorter than claws; claws slender and simple.

Abdomen: most tergites and sternites weakly divided (Fig. 3A & B). Anal plates (tergite XII and sternite XII) situated between tergite XI and sternite XI. Pleural membrane striate and slightly wrinkled, without setae. Spiracles simple, with spiracular helix.

Genitalia: male of typical chernetid conformation; female with a pair of medium length, thin, slightly curved spermathecae that lack terminal bulbs (Figs. 2J, 4G, 6D).

Description (tritonymph).—*Chelicera:* hand with 4 setae, *sbs* absent.

Pedipalp: fixed finger with 7 trichobothria, movable finger with 3 trichobothria (Fig. 2F); *isb* and *sb* absent.

Description (deutonymph).—*Chelicera:* hand with 4 setae, *sbs* absent.

Pedipalp: fixed finger with 6 trichobothria, movable finger with 2 trichobothria (Fig. 2G); *esb*, *isb*, *sb* and *st* absent.

Remarks.—The genus *Haplochernes* is here restricted to those species of Chernetidae with only four setae on the cheliceral hand and a single pair of thin, slightly curved spermathecae that lack terminal bulbs. While the majority of chernetids have five setae on the cheliceral hand, and others have six or more, very few have four setae and none have fewer than four. Those species that have four setae include some, but not all, species of *Americhernes* Muchmore, 1976, *Anaperochernes* Beier, 1964, *Coprochernes* Beier, 1976, *Neoallochernes* Hoff, 1947, *Rhopalochernes* Beier, 1932 and the sole species of *Meiochernes* Beier, 1957 (Beier 1957, 1964, 1976a; Muchmore 1976, 1992; Mahnert 1985; Harvey 1990; Heurtault 1998).

The only described species that conform to the diagnosis of *Haplochernes* presented here are *H. boncicus* and *H. hagai* Morikawa, 1953 from Japan and *H. madagascariensis* from Madagascar. We also describe a new species from Hainan Island. The other species of *Haplochernes* differ by the presence of five setae on the cheliceral hand, the subbasal position of trichobothrium *est* and the paired spermathecae with short ducts and enlarged receptacula (e.g., Harvey 1988), and their systematic position will be assessed in another publication (Harvey, unpublished data).

Haplochernes boncicus (Karsch, 1881)
Figs. 1, 2

Chelifer boncicus Karsch, 1881: 37.
Chelifer nipponicus Kishida, 1927: 954, fig. 1844 (synonymised by Judson, 2010: 11).
Haplochernes madagascariensis Beier, 1932: 110, fig. 127. **Syn. nov.**
Haplochernes hagai Morikawa, 1953: 350, fig. 2c–f. **Syn. nov.**

Type material.—*Syntypes of* Chelifer boncicus. JAPAN: 2 ♂, 3 ♀, no other locality data [F.K.W. Dönitz and F.M. Hilgendorf] (ZMB Arach-3514).

Holotype female of *Haplochernes madagascariensis*. MADAGASCAR: "N.W. Madagaskar", [J.M.] Hildebrandt (ZMB, Arachnida-3797).

Other material examined.—JAPAN: 2 ♂, 1 ♀, no other data (ZMB Arach-31982); 2 ♀, no other data, Hilgendorf (ZMB Arach-31983); 1 ♂, 1♀, no other data (ZMB Arach-31984); Gifu Prefecture: 1 ♂, 7 ♀, 1 tritonymph, 1 deutonymph, trail above Fuwa no Taki, Fuwa District, 35°24′50"N, 136°31′05"E, alt. 303 m, 3 June 2010, under tree bark, D. Harms, M.S. Harvey, Y. Konishi (WAM T129559–4, T130741, T130742).

Diagnosis.—*Haplochernes boncicus* is much smaller than *H. wuzhiensis* sp. nov., e.g., pedipalpal femur 0.585–0.87 (♂),

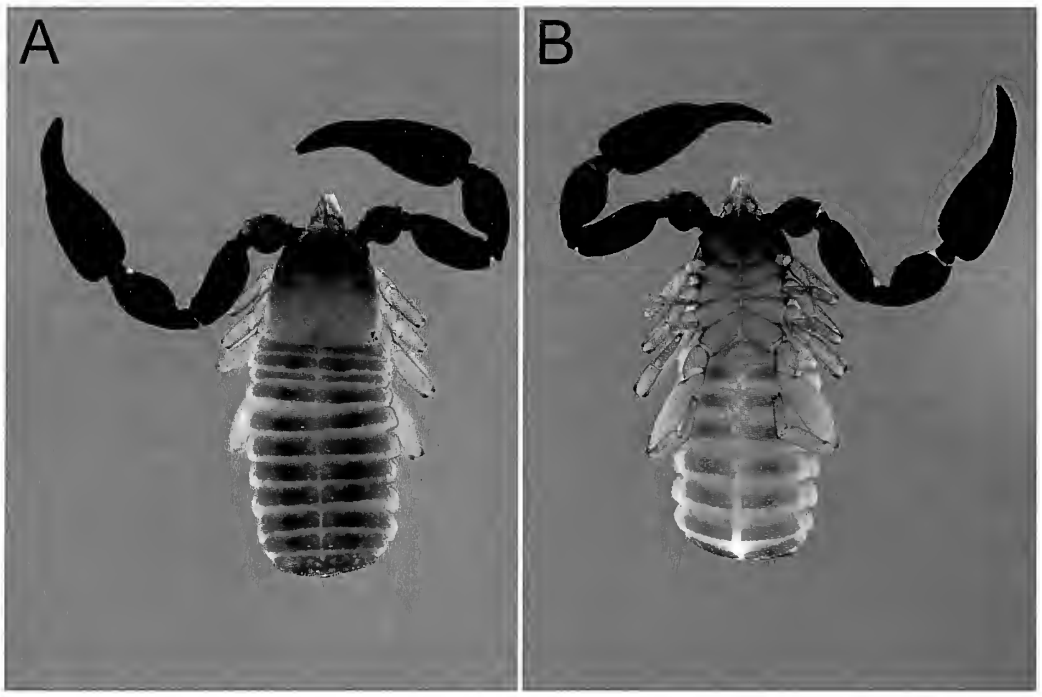

Figure 1.—*Haplochernes boncicus* (Karsch) (WAM T129560), female: A. Dorsal view. B. Ventral view.

0.655–0.79 (♀) mm, and chela (with pedicel) 1.05–1.46 (♂), 1.18–1.34 (♀) mm, compared with pedipalpal femur 1.20–1.25 (♂), 1.13–1.28 (♀) mm and chela (with pedicel) 2.15–2.16 (♂), 1.93–2.08 (♀) mm of *H. wuzhiensis*.

Description (adults).—*Color:* pedipalps deep red-brown, carapace red-brown, becoming paler in posterior half; legs yellow-brown (Fig. 1A, B).

Setae: most setae apically denticulate.

Chelicera (Fig. 2B): with 4 setae on hand and 1 subdistal seta (*gls*) on movable finger; seta *sbs* absent; *bs* dentate, *ls, is* and *es* smooth; with 2 dorsal lyrifissures and 1 ventral lyrifissure; galea of ♂ and ♀ thick, with 5–6 small distal rami; rallum of 3 blades (Fig. 1C); serrula exterior with 18 (♂, ♀) blades; lamina exterior present.

Pedipalp (Fig. 2D): all surfaces, except chelal fingers, granulate; patella with 3 small sub-basal lyrifissures; without tactile setae; trochanter 1.87 (♂), 1.63 (♀), femur 2.60–2.79 (♂), 2.46–2.81 (♀), patella 2.03–2.24 (♂), 3.01–3.33 (♀), chela (with pedicel) 2.99–3.41 (♂), 3.01–3.33 (♀), chela (without pedicel) 2.95–3.24 (♂), 2.92–3.21 (♀), hand 1.59–1.84 (♂), 1.67–1.84 (♀) x longer than broad, movable finger 0.78–0.87 (♂), 0.85–0.90 (♀) x longer than hand. Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Fig. 2E): *eb* and *esb* situated basally, *est* situated slightly closer to *esb* than to *et*, *ib* and *ist* situated subbasally; *isb* and *it* situated medially, with *isb* closer to *it* than to *ist*; *t* situated subdistally, *st* situated slightly closer to *sb* than to *t*. Venom apparatus only present in movable chelal finger, venom duct long, terminating in nodus ramosus which is closer to *t* than to *st*. Chelal teeth rounded and juxtadentate; fixed finger with ca. 38 (♂), 43 (♀)teeth, plus 4 (♂), 7 (♀) retrolateral accessory teeth and 3 (♂), 1 (♀) prolateral accessory teeth; movable finger with ca. 42 (♂), 46 (♀) teeth, plus 7 (♂), 6 (♀) retrolateral accessory teeth and 2 (♂, ♀) prolateral accessory teeth; fixed finger with 1 retrolateral and 1 prolateral sense spots, movable finger with 1 retrolateral and 0 prolateral sense spots.

Carapace (Fig. 2A): evenly granulate; 1.02–1.21 (♂), 0.94–1.19 (♀) x longer than broad; with 1 pair of very faint eye-spots (♀) or eye-spots not visible (♂); with 56 (♂), 53 (♀) setae, including 8 (♂), 6 (♀) setae near anterior margin and 8 (♂), 10 (♀) setae near posterior margin; without furrows.

Coxal region: maxillae granulate anteriorly; coxae smooth; manducatory process somewhat pointed, with 3 apical acuminate setae, with 1 small sub-oral seta, and 23 (♂), 24 (♀) additional setae; median maxillary lyrifissure rounded and situated submedially; posterior maxillary lyrifissure rounded. Chaetotaxy of coxae I–IV: ♂, 12: 12: 14: 19; ♀, 10: 12: 11: 22.

Legs: junction between femora and patellae I and II strongly oblique to long axis; junction between femora and patellae III and IV very angulate; femora III and IV much smaller than patellae III and IV; femur + patella of leg IV 3.35 (♂), 3.07 (♀) x longer than broad; patella and tibia without 'pseudotactile' seta; tarsus IV with very long tactile seta located in basal half (Fig. 2H), TS ratio = 0.33 (♂), 0.29 (♀); subterminal tarsal setae arcuate and acute; claws not modified; arolium slightly shorter than claws.

Abdomen: tergites II–X and sternites III–X with faint median suture line. Tergal chaetotaxy: ♂, 10: 12: 10: 15: 20: 18: 17: 17: 17: 15: 16 (including 4 tactile setae): 2; ♀, 12: 12: 12: 14: 17: 17: 16: 15: 14: 13: 18: 2; all setae acuminate. Sternal chaetotaxy: ♂, 48: (2) 13 [3 + 3] (2): (2) 10 (2): 20: 18: 19: 17: 19: 16: 21 (including 4 tactile setae): 2; ♀, 28: (2) 12 (2): (2) 12 (2): 18: 18: 20: 16: 18: 15: 12 (including 4 tactile setae): 2. Sternite III of female with setae arranged in inverted-U (Fig. 2I). Spiracles with helix. Pleural membrane striate and slightly wrinkled, without setae.

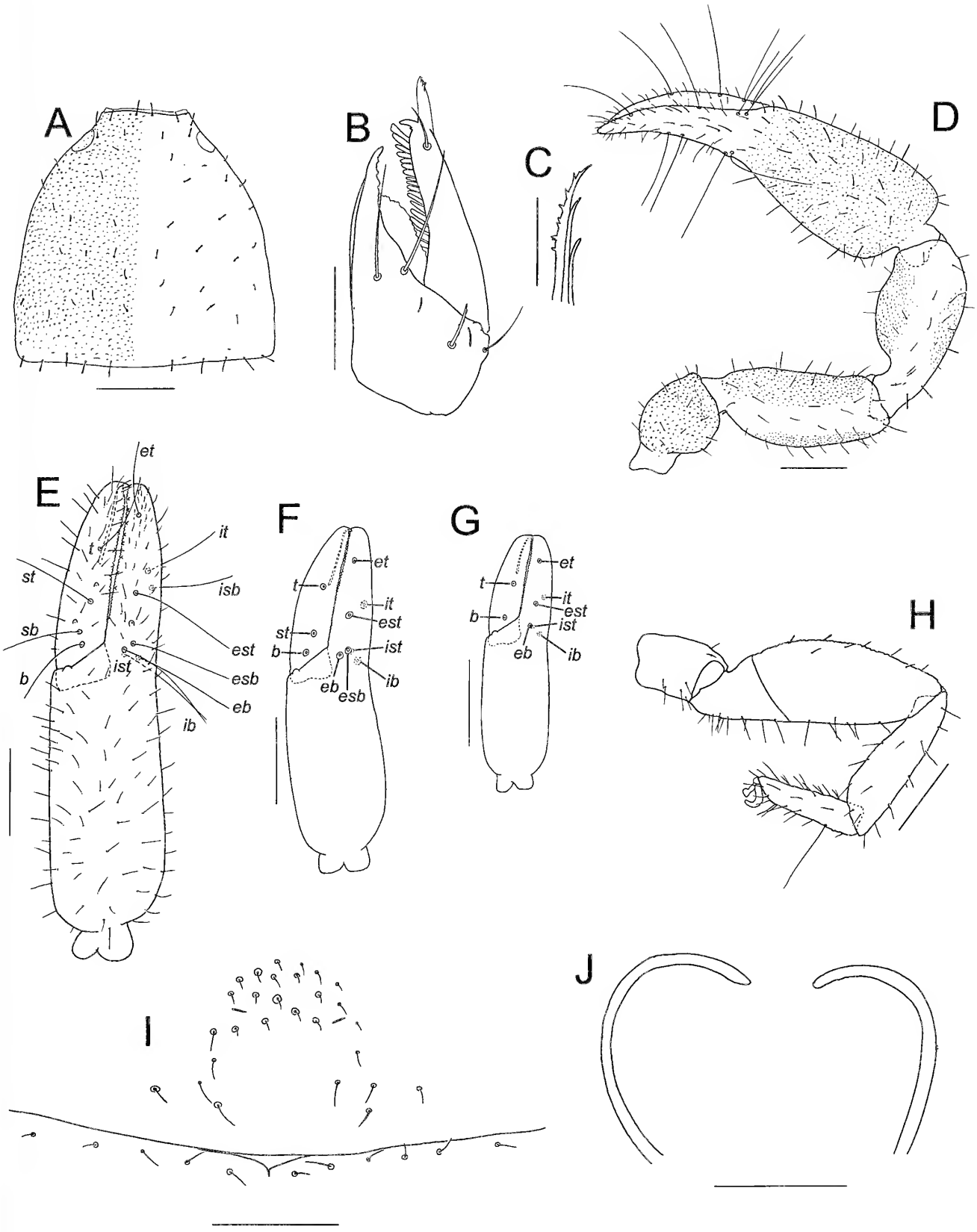

Figure 2.—*Haplochernes boncicus* (Karsch), female (WAM T129559), unless stated otherwise: A. Carapace. B. Right chelicera, dorsal view. C. Right rallum. D. Right pedipalp, dorsal view. E. Left chela, lateral view. F. Left chela, lateral view, tritonymph (WAM T129563). G. Left chela, lateral view, deutonymph (WAM T129564). H. Right leg IV, lateral. I. Genital sternites, ventral view. J. Spermathecae, ventral view. Scale lines = 0.25 mm (A, D–H); 0.1 mm (B, I, J); 0.05 mm (C).

Genitalia: male typical of Chernetidae, internal setae acicular and slightly curved; female with single pair of moderately long spermathecae, gently curved (Fig. 2J).

Dimensions (mm): males: WAM T130742, followed by other males (when measured): Body length 2.21 (2.36–3.04). Pedipalps: trochanter 0.44/0.235, femur 0.725/0.26 (0.585–0.87/0.225–0.325), patella 0.67/0.305 (0.545–0.805/0.25–0.36), chela (with pedicel) 1.26/0.37 (1.05–1.46/0.34–0.45), chela (without pedicel) 1.20 (1.01–1.39), hand length 0.68 (0.55–0.83), movable finger length 0.59 (0.525–0.66). Chelicera 0.255/0.14, movable finger length 0.205. Carapace 0.795/0.68 (0.755–0.92/0.625–0.86). Leg I: femur 0.25/0.145, patella 0.345/0.13, tibia 0.285/0.08, tarsus 0.245/0.07. Leg IV: femur + patella 0.67/0.20, tibia 0.445/0.125, tarsus 0.315/0.085, TS = 0.105.

Females: WAM T129559, followed by other females (when measured): Body length 2.25 (2.54–3.15). Pedipalps: trochanter 0.444/0.272, femur 0.79/0.281 (0.655–0.77/0.25–0.29), patella 0.672/0.217 (0.635–0.70/0.285–0.335), chela (with pedicel) 1.313/0.402 (1.18–1.34/0.37–0.43), chela (without pedicel) 1.265 (1.15–1.30), hand length 0.670 (0.64–0.75), movable finger length 0.603 (0.575–0.63). Chelicera 0.294/0.155, movable finger length 0.224. Carapace 0.878/0.867 (0.74–0.90/0.685–0.81); eye diameter 0.085. Leg I: femur 0.270/0.154, patella 0.360/0.132, tibia 0.301/0.090, tarsus 0.273/0.072. Leg IV: femur + patella 0.736/0.240, tibia 0.484/0.134, tarsus 0.335/0.090, TS = 0.097.

Description (tritonymph).—*Color:* sclerotized portions generally pale yellow-brown.

Chelicera: with 4 setae on hand and 1 subdistal seta (gls) on movable finger; seta *sbs* absent; seta *bs* dentate, remaining setae acuminate; seta *bs* shorter than others; galea with 5 small distal rami; rallum with 3 blades; serrula exterior with 16 blades.

Pedipalp: trochanter 1.68, femur 2.37, patella 1.98, chela (with pedicel) 3.30, chela (without pedicel) 3.15, hand 1.75 x longer than broad, movable finger 0.87 x longer than hand. Fixed chelal finger with 7 trichobothria, movable chelal finger with 3 trichobothria (Fig. 2F): *eb*, *esb*, *ib* and *ist* situated subbasally, *est* situated slightly closer to *esb* than to *et*, *it* situated medially, and *st* much closer to *b* than to *t*. Venom apparatus only present in movable chelal finger, venom duct long, terminating in nodus ramosus near *t*. Fixed finger with 38 marginal teeth, plus 1 retrolateral and 1 prolateral accessory teeth; movable finger with 39 marginal teeth, plus 1 retrolateral and 3 prolateral accessory teeth.

Carapace: 1.05 x longer than broad; eye-spots not visible; with ca. 40 setae, with 4 near anterior margin and 7 near posterior margin; without furrows.

Coxal region: chaetotaxy of coxae I–IV: 7: 9: 8: 11.

Legs: tarsus IV with sub-distal tactile seta, TS ratio = 0.30.

Abdomen: tergal chaetotaxy: 8: 9: 7: 10: 12: 12: 13: 12: 12: 12: 15 (including 4 tactile setae). Sternal chaetotaxy: 7: (1) 8 (1): (1) 8 (1): 14: 15: 14: 15: 14: 13: 16 (including 4 tactile setae): 2.

Dimensions (mm): WAM T129563: Body length 1.89. Pedipalps: trochanter 0.345/0.205, femur 0.51/0.215, patella 0.475/0.24, chela (with pedicel) 0.99/0.30, chela (without pedicel) 0.945, hand length 0.525, movable finger length 0.455. Carapace 0.725/0.69.

Description (deutonymph).—*Color:* sclerotized portions generally pale yellow-brown.

Chelicera: with 4 setae on hand and 1 subdistal seta (*gls*) on movable finger; seta *sbs* absent; seta *bs* dentate, remaining setae acuminate; seta *bs* shorter than others; galea with 4 small distal rami; rallum with 3 blades; serrula exterior with 13 blades.

Pedipalp: trochanter 1.13, femur 2.24, patella 2.00, chela (with pedicel) 3.43, chela (without pedicel) 3.29, hand 1.88 x longer than broad, movable finger 0.78 x longer than hand. Fixed chelal finger with 6 trichobothria, movable chelal finger with 2 trichobothria (Fig. 2G): *eb*, *ib* and *ist* situated subbasally, *est* situated closer to *esb* than to *et*, and *it* situated medially. Venom apparatus only present in movable chelal finger, venom duct long, terminating in nodus ramosus distal to *t*. Fixed finger with 28 marginal teeth and no accessory teeth; movable finger with 36 marginal teeth and no accessory teeth.

Carapace: 1.06 x longer than broad; eye-spots not visible; with 34 setae, with 4 near anterior margin and 6 near posterior margin; without furrows.

Coxal region: chaetotaxy of coxae I–IV: 5: 5: 5: 5.

Legs: tarsus IV with sub-distal tactile seta, TS ratio = 0.29.

Abdomen: tergal chaetotaxy: 6: 6: 6: 6: 10: 8: 10: 10: 10: 8: 12 (including 4 tactile setae). Sternal chaetotaxy: 0: (1) 4 (1): (1) 6 (1): 10: 10: 10: 10: 10: 10: 11 (including 4 tactile setae): 2.

Dimensions (mm): WAM T129564: Body length 1.30. Pedipalps: trochanter 0.255/0.155, femur 0.37/0.165, patella 0.35/0.175, chela (with pedicel) 0.72/0.21, chela (without pedicel) 0.69, hand length 0.395, movable finger length 0.31. Carapace 0.58/0.545.

Remarks.—The syntypes of *C. boncicus* were collected by two German scientists: Friedrich K. W. Dönitz (1838–1912) and Franz M. Hilgendorf (1839–1904). Dönitz transferred to the Imperial Medical Academy in Tokyo in 1873, and was based in Japan for 13 years (Nuttall 2009). Hilgendorf was also based at the Academy, between 1873 and 1876 (Yajima 2007). The precise provenance of the specimens is not known. The vial originally contained six specimens, but only five were present when audited in 1999 (see http://www.biologie.uni-ulm.de/cgi-bin/herbar.pl?herbid=95200&sid=T&lang=e; accessed 22 January 2014), and when borrowed for the present study. As there are no appreciable differences between the syntypes and no taxonomic controversy of the species, we feel there is no need to designate a leetotype. The other three vials in the ZMB collection appear to be those mentioned by Ellingsen (1907, 1910) which also lack locality data other than Japan.

The species was briefly redescribed by Beier (1932), as *H. boncicus*, where illustrations of the pedipalp of a male and female were provided, probably based on the ZMB specimens. A more detailed redescription and additional illustrations were provided by Sato (1979b), in which the presence of only four setae on the cheliceral hand was first noted.

Two other taxa are included as synonyms of *H. boncicus*. *Chelifer nipponicus* Kishida, 1927, also with an unspecified type locality in Japan (Kishida 1927), was synonymized with *C. boncicus* by Judson (2010). *Haplochernes hagai* was described by Morikawa (1953) from three collections, all from

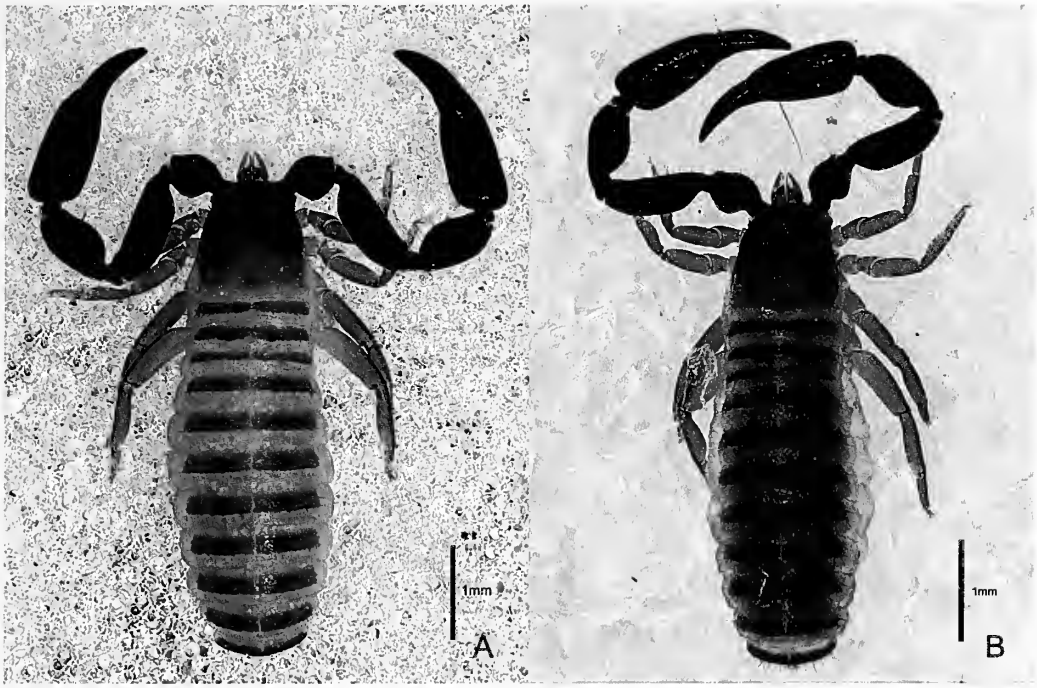

Figure 3.—*Haplochernes wuzhiensis* sp. nov., dorsal view: A. Female holotype. B. Male paratype.

within the city of Tokyo. The species was later regarded as a subspecies of *H. boncicus* by Morikawa (1960), from which it was separated by the larger body length and pedipalps, lack of eye-spots, and lower numbers of accessory teeth on the chelal fingers. Although the type specimens of *H. hagai* have not been available for study, we have compared the original description with the other specimens examined for this study, including the type material, and cannot ascertain any features that would warrant *H. hagai* to be retained as a distinct species or subspecies. Therefore, *H. hagai* is treated as a junior synonym of *C. boncicus*.

Haplochernes madagascariensis was described from a single female collected in north-western Madagascar (Beier 1932, 1933), but has not been reported since. The holotype was collected by Johannes Maria Hildebrandt during an expedition to Madagascar (Beentje 1998). Beier (1932) distinguished *H. madagascariensis* from *H. boncicus* based on perceived differences in the relative lengths of the movable chelal finger which was claimed to be much shorter than the chelal hand (without pedicel) and the pedipalpal patella. Examination of the holotype shows that the chelal finger is indeed shorter than the chelal hand and the tibia, but not shorter than that found in *H. boncicus*. Therefore, we place *H. madagascariensis* as a synonym of *H. boncicus*.

Haplochernes boncicus has been previously recorded from numerous localities in Japan, all situated on the island of Honshu within the following Prefectures: Chiba, Kanagawa, Kyoto, Mie, Okayama, Saitama, Shimane, Tokyo and Yamagata (Sato 1978, 1979b, 1979a, 1980; Sato et al. 1988; Takano et al. 1989; Nakajima et al. 1991). The specimens reported here are the first from Gifu Prefecture. Beier (1932) also recorded *H. boncicus* from "Formosa", now known as Taiwan, but the material on which this was based has not been traced.

Haplochernes wuzhiensis Gao & Zhang, sp. nov.
Figs. 3–6

http://zoobank.org/?lsid=urn:lsid:zoobank.org:act:CD418092-9235-474B-A355-1D380A0DB440

Type material.—*Holotype female.* CHINA: Hainan Province: Hainan Island, Wuzhishan City, Wuzhishan Mountain [18°54′N, 109°39′E], alt. 703 m, 16 May 2011, Zhizhong Gao (Ps.-MHBU-HN110516).

Paratypes: CHINA: 6 ♂, 9 ♀, same data as holotype (MHBU).

Diagnosis.—*Haplochernes wuzhiensis* is much larger than *H. boncicus*, e.g., pedipalpal femur 1.20–1.25 (♂), 1.13–1.28 (♀) mm and chela (with pedicel) 2.15–2.16 (♂), 1.93–2.08 (♀) mm compared with pedipalpal femur 0.585–0.87 (♂), 0.655–0.79 (♀) mm, and chela (with pedicel) 1.05–1.46 (♂), 1.18–1.34 (♀) mm.

Description (adults).—*Color* (Fig. 3): mostly reddish brown, carapace and palps dark brown, remaining parts (legs, sternites and pleural membranes) light yellowish brown.

Setae: most setae apically denticulate.

Chelicera (Figs. 4A, 5A): with 4 setae on hand and 1 subdistal seta (*gls*) on movable finger; seta *sbs* absent; *bs* apically dentate, *ls* and *es* smooth; with 2 dorsal lyrifissures and 1 ventral lyrifissure; with poorly-visible scale-shaped sculpture; galea thick, of ♂ with 5, of ♀ with 3 short distal rami; rallum of 3 blades, the distal blade dentate, the others smooth; serrula exterior with 20–22 (♂), 18–20 (♀) blades; lamina exterior present.

Pedipalps (Figs. 4D, 5D, 6A, 6G): most segments finely granulate, except for chelal fingers which are smooth; setae acuminate and weakly apically dentate; without tactile setae; trochanter with distinct rounded dorsal hump; proportions (based on 3 specimens): trochanter 1.39–1.70 (♂), 1.48–1.52

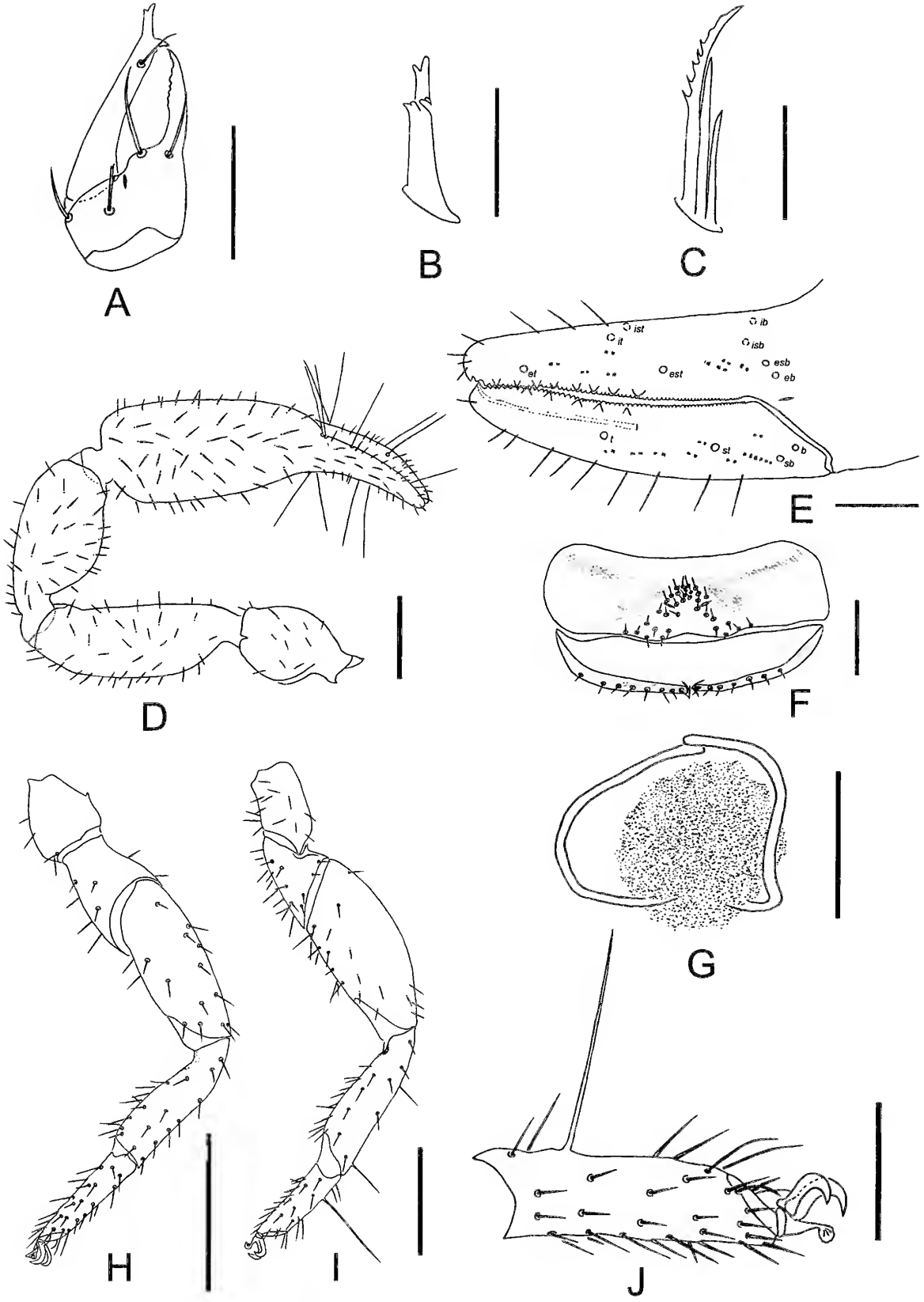

Figure 4.—*Haplochernes wuzhiensis* sp. nov., female holotype: A. Chelicera, dorsal view. B. Galea, dorsal view. C. Rallum. D. Left pedipalp, dorsal view. E. Right chelal fingers, lateral view. F. Genital operculum. G. Spermathecae. H. Leg I, lateral view. I. Leg IV, lateral view. J. Tarsus IV, lateral view. Scale lines = 0.5 mm (D, H, I); 0.2 mm (A, E–G, J); 0.05 mm (B, C).

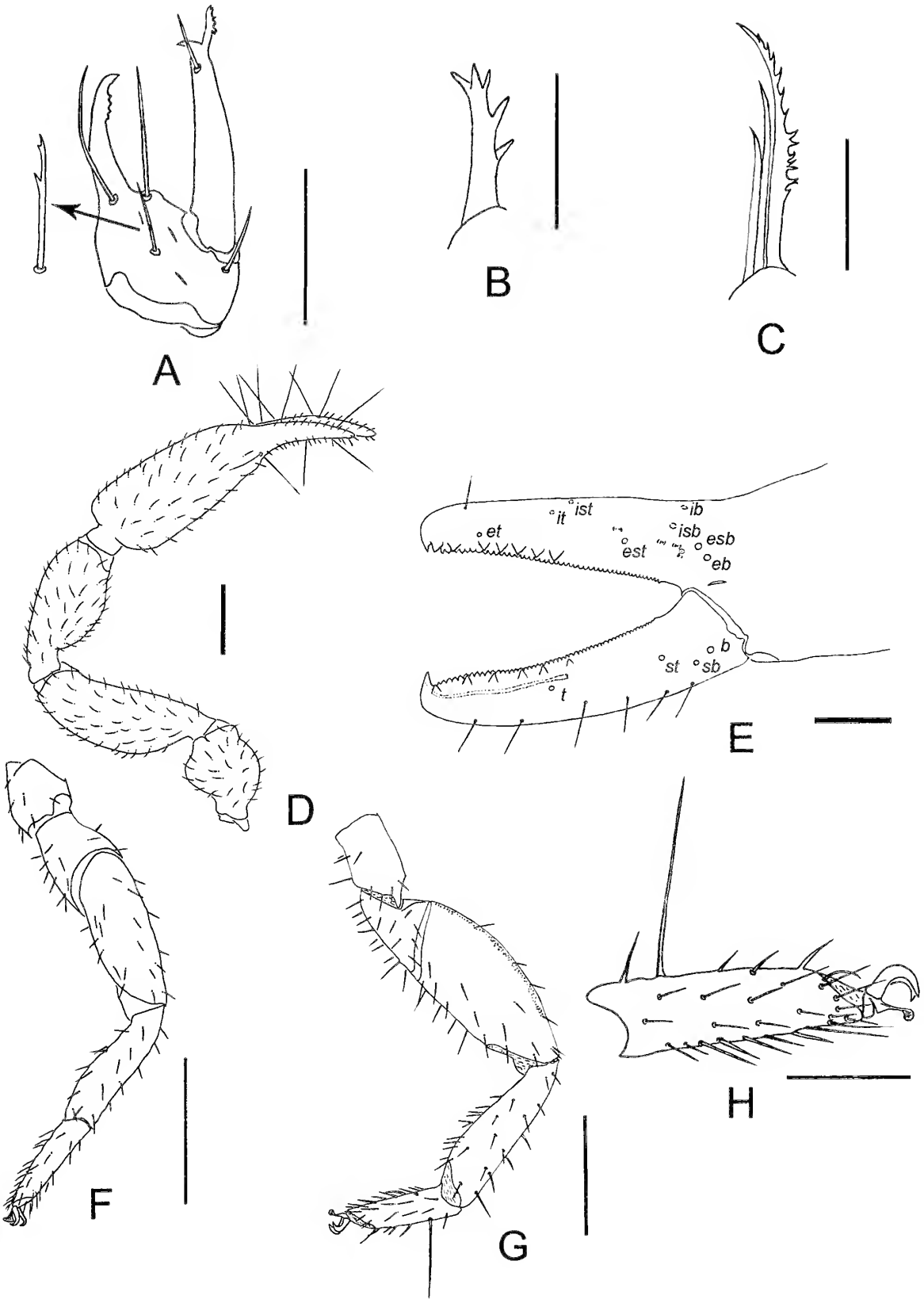

Figure 5.—*Haplochernes wuzhiensis* sp. nov., male paratype: A. Chelicera, dorsal view. B. Galea; dorsal view. C. Rallum. D. Left pedipalp, dorsal view. E. Right chelal fingers, lateral view. F. Leg I, lateral view. G. Leg IV, lateral view. H. Tarsus IV, lateral view. Scale lines =0.5 mm (D, F, G); 0.2 mm (A, E, H); 0.05 mm (B, C).

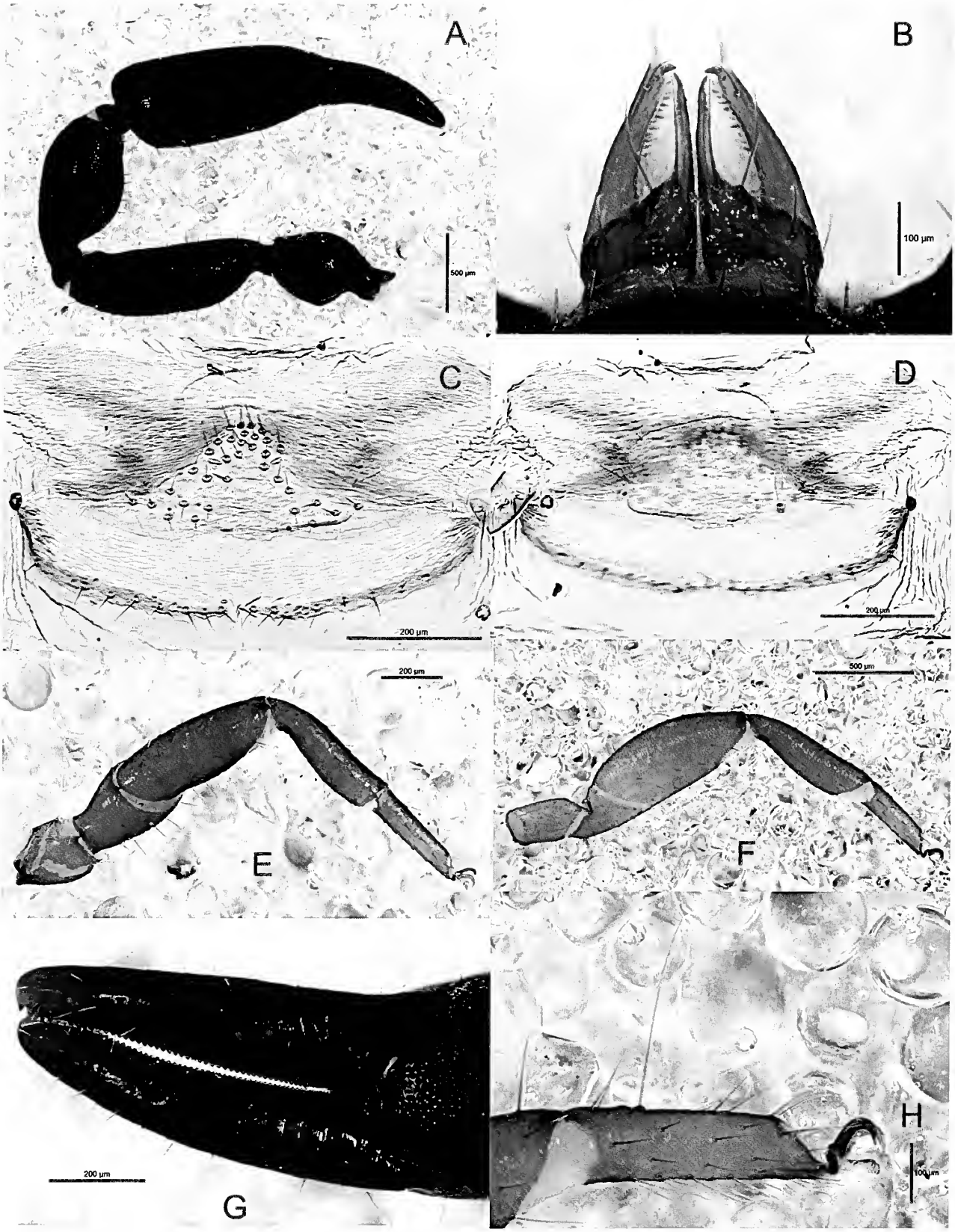

Figure 6.—*Haplochernes wuzhiensis* sp. nov., female holotype: A. Left pedipalp, dorsal view. B. Chelicera, dorsal view. C. Genital operculum. D. Spermathecae. E. Leg I, lateral view. F. Leg IV, lateral view. G. Right chelal fingers, lateral view. H. Tarsus IV, lateral view.

(♀), femur 2.93–2.98 (♂), 2.88–3.04 (♀), patella 2.23–2.50 (♂), 2.15–2.27 (♀), chela (with pedicel) 3.84 (♂), 3.50–3.52 (♀), chela (without pedicel) 3.57–3.62 (♂), 3.32–3.39 (♀), hand (with pedicel) 2.32–2.55 (♂), 2.24–2.29, hand (without pedicel) 2.20–2.28 (♂), 2.07–2.11 x longer than broad; movable finger 0.60– 0.66 (♂), 0.67–0.68 (♀) times as long as hand (with pedicel), and 0.66–0.70 (♂), 0.72–0.74 (♀) times as long as hand (without pedicel). Fixed chelal finger with 8 trichobothria, movable chelal finger with 4 trichobothria (Figs. 4E, 5E): *eb* and *esb* situated basally, *est* situated slightly closer to *esb* than to *et*, *ib* and *ist* situated subbasally; *isb* and *it* situated medially, with *isb* closer to *it* than to *ist*; *t* situated subdistally, *st* situated slightly closer to *sb* than to *t*. Venom apparatus only present in movable chelal finger, venom duct long, terminating in nodus ramosus slightly basal to *t*. Chelal teeth rounded and juxtadentate; fixed finger with 44–46 (♂, ♀) teeth, plus 1–2 (♂), 2–3 (♀) retrolateral and 6–8 (♂), 5–6 (♀) prolateral accessory teeth; movable finger with 54–56 (♂), 40–44 (♀) teeth, plus 2–3 (♂), 1–2 (♀) retrolateral and 3–5 (♂), 4–5 (♀) prolateral accessory teeth.

Carapace (Fig. 3A, B): evenly and densely granulate; prozone darker than mesozone and metazone; slightly broader than long, 0.93–0.96 (♂), 0.96–1.00 (♀) times; eye-spots absent or very indistinct; with *ca.* 75 (♂), 80 (♀) setae, including 6 (♂, ♀) on anterior margin and 8 (♂), 8–10 (♀) on posterior margin; all setae acuminate and apically dentate; with 2 regularly granular transverse furrows, median furrow narrower and deeper, the subbasal one more or less indistinct and nearer to posterior margin.

Coxal region: maxillae with scale-like sculpturing; coxae smooth; manducatory process somewhat pointed, with 3 apical acuminate setae, with 1 small sub-oral seta, and *ca.* 23–25 (♂), 21–23 (♀) additional setae; median maxillary lyrifissure rounded and situated submedially; posterior maxillary lyrifissure rounded. Chaetotaxy of coxae I–IV: ♂, 13–15: 13–15: 14–16: 27–31; ♀, 16: 15: 17: numerous.

Legs (Figs. 4H & I, 5F & G, 6E & F): junction between femora and patellae I and II strongly oblique to long axis; junction between femora and patellae III and IV very angulate; femora III and IV much smaller than patellae III and IV; femur + patella of leg IV 3.00–3.06 (♂), 2.94–3.08 (♀) x longer than broad; patella and tibia without 'pseudotactile' seta; tarsus IV with very long tactile seta located in basal half (Figs. 4J, 5H, 6H), TS ratio = 0.30–0.31 (♂), 0.28–0.29 (♀); subterminal tarsal setae arcuate and acute; claws not modified; arolium slightly shorter than claws.

Abdomen: all tergites divided except tergite XI (Fig. 3A, B); with weakly scale-shaped sculpture; tergites III narrower than others. Tergal chaetotaxy: ♂, 6(7)–6: 7(6)–6(8): 6(7)–5(7): 9(8)–9(7): 9–10(9): 7(8)–9(8): 9(8)–9: 8(9)–9: 9(8)–8(9): 8(7)–7(8): 18(19) (13+6 long tactile setae): 2; ♀, 7(6)–6: 7–8: 6–8(7): 9(8)–9(7): 9–10(8): 8(10)–9(7): 10 (8)–9: 8(9)–7(8): 9(8)–8(9): 7–7(8): 18(19) (including 1–2 long tactile setae): 2. All sternites divided except VI, weakly scaly sculptured, setae slightly dentate and long, chaetotaxy of sternites IV–XI: ♂, 9(8)–10(9): 9(10)–12(10): 9(10)–10(11): 9–10(11): 9(10)–11(10): 9–9(10): 9(10)–9(10): 18 (include 4 long tactile setae): 2; ♀, 6(5)–6: 9(10)–11(9): 11(10)–10(11): 9(11)–10: 9(11)–9(11): 10–9(10): 9(10)–9(10): 18 (include 2 long tactile setae): 2 (simple and acuminate setae).

Genitalia: male typical of Chernetidae, internal setae acicular and slightly curved; female with a single pair of moderately long spermathecae, gently curved (Figs. 4G, 6D). Anterior genital operculum (sternite II) of ♂ with 30–34 setae, of ♀ with *ca.* 35 scattered setae (Figs. 4F, 6C).

Dimensions (mm): male: based on 3 specimens: Total length 4.20–4.75. Pedipalp: trochanter 0.64–0.68/0.40–0.46, femur 1.20–1.25/0.41–0.42, patella 1.03–1.18/0.46–0.47, chela (with pedicel) 2.15–2.16/0.56–0.87, chela (without pedicel) 2.00–2.03, hand (with pedicel) length 1.30–1.43, hand (without pedicel) 1.23–1.28, movable finger length 0.86–0.87. Carapace 1.00–1.13/1.10–1.18. Leg I: trochanter 0.25/0.20–0.21, femur 0.39–0.40/0.22–0.23, patella 0.55–0.56/0.21–0.22, tibia 0.48–0.49/0.12–0.13, tarsus 0.35–0.38/0.09. Leg IV: trochanter 0.40–0.41/0.23–0.24, femur + patella 1.05–1.10/0.35–0.36, tibia 0.72–0.73/0.19–0.20, tarsus 0.45–0.46/0.12, length of tactile seta 0.35–0.45.

Females: based on 3 specimens: Total length 4.75–5.00. Pedipalp: trochanter 0.64–0.68/0.42–0.46, femur 1.13–1.28/0.39–0.42, patella 0.98–1.08/0.43–0.50, chela (with pedicel) 1.93–2.08/0.55–0.59, chela (without pedicel) 1.83–2.00, hand (with pedicel) length 1.26–1.32, hand (without pedicel) length 1.16–1.22, movable finger length 0.84–0.90. Carapace 1.08–1.10/1.08–1.15. Leg I: trochanter 0.24–0.27/0.20–0.22, femur 0.35–0.40/0.23–0.25, patella 0.51–0.57/0.19–0.21, tibia 0.45–0.49/0.13–0.14, tarsus 0.35–0.36/0.09. Leg IV: trochanter 0.39–0.44/0.23, femur +patella 1.00–1.11/0.34–0.36, tibia 0.66–0.70/0.20, tarsus 0.43–0.44/0.12, length of tactile seta 0.38–0.40.

Etymology.—The specific name refers to the type locality, Wuzhishan.

ACKNOWLEDGMENTS

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Comparative cytogenetic analysis among filistatid spiders (Araneomorphae: Haplogynae)

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Abstract. The family Filistatidae is considered sister to Synspermiata or sister to Hypochilidae. Cytogenetic knowledge of this family could be useful for understanding the mechanism of chromosome evolution that has occurred within the group. In this work, two filistatid species belonging to distinct subfamilies, *Kukulcania hibernalis* (Hentz, 1842) (Filistatinae) and *Misionella mendensis* (Mello-Leitão, 1920) (Prithinae), were investigated using standard and differential chromosome staining. Analysis of mitotic and meiotic cells revealed the diploid $2n♂ = 25$ for *K. hibernalis* and $2n♂ = 21$ for *M. mendensis*. Both species exhibited a sex chromosome system of the X_1X_2Y type and metacentric/submetacentric chromosomes. In prophase I cells, the sex chromosomes were in a trivalent configuration with all elements associated without chiasma through their terminal regions. Both species revealed six nucleolar organizer regions on the terminal region of three autosomal pairs. In *K. hibernalis*, constitutive heterochromatin was located mainly in the terminal regions of autosomes and sex chromosomes while in *M. mendensis*, the heterochromatin occurred in the pericentromeric region of all chromosomes. Despite the scarcity of cytogenetic information for Filistatidae, the available results show the occurrence of high variability in the diploid number but with the maintenance of the X_1X_2Y sex chromosome system. Additionally, the karyotype differentiation in the species of this family seems to have involved not only the number of autosomes but also specific chromosomal sites, such as the constitutive heterochromatic regions.

Keywords: constitutive heterochromatin, karyotype, meiosis, nucleolar organizer region, sexual trivalent

The spider family Filistatidae is composed of 147 species and 19 genera, having a worldwide distribution, with the greatest diversity in tropical and subtropical biogeographic regions (Gray 1995; Ramírez & Grismado 1997; World Spider Catalog 2016). The phylogenetic position of Filistatidae is in dispute. While some studies on spinneret morphology (Platnick et al. 1991) and respiratory system morphology (Ramírez 2000) point towards a sister relationship between Filistatidae and the ecribellate haplogynes (=Synspermiata as proposed in Michalik & Ramírez 2014), forming the Haplogynae clade, others, focusing on phylogenomics (Bond et al. 2014; Garrison et al. 2016), placed Filistatidae (*Kukulcania* Lehtinen, 1967) as sister to basal araneomorph Hypochilidae (*Hypochilus* Marx, 1888).

There are few studies regarding the phylogenetic relationships between the genera of Filistatidae. However, Gray (1995) and Ramírez & Grismado (1997) subdivided the family into Filistatinae and Prithinae. The subfamily Filistatinae comprises three genera, *Filistata* Latreille, 1810, *Kukulcania*, and *Sahastata* Benoit, 1968, whereas Prithinae includes *Afrofilistata* Benoit, 1968, *Andoharano* Lehtinen, 1967, *Filistatinella* Gertsch & Ivie, 1936, *Filistatoides* F. O. Pickard-Cambridge, 1869, *Lihuelistata* Ramírez & Grismado, 1997, *Misionella* Ramírez & Grismado, 1997, *Pikelinia* Mello-Leitão, 1946, *Pritha* Lehtinen, 1967, *Wandella* Gray, 1994, and *Yardiella* Gray, 1994, totaling ten genera (Ramírez & Grismado 1997). This phylogenetic hypothesis did not include the six other filistatid genera, *Antilloides* Brescovit, Sánchez-Ruiz & Alayón, 2016, *Microfilistata* Zonstein, 1990, *Mystes* Bristowe, 1938, *Pholcoides* Roewer, 1960, *Tricalamus* Wang, 1987 and *Zaitunia* Lehtinen, 1967 (World Spider Catalog 2016).

Only three species of Filistatidae have been cytogenetically investigated, *Filistata insidiatrix* (Forsskål, 1775) from Greece, with $2n♂ = 33$, X_1X_2Y, *Kukulcania hibernalis* (Hentz, 1842) from Argentina, and *Kukulcania* aff. *hibernalis*, which showed karyotypes with $2n♂ = 24$, X_1X_20 and $2n♂ = 25$, X_1X_2Y, respectively. In these three species, the chromosomes exhibited metacentric and submetacentric morphology (Rodríguez Gil et al. 2002; Král et al. 2006; Kořínková & Král 2013). In the present work, two species of Filistatidae belonging to different subfamilies, *Kukulcania hibernalis* (Filistatinae) and *Misionella mendensis* (Mello-Leitão 1920) (Prithinae), were analyzed using standard and differential chromosome staining techniques. This is the first cytogenetic study of *M. mendensis* and the identification of specific chromosome regions in filistatid spiders. Taking into account that Filistatidae is likely relatively basal within araneomorph spiders, the cytogenetic knowledge of this family is useful for understanding the mechanisms of chromosome evolution that occurred within the group.

METHODS

The cytogenetic data of the Brazilian Filistatidae examined in this work corresponded to a sample of eight male and four female individuals of *K. hibernalis* from Barra do Jacaré (23°06′54″S, 50°10′51″W), state of Paraná, and three male specimens and four embryos (three males and one female) of *M. mendensis* collected in the municipalities of Rio Claro (22°24′39″S, 47°33′39″W) and São Paulo (23°32′52″S,

* *In memoriam*

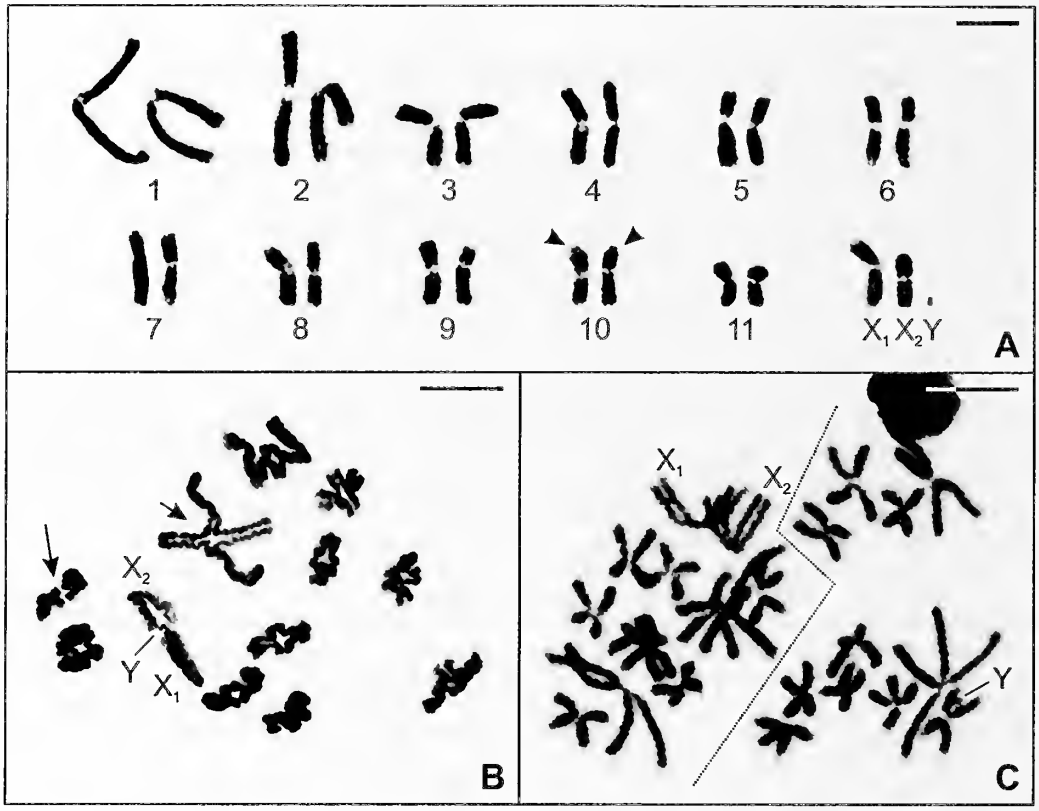

Figure 1.—Testicular cells of *Kukulcania hibernalis* stained with Giemsa. A. Karyotype, $2n♂ = 25$, X_1X_2Y, with metacentric chromosomes. Note the heteromorphism of the chromosomes of pair 9. Arrowheads indicate secondary constrictions on pair 10. B. Diplotene, exhibiting bivalents with interstitial (small arrow) or terminal (large arrow) chiasmata. C. Metaphase II, showing $n = 13$, X_1X_2 (left pole) and $n = 12$, Y (right pole). Scale = 10 μm.

46°38′9″W), state of São Paulo. The voucher specimens were deposited in the collection of the Laboratório Especial de Coleções Zoológicas, Instituto Butantan (IBSP, curator A. D. Brescovit), São Paulo, Brazil. The chromosomal preparations were obtained from embryos and gonads of adult individuals, following the methodology described by Araujo et al. (2005). All the cytological preparations were standard stained with 3% Giemsa solution (3% of commercial Giemsa and 3% of phosphate buffer pH 6.8 in distilled water). For identification of the nucleolar organizer regions (NORs) and location of constitutive heterochromatin regions, chromosome preparations were submitted to silver impregnation (Howell & Black 1980) and C-banding (Sumner 1972), respectively. To obtain a better resolution of the C-banding pattern, chromosomes were stained with 4-6′-diamidino-2-phenylindole (DAPI). All cells were photographed using an Olympus BX51 light microscope coupled to an Olympus DP71 digital camera with DP Controller software. The chromosomes were measured using LEVAN, a plugin for Image J software, developed by Sakamoto & Zacaro (2009), and morphologically classified following Levan et al. (1964).

RESULTS

Kukulcania hibernalis.—Mitotic metaphase cells of *K. hibernalis* revealed the diploid number $2n = 25$ for males and $2n = 26$ for females. The comparative study of both mitotic cells of the males and females and metaphase II cells of the males, showed the presence of a sex chromosome system of the $X_1X_2Y/X_1X_1X_2X_2$ type for this species (Fig. 1). The male karyotype was composed of chromosomes of large (pairs 1 and 2), medium (pairs 3 to 10) and small (pair 11) sizes. The X_1 and X_2 sex chromosomes were medium-sized whereas the Y chromosome was extremely small, being identified as the smallest element of the karyotype. All chromosomes showed a metacentric morphology, with the exception of one element of pair 9, which was classified as submetacentric (Fig. 1A). This morphological heteromorphism of pair 9 was verified in three male specimens, in which a detailed karyotype analysis was accomplished. A secondary constriction was easily visualized in the short arm terminal region of pair 10.

Early prophase I nuclei exhibited three (two large and one small) positive heteropycnotic blocks of sexual chromatin. Diplotene cells exhibited 11 autosomal bivalents with one terminal or interstitial chiasma (Fig. 1B), except the large bivalent that occasionally presented two chiasmata, one terminal and one interstitial. The sex chromosomes were easily identified since they formed a trivalent configuration, with all elements associated through their terminal regions. In this association, both arms of the X_1 and X_2 chromosomes were in an achiasmate pairing with both arms of the Y chromosome, which always assumed a central position in this trivalent configuration.

Silver-impregnated spermatogonial metaphase cells revealed six NORs located on the short arm terminal region of pairs 1, 5 and 10 (Fig. 2A, B). However, not all NORs appeared in the

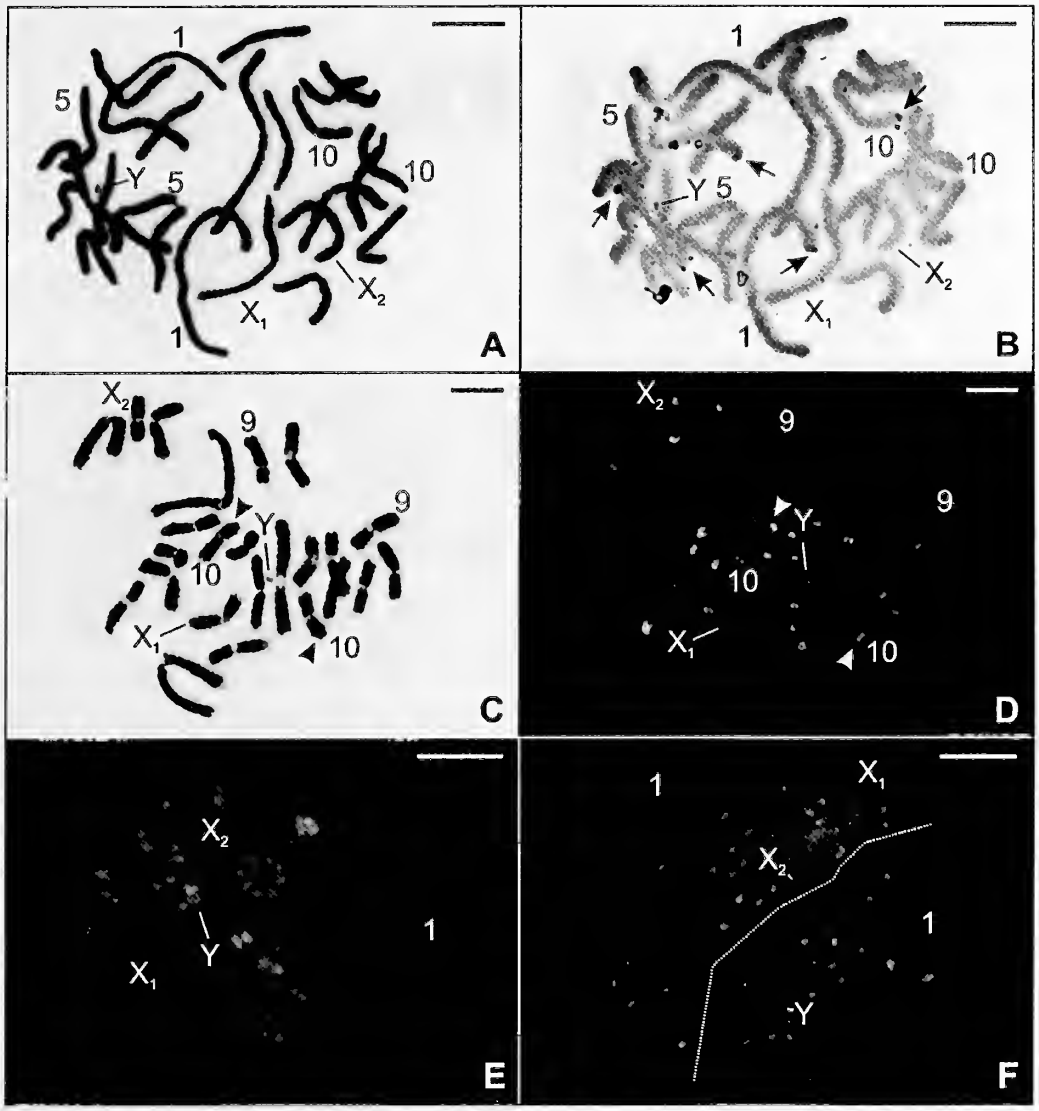

Figure 2.—Testicular cells of *Kukulcania hibernalis*, stained with Giemsa (A, C), silver-impregnated (B) and DAPI C-banded (D–F). A, B. Mitotic metaphase, revealing nucleolar organizer regions (arrows) on the terminal regions of pairs 1, 5 and 10. C, D. Mitotic metaphase, showing the predominance of constitutive heterochromatin in the terminal regions of the chromosomes. The arrowheads in pair 10 point to heterochromatin colocalized with the secondary constrictions. E, F. Diplotene and metaphase II, respectively, exhibiting pericentromeric heterochromatin in X_2 and the totally heterochromatic Y chromosome. Scale = 10 μm.

same cell, with the number of active NORs varying from two to five. Additionally, the NORs located on pair 10 were coincident with secondary constriction observed in Giemsa-stained cells. DAPI C-banded testicular cells showed constitutive heterochromatin in the short arm terminal region of all autosomal pairs and X_1 and X_2 sex chromosomes, with the exception of pairs 5 and 9 (Fig. 2C, D). Furthermore, blocks of constitutive heterochromatin were visualized in the long terminal region of pairs 4, 5, 6, 7, 8, 10, 11 and X_2 sex chromosome. Additional bands were also found in the short arm interstitial region of pair 4. The Y chromosome was entirely heterochromatic. The constitutive heterochromatin present in the short arm of pair 10 was colocalized with the secondary constriction. In addition to the DAPI C-band pattern observed in mitotic cells, the study of meiotic cells allowed us to identify blocks of heterochromatin in the pericentromeric region of the X_2 sex chromosome (Fig. 2E, F). Metaphase II nuclei confirmed that the DAPI C-banded positive regions of pair 1 were tenuous when compared with those of the other chromosomes.

Misionella mendensis.—Male karyotype analysis of *M. mendensis* revealed $2n = 21$, X_1X_2Y metacentric chromosomes, with the exception of pair 1 that was submetacentric (Fig. 3A). The autosomal chromosomes gradually decreased in size, but the X_1 and X_2 sex chromosomes were the largest and the Y chromosome, the smallest elements of the karyotype. Secondary constrictions were located in the long arm interstitial region of pairs 1 and 2. The study of meiotic cells confirmed the diploid number and type of sex chromosome system established for this species (Fig. 3B, D). In diplotene nuclei, the autosomal bivalents exhibited one terminal or interstitial chiasma and the sex chromosomes were associated in a trivalent configuration (Fig. 3B), similar to that observed in *K. hibernalis*. Metaphase II cells showed $n = 11$, X_1X_2 and $n = 10$,

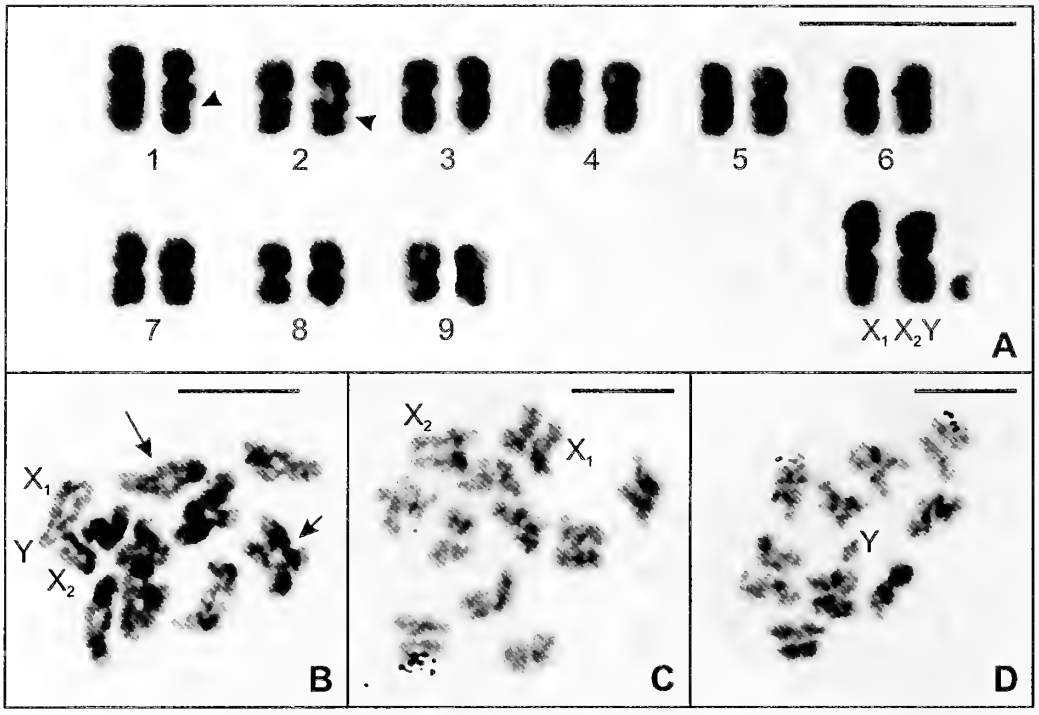

Figure 3.—Testicular cells of *Misionella mendensis*, stained with Giemsa. A. Karyotype, $2n♂ = 21$, X_1X_2Y with chromosomes predominantly metacentric. The arrowheads indicate constrictions. B. Diplotene, showing autosomal bivalents with one interstitial (small arrow) or terminal chiasma (large arrow). C, D. Metaphase II with n=11, X_1X_2 and n=10, Y, respectively. Scale = 10 μm.

Y (Fig. 3C, D), indicating the balanced segregation of all chromosomes.

Mitotic cells of embryos examined with Giemsa staining and silver impregnation revealed six NORs on the short arm terminal region of pairs 1, 3 and 5 (Fig. 4A, B). In this species, the constrictions revealed by Giemsa staining were not silver impregnated. Mitotic metaphase cells submitted to C-banding and stained with DAPI showed constitutive heterochromatin in the pericentromeric region of all chromosomes; additional bands were verified in the short arm terminal region of pairs 5 and 8 (Fig. 4C, D). The terminal heterochromatin of pair 5 was located in an NOR-bearing region.

DISCUSSION

The $2n♂ = 21$ observed in *M. mendensis* (Prithinae) is the lowest diploid number described until now for Filistatidae. The number of autosomes found in *K. hibernalis* (Filistatinae) is the same as that previously described for one population of this species from Argentina (Rodríguez Gil et al. 2002). The metacentric and submetacentric chromosomal morphology is common for all filistatids, including the species analyzed here, as also occurs for most haplogyne spiders (Araujo et al. 2016).

In Filistatinae, cytogenetic information is available for three species, *Filistata insidiatrix* with $2n♂ = 33$, X_1X_2Y (Král et al. 2006), *Kukulcania* aff. *hibernalis* with $2n♂ = 25$, X_1X_2Y (Kořínková & Král 2013), and *Kukulcania hibernalis* with $2n♂ = 24$, X_1X_20 (Rodríguez Gil et al. 2002) and $2n♂ = 25$, X_1X_2Y (present study). In Prithinae, the only species that has been cytogenetically examined is *Misionella mendensis*, $2n♂ = 21$, X_1X_2Y. These data show that the highest diploid numbers occur in Filistatinae, but the X_1X_2Y sex chromosome system is a shared characteristic for the species of both subfamilies.

The cytogenetic data did not reveal new information about the Filistatidae affinities, because the X_1X_2Y sex chromosome system found in this family has a morphology and meiotic behavior similar to that described for *Hypochilus* and known for some Synspermiata families (Drymusidae, Pholcidae and Sicariidae) (Král et al. 2006). However, taking into account the presence of the X_1X_2Y system in Hypochilidae and Synspermiata, and considering its absence in Mygalomorphae (Araujo et al. 2016), this system probably reflects the ancestral condition for Araneomorphae (Silva 1988; Oliveira et al. 1996, 1997; Rodriguez Gil et al. 2002; Silva et al. 2002; Král et al. 2006).

The difference between the sex chromosome system described for *K. hibernalis* herein (X_1X_2Y) and from Argentina (X_1X_2) (Rodríguez Gil et al. 2002) could be a case of population variation, however, the possibility of misinterpretation of the sex chromosome system in the paper of Rodríguez Gil et al. (2002) cannot be ruled out. The misidentification of the X_1X_2Y sex chromosome system, due to the tiny size of the Y chromosome, is a problem already pointed out by Král et al (2006). The stage of chromosome condensation in the pictures of *K. hibernalis* presented by Rodríguez Gil et al. (2002) do not allow an unambiguous identification of the Y absence requiring a reanalysis of the Argentinean population.

Cytogenetic data in regard to the identification of specific chromosomal regions are scaree in spiders, considering that less than 10% of the species have been characterized in relation to the distribution of NORs and constitutive heterochromatin (Araujo et al. 2012, 2014, 2015; Forman et al. 2013; Kořínková

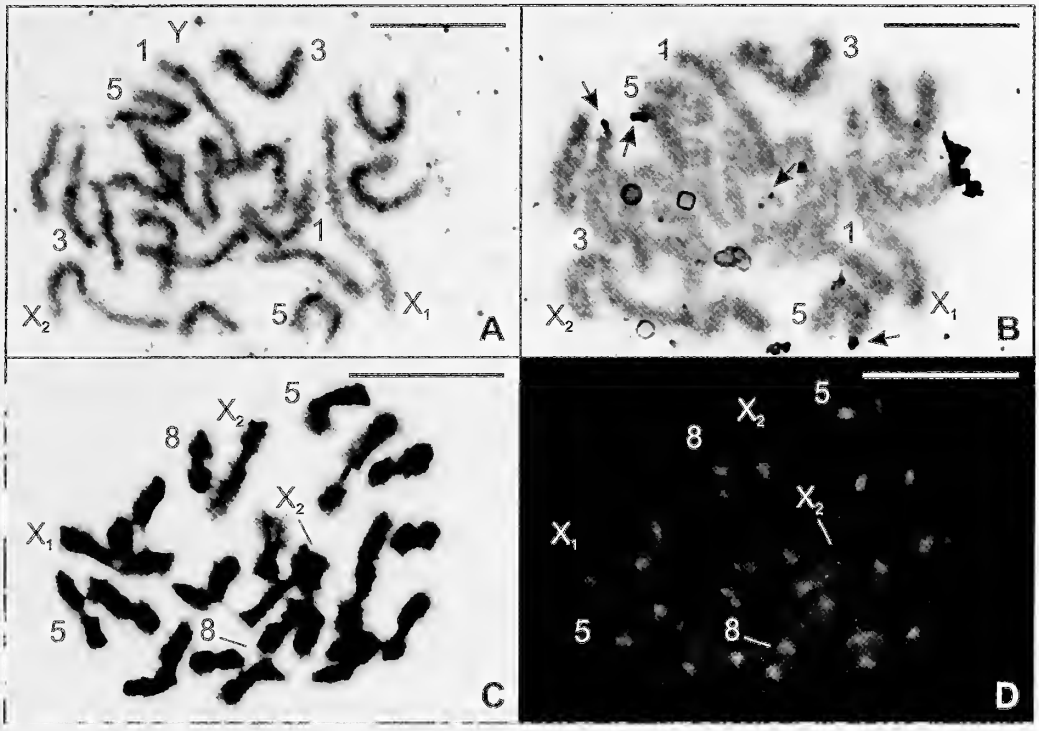

Figure 4.—Embryonic mitotic cells of *Misionella mendensis* stained with Giemsa (A, C), silver-impregnated (B) and DAPI C-banded (D). A, B. Metaphase, $2n♂ = 21$, X_1X_2Y, revealing nucleolar organizer regions (arrow) on the terminal regions of pairs 1, 3 and 5. In B, the Y chromosome is not evident. C, D. Metaphase, $2n♀ = 22$, $X_1X_1X_2X_2$, showing constitutive heterochromatin in the pericentromeric region of all chromosomes. Scale = 10 μm.

& Král 2013; Král et al. 2013). In Mygalomorphae and Araneomorphae, NORs are predominantly located on the terminal region of one to three autosomal pairs. According to Král et al. (2013), this pattern could be a symplesiomorphy of these two suborders of Araneae. Nevertheless, in the Haplogynae lineage, the species possessing X0 and XY systems showed NORs on autosomal chromosomes and the X chromosome, or only on the X chromosome (Král et al. 2006; Oliveira et al. 2007; Araujo et al. 2008). Additionally, the only species with X_1X_2Y sex chromosome system investigated regarding the distribution of NORs, *Hypochilus pococki* Platnick, 1987 (Hypochilidae) with $2n♂ = 29$, showed two pairs of autosomal chromosomes impregnated by silver (Král et al. 2006). Despite the two species of Filistatidae analyzed in this study that showed different diploid numbers, in both species the silver-impregnated regions (Ag-NORs) were located on the terminal region of three autosomal pairs, including pairs 1 and 5. Autosomal NORs are the most common condition in spiders (Araujo et al. 2012)

In spiders, the constitutive heterochromatin commonly exhibits a similar pattern in autosomes and sex chromosomes, occurring in the pericentromeric region (Araujo et al. 2012). In the Filistatidae species studied herein, a clear difference in relation to distribution of constitutive heterochromatin was observed, taking into account that in *K. hibernalis* terminal C-bands were predominant while in *M. mendensis* the positive heterochromatic regions were pericentromeric. This result indicated that in addition to the change in diploid number, the dispersion and/or accumulation of constitutive heterochromatin in specific chromosomal regions may be related to karyotype differentiation in Filistatidae species. Furthermore, a change in the amount of heterochromatin was probably the key event responsible for the heteromorphism observed in the chromosomes of pair 9 of *K. hibernalis*. This is supported by the morphology of the submetacentric element which did not show a positive DAPI C-band in the short arm terminal region. In Haplogynae taxa with a X_1X_2Y sex chromosome system, the Y chromosome is completely heterochromatic. This pattern was observed in *K. hibernalis* and *M. mendensis*, as well in species belonging to other families, e.g., *Loxosceles intermedia* Mello-Leitão, 1934, *Loxosceles laeta* (Nicolet, 1849) (Sicariidae) and *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae) (Silva et al. 2002; Král et al. 2006).

Although cytogenetic information is restricted to only four species of Filistatidae, the available data revealed that this family has a high karyotype diversity, mainly related to the number of autosomal chromosomes and the distribution of constitutive heterochromatin. Additionally, the diversity in karyotype constitution seems to be a common feature of both basal (Filistatidae) and Synspermiata species, differing from the uniform karyotype pattern observed in most Entelegynae spiders.

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Use of alternative habitats by spiders in a desert agroecosystem

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Abstract. Annual crop fields are short-lived and disturbed environments. Therefore, sustainable populations of natural enemies in these fields must be maintained by repeated colonization each season from habitats outside the crop fields. In desert agroecosystems, unmanaged habitats differ greatly in abiotic and biotic conditions from croplands, creating potentially significant barriers to movement of predators. We asked here: to what extent do predators use non-crop habitats as refuges or breeding sites in the desert agroecosystem of the northern Negev, Israel? We investigated the use of natural desert habitat, planted trees (*Eucalyptus*), and a summer crop (sunflowers) by winter-wheat inhabiting spiders. We collected spiders using pitfall traps and a suction device from wheat fields and adjacent to non-wheat habitats during the wheat season and between seasons. We found that two crop specialist species, *Trichoncoides piscator* (Simon, 1884) (Linyphiidae) and *Thanatus vulgaris* Simon, 1870 (Philodromidae), switched to an alternative crop during the inter-wheat season. Habitat generalist species, such as *Nomisia* sp. (Gnaphosidae), *Enoplognatha* spp. (Theridiidae) and *Alioranus pastoralis* (O. Pickard-Cambridge, 1872) (Linyphiidae) used alternative non-crop habitats as refuges and breeding sites to differing degrees in both seasons. While all habitat generalist species used the desert habitat, none used planted trees exclusively as an alternative habitat. We conclude that crop-inhabiting, desert species may be unable to colonize the wheat fields if nearby desert habitat is supplanted by other crops or by tree plantations.

Keywords: breeding site, colonization, planted trees, refuge

Crop fields may provide high quality habitats for predators that are attracted to the fields by an abundance of prey. Nevertheless, the fields are often short-lived and disturbed habitats owing to crop management practices, qualities that may make them less suitable for predators. Seasonal crops in particular favor herbivore species that can survive and reproduce in spatially and temporally changing environments, and have developed good dispersal abilities and short life cycles that are completed during a single crop season (Ehler & Miller 1978). Many predators, however, have long life cycles relative to the crop cycle. In order to maintain stable populations of predators that can act as natural enemies of crop herbivores, alternative habitats must be available between crop seasons. These habitats may provide refuge, prey and breeding sites, and thus serve as sources of populations that will colonize the crop fields in the following season (Landis et al. 2000).

The suitability of alternative habitats is determined by habitat characteristics such as the abiotic and biotic conditions they provide, their stability over time, and above all by the permeability of their boundary with the crop fields (Burel et al. 2000; Hunter 2002). In spite of the presumed importance of these habitats, relatively few studies have demonstrated the use of multiple alternative habitats by crop-inhabiting predators. Here, wheat fields in a desert agroecosystem serve as a case study of alternative habitat use by spiders that colonize the wheat fields. Spiders are generalist predators with diverse predatory behaviors, habitat preferences and dispersal abilities (Nyffeler & Benz 1987; Uetz et al. 1999). They can be important predators of crop pests in temperate regions (Nyffeler & Sunderland 2003; Symondson et al. 2003) and also in desert crops (Opatovsky et al. 2012). Spiders in annual crops can be divided generally into agrobiont species that are phenologically synchronized with the disturbance regime in the crop fields (Birkhofer et al. 2013) and those with long life cycles that require additional habitats for survival. For the latter species, the presence of alternative habitats to complete their life cycle, and the ability to move between habitats, are essential features of the system that will enable them to sustain activity in the fields.

Desert agroecosystems, unlike temperate ones, are characterized by strong contrasts between the crop fields and neighboring habitats, which may restrict the ability of predators to take advantage of alternative habitats. Nevertheless, Pluess et al. (2008) showed that during the wheat season, more than 50% of the spider species occurring in wheat fields are found also in the adjacent desert habitat. However, while several spider species were shown to immigrate into the wheat fields from habitats outside the crop fields (Gavish-Regev et al. 2008), only a few species were found to move across the boundary into the desert habitat immediately after the wheat harvest (Opatovsky & Lubin 2012). These possibly contradictory results led us to investigate the use of alternative habitats by crop-inhabiting spider species during both crop and inter-crop seasons in this desert agroecosystem. We asked whether desert habitats serve as refuges and breeding sites for wheat-inhabiting spiders between crop seasons. Alternatively, spiders could move to planted trees or other crops as the season progresses. These different possibilities can have important implications for management of the desert agroecosystem, namely whether or not to maintain natural habitat surrounding the crop fields.

The aim of this research was to reveal how different habitats are used by wheat-inhabiting spiders in the crop and inter-crop seasons. We sampled spiders in paired, adjacent habitat patches in the northern Negev desert: wheat fields paired with

Table 1.—Description of substrate and vegetation characteristics in each habitat at each sampling session.

	Jan	Feb	Apr	Jun	Aug	Sep	Nov
Desert	Perennials & green annuals			Perennials & dry annuals	Perennials & sparse dry annuals		
Trees	Moist leaf litter				Dry leaf litter		
Wheat	Green		Dry	Dry stubble	Plowed fields		Newly seeded fields
Sunflowers	-			Young plants	Dry plants	Dry stubble	Plowed fields

adjacent desert habitat or with planted eucalyptus trees, and post-harvest (fallow) wheat fields paired with desert, planted trees or a summer crop (sunflowers). These different habitat types are characterized by different biotic and abiotic conditions and by their degree of stability over the seasons. The wheat fields are covered by homogenous vegetation during the crop season and are bare between seasons, while the natural desert habitat is more stable, but is dry most of the year with a short period with annual vegetation after the rainy season. The planted tree habitat combines the stability of the natural environment with higher vegetation cover and cooler micro-climate also during the summer when the desert habitat and wheat fields are dry. The summer crops (sunflowers in our study) are usually irrigated during the summer and therefore provide moist habitat in this dry environment. The phenology of these different habitats and the environmental conditions provided could determine their availability to wheat-inhabiting spiders.

METHODS

Study sites.—Spiders were sampled in an area of approximately 30 km^2 of agricultural fields of Kibbutz Be'eri, Israel (31° 25′ 37″ N, 34° 29′ 34″ E), an area that is dominated by large annual crop fields. During the winter, the main crop is winter wheat (*Triticum aestivum* L.), which is sown after the first rain (November) and harvested in March for green fodder or in May for grain. Most of the wheat fields are dryland crops that rely on the annual precipitation (ten year average: 271 mm, data from the Israel Meteorological Service). During the summer, the agricultural fields either remain as plowed, bare soil or a summer crop is grown. The sampling was done in 14 sites that included wheat fields adjacent to different non-wheat habitats. Six wheat field sites were adjacent to planted trees ("tree"), four sites were adjacent to natural, desert habitat ("desert") and four fallow wheat field sites were adjacent to sunflowers (*Helianthus annuus* - "sunflower"). The latter sites were sampled during the summer, inter-wheat season. The "wheat", "desert" and "tree" habitats were not irrigated, with the exception of two wheat fields near planted trees, which received irrigation during November right after sowing, while the "sunflower" habitat was irrigated throughout the sampling sessions. The planted trees were non-indigenous *Eucalyptus* (mainly *Eucalyptus camaldulensis*) planted along the dry riverbanks to prevent soil erosion (180–330 trees per hectare). The soil cover in the tree habitats was mostly dry leaf litter and sparse shrubs. The cover in the desert habitats was composed of annual vegetation appearing mainly after the rainy season, but dry the rest of the year, and scattered shrubs and perennial grasses (*Asphodelus aestivus*, *Lyceum shawii*, *Stipa capensis*) (Table 1).

Spider sampling.—Three samples were taken during the wheat-growing season (January, February and April, 2011), three samples in the inter-wheat season (June, August and September, 2011) and one sample at the beginning of the following wheat crop season (November, 2011). The spiders were sampled using pitfall traps and a suction device (except the sample in November 2011, which was done only with pitfall traps). Eight pitfall traps were located parallel to the field's edge, 50 m into the field and 50 m into the adjacent habitat respectively (a total of 16 traps for each site) and were separated from one another by 3 m. In the planted tree habitat, the traps were located near the center of the habitat, between 10 and 50 m into the habitat, owing to the restricted width of the *Eucalyptus* habitat at some sites. The traps were 10 cm deep with a 9 cm diameter opening, buried in the ground so the rim was level with the surface, and each contained 100 ml of 50% ethylene glycol with a drop of detergent to break the surface tension. The traps were open for a week each sampling session.

The suction samples were taken using a Stihl SH55 suction device with a tube opening of 65 mm diameter. Samples were taken along five transects in eaeh habitat, 50 m from the habitat edge and parallel to it, except in the planted trees habitat, which was sampled in the center of the habitat (10 to 50 m from the habitat edge). Each transect was 20 m long and the suction device was lowered for 10 s at each 1 m along the transect (total of 20 collections per sample and 10 samples per site). A fine mesh sleeve was inserted into the collecting tube of the device, and after each transect the contents of the sleeve were emptied into a bag that was cooled until the spiders were separated in the laboratory using a hand-held aspirator. The spiders were stored in 70% ethanol until they were identified. Adult spiders were identified to species level using taxonomic keys (Levy 1985, 1988; Roberts 1995; Proszynski 2003). Nomenclature was adapted to the World Spider Catalogue (World Spider Catalog 2016). Immature individuals were identified to genus or family level. Voueher specimens are deposited in the arachnid collection of the Hebrew University of Jerusalem.

Data analysis.—The analysis was done on the lowest taxonomic level possible of the four most common spider families (with more than 10% of the total number of individuals collected). First, the effect of two factors, season (wheat season and inter-wheat season) and habitat (planted tree, desert, summer crop and adjacent wheat fields), was tested. We used a generalized linear model with a Poisson distribution on the average number of individuals per pitfall trap or suction sample, with habitat type and season as fixed categorical factors and the site as a random factor. The response variable (average number of individuals per trap or suction sample) was chosen from the sampling method that collected the largest total number of individuals (Table 2).

Table 2.—The total number of individuals of each spider group collected in each sampling method and the average number of individuals per trap or suction sample. Significant differences between the numbers of individuals collected in each method (t-test) are marked in bold. For analysis of the effects of habitat and season on abundance, we used the data from the sampling method that yielded the largest number of individuals.

Group	Collecting method	No. of individuals caught in each method	Average of individuals per trap/suction sample	t	*P*
Linyphiidae					
Alioranus pastoralis	Pitfall	36	0.07	0.72	0.47
	Suction	10	0.04		
Trichoncoides piscator	Pitfall	34	0.03	1.82	0.07
	Suction	0	0		
Gnaphosidae					
Nomisia	Pitfall	29	0.04	1.42	0.16
	Suction	6	0.01		
Juveniles of *Nomisia*	Pitfall	92	0.09	0.69	0.48
	Suction	36	0.08		
Theridiidae					
Enoplognatha	Pitfall	46	0.14	**2.53**	**0.01**
	Suction	9	0.04		
Juveniles of *Enoplognatha*	Pitfall	16	0.02	**3.1**	**0.002**
	Suction	33	0.1		
Philodromidae					
Thanatus vulgaris	Pitfall	179	0.17	**3.04**	**0.002**
	Suction	15	0.03		
Thanatus fabricii	Pitfall	225	0.25	**2.39**	**0.02**
	Suction	1	0.001		
Juveniles of *Thanatus*	Pitfall	32	0.03	**3.94**	**<0.001**
	Suction	681	1.71		

Second, we tested the differences in spider abundance between the main habitats by using multiple comparisons of the significant factors. In cases where interactions between the habitat type and season were significant, the comparisons were done between habitats in each season separately. To evaluate the importance of the alternative habitats as breeding sites, the analysis described above was repeated for the juvenile stages of the main spider groups. In addition, the abundances of adults and juveniles in the wheat fields and alternative habitats were plotted over the year to examine patterns of change.

The statistical analyses were done using R 3.1.2 (R Core Team 2014) with nlme package (Pinheiro et al. 2016).

RESULTS

A total of 4133 individuals were collected in the two sampling methods in both seasons and in all habitats combined. Of these, 468 individuals belonging to 18 families were collected in the wheat fields during the crop season. The most common families in the wheat fields were Linyphiidae (sheet-web spiders, 25% of the total individuals), Gnaphosidae (ground spiders, 17%), Theridiidae (tangle-web spiders, 14%) and Philodromidae (running crab spiders, 13%).

Linyphiidae.—Adult linyphiids were collected mainly in pitfall traps and no juveniles were found. Of five species, two species dominated the samples: *Alioranus pastoralis* (O. Pickard-Cambridge, 1872) and *Trichoncoides piscator* (Simon, 1884) (28% and 22%, respectively, in the wheat fields).

During the wheat season, *A. pastoralis* was collected in wheat fields and desert habitat only, and it was not found in the inter-wheat season at all (Fig. 1A, $F_{2,61} = 0.83$, $P = 0.41$; Table 3). The seasonal dynamics of *A. pastoralis* show low abundance in the desert habitat and in adjacent wheat fields at the beginning of the season (Fig. 1B). By April, this species disappeared from the desert habitat and appeared in large numbers in wheat fields adjacent to planted trees, but not in the adjacent trees (Fig. 1B).

Trochonchoides piscator occurred during the wheat season in the wheat fields and trees, but not in the desert habitat (Fig. 1C; overall $F_{2,61} = 1.84$, $P = 0.07$; Table 3). In the inter-wheat season, *Tr. piscator* occurred in fallow wheat fields and in sunflowers and was significantly more abundant in the sunflower crop (Fig. 1C; overall, $F_{3,78} = 3.55$, $P < 0.001$, sunflowers vs. wheat, $P < 0.001$; Table 3). The decrease in abundance of *Tr. piscator* in wheat fields at the end of the season was followed by an increase in the sunflower fields (Fig. 1D).

Gnaphosidae.—The genus *Nomisia* Dalmus, 1921 constituted 27% of the gnaphosid individuals collected in pitfall traps in the wheat fields. The only species of *Nomisia* found in all habitats was *Nomisia riparienses* (O. Pickard-Cambridge, 1872), however, there were too few individuals to analyze habitat preference at the species level, due to the low proportion of adults and the inability to separate juveniles to species. Adults and juveniles were found in both seasons in all habitats except sunflowers. Their abundances did not differ significantly among wheat fields, trees and desert habitat (Adult: Fig. 2A; Season, $F_{1,141} = 0.09$, $P = 0.92$, Habitat: $F_{3,141} = 1.11$, $P = 0.27$; Juveniles: Fig. 2C; Season, $F_{1,141} = 0.04$, $P = 0.97$, Habitat: $F_{3,141} = 0.81$, $P = 0.42$; Table 3). Adults were found in tree habitats at the end of the wheat season while juveniles appeared in low abundances in the tree and desert habitats earlier in the season (Fig. 2B, D).

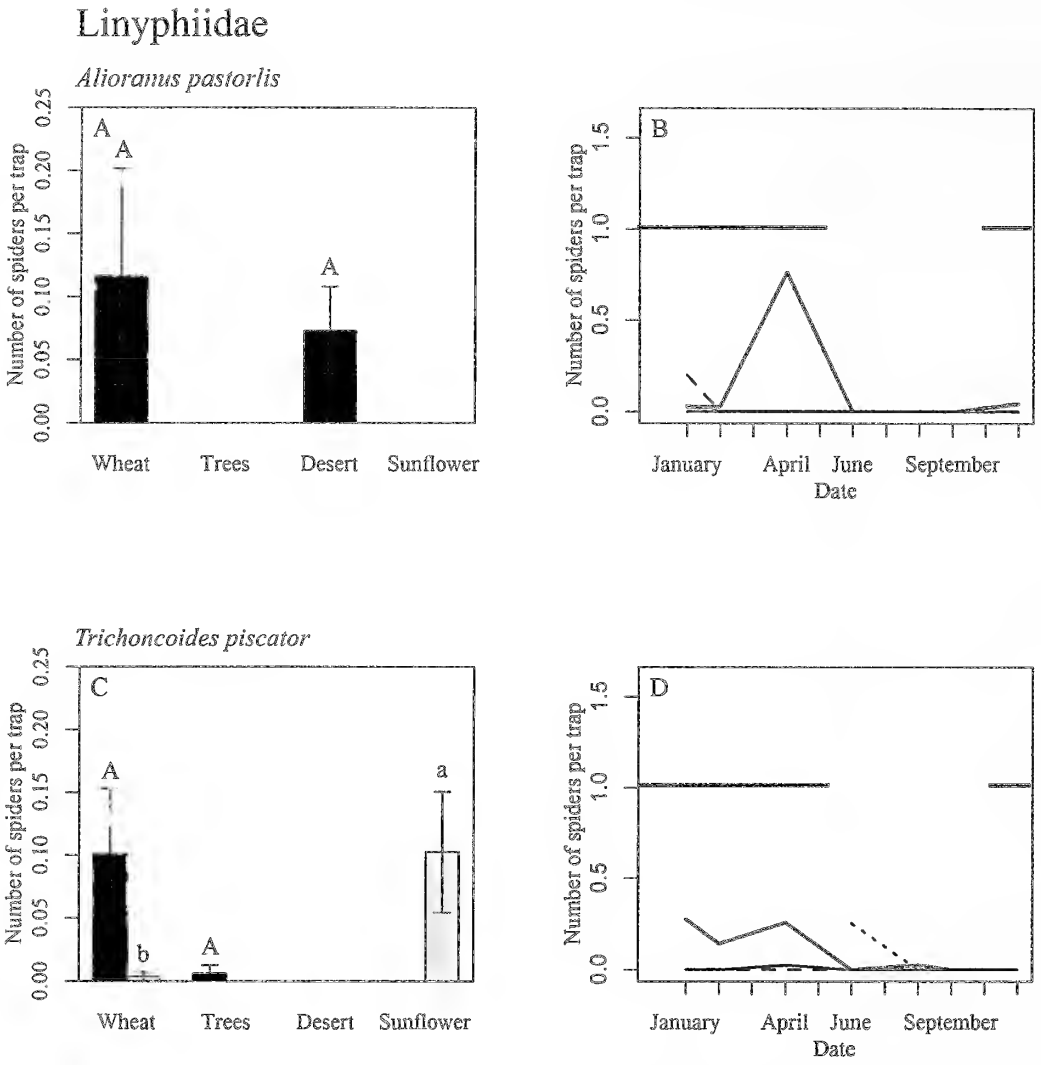

Figure 1.—Abundance of *Alioranus pastoralis* (A, B) and *Trichoncoides piscator* (C, D) (Linyphiidae) across habitat types and seasons (mean number of individuals per pitfall trap ± s.e.). A, C. The average numbers found in the four different habitat types (wheat fields, planted eucalyptus trees, desert and sunflower fields). The black bars represent the wheat season (October–May) and the grey bars represent the inter-wheat season (May–October). The letters above the bars represent significant differences ($P < 0.05$) between habitat types within each season. B, D. Changes in abundance in wheat adjacent to trees (solid black line), wheat adjacent to desert (broken black line), planted trees (solid grey line), and desert (broken grey line). Horizontal lines at the top indicate the wheat season.

Theridiidae.—The genus *Enoplognatha* Pavesi, 1880 constituted 52% of the total theridiid spiders collected in the wheat fields. The adults were collected in pitfall traps and the juveniles mainly by suction device (Table 2). There were two common species, *E. gemina* Bosmans & Van Keer, 1999 and *E. macrochelis* Levy & Amitai, 1981, which were combined, as there were not enough individuals of each species alone to test for habitat use. Adults and juveniles were trapped only during the wheat season, in wheat, planted trees and desert habitat. Adults occurred in significantly lower numbers in the trees than in the desert habitat (Fig. 3A; overall $F_{2,61} = 2.27$, $P = 0.03$; trees vs. desert, $P = 0.04$; Table 3), while juveniles were found in all habitats except sunflowers (Fig. 3C; $F_{2,61} = 1.1$, $P = 0.29$; Table 3). Adults and juveniles were present in the desert habitat and adjacent wheat fields early in the wheat season (Fig. 3B, D).

Philodromidae.—There were two common species, out of five species: *Thanatus fabricii* (Audouin, 1826) (50% of total adult philodromids in pitfall samples) and *Th. vulgaris* Simon, 1870 (45%). Adults were collected in pitfall traps and juveniles by suction device (Table 2). *Thanatus fabricii* was found mainly in the desert habitat with no differences between seasons (Fig. 4A; overall $F_{3,141} = 2.73$, $P = 0.01$, desert vs. wheat $P = 0.001$, desert vs. trees $P = 0.001$; desert vs. sunflowers $P = 0.02$; Table 3).

Thanatus vulgaris dominated the samples collected from the wheat fields (87% of philodromids from wheat fields). *Thanatus vulgaris* was found in higher abundance during the inter-wheat season ($F_{1,141} = 1.96$, $P = 0.04$; Table 3). During this season, *Th. vulgaris* adults were collected mostly in sunflower fields (Fig. 4C; overall, $F_{3,80} = 2.8$, $P = 0.006$, sunflowers vs. trees $P = 0.01$, sunflowers vs. desert $P = 0.01$, sunflowers vs. wheat $P = 0.04$; Table 3). During the wheat season *Th. vulgaris* occurred in all habitats ($F_{2,61} = 1.69$, $P = 0.09$; Table 3), however its abundance increased in the wheat fields toward the end of the wheat season (Fig. 4D)

Juvenile *Thanatus* were found mostly in the inter-wheat season and in higher abundance in the sunflower fields (Fig.

Table 3.—Habitat preference of the main spider groups (family, genus and dominant species) between the wheat fields and adjacent alternative habitats during the wheat season (desert, planted trees) and between fallow wheat fields and a summer crop (sunflowers) between wheat seasons. Significant effects from GLMM and post hoc comparisons are marked in bold.

Group	Factor	F(df)	*P*	Significant differences
Linyphiidae				
Alioranus pastoralis	Season	-	-	Found only in the wheat season
	Habitat (wheat season)	0.83 (2,61)	0.41	
Trichoncoides piscator	Season	**3.35 (1,141)**	**0.001**	**Between seasons>wheat season**
	Habitat	**2.97 (3,141)**	**0.003**	
	Season*Habitat	**3.0**	**0.003**	
	Habitat (wheat season)	1.84 (2,61)	0.07	
	Habitat (between seasons)	**3.55 (3,78)**	**<0.001**	**Sunflower>wheat (<0.001)** **Sunflower>trees (<0.001)** **Sunflower>desert (<0.001)**
Gnaphosidea				
Nomisia	Season	0.09 (1,141)	0.92	
	Habitat	1.11 (3,141)	0.27	
Nomisia juveniles	Season	0.04 (1,141)	0.97	
	Habitat	0.81 (3,141)	0.42	
Theridiidae				
Enoplognatha	Season	-	-	Found only in the wheat season
	Habitat (wheat season)	**2.27 (2,61)**	**0.03**	**Desert>trees (0.04)**
Enoplognatha juveniles	Season	-	-	Found only in the wheat season
	Habitat (wheat season)	1.1 (2,61)	0.29	
Philodromidae				
Thanatus fabricii	Season	1.24 (1,141)	0.21	Wheat season>between seasons
	Habitat	**2.73 (3,141)**	**0.01**	**Desert>wheat (<0.001)** **Desert>trees (<0.001)** **Desert>sunflower (0.02)**
Thanatus vulgaris	Season	**1.96 (1,141)**	**0.04**	**Between seasons>wheat season**
	Habitat	**2.21 (3,141)**	**0.02**	
	Season*Habitat	**2.87**	**0.004**	
	Habitat (wheat season)	1.69 (2,61)	0.09	
	Habitat (between seasons)	**2.8 (3,80)**	**0.006**	**Sunflower>wheat (0.04)** **Sunflower>trees (0.01)** **Sunflower>desert (0.01)**
Thanatus juveniles	Season	**3.19 (1,141)**	**0.001**	**Between seasons>wheat season**
	Habitat	**2.26 (3,61)**	**0.02**	
	Season*Habitat	**2.05**	**0.04**	
	Habitat (wheat season)	**2.45 (2,40)**	**0.01**	**Desert>wheat (0.04)** **Desert>trees (0.04)**
	Habitat (between seasons)	**2.15 (3,73)**	**0.03**	**Sunflowers>wheat (0.04)**

4E; season, $F_{1,141} = 3.19$, $P = 0.001$, habitat, $F_{1,161} = 2.26$, $P = 0.02$, habitat (inter-wheat), $F_{3,73} = 2.15$, $P = 0.03$, sunflowers vs. wheat $P = 0.04$; Table 3). Juveniles increased in abundance in all non-wheat habitats at the end of the summer (Fig. 4F). During the wheat season juvenile abundance was low but was significantly higher in the desert habitat (overall, $F_{2,40} = 2.45$, $P = 0.01$, desert vs. wheat $P = 0.04$, desert vs. trees $P = 0.04$; Table 3).

DISCUSSION

Overall, spider abundance was low in our samples, as is typical of these desert agroecosystems (Pluess et al. 2008; Opatovsky et al. 2010; Opatovsky & Lubin 2012). By comparison, cereal fields and adjacent grasslands in temperate regions of Europe have abundances several times greater than in our samples (e.g., Schmidt & Tscharntke 2005a; Schmidt-Entling & Döbeli 2009). However, in both regions, the natural habitats harbor higher spider abundance and species diversity than the adjacent crop fields (Schmidt & Tscharntke 2005b; Pluess et al. 2008).

The use of two sampling methods, pitfall traps and suction sampling, provided an additional level of information and allowed us to track the different life stages of spiders, as in some instances juveniles and adults were collected by different methods. For example, adults of *Th. vulgaris* and *Th. fabricii* are terrestrial and were collected almost exclusively by pitfall traps, while the juveniles of these species occur in the vegetation layer and were collected mainly by suction sampling. Thus, we were able to determine the presence of juveniles and adults in each of the habitats in each season, as well as the changes in their abundance over time.

Our results indicate differences in the patterns of habitat use in the different spider groups, and also between juveniles and adults. As predicted, crop specialists switched to an alternative crop during the inter-wheat season, while habitat generalist

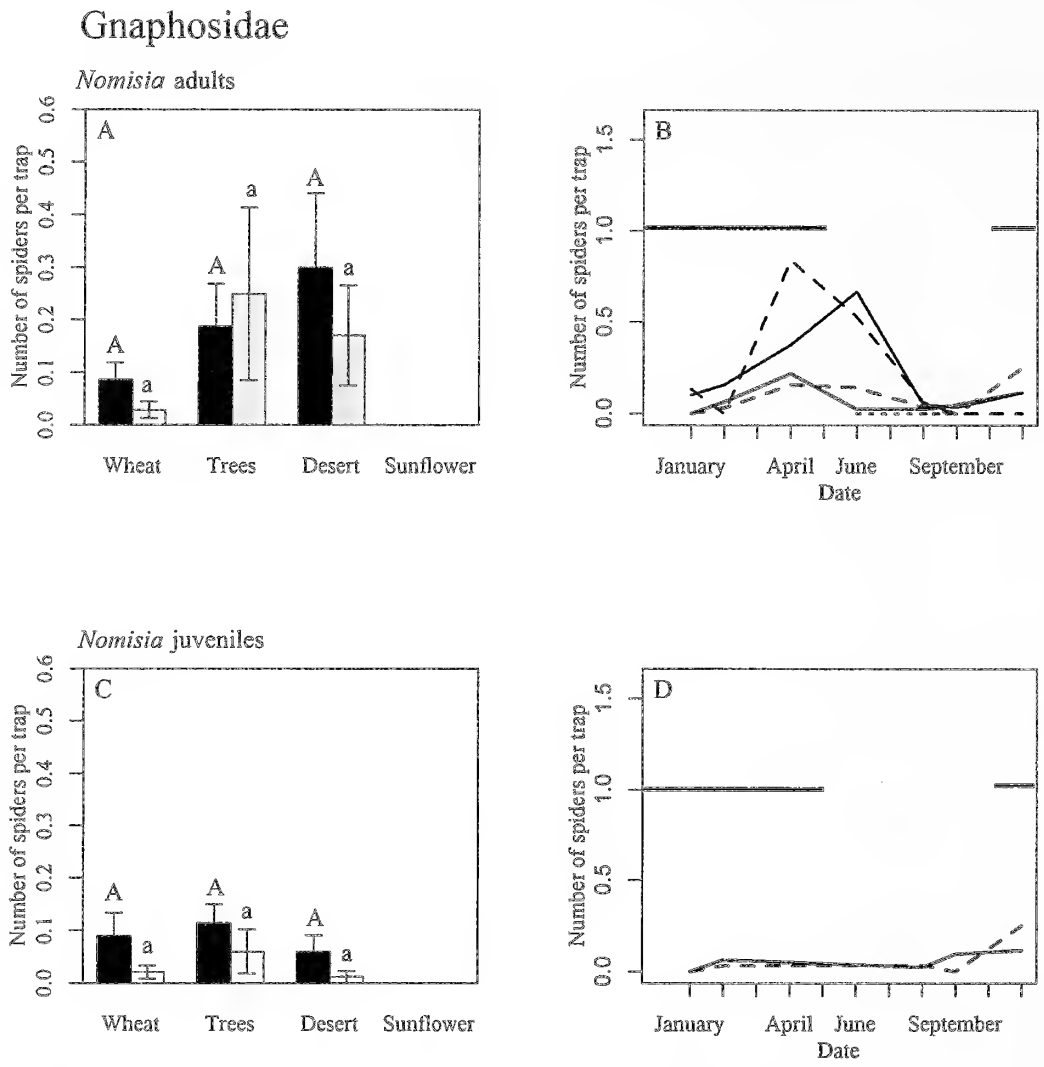

Figure 2.—Abundance of *Nomisia* (Gnaphosidae) adults and subadults (A, B) and juveniles (C, D) across habitat types and seasons (mean number of individuals per pitfall trap ± s.e.). A, C. The average numbers found in the four different habitat types (wheat fields, planted eucalyptus trees, desert and sunflower fields). The black bars represent the wheat season (October–May) and the grey bars represent the inter-wheat season (May–October). The letters above the bars represent significant differences ($P < 0.05$) between habitat types within each season. B, D. Changes in abundance in wheat adjacent to trees (solid black line), wheat adjacent to desert (broken black line), planted trees (solid grey line), and desert (broken grey line). Horizontal lines at the top indicate the wheat season.

species used desert and tree habitats to differing degrees in both seasons. In this system, two species can be considered crop specialists: *Trichoncoides piscator* (Linyphiidae) and *Thanatus vulgaris* (Philodromidae). The former is noted as an agrobiont species in Europe and is associated with different crops (e.g., oilseed rape, Drapela et al. 2008). *Thanatus vulgaris*, to our knowledge, was not previously noted as a crop specialist spider. In Israel, it is recorded throughout the country (Levy 1977). Possibly the species is typical of more mesic habitats, and can survive in the Negev desert only in crop fields.

Trichoncoides piscator disappeared from the wheat at the end of the season and simultaneously appeared in the sunflowers fields. Similarly, *Th. vulgaris* invaded sunflower fields during the inter-wheat season, but nevertheless also remained in fallow wheat fields after the wheat harvest (Opatovsky & Lubin 2012), indicating the possibility of surviving the inter-crop season as adults in the fallow fields. Juveniles may have a broader habitat tolerance than adults, as they were found in the eucalyptus trees and desert during the inter-wheat season as well as in the sunflower fields. However, we could not distinguish juveniles of *Th. fabricii* from those of *Th. vulgaris*. Thus, it is possible that juveniles found in the tree and desert habitats were *Th. fabricii*, while those in the sunflowers were largely *Th. vulgaris*. This interpretation is supported by the fact that during the inter-wheat season *Th. fabricii* adults inhabited the tree and desert habitats, while *Th. vulgaris* adults were infrequent in these habitats.

Spill-over of natural enemies into the surrounding natural environment at the end of the crop season is known in temperate agroecosystems (Rand et al. 2006). Apparently, crop specialist species in the desert agroecosystem are unable to disperse into the desert environment at the end of the wheat season and have to disperse to more mesic environments such as other crop fields. Therefore, the crop specialist spiders such as *Tr. piscator* and *Th. vulgaris* do not necessarily benefit from a diversified agroecosystem with non-crop habitats, as was found also for *Tenuiphantes tenuis* (Blackwall, 1852) (Liny-

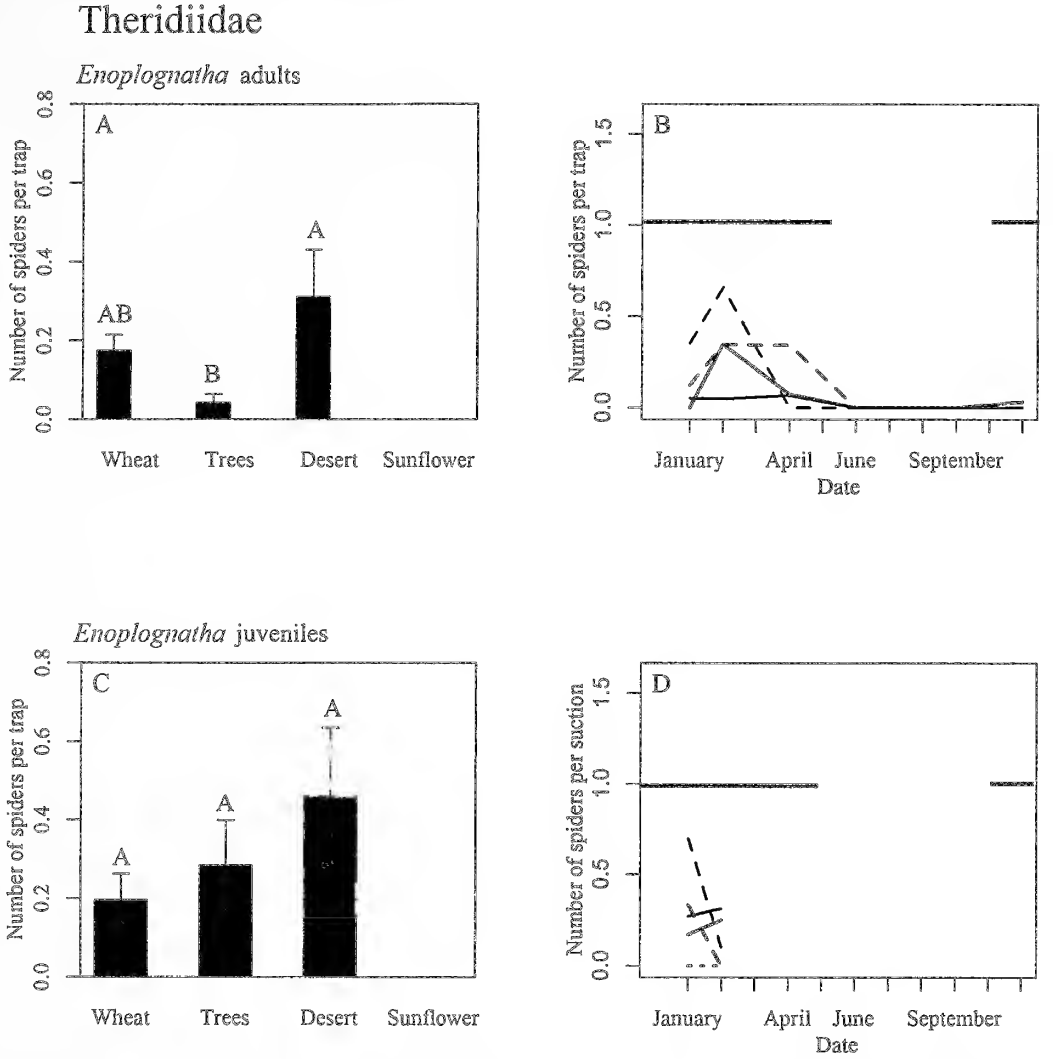

Figure 3.—Abundance of *Enoplognatha* (Theridiidae) adults and subadults (A, B) and juveniles (C, D) across habitat types and seasons (mean number of individuals per pitfall trap/suction sample, respectively ± s.e.). A, C. The average numbers found in the four different habitat types (wheat fields, planted eucalyptus trees, desert and sunflower fields). The black bars represent the wheat season (October–May) and the grey bars represent the inter-wheat season (May–October). The letters above the bars represent significant differences ($P < 0.05$) between habitat types within each season. B, D. Changes in abundance in wheat adjacent to trees (solid black line), wheat adjacent to desert (broken black line), planted trees (solid grey line), and desert (broken grey line). Horizontal lines at the top indicate the wheat season.

phiidae) in the temperate region (Schmidt et al. 2008). While natural habitats provide refuge during the winter in temperate regions (Pfiffner & Luka 2000), we suggest that in desert agroecosystems summer crops are refuges for agrobiont species that cannot survive in the desert habitat during the summer.

Both species of linyphiids (*Tr. piscator* and *A. pastoralis*) occurred in high abundance in the two irrigated wheat fields adjacent to planted trees, leading to large variance in the abundance of these two species in this habitat. *Alioranus pastoralis* was absent from the non-irrigated wheat fields adjacent to trees, and *Tr. piscator* had ten times higher abundance in the irrigated compared to non-irrigated wheat fields adjacent to trees. It is likely that the higher humidity and plant productivity favors these linyphiids (Nyffeler & Sunderland 2003). *Alioranus pastoralis* was not found at all in the inter-crop season, but surprisingly, it occurred in the desert habitat at the beginning of the wheat season, increasing in abundance in the wheat fields only around the middle of the crop season. *Alioranus pastoralis* was observed to lay eggs in the wheat fields (I. Opatovsky, personal observation) and Gavish-Regev et al. (2008) suggested that linyphiid eggs might survive in the soil until the next wheat season. Our results suggest, however, that populations of *A. pastoralis* are resident also in the desert habitat (see also Pluess et al. 2008), and this habitat may act as a dispersal source at the beginning of the wheat season.

Spider groups that used non-wheat habitats to a significant extent during part of their life cycle include the crop residents, *Nomisia* (Gnaphosidae) and *Enoplognatha* (Theridiidae), and desert species such as *Thanatus fabricii* (Philodromidae), and possibly *Alioranus pastoralis* (see above). *Nomisia* are nocturnally active hunting spiders that maintained stable populations of juveniles and adults in the desert and tree habitats and entered the wheat fields at the beginning of the crop season. The generalist habitat preference of these spiders allows each habitat in the agroecosystem to serve as dispersal source. This may explain the early colonization of the wheat fields by

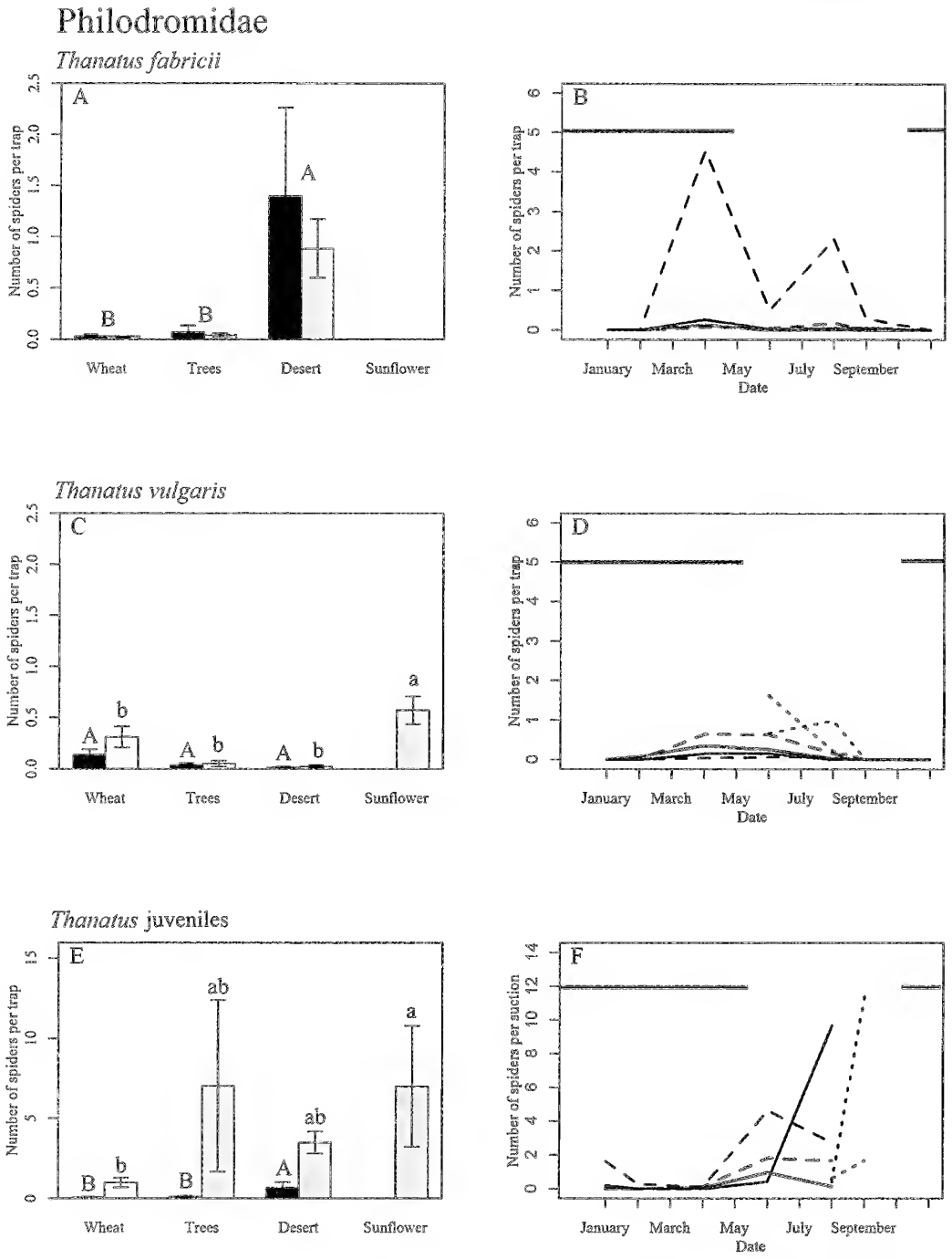

Figure 4.—Abundance of *Thanatus fabricii* adults (A, B) and *T. vulgaris* adults (C, D), and juveniles of *Thanatus* (Philodromidae) (E, F) across habitat types and seasons (mean number of individuals per pitfall trap/suction sample, respectively ± s.e.). A, C. The average numbers found in the four different habitat types (wheat fields, planted eucalyptus trees, desert and sunflower fields). The black bars represent the wheat season (October–May) and the grey bars represent the inter-wheat season (May–October). The letters above the bars represent significant differences ($P < 0.05$) between habitat types within each season. B, D, F. Changes in abundance in wheat adjacent to trees (solid black line), wheat adjacent to desert (broken black line), fallow wheat adjacent to sunflowers (dotted black line), planted trees (solid grey line), and desert (broken grey line) and sunflowers (dotted grey line). Horizontal lines at the top indicate the wheat season.

Nomisia in spite of having cursorial dispersal. Such early immigration into the field from the surrounding habitats may be important in controlling populations of the herbivorous insects early in the season (Birkhofer et al. 2008). Adult and juvenile *Enoplognatha* had a similar distribution pattern to *Nomisia*. Both species of *Enoplognatha* are small spiders that construct sheet webs near the ground. Theridiid juveniles, primarily *Enoplognatha* species, were found to immigrate into Negev wheat fields at the beginning of the crop season, most likely by ballooning, as they appeared simultaneously throughout the field (Gavish-Regev et al. 2008; Opatovsky et al. 2016). *Thanatus fabricii*, unlike the crop specialist *Th. vulgaris*, appears to be mainly a desert species that occurred also in low abundance in the adjacent wheat fields and in

eucalypt trees. It is recorded as occurring in sandy habitats in the Middle East and North Africa (Levy 1977).

The planted eucalyptus trees are alien species and are generally thought to harbor lower insect species diversity and abundance in comparison with native trees (Gardner et al. 2008; Gries et al. 2012). However, Herrmann et al. (2015) found that the eucalyptus plantings increase spider species diversity in the semi-desert agroecosystem of Israel. Nevertheless, we found that this habitat was not a uniquely occupied alternative habitat for any of the spider groups that dominated the wheat fields. Some species even avoided the planted trees, for example *A. pastoralis* and adults of *Enoplognatha*, perhaps due to unsuitable conditions for web building. Species that used the tree habitat invariably were found in the desert habitat as well, leading to the conclusion that wheat-inhabiting spiders might not derive special benefit from eucalyptus groves surrounding the crop fields.

With the exception of the two crop-resident species, the linyphiid *Tr. piscator* and the philodromid *Th. vulgaris*, all other species investigated here are most likely desert or disturbed habitat species that invade agricultural fields during the cropping season. In temperate regions, the presence of grassland and forest habitats near cereal fields was shown to have a positive effect on spider species abundance in the crop fields (Schmidt & Tscharntke 2005a, b; Öberg et al. 2007; Hogg & Daane 2010). In general, increasing habitat diversity within the agroecosystem can increase the abundance and diversity of generalist predator species (Sunderland & Samu 2000; Birkhofer et al. 2014). In this desert region, proximity of these natural habitats to the crop fields can facilitate the dispersal of the spiders into the crop, as some crop-inhabiting desert species may be unable to colonize the wheat fields if nearby desert habitat is supplanted by other crops or even by tree plantations. Consequently, in desert agroecosystems, natural or semi-natural habitats should be conserved in order to increase spider abundance and potential biocontrol services provided by them.

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SHORT COMMUNICATION

Variation in web-building spider communities among three tropical tree species in a young experimental plantation

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Abstract. We documented the presence and abundance of spider species (Arachnida: Araneae) on young trees of *Swietenia macrophylla*, *Ceiba pentandra* and *Cordia dodecandra* found in an experimental plantation. Surveys of spider abundance and species identity conducted twice during the growing season indicated marked differences in web-building spider assemblages associated with each tree species. *Swietenia* exhibited the lowest spider abundance, whereas *Cordia* and *Ceiba* had similarly higher abundances. *Leucauge venusta* (Walckenaer, 1841) was the dominant spider on all tree species, but different spider species were co-dominant on *Cordia* and *Ceiba* (*Araneus pegnia* (Walckenaer, 1841) and *Argiope argentata* (Fabricius, 1775) respectively), and several spider species were exclusive to each tree species. These results highlight the influence of tree species identity on community structure at higher trophic levels, particularly in the case of web-building spiders inhabiting tropical tree communities.

Keywords: Abundance, Araneae, plant traits, predator, species composition

The effects of plant phenotypic variation on consumer communities have been extensively documented (Mooney & Singer 2012). Such effects are generally attributed to plant genotypes or species varying in associated key traits, for example, chemical defenses and nutritional quality for herbivores or refuge availability for mutualists (Karban 1992; Mooney & Singer 2012). Within this context, research on the consequences of plant species variation on herbivores has historically received much attention particularly for herbaceous plants (Hunter et al. 2000). In contrast, fewer studies have rigorously evaluated tree species variation in associated consumer communities despite the fact that arboreal plants dominate many types of terrestrial ecosystems, and few of these studies have looked at effects on predators and parasitoids (for exceptions see: Lill et al. 2002; Vehviläinen et al. 2008; Singer et al. 2014).

Spiders (Araneae) are one of the most diverse and abundant invertebrate predators in terrestrial ecosystems (Platnick 2015). Within this order web-building spiders, which represent ca. 30% of all spider species, are ubiquitous predators in terrestrial food webs (Pp. 25–38, 68–74 & 235–243 in Ubick et al. 2005). Plant species variation in web-building spider communities is strongly and directly mediated by plant physical traits such as leaf position, thickness, or branch/leaf architecture which determine site-choosing preferences for web-building (Langelloto & Deno 2004; Jiménez-Valverde & Lobo 2007), as well as by the availability of refuges from other predators (Gunnarsson 1990; De la Cruz et al. 2009). However, the effects of arboreal species identity on spiders have been poorly studied despite the fact that long-lived tree species vary substantially in many of the aforementioned traits and presumably provide ample opportunity for bottom-up effects on predator abundance and diversity.

We report on the results of a study conducted in a four-year-old experimental tree planation in Yucatán, México. We used a subset of plots for this experiment, containing big-leaf mahogany (*Swietenia macrophylla* King), *Ceiba pentandra* (L.) Gaertn, and *Cordia dodecandra* A. DC., and evaluated whether there were differences in the web-building spider assemblages recruiting to these tree species. We expected that differences among tree species in physical traits (e.g., architecture, size, leaf arrangement) would lead to variation in spider abundance and species composition.

The plantation was established in December 2011 at a site in Yucatán, México (20°24′44″N, 89°45′13″W), and included six tree species: *Swietenia macrophylla* King (Meliaceae), *Tabebuia rosea* (Bertol.) DC. (Bignonaceae), *Ceiba pentandra* (L.) Gaertn. (Malvaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae), *Piscidia piscipula* (L.) Sarg. (Fabaceae), and *Cordia dodecandra* A. DC. (Boraginaceae). Seeds were collected from adult trees located in southern Quintana Roo (México), and seeds from a single parental tree represented a maternal source. For details see: Abdala-Roberts et al. (2015).

The plantation consisted of 74 plots, 21×21 m each, with a planting density of 64 plants per plot and 3-m spacing among trees, for a total of 4780 trees. Plots were classified as species monocultures or polycultures, the latter composed of random mixtures of four out of the six species (Abdala-Roberts et al. 2015). We selected three out of the six tree species for this study, namely: *S. macrophylla* (hereafter *Swietenia*), *Cordia dodencandra* (hereafter *Cordia*), and *Ceiba pentandra* (hereafter *Ceiba*), as these species exhibit marked differences in chemical traits (e.g., phenolics) (Moreira et al. 2014; Abdala-Roberts et al. 2015; S. Rosado-Sánchez, unpublished) which might influence herbivore recruitment, as well as in physical traits (e.g., branching pattern and canopy cover) which may influence web-building spiders (Table S1, online at http://dx.doi.org/10.1636/JoA-S-16-016.s1). For this study, we used seven polyculture plots within which these species were present, in addition to a fourth species (*T. rosea*, *P. piscipula*, or *E. cyclocarpum*) which was not sampled and varied in identity across plots (see Table S2, online at http://dx.doi.org/10.1636/JoA-S-16-016.s1). The selected plots were the only polycultures where the three focal species co-occurred.

We conducted two surveys of web-building spiders, one in May 2013 and another in September 2013. During each survey, we sampled the same plots but inspected a different set of trees within each plot because collection of spider specimens during the first survey could influence spider abundance or species composition during the second survey. For each plot, we randomly sampled a total of 20 trees across both surveys (10 trees per plot, per survey) (see Table S2). At the time

of sampling, trees were two (*Cordia*) to four (*Ceiba*, *Swietenia*) m tall. To reduce edge effects on spider recruitment, we avoided plants located on the outer rows of each plot. Across plots and surveys, a total of 140 plants were sampled: 42 for *Swietenia*, 52 for *Ceiba*, and 46 for *Cordia*.

Surveys were conducted in the morning (700 to 1300 hrs) by "looking down", in which the plant is inspected from ground level up to a height of 0.5 m, and then "looking up" by continuing the search up to two m of height (Coddington et al. 1991). This resulted in a thorough sampling of the main stem and the lower- to mid-portion of the canopy of all the trees. The examination of each plant lasted six minutes and we recorded all web-building spiders regardless of web structure. Specimens were preserved in 70% ethanol and transported to the laboratory for species identification using specialized literature (e.g., Levi 1955, 1978, 1991; Ubick et al. 2005). Scientific names were updated using the World Spider Catalog (Platnick 2015). Unidentified individuals were classified as morphospecies.

To test for differences among tree species in spider community composition, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2001) in the VEGAN package of R ver. 3.0.2 (R Core Team, 2013) with 1000 random permutations using a dissimilarity distance matrix with spider species abundances based on the Jaccard index (Chao et al. 2006). We previously ran this analysis restricting the permutations to each plot ("strata" option) to account for spatial structure (i.e., autocorrelation) and results remained unchanged; therefore, we report results for the unrestricted analysis.

We tested for tree species differences in spider abundance with a generalized linear mixed model using a Poisson distribution and log link in PROC GLIMMIX, SAS version 9.2 (SAS Institute 2009, Cary NC). We used data at the plant level and included tree species (fixed effect), survey (random), plot (random), and maternal source (random, nested within plot) as independent variables. This analysis was repeated excluding the most abundant spider (*Leucuage venusta* (Walckenaer, 1841)) to determine whether tree species differences were driven by this spider. We compared differences between tree species means using Bonferroni-adjusted least-square means.

A total of 426 spider specimens were collected across all tree species, representing four families, 24 genera, and 28 species (Table 1). The family Araneidae had the highest species richness with 14 species, followed by Theridiidae with 12 species. The families Uloboridae and Tetragnathidae were each represented by only one species. The most common species were *Leucauge venusta* with 231 individuals (54.2% of the sample) and *Araneus pegnia* (Walckenaer, 1841) with 54 individuals (12.6%).

Results from the PERMANOVA indicated a significant effect of tree species on spider species composition ($F_{2,91} = 3.29$, $P < 0.001$). With the exception of *L. venusta*, which was consistently the most common species on all tree species, we found that the composition and relative abundance of the following most abundant spider species varied among tree species. For *Swietenia*, the second most abundant species was *Eriophora ravilla* (C. L. Koch, 1844) representing 9% of the specimens sampled on this tree species, whereas for *Ceiba* the second most abundant species was *Argiope argentanta* (Fabricius, 1775) (11%) and for *Cordia* it was *Araneus pegnia* (23%). A follow-up (2 by 2) contingency table indicated a significant association of *Arg. argentata* and *Aran. pegnia* abundance with *Cordia* and *Ceiba*, respectively ($\chi^2 = 37.71$, df = 1, $P < 0.0001$). We found a similar number of rare species (i.e., represented by one individual for each tree species) on all tree species (eight for *Swietenia* and seven each for *Ceiba* and *Cordia*), but many of these were exclusive to each tree species (see Table 1).

For spider abundance, *Cordia* accounted for 42% ($n = 182$) of all specimens recorded, followed by *Ceiba* with 33% ($n = 142$) and *Swietenia* with 25% ($n = 102$) (Table 1). The generalized linear mixed model indicated a significant effect of tree species on the abundance of web-building spiders per plant ($F_{2,14} = 11.55$, $P = 0.001$). There was also a significant effect of tree species on spider abundance after excluding *L. venusta* ($F_{2,14} = 5.93$, $P = 0.013$), suggesting that tree species differences were not predominantly driven by this dominant spider species. Comparison of least-square means (model including *L. venusta*) indicated that the highest abundance was for *Cordia* (2.12 ± 0.23 spiders), followed by *Ceiba* (1.9 ± 0.2 spiders), and lastly *Swietenia* (1.18 ± 0.15 spiders). Mean abundances on *Cordia* and *Ceiba* did not differ significantly, but mean abundances on both of these species differed from those on *Swietenia* ($t_{1,14} > -4.71$, $P < 0.01$).

Overall, the above results indicated a clear differentiation in web-building spider assemblages among the tropical tree species studied. The observed patterns are noteworthy considering that at the time of sampling plants were two years old, and indicate that tree inter-specific variation in associated predator faunas may arise relatively early in tree ontogeny. In turn, the observed effects of tree species on spider communities are likely to further increase with tree age as new phenotypic features arise (e.g., increased architectural complexity).

This study's findings are consistent with findings from previous work in southern Mexico which reported that Theridiidae and Araneidae were the most species rich and abundant groups in both agricultural (Ibarra-Núñez & García-Ballinas 1998) and natural ecosystems (Maya-Morales et al. 2011). In addition, the most abundant species in our study, *Leucauge venusta*, has been reported, along with other species of the same genus (e.g., *L. mariana* (Taczanowski, 1881) and *L. argyra* (Walckenaer, 1841)), as a dominant web-building spider in cacao agroecosystems (De la Cruz et al. 2009) and coffee plantations (Pinkus-Rendón et al. 2006) in southern Mexico, as well as in managed ecosystems in temperate North America (Young & Edwards 1990). Species of the genus *Leucauge* White, 1841 build horizontal webs with a high number of radii and spirals which provide greater structural resistance (Dondale 2003) and also exhibit a broad diet breadth (De la Cruz et al. 2007), traits which have likely contributed to their colonization success and dominance.

The relative abundance and identity of common and rare web-building spiders exhibited marked differences among tree species. Biases in the preference for a particular tree species were especially evident for two of the most abundant spiders in our sample, *Araneus pegnia* and *Argiope argentata*. Field observations indicated that *Ara. pegnia* uses the leaves of *Cordia* for protection during the daytime by bending the leaf edges over them to create a shelter, whereas *Arg. argentata* uses the thorns of the main trunk on *Ceiba* as support structures to build their web and perhaps also as protection against other predators (L. Esquivel-Gómez, personal observation). These observations suggest that tree species variation in spider species recruitment was mediated (at least partly) by plant physical traits of leaves and stems (e.g., see Langelloto & Denno 2004; Jiménez-Valverde & Lobo 2007).

Variation in spider abundance between tree species could also have resulted from differences in the availability of web-building sites (i.e., attachment sites and branch or leaf arrangement; Jiménez-Valverde & Lobo 2007), shelters against other predators (Rypstra 1986), and microhabitat conditions (Rypstra 1986). For example, a higher abundance of orb weavers (Araneidae, Tetragnathidae) observed on *Cordia* and *Ceiba* could be explained because these species provide suitable habitat requirements such as a large separation between branches which allows the construction of the large-size webs (Stenchly et al. 2011). Plant size *per se* appeared not to be a main driver of differences in abundance, because *Cordia* was the smallest of the three species and exhibited the highest abundance. Further work is necessary to formally assess which physical traits are predictors of spider recruitment for the studied tree species. Interestingly, previous work conducted in the same experimental system reported no differences among tree species in the abundance of cursorial spiders

Table 1.—List of the web-building species sampled on the tropical trees Swietenia macrophylla ("sw"), Ceiba pentandra ("ce"), and Cordia dodecandra ("co"), in polyculture plots from a tree diversity experiment in southern Mexico (Yucatan). Total abundances are shown for each species of spider as well as spider abundances separately for each tree species. The top three most abundant spiders on each tree species are typed in bold.

Family	Species	Authority	key	sw	ce	co	total
Araneidae	*Acacesia hamata*	(Hentz, 1847)	Ah	0	0	2	2
	Araneus pegnia	(Walckenaer, 1842)	Ap	4	9	**41**	54
	Argiope argentata	(Fabricius, 1775)	Aa	3	**21**	1	25
	Cyclosa berlandi	Levi, 1999	Cb	3	**10**	3	16
	Cyclosa caroli	(Hentz, 1850)	Cc	1	8	2	11
	Eriophora ravilla	(C.L.Koch, 1844)	Er	**9**	3	6	18
	Gasteracantha cancriformis	(Linnaeus, 1758)	Gc	5	2	4	11
	Mangora itza	Levi, 2005	Mi	0	0	1	1
	Mecynogea lemniscata	(Walckenaer, 1842)	Ml	0	0	1	1
	Metepeira c. olmec	Piel, 2001	Mo	0	0	3	3
	Micrathena gracilis	(Walckenaer, 1805)	Mg	0	1	0	1
	Micrathena sagittata	(Walckenaer, 1842)	Ms	3	3	2	8
	Neoscona oaxacensis	(Keyserling, 1864)	No	0	1	1	2
	Verrucosa arenata	(Walckenaer, 1842)	Va	0	0	2	2
Theridiidae	*Achaearanea* sp.		Ach	1	0	0	1
	Achaearanea tesselata	(Keyserling, 1884)	Pt	1	1	0	2
	Ameridion signum	(Levi, 1959)	As	0	0	1	1
	Anelosimus studiosus	(Hentz, 1850)	Ans	0	1	0	1
	Argyrodes elevatus	Taczanowski, 1873	Ae	1	1	0	2
	Chrysso albomaculata	O.P. Cambridge, 1882	Ca	**8**	3	**12**	23
	Chrysso sp.		Cs	1	0	1	2
	Emertonella emertoni	(Bryant, 1933)	Ee	1	0	0	1
	Euryopis lineatipes	O.P. Cambridge, 1893	El	0	2	0	2
	Faiditus caudatus	(Taczanowski, 1874)	Fc	1	0	0	1
	Neospintharus rioensis	(Exline & Levi, 1962)	Ar	0	1	0	1
	Tidarren sisyphoides	(Walckenaer, 1842)	Ts	1	1	0	2
Tetragnathidae	*Leucauge venusta*	(Walckenaer, 1841)	Lv	**59**	**74**	**98**	231
Uloboridae	*Uloborus sp.*		Ulo	0	0	1	1
Total abundances				102	182	142	426

(Salticidae) (Abdala-Roberts et al. 2015), suggesting that tree species variation in web spider communities depends on traits associated with web construction.

Although direct effects of plant traits on spider recruitment are likely to be important for explaining our results, we cannot rule out the influence of indirect effects occurring through differences in herbivore abundance or diversity among tree species. Although spiders are generalist predators and frequently exhibit euryophagous behavior (Pekár et al. 2012), species vary largely in their hunting strategies and prey preferences (Nyffeler 1999). Some species build webs designed to capture specific prey such as adult Lepidoptera and ants and display oligophagous or even stenophagous behavior (Pekár et al. 2012). Thus, differences in herbivore composition among tree species would be expected to lead to variation in spider recruitment and species composition. Interestingly, *Swietenia* has the highest levels of leaf phenolics of the three tree species (S. Rosado-Sánchez unpublished) which may reduce insect herbivore abundance and diversity and in turn (at least partly) explain why spider abundance was lowest for this species. Further work is needed in order to determine the relative importance of direct vs. indirect effects of plant phenotypic variation on web-building spider communities.

Our findings have important implications provided that web-building spiders exert strong impacts on arthropod community structure. Reduced overlap among plant species in predator species composition is expected to lead to non-additive increments in predator diversity with increasing tree species diversity, as observed for spiders and other groups of predators in this experimental system (Campos-Navarrete et al. 2015; Esquivel-Gómez et al. in press). This may ultimately lead to higher predation rates. Indirect effects of spiders on plants may vary depending on the degree to which they feed upon other carnivorous vs. herbivorous arthropods, provided that spider top-down net effects on plants are positive. In that context, our results argue in favor of conserving tree diversity in forest patches and establishing mixed tree plantations to maintain or increase predator abundance and diversity, and to ultimately achieve top-down regulation of herbivore populations.

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