



El Colegio de la Frontera Sur

Taxonomía y biología de dos especies de arañas del género
Phonotimpus Gertsch & Davis, 1940 (Araneae: Phrurolithidae)

Tesis

presentada como requisito parcial para optar al grado de
Doctor en Ciencias en Ecología y Desarrollo Sustentable
Con orientación en Ecología de Artrópodos y Manejo de Plagas

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1940 (Araneae: Phrurolithidae)

para obtener el grado de **Doctor en Ciencias en Ecología y Desarrollo Sustentable**

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DEDICATORIA

A mis padres, hermanos, sobrinos y Doña Lucherito quienes me han brindado su apoyo y muchos momentos de alegría.

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RESUMEN

Las arañas de la familia Phrurolithidae son muy pequeñas (de 2 a 3 mm) y de coloraciones crípticas que usualmente deambulan debajo de rocas y entre la hojarasca. La información taxonómica que se tiene de ellas en México es limitada, pues se considera que existen muchas especies por describir; lo que se conoce sobre su biología es aún más exiguo. En el Volcán Tacaná (Chiapas) se encontraron dos especies de Phrurolithidae que son comunes entre las de arañas de la hojarasca, las cuales no habían sido objeto de estudio hasta ahora. En este trabajo se abordaron varios aspectos sobre ellas, como su taxonomía, la fenología, el cuidado maternal y el periodo de gestación. En el primer manuscrito se describieron a las dos especies como nuevas para la ciencia pues tenían características particulares. Ambas especies fueron asignadas al género *Phonotimpus* por compartir una serie de características con dicho género, una fue denominada *Phonotimpus pennimani* y la otra *Phonotimpus talquian*. También, se incluyó la re-descripción de la hembra de *P. separatus* (especie tipo del género) con la que se profundizó en la correcta separación del género.

En el segundo manuscrito se demuestra que las dos especies se encuentran presentes casi todo el año (juveniles y adultos), por lo que ambas son eurícronas sin un periodo fijo de reproducción. Los estadios juveniles y penúltimos de ambas especies construyen un refugio temporal cuando realizan la muda. Además, las dos especies exhiben dimorfismo sexual y ambas utilizan la emboscada para capturar a sus presas (coleómbolos). Las hembras de las dos especies depositan sus huevos en ovisacos con forma de disco y les proveen cuidado. *Phonotimpus pennimani*, y probablemente *P. talquian*, son especies iteróparas pues producen hasta cuatro ovisacos. Por último, se reportó el parasitismo de huevos de *P. pennimani* por una avispa del género *Idris* sp. (Platygastridae).

PALABRAS CLAVES

Arañas, cuidado maternal, fenología, parasitoide, refugio, taxonomía.

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CAPITULO I. INTRODUCCIÓN

A nivel mundial, se conocen cerca de 49,000 especies de arañas en 120 familias (World Spider Catalog 2019). En México, Chiapas cuenta con una elevada diversidad de arañas y hasta el momento se han registrado 487 especies, 212 géneros y 50 familias, pero se considera que existe un mayor sesgo hacia la recolecta y el estudio de arañas tejedoras que de arañas errantes (Ibarra-Núñez 2013). Estudios recientes realizados en la Sierra Madre de Chiapas han proporcionado indicios de que el conocimiento de la diversidad de arañas en Chiapas dista de ser completo. Dichos estudios encontraron la presencia de especies, géneros e incluso familias no registradas previamente para el estado o el país, además revelaron que varias de esas especies corresponden a taxa aún no descritos (Chame-Vázquez 2011; Ibarra-Núñez et al. 2011; Campuzano-Granados 2014; Angulo-Ordoñes 2015; Chame-Vázquez 2015; Gómez-Rodríguez 2015). Dos de esas especies nuevas para la ciencia, de tamaño pequeño y habitantes de la hojarasca, correspondieron a una familia poco estudiada (Phrurolithidae), cuya biología es prácticamente desconocida. Por lo anterior, estas especies se escogieron como objeto de estudio para esta tesis.

Si bien se han incrementado los esfuerzos en los estudios sobre la diversidad de arañas, el número de trabajos que abordan aspectos de biología o historia natural en México es aún muy limitado. Primeramente, hay que reconocer que un grupo tan diverso como el de las arañas sin duda incluye un rango amplio de estilos de vida y comportamientos, aunado a las variadas adaptaciones fisiológicas y morfológicas (Turnbull 1973). La gran diversidad contrasta con la poca información existente acerca de la biología de muchas de estas especies.

Phrurolithidae es una familia de arañas relativamente poco diversa con 13 géneros y 223 especies a nivel mundial (World Spider Catalog 2019). El tamaño corporal de las Phrurolithidae es menor a los 5 mm, son arañas errantes del suelo que deambulan debajo de rocas o entre la hojarasca. Algunas especies son de hábitos nocturnos y otros diurnos, además de que ciertas especies tienen semejanza morfológica con las hormigas (Penniman 1978; Draney 1997; Ubick y Richman 2005; Pekár y Jarab 2011). En México, se han reportado 4 géneros y 15 especies, pero desde la publicación de las descripciones originales no se han realizado estudios taxonómicos o biológicos que involucren algunas

de estas especies (Chamberlin y Ivie 1936; Gertsch y Davis 1940; Platnick y Ubick 1989). Ubick y Richman (2005) consideraron que la taxonomía e historia natural de muchos miembros de la actual familia Phrurolithidae es parcial e incierta.

Estudios realizados sobre la diversidad de arañas en dos zonas de la parte alta del Volcán Tacaná en Chiapas (Chamé-Vázquez 2011; Chamé-Vázquez 2015) revelaron la existencia de dos especies de Phrurolithidae con gran afinidad morfológica entre sí, fueron asignadas inicialmente al género *Piabuna* Chamberlin & Ivie, 1933 por sus semejanzas con las estructuras genitales de los miembros de dicho género (Ibarra-Núñez et al. 2011; Chamé-Vázquez 2015). Sin embargo, estudios preliminares nos llevaron a concluir que la asignación no era totalmente correcta, ya que las hembras de dichas especies también tenían semejanzas con las especies del género *Phonotimpus* Gertsch & Davis, 1940, el cual es cercano a *Piabuna*, por lo que aún se desconocen las relaciones taxonómicas de las especies encontradas en el Volcán Tacaná, con las especies de los géneros *Piabuna* y *Phonotimpus*. Aunado a lo anterior, tampoco se dispone de información sobre casi ningún aspecto de la biología de ambos géneros. Ante la limitada información disponible, consideramos que la combinación de los estudios taxonómicos y biológicos nos permitirá caracterizar mejor a estas especies, y al mismo tiempo nos proporcionarán los primeros estudios detallados sobre la biología de un grupo de arañas que habitan en la hojarasca de los ambientes tropicales del sureste de México.

ANTECEDENTES

Las arañas errantes

La seda es una de las características más distintivas de las arañas, si bien todas las arañas producen seda no todas construyen telarañas (Wise 1993; Foelix 2011). Las arañas usan la seda para múltiples propósitos, de hecho, producen distintos tipos de seda para una función específica (Turnbull 1973). Las arañas pueden ser divididas en dos grandes grupos basado en su estrategia de caza: las tejedoras de redes son aquellas arañas con hábitos relativamente sedentarios que fabrican una trampa hecha con seda, que usualmente está suspendida en alguna estructura de su entorno, mientras que las arañas errantes son aquellas que no fabrican trampas de seda, sino que deambulan por el sustrato en la búsqueda de sus presas (Turnbull 1973; Wise 1993).

Con excepción de las especies de la familia Salticidae, quienes han sido objeto de numerosos estudios, los hábitos de las arañas errantes no han facilitado la recopilación de información acerca de su historia natural, ya que la mayoría de estas arañas son con frecuencia de coloraciones crípticas, de movimientos rápidos y fácilmente perturbadas, además de que muchas viven ocultas entre la hojarasca, debajo de rocas o troncos (Felix 2011; Turnbull 1973). Las estrategias de caza de estas arañas varían de acuerdo con el género o incluso la familia considerada, existiendo tres tipos generales: las acechadoras, las emboscadoras y por último las corredoras. La estrategia acechadora implica detectar una presa potencial, acercarse lentamente y lo bastante cerca para dar un salto y atrapar a su presa (p. ej. Salticidae). Las emboscadoras se ubican inmóviles en un sitio por donde transitan las presas potenciales o sobre un recurso que las atrae, como las flores, para que la presa se acerque a ellas a una corta distancia de ataque (p. ej. muchas Thomisidae). La estrategia de las corredoras consiste en detectar y perseguir a la presa hasta atraparla (p. ej. Lycosidae) (Turnbull 1973; Wise 1993). El uso de la seda en las arañas errantes tiene otras funciones como línea de seguridad, soporte para desplazamientos, sustrato portador de feromonas sexuales, como recubrimiento de refugios, para construir la red de esperma o para fabricar los ovisacos (Wise 1993; Foelix 2011).

Particularidades de la familia Phrurolithidae

Las arañas de la familia Phrurolithidae forman parte de los grupos Entelegynae (arañas con órganos genitales complejos), del clado RTA (machos con una apófisis en la cara retrolateral de la tibia del pedipalpo) y del clado Dionycha (arañas con solo 2 uñas en las patas ambulatorias). Dentro de este último grupo las Phrurolithidae comparten varias características con la familia Trachelidae como: la presencia de brochas tarsales compuestas por sedas fuertemente plegadas, presencia de sujetadores de la brocha tarsal, una reducción en el número de espinas de las patas posteriores y ausencia de una apófisis media en el bulbo copulatorio del macho. Sin embargo, se distinguen de las Trachelidae por tener una serie de macrosetas ventrales muy largas en las tibias de las patas anteriores y por carecer de espínulas (“cusps” en inglés) en las patas. Además, los machos tienen modificaciones en la cara ventral del fémur del palpo (apófisis femoral). Todas las Phrurolithidae, con excepción de las especies del género *Drassinella*, tienen un receptáculo globoso característico en la genitalia interna de las hembras, adicional a las espermatecas primarias y secundarias (Ramírez 2014).

La taxonomía de la familia Phrurolithidae en Norteamérica es limitada, el estudio más reciente es el de Penniman (1985), quien propuso una reclasificación de este grupo. Posterior a esto no existen estudios recientes que consideren a todos los géneros que tienen distribución en esta región, solo existe un estudio de Platnick y Ubick (1989) sobre el género *Drassinella*, y solo dos estudios que incluyeron varios géneros americanos de esta familia para análisis cladísticos (Bosselaers y Jocqué 2002; Ramírez 2014). En contraste, recientemente en Asia se han llevado a cabo estudios taxonómicos de varios géneros, entre los que se incluye al género *Abdosetae* Fu, Zhang & MacDermott, 2010, *Otacilia* Thorell, 1897 y algunos grupos de especies del género *Phrurolithus* C. L. Koch, 1839 (World Spider Catalog 2019).

Hábitat y fenología

Las arañas errantes se pueden encontrar sobre la vegetación o por debajo de troncos, rocas, y también deambulan entre la hojarasca y en el suelo, lugares en donde cazan a sus presas (Wise 1993). La distribución geográfica conocida de las especies mexicanas de Phrurolithidae, se limita a las localidades donde fue recolectado el material tipo y sobre

el cual se basaron las descripciones taxonómicas. En estos trabajos no se incluyeron datos relacionados con el hábitat o la historia natural de las especies. Para otras especies de Norteamérica, la información acerca de los hábitats que ocupan es exigua, por ejemplo, Chamberlin e Ivie (1935) mencionaron que *Piabuna brevispina*, *P. longispina* y *P. xerophila* fueron recolectadas debajo de rocas en una ladera seca. Mientras que *Scotinella fratrella* (Gertsch, 1935) es común en campos de cultivo abandonados y en suelos de hábitats con etapas sucesionales intermedias en Ohio (EUA), al menos los machos adultos de esta especie parecen pasar el invierno en estado adulto (Penniman 1978). Draney (1997) estudió la fenología y selección de hábitat de arañas de suelo en Georgia (EUA), tal autor encontró que *Phrurotimpus alarius* (Hentz, 1847) tiene una preferencia por áreas boscosas y consideró a *P. alarius* como una especie con ciclo anual y con la temporada de apareamiento en primavera, pues la mayoría de los machos fueron recolectados en abril.

Las dos especies de Phrurolithidae en estudio fueron recolectadas en las faldas del Volcán Tacaná y son consideradas como habitantes del suelo, ya que sólo han sido capturadas mediante trampas de caída y cuando se escrudiñaba la hojarasca. La primera morfoespecie, “*Piabuna*” sp1 se encontró entre la hojarasca de un bosque mesófilo de montaña a una altitud de 2021 a 2048 m s.n.m. En esa localidad las hembras adultas se recolectaron de diciembre 2006 a noviembre 2007 (con excepción de enero), los machos adultos de febrero a mayo y los juveniles de diciembre a noviembre, aunque fueron muy escasos en abril y mayo, meses en que los machos y las hembras fueron más abundantes (Chame-Vázquez 2011). Por otro lado, “*Piabuna*” sp2 fue capturada entre la hojarasca de cafetales que se encuentran a una altitud de 922 a 1069 m s.n.m. y los adultos de esta especie se colectaron solo en marzo, junio y agosto (Chame-Vázquez 2015). Lo anterior parece indicar que los adultos emergen a finales de la temporada seca y continúan presentándose en los primeros meses de la temporada de lluvias, pero se desconoce si los adultos continúan apareciendo a finales de esta temporada, ya que las recolectas en ese sitio se realizaron solamente entre febrero y agosto.

Reproducción

La reproducción en arañas varía desde procesos muy simples a muy complejos, en el cortejo existen señales químicas, físicas o visuales. Además, involucra una gran variedad de posiciones de apareamiento, así como diferentes interacciones antagónicas sobre todo cuando existe un competidor (Wise 1993; Foelix 2011). En arañas errantes existe una amplia heterogeneidad de comportamientos de cortejo y cópula. Algunos tomísimos realizan un cortejo modesto, mientras que los salticidos despliegan muchas señales visuales con una variedad de movimientos y danzas utilizando su abdomen y patas, en tanto que algunos machos de la familia Lycosidae aparte de danzar, envían estímulos vibratorios y químicos para evitar que las hembras los confundan con presas potenciales (Felix 2011). En el caso de las arañas de la familia Phrurolithidae, como muchas otras familias, no existen estudios sobre este tipo de comportamiento.

El único estudio que aborda algunos aspectos de la biología reproductiva de algunas especies de Phrurolithidae fue el realizado por Pekár y Jarab (2011) quienes observaron que *Liophrurillus flavitarsis* (Lucas, 1846) y *Phrurolithus festivus* (C. L. Koch, 1835) no presentaban un cortejo, sino que el macho de ambas especies corría directamente hacia la hembra e inmediatamente empezaban a aparearse. Para ello, el macho se colocó sobre un costado de la hembra e inició la cópula, esta posición corresponde al tipo III de la clasificación de posiciones de cópula de von Helversen (1976 citado por Foelix 2011), que consiste en que el macho se dirige de frente hacia la hembra, se monta sobre su prosoma, después gira hacia el lado derecho o izquierdo de tal manera que uno de sus palpos pueda ser insertado en el epigineo de la hembra. Además, Pekár y Jarab (2011) indicaron que el tiempo promedio de apareamiento para *L. flavitarsis* fue de 84 ± 4.9 minutos (prácticamente una hora y media), mientras que para *P. festivus* duró 252 ± 15.7 minutos (prácticamente cuatro horas y cuarto). El tamaño de la puesta en *L. flavitarsis* fue en promedio de 4.7 huevos comparado con el promedio de 4.1 de *P. festivus*. Por último, las hembras de ambas especies produjeron más de un ovisaco en cautiverio.

Cuidado parental

Después de la copula las hembras realizan la postura de huevos y producen un ovisaco, el cual es un contenedor hecho con varias capas de diferentes tipos de seda. La

fertilización de los huevos se realiza al momento que estos pasan a través del útero externo y después pasan por la abertura genital para ser depositados en el ovisaco (Foelix 2011). La cantidad de huevos puestos dependen de cada especie de araña, va desde uno solo como en el caso de *Monoblemma muchmorei* (Tetrablemmidae), hasta aproximadamente 2,500 huevos depositados por *Cupiennius* sp. (Trechaleidae) (Edwards y Edwards 2006; Foelix 2011). El cuidado parental en arañas va desde la protección de los huevos contra los depredadores, el transporte de los huevos o arañuelas, la provisión de alimento a las arañuelas pequeñas mediante la regurgitación de fluidos hasta la matrifagia, que es cuando la madre sirve de alimento a su progenie (Vieira y Romero 2008). Para el caso de la familia Phrurolithidae, no existen estudios que aborden este tema a detalle.

JUSTIFICACIÓN

El estudio taxonómico preliminar de las dos especies de Phrurolithidae recolectadas en las faldas de Volcán Tacaná (Chame-Vázquez 2011; 2015) nos proporcionó evidencias de las semejanzas y diferencias morfológicas con las especies descritas de los géneros *Piabuna* y *Phonotimpus*, lo que nos llevó a concluir que ambas especies son afines entre sí. Debido a la incertidumbre de las relaciones taxonómicas entre los géneros de la familia Phrurolithidae, un estudio detallado coadyuvaría a un mejor conocimiento taxonómico de los géneros *Piabuna* y *Phonotimpus* puesto que desde las descripciones originales, que datan de 1933, 1935 y 1940, no se han descrito más especies relacionadas.

Los registros previos de distribución de la familia Phrurolithidae en México están concentrados en su mayoría en los estados del norte y centro del país (*Drassinella*: Baja California, Guerrero; *Phonotimpus*: San Luis Potosí, Nuevo León; *Phrurolithus*: Coahuila, Hidalgo, Veracruz, Tamaulipas; *Piabuna*: Coahuila). Por ende, la distribución disyunta de las especies del Volcán Tacaná podría proveernos de más información biogeográfica acerca de este grupo. Por su parte, la distribución de ambas especies enmarcadas en este estudio está restringida al Volcán Tacaná, una zona con pocos estudios faunísticos y con fauna característica que incluye algunas aves, mamíferos y reptiles enlistados en el CITES y en la NOM-059-SEMARNAT-2010 (SEMARNAT y CONANP 2013). Asimismo, la población original de “*Piabuna*” sp1 fue encontrada en un bosque mesófilo de montaña dentro de la Reserva de la Biósfera Volcán Tacaná, este tipo de vegetación es considerada como una de las más amenazadas en México y el de menor extensión a nivel mundial (CONABIO 2010). Esta distribución les confiere a las especies en estudio el estatus de especies endémicas lo que resalta la importancia de emprender más estudios que incrementen el conocimiento de la fauna y flora que residen en la región, pero también de la necesidad de implementar estrategias que ayuden al uso, manejo y preservación de los sitios que los albergan.

La elección de estas arañas como modelos de análisis se fundamenta en que algunos estudios han demostrado que son integrantes frecuentes de las comunidades de arañas del suelo en México (Chamé-Vázquez 2011; Ibarra-Núñez et al. 2011; Angulo-Ordoñes 2015; Chamé-Vázquez 2015; Rivera-Quiroz et al. 2016) y podrían desempeñar papeles importantes en la dinámica de los procesos biológicos de los hábitats en los cuales

residen. Además, en general la familia Phrurolithidae probablemente sea más diversa de lo que se conoce actualmente (*obs. pers.*), pues podría ser otro caso como el de la familia Oonopidae, la cual era considerada como poco diversa y que mediante el proyecto “The Planetary Biodiversity Inventories” incrementó considerablemente el número de sus especies a nivel mundial (The Goblin Spider PBI 2017).

La escasa información publicada sobre la biología de las arañas de la familia Phrurolithidae, hace evidente la necesidad de realizar estudios sobre este grupo. Como ejemplo tenemos a *Scotinella* Banks, 1911, uno de los géneros mejor conocidos en cuanto a su taxonomía (World Spider Catalog 2019), pero del cual no se ha estudiado su comportamiento reproductor, cortejo, oviposición u otro comportamiento para alguna de sus especies (Penniman 1985).

Por lo anterior se hace evidente la necesidad de indagar más acerca de la taxonomía y biología de las arañas de la familia Phrurolithidae en el Volcán Tacaná.

OBJETIVO GENERAL

- Caracterizar la identidad taxonómica y estudiar aspectos de la historia de vida de dos especies de arañas de la familia Phrurolithidae que residen en el Volcán Tacaná en Chiapas, México.

Objetivos específicos

- Describir, ilustrar y comparar los caracteres morfológicos de las dos especies de Phrurolithidae del Volcán Tacaná.
- Analizar, a través de sus caracteres morfológicos, las relaciones taxonómicas que sostienen estas especies con otras de la familia Phrurolithidae en Norteamérica.
- Describir el ciclo de vida de las dos especies de Phrurolithidae (número de estadios para alcanzar la madurez y su duración bajo condiciones de laboratorio).
- Determinar aspectos relativos a la reproducción relacionados con los ovisacos, el número de huevos, tiempo de gestación y cuidado maternal.

MÉTODOS

Sitios de estudio

Las recolectas de especímenes se llevaron a cabo en los dos sitios donde fueron localizadas previamente las arañas, ambos sitios están ubicados en las faldas del Volcán Tacaná (Figura 1). El primer sitio es un remanente de bosque mesófilo de montaña localizado en el ejido Talquián en el municipio de Unión Juárez ($15^{\circ}05'14.8''$ N y $92^{\circ}05'55''$ O, entre los 2021–2048 m de altitud). El tipo de clima del municipio es semicálido húmedo a templado húmedo con abundantes lluvias en verano, con temperatura media anual de 20.9 °C (rango de 14.5 – 27.4 °C) y una precipitación anual de 3,565.5 mm acorde a la estación más cercana (estación 7146; INEGI 2019). El segundo sitio es un cafetal de

sombra localizado en la comunidad de Alpujarras en el municipio de Cacahoatán ($15^{\circ}4'20.76''$ N y $92^{\circ}9'57''$ O, entre los 922–1069 m de altitud). El tipo de clima del municipio es cálido húmedo a templado húmedo con abundantes lluvias en verano, con temperatura media anual de 24.8 °C (rango de 17.5 – 32 °C) y una precipitación anual de 4,423.8 mm acorde a la estación más cercana (estación 7172; INEGI 2019).

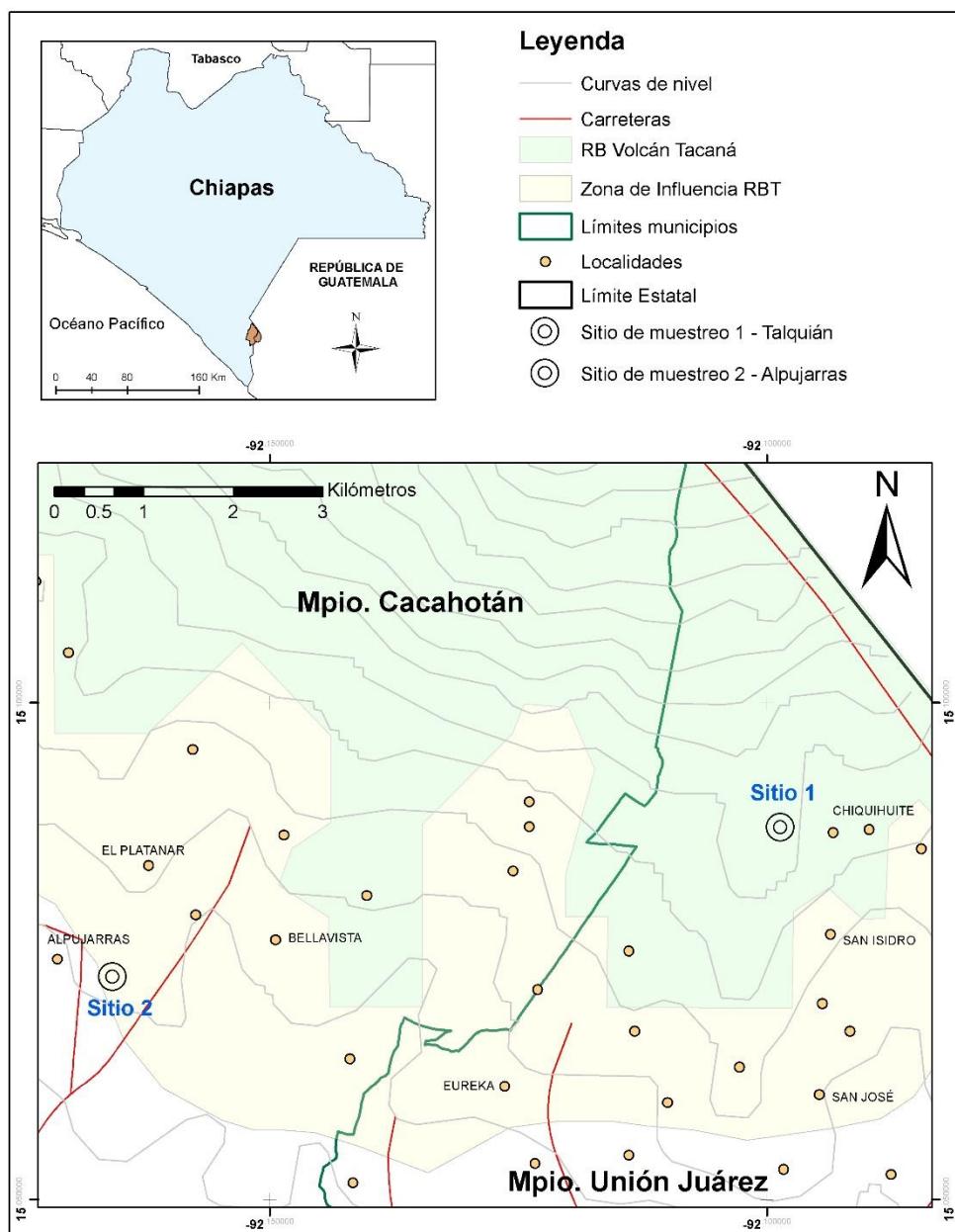


Figura 1. Ubicación de los sitios donde se han registrado previamente a las especies de “*Piabuna*” spp. (Phrurolithidae). Sitio 1, Talquián, Mpio. Unión Juárez; Sitio 2, Alpujarras, Mpio. Cacahoatán.

Revisión taxonómica

Se revisó el material depositado en la Colección de Arácnidos del Sureste de México (ECOTAAR) de El Colegio de la Frontera Sur (ECOSUR), Tapachula, Chiapas, México. Además, se solicitaron en préstamo ejemplares de las siguientes colecciones: Colección Nacional de Arácnidos de la Universidad Nacional Autónoma de México, Ciudad de México (CNAN); Colección de Arácnidos del Centro de Investigaciones Biológicas del Noroeste, Baja California Sur (CARCIB), Colección del Laboratorio de Aracnología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México (CAFC-UNAM), Colección de Arácnidos del Estado de México, Universidad Autónoma del Estado de México, Estado de México (UAMEX), Laboratorio de Sistemática Animal, Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo de Hidalgo (UAEH).

El trabajo taxonómico consistió en la toma de medidas de diferentes partes del cuerpo, registro de caracteres de interés para la diferenciación entre las especies en estudio y las especies previamente descritas de los géneros considerados como relacionados, adquisición de fotografías y la elaboración de ilustraciones de las características distintivas de los adultos de cada sexo y su correspondiente descripción. Las observaciones morfológicas, medidas, dibujos y fotografías se realizaron con un microscopio estereoscópico Nikon SMZ 1500, provisto con una cámara digital Nikon D5200 y micrómetro ocular. Se tomaron fotografías en diferentes planos focales de las diferentes estructuras de los especímenes y se combinaron con Helicon Focus versión 6.7.1 (<http://www.heliconsoft.com/heliconsoft-products/helicon-focus/>), un software de apilado de imágenes para producir imágenes con mejor profundidad de campo. Las imágenes fueron editadas con Adobe Photoshop CC para producir las ilustraciones finales. Además, se tomaron fotografías de estructuras importantes mediante un microscopio electrónico de barrido (MEB) marca TOPCON modelo SM-510 de El Colegio

de la Frontera Sur. Para ello, los especímenes seleccionados fueron deshidratados en series de alcohol y secados con hexametildisilazano, después fueron montados en cilindros de aluminio y recubiertos con oro-paladio para su observación.

Las comparaciones taxonómicas se sustentaron principalmente en la forma y arreglo de las estructuras que componen el aparato genital de ambos sexos y otras estructuras relacionadas. Adicionalmente, se tomaron medidas de los ojos (amplitud de las filas, diámetro y separación), altura del clípeo, la longitud de los artejos de las patas (fémur, patela, tibia, metatarso y tarso), finalmente la longitud y anchura del prosoma y opistosoma. Se contabilizó el número de macrosetas y la disposición de éstas en las patas I y II, siguiendo la terminología de Jin et al. (2016). Toda la información anterior se utilizó para la elaboración de las descripciones de las especies y el análisis de las relaciones taxonómicas con otras especies del género *Piabuna* y *Phonotimpus*.

Captura de ejemplares y mantenimiento en laboratorio

Para el estudio de la historia de vida, se recolectaron periódicamente individuos de las dos especies de arañas en los sitios donde fueron previamente registrados (Chamé-Vázquez 2011; 2015). La búsqueda se realizó manualmente mediante la revisión de la hojarasca *in situ* con ayuda de una manta de color blanco y la captura con aspiradores bucales. Adicionalmente a las recolectas directas, también se llevaron 10 muestras de hojarasca al laboratorio, en donde se revisaron posteriormente el mismo día para continuar la búsqueda de arañas.

Todas las arañas capturadas fueron alojadas individualmente en pequeños contenedores de plástico de 9 x 9 x 7 cm (jaulas) y mantenidas en condiciones de laboratorio ($26 \pm 1.3^\circ\text{C}$, $57 \pm 4.3\%$ de humedad relativa y un régimen de 12 horas luz: 12 horas oscuridad). El fondo de las jaulas consistió en una capa de yeso con carbón activado de 0.5–1 cm de profundidad para mantener la humedad, para lo cual fue asperjado con agua regularmente. Se agregaron fragmentos de viales o popotes transparentes como elementos en donde las arañas pudiesen resguardarse, construir un refugio o como soporte para cuando realizaron la muda.

Alimentación y ciclo de vida

Todas las arañas se alimentaron con una dieta de cinco colémbolos (*Collembola*) dos veces por semana. A la par de la alimentación, se llevó un registro de la fecha de muda de cada uno de los individuos recolectados, la exuvia se retiró y se guardó en un vial con su respectiva etiqueta. La información anterior nos ayudó a determinar el número de estadios, el tiempo promedio entre cada estadio y el tiempo acumulado promedio que necesitó un individuo para alcanzar la madurez (por sexo/especie).

Reproducción

Periódicamente se realizaron observaciones para registrar las posturas (número de ovisacos y frecuencia de elaboración). Se describió la forma y el tamaño del ovisaco y se disecaron para realizar el conteo del número total de huevos, el tamaño promedio de los huevos y el tiempo promedio que tardaron en emerger desde la postura. Finalmente, se hicieron anotaciones del comportamiento de la hembra después de la elaboración del ovisaco hasta la eclosión de la progenie para detectar el comportamiento de cuidado parental.

**CAPÍTULO II Redescription of *Phonotimpus separatus* Gertsch & Davis, 1940
(Araneae: Phrurolithidae) and description of two new species of *Phonotimpus*
from Mexico.** (Manuscrito publicado en Zootaxa).

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Redescription of *Phonotimpus separatus* Gertsch & Davis, 1940 (Araneae: Phrurolithidae) and description of two new species of *Phonotimpus* from Mexico

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Abstract

The female of *Phonotimpus separatus* Gertsch & Davis (the type species of the genus) is redescribed from a specimen collected at the type locality, and two new species of *Phonotimpus* from Mexico are described: *P. pennimani* sp. nov. and *P. talquian* sp. nov. A more detailed description of *P. separatus* is provided to better distinguish them from related taxa. The two new species are closely related; males and females of both species share several somatic and genitalic characters not found in *P. separatus*. The resemblance of both new species to *P. separatus* is discussed.

Key words: spiders, neotropical, *Piabuna*, Chiapas, Tacana volcano, taxonomy

Resumen

Se redescribe a la hembra de *Phonotimpus separatus* Gertsch & Davis (la especie tipo de este género) a partir de un espécimen colectado en la localidad tipo y se describen dos especies nuevas de *Phonotimpus* de México: *P. pennimani* sp. nov. y *P. talquian* sp. nov. Se proporciona una descripción más detallada de *P. separatus* para apoyar mejor su discriminación con los taxa relacionados. Las dos nuevas especies están estrechamente relacionadas entre sí, machos y hembras de ambas especies comparten varios caracteres somáticos y de genitalia que no se encuentran en *P. separatus*. Finalmente, se discute la semejanza de las dos nuevas especies con *P. separatus*.

Palabras clave: arañas, neotrópico, *Piabuna*, Chiapas, Volcán Tacaná, taxonomía.

Introduction

Phrurolithidae is a relatively small family with 13 genera and 203 species, of which seven genera are known from America: *Drassabella* Banks, *Phonotimpus* Gertsch & Davis, *Phrurolithus* C. L. Koch, *Phrurolinellus* Chamberlin, *Phrurotimpus* Chamberlin & Ivie, *Piabuna* Chamberlin & Ivie and *Scotinella* Banks (World Spider Catalog 2018). However, most of the American species are poorly known (i.e. very brief descriptions or only known from one sex) and some of them are misplaced (Penniman 1978; Dondale & Redner 1982; Platnick & Ubick 1989).

The genus *Phonotimpus* has two species, *P. separatus* Gertsch & Davis, 1940 (the genotype) and *P. eutypus* Gertsch & Davis, 1940. Both are endemic to Mexico and were described by Gertsch & Davis (1940), only from female specimens. Those authors did not give a proper diagnosis, but they emphasized that *Phonotimpus* “is distinct from *Phrurotimpus* only in the eye relations and type of epigynum. The eyes of the second row are gently recurved and the medians are very much smaller than the lateral eyes”. According to Penniman (1985), the genera *Phonotimpus* and *Piabuna* form a monophyletic group (within his higher Phrurolithinae), because males of both genera share the presence of a dorsal tibial apophysis, although no males of *Phonotimpus* are formally described to date (but see Penniman 1985, fig. 26). Gertsch & Davis (1940) stated that the females of *P. separatus* and *P.*

eutypus have a dorsal scutum in the opisthosoma. Penniman (1985) corroborated that among the females of Phrurolithinae he examined, the dorsal scutum is found solely in *Phonotimpus* and in other three species of *Scotinella* (he did not specify which ones), whereas the females of *Piabuna* lack a dorsal scutum (Chamberlin & Ivie 1933, 1935; Gertsch & Davis 1940). Penniman (1985) also noted four other characters shared by the *Phonotimpus* species that he examined (two characters were previously observed by Gertsch & Davis): PER recurved, PME closer to PLE than to each other, PME smaller than PLE, and femur II with one prolateral macroseta.

We provide a redescription of the female of *P. separatus* based on a specimen collected at the type locality in San Luis Potosí, Mexico. Furthermore, through two spider inventories carried out in Chiapas, Mexico, we collected two species of Phrurolithidae that (based on Gertsch & Davis 1940 and Penniman 1985) can be assigned to *Phonotimpus*, but do not correspond with either of the described species in this genus; therefore, we describe two new species, *P. pennimani* sp. nov. and *P. talquian* sp. nov.

Material and methods

Specimens were examined and measured with an ocular micrometer under an Olympus SZX16 stereomicroscope. All measurements are in millimeters. Total body length is the sum of the carapace plus opisthosoma lengths. The eye sizes were measured as the maximum diameter seen from above. Leg measurements are noted as: total length (femur, patella, tibia, metatarsus, tarsus). Epigyna were cleared with 85% lactic acid. Color descriptions were based on specimens preserved in 96% ethanol. Photographs of habitus and epigyna were taken using a Nikon D5200 camera attached to a Nikon E400 compound microscope, then multiple focal planes were merged with Helicon Focus software ver. 6.7.1 (<http://www.heliconsoft.com/heliconsoft-products/helicon-focus/>) following the guidelines of the Alvarez-Padilla Laboratory (2017, microscopy methods). Scanning electron microscope (SEM) photographs were taken using a TOPCON SM-510 at El Colegio de la Frontera Sur, Tapachula. Before image acquisition, male and female body parts were dehydrated in an ethanol series, then dried to critical point, before being mounted on an aluminum stub and coated with gold/palladium.

Spine notation follows Jin *et al.* (2016) and general terminology follows Ramírez (2014). Abbreviations: A, atrium; AER, anterior eye row; ALE, anterior lateral eye; AME, anterior median eye; B, bursa; C, conductor; CD, copulatory duct; CO, copulatory opening; Cb, cymbium; DTA, dorsal tibial apophysis; E, embolus; EBP, embolar basal process; FD, fertilization duct; MF, median field of epigynum; MOA, median ocular area; PER, posterior eye row; PFS, prolateral femoral setae; PLE, posterior lateral eye; PME, posterior median eye; RFC, retrolateral femoral concavity; RTA, retrolateral tibial apophysis; S1, primary spermatheca; S2, secondary spermatheca; T, tegulum. Here, we used the term bursa for the membranous blind sac that originates from the copulatory duct, and we consider it homologous with the “globose membranous extension of proximal copulatory duct” of Ramírez (2014).

The examined specimens are deposited in the following collections (acronyms and curators in parentheses): Colección de Arácnidos del Sureste de México, Chiapas, Mexico (ECOTAAR, G. Ibarra-Núñez); Colección Nacional de Arácnidos at Universidad Nacional Autónoma de México, Ciudad de México, Mexico (CNAN, O.F. Francke); Colección de Arácnidos del Centro de Investigaciones Biológicas del Noroeste, Baja California Sur, Mexico (CARCIB, M.L. Jiménez) and American Museum of Natural History, New York, USA (AMNH, L. Prendini). The distribution map was generated with Simple Mappr (Shorthouse 2010).

Taxonomy

Phrurolithidae Banks, 1892

Phonotimpus Gertsch & Davis, 1940

Type species: *Phonotimpus separatus* Gertsch & Davis, 1940, by original designation.

Phonotimpus separatus Gertsch & Davis, 1940

Fig. 1

Note. Although the holotype of *Phonotimpus separatus* has not been examined by us, the studied specimen was collected at the type locality and is consistent with most of the descriptive characters provided by Gertsch & Davis (1940), including the illustration of the epigynum. Dr. N. Platnick (American Museum of Natural History, New York) compared our figures of *P. separatus* with the holotype specimen and confirmed that they are conspecific.

Material examined. MEXICO: San Luis Potosí, Municipio de Matlapa, 2.5 km N of Matlapa ($21^{\circ}21'39.5''N$ $98^{\circ}49'51.9''W$), 29 July 2017, in leaf litter, leg. J.F. Gómez, 1♀ (ECOTAAR-9018).

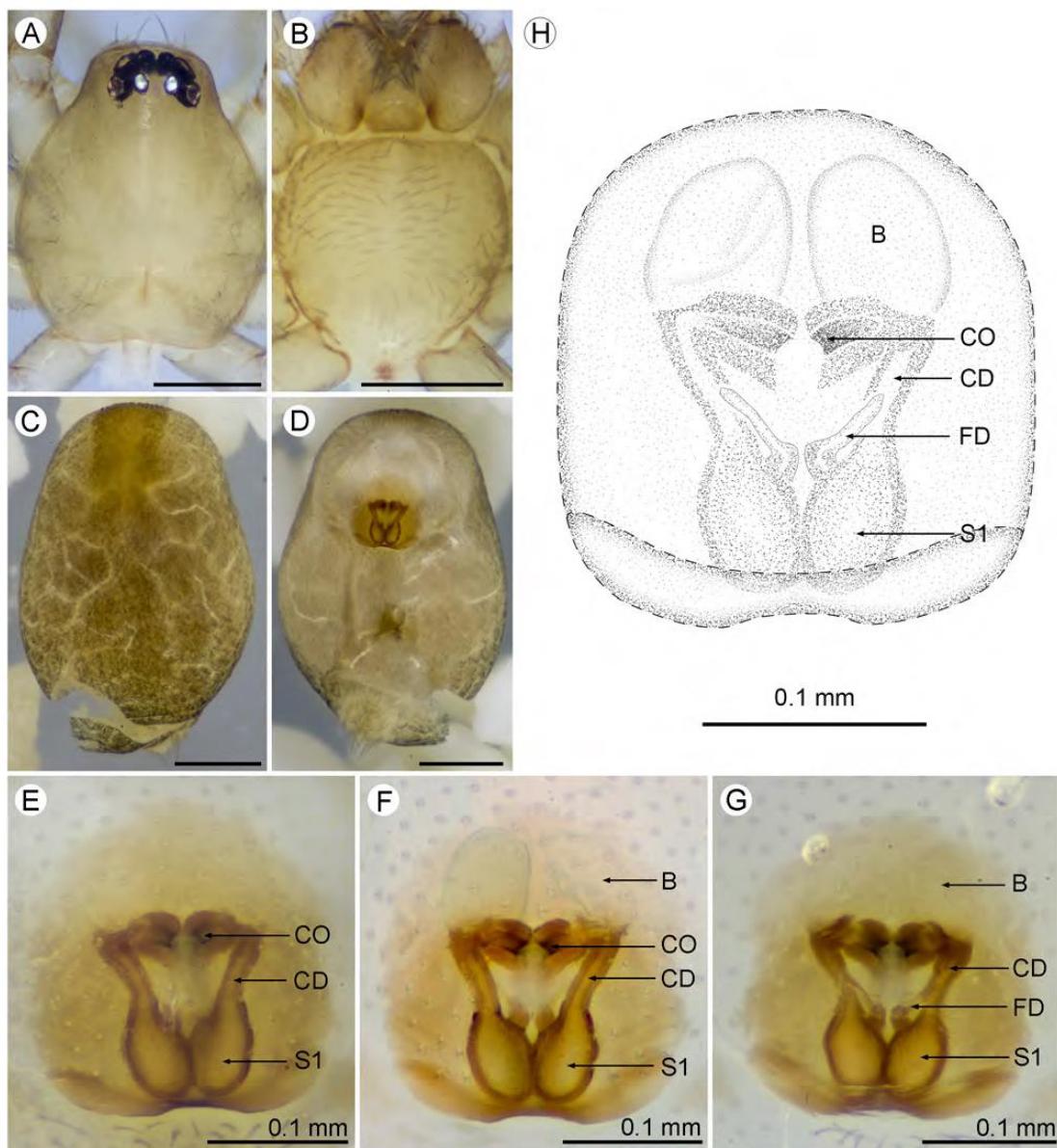


FIGURE 1. Female of *Phonotimpus separatus*. A, C Habitus, dorsal view; B, D Habitus, ventral view; E–H Epigyne, E Intact, ventral view, F Dissected, ventral view, G Dissected, dorsal view, H Dorsal view. Scale bars (A–D): 0.25 mm.

Diagnosis. *P. separatus* differs from *P. eutypus* by having only one small and very shallow atrium (Figs 1E–F), while *P. eutypus* has two separate slit-like atria (Gertsch & Davis 1940: fig. 27). The female of *P. separatus* differs from those of *P. pennimani* sp. nov. and *P. talquian* sp. nov. by having only one small and very shallow atrium, S1 posterior to CO, and FD that arise from the anterior part of the S1 (Figs 1E–H), the carapace that is slightly longer than wide, and the opisthosomal scutum that is narrow and short (Figs 1A, C), while *P. pennimani* sp. nov. and *P. talquian* sp. nov. have two large oval atria, the S1 lie ectal to the CD, the FD arise from the posterior part of the S1 (Figs 5A–D, 10A–D), the carapace is almost as wide as long, and the opisthosomal scutum is wider and longer (Figs 2C, 7C).

Description. Female. Carapace, labium, sternum, endites and all legs dull yellow; opisthosoma dusky-yellow, scutum yellowish (Figs 1A–D). Total length 1.64; carapace 0.68 long, 0.58 wide; opisthosoma 0.96 long, 0.68 wide. Carapace pear-shaped, fovea longitudinal. AER almost straight, PER recurved as seen from above. Eyes sizes and interdistances: AME 0.03, ALE 0.05, PME 0.03, PLE 0.05. AME-AME 0.01, AME-ALE touching, PME-PME 0.04, PME-PLE 0.02, ALE-PLE 0.01. MOA 0.10 long, front width 0.08, back width 0.10. Clypeus height 0.03. Paturon with two frontal spines, mesal one strong, ectal one smaller. Labium slightly wider than long (0.11/0.08), endites longer than wide (0.20/0.13), sternum slightly longer than wide (0.43/0.41). Opisthosoma oval, with dorsal scutum narrow and small, covering 1/3 of the opisthosoma. Leg measurements: I 2.14 (0.59, 0.23, 0.55, 0.50, 0.27), II 1.81 (0.50, 0.22, 0.40, 0.41, 0.28), III 1.67 (0.45, 0.19, 0.31, 0.42, 0.30), IV 2.32 (0.62, 0.21, 0.52, 0.60, 0.37). Leg formula 4123. Leg spination: femur I with 2 prolateral spines in distal half; right tibia I with 6 pairs of ventral spines but left tibia I lacks 1 retroventral spine; metatarsus I with 4 proventral spines and 3 retroventral spines. Femur II with 1 prolateral spine in distal half; tibia II with 5 proventral and 4 retroventral spines; metatarsus II with 4 proventral spines and 2 retroventral spines; left femur IV with one dorso-basal macroseta but right femur IV without such spine; metatarsus III with some distal setae, forming a kind of preening comb. Palpus: femur with one dorso-distal spine, patella with one prolateral spine on its basal half, tibia with one dorso-basal, one dorso-distal and one prolateral-basal spine; with ventral patch of setae on tarsus and small claw. Epigynum: CO opposite one another, sharing single small and shallow atrium (Figs 1E–F), oval B bigger than S1; egg-shaped S1 lie posterior to CO (Figs 1F, 1H). In dorsal view, B arise near to CO; FD arise from mesal side of anterior part of S1 (Figs 1G–H).

Taxonomic notes. Gertsch & Davis (1940: 21) stated about *P. separatus* “The atriobursal orifices are widely separated whereas in *eutypus* they are closely approximated.” The examination of the specimen described here show that they confused the bursae (visible through the integument) with the copulatory openings. They also stated about the PER in this genus (1940: 20) “In *P. separatus* the median eyes are much nearer the laterals but in *P. eutypus* the four posterior eyes are subequidistantly spaced”, Dr. N. Platnick (who examined both holotypes) informed us that this is also inaccurate, as *P. eutypus* has the same eye pattern as *P. separatus*.

Habitat. Gertsch & Davis (1940) did not give information about the habitat. The specimen described here was collected from leaf litter from a secondary vegetation forest, near to maize crops.

Distribution. The female described by Gertsch & Davis (1940) was found “5 miles north Tamazunchale”; the town of Matlapa is located about 8 km north (5 miles) of Tamazunchale; therefore, this corresponds to the area of the type locality (Fig. 12).

Phonotimpus pennimani sp. nov.

Figs 2–6

Type material. Holotype ♂: MEXICO: Chiapas, Municipio de Cacahoatán, Ejido Alpujarras (15°4'20.76"N, 92°9'57.00"W, 922 m), 21 April 2016, in leaf litter of shade-grown coffee, leg. D. Chamé, E. Chamé, H. Montaño, G. Suárez (ECOTAAR-9000).

Allotype ♀: same data except 15 March 2016 (ECOTAAR-8999).

Paratypes: 1♂, same data except 16 May 2016 (CNAN-T1214); 1♀, same data except 22 June 2016 (CNAN-T1213); 1♂, 1♀, same data except 16 May 2016 (AMNH); 1♀, same data except 18 May 2016 (CARCIB-205); 1♂, same data except 13 March 2017, leg. G. Angulo, D. Chamé, H. Montaño (CARCIB-206); 1♀, same data except 13 April 2016, leg. D. Chamé, E. Chamé, H. Montaño, G. Suárez (ECOTAAR-9001); 1♂, same data except 16 May 2016 (ECOTAAR-9003); 1♀, same data except 20 June 2016 (ECOTAAR-9005); 1♂, 1♀, same data

except 13 March 2017, leg. G. Angulo, D. Chamé, H. Montaño (ECOTAAR-9006); 2♀, 3 juv., same data except 24 March 2014, leg. D. Chamé, H. Montaño, E. Chamé (ECOTAAR-8996); 3♀, 1 juv., same data except 12 August 2014 (ECOTAAR-8998).

Etymology. The specific epithet is a patronym in honor of Dr. Andrew J. Penniman (U.S.A.), who studied the genus *Scotinella* and improved the knowledge of North American phrurolithids.

Diagnosis. The females of *P. pennimani* sp. nov. differ from *P. eutypus* by having two oval atria (Fig. 5A) and the dorsal scutum is long and wide (Fig. 2C), while *P. eutypus* has two slit-like atria (Gertsch & Davis 1940: fig. 27) and the dorsal scutum covers only the base of the opisthosoma. The females of *P. pennimani* sp. nov. differ from *P. separatus* by having two large atria, S1 ectal to the CD, FD arising from the posterior part of the S1 (Figs 5A–D), the carapace that is almost as wide as long, and the opisthosomal scutum that is wide and long (Fig. 2C), while in *P. separatus* there is only one small atrium, S1 lie posterior to the CD, FD arise from the anterior part of the S1 (Figs 1E–H), the carapace is slightly longer than wide, and the opisthosomal scutum is narrow and short (Figs 1A, C). The females of *P. pennimani* sp. nov. differ from *P. talquian* sp. nov. by having two shallow epigynal atria (Fig. 5A), with the CO visible in ventral view (Figs 5A, 5C, 6C), oval S1, and by the apparent absence of S2 (Fig. 5B), while in *P. talquian* sp. nov. the epigynal atria are deeper, with the CO not visible in ventral view (Figs 10A, 10C, 11C), the S1 are liver-shaped, and by the presence of small S2 (Figs 10B, 10D). The males of *P. pennimani* sp. nov. differ from *P. talquian* sp. nov. by having a conical RTA with its tip very slender (thread-like, Figs 3A, 4A), by the shape of the DTA, finger-like when seen dorsally (Fig. 4B), and by the C tip widened in ventral view (Fig. 3B), while in *P. talquian* sp. nov. the RTA is tapering but the tip is not thread-like (Figs 8A, 9A), DTA in dorsal view is S-shaped (Figs 9B), and the C is not noticeably widened distally (Fig. 8B).

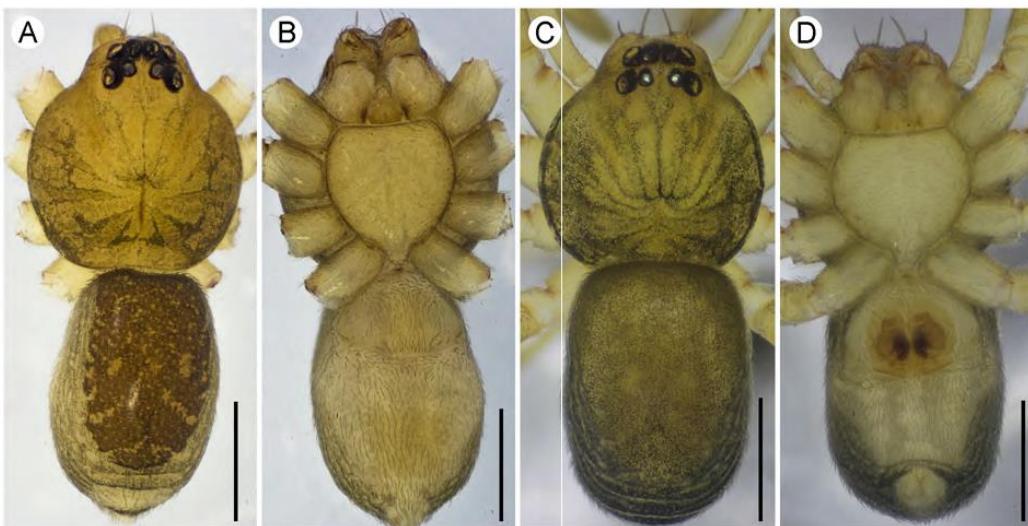


FIGURE 2. *Phonotimpus pennimani* sp. nov. A Male habitus, dorsal view; B Male habitus, ventral view; C Female habitus, dorsal view; D Female habitus, ventral view. Scale bars: 0.5 mm.

Description. Male holotype. Carapace and chelicerae yellowish-brown, with dark grey markings, labium, endites and sternum yellowish. Legs yellowish, with sparse dusky mottling. Dorsum of opisthosoma dark grey, with sparse pale-yellow spots and bright brown scutum. Venter pale yellow, bordered laterally with dark grey (Figs 2A–B). Total length 2.13; carapace 1.01 long, 0.90 wide; opisthosoma 1.12 long, 0.73 wide. Carapace, AER and PER as in *P. separatus*, except carapace almost as wide as long. Eye sizes and interdistances: AME 0.07, ALE 0.07, PME 0.05, PLE 0.07. AME-AME 0.02, AME-ALE 0.01, PME-PME 0.08, PME-PLE 0.03, ALE-PLE 0.05. MOA 0.17 long, front width 0.15, back width 0.20. Clypeus height 0.09. Chelicerae with 2 promarginal teeth separated by roughly two times base width of tooth; retromargin with two teeth, proximal tooth slightly larger than distal one. Frontal spines on paturon as in *P. separatus*. Labium wider than long (0.15/0.11), endites longer than wide (0.33/0.21), sternum about as long as wide (0.57/0.58). Opisthosoma oval, with dorsal scutum covering 3/4 of the opisthosoma length. Leg measurements: I 3.87 (1.00, 0.36, 1.06, 0.98, 0.47), II 3.10 (0.84, 0.33, 0.73, 0.74, 0.46),

III 2.84 (0.77, 0.30, 0.57, 0.75, 0.45), IV 3.92 (1.03, 0.32, 0.87, 1.08, 0.61). Leg spination: femur I with 2 prolateral spines in distal half; tibia I with 6 pairs of ventral spines; metatarsus I with 4 proventral spines and 3 retroventral spines. Femur II with 1 prolateral spine in distal half; tibia II with 5 pairs of ventral spines; metatarsus II with 4 proventral spines and 3 retroventral spines. Femora without dorsal macrosetae. Tarsal claw pectinate, onychium with pair of dorsal tactile hairs (Fig. 6D). Tarsal organ capsulate, with oval opening (Figs 4C–F). Palpus: femur with one dorso-distal spine, with central, broad and shallow depression on ectal side, with cluster of setae on mesal side (Figs 3C–D) and inconspicuous ventral apophysis perceived as slight swelling between the setae and depression (Fig. 3C). RTA long and conical, with distal part thread-like, as seen retro-laterally (Figs 3A, 4A). DTA tapering in lateral view, with its tip blunt (Fig. 3A), finger-like, directed towards ectal side in dorsal view (Fig. 4B). Cb with few short and thick setae on dorsal side and longitudinal narrow area without setae in its basal half (Fig. 4B). T large, protruding ectally at its proximal side (Figs 3B, 4A). E, EBP and C similar in length (Figs 6A–B). C with its tip widened and covering tips of E and EBP in ventral view (Fig. 3B).

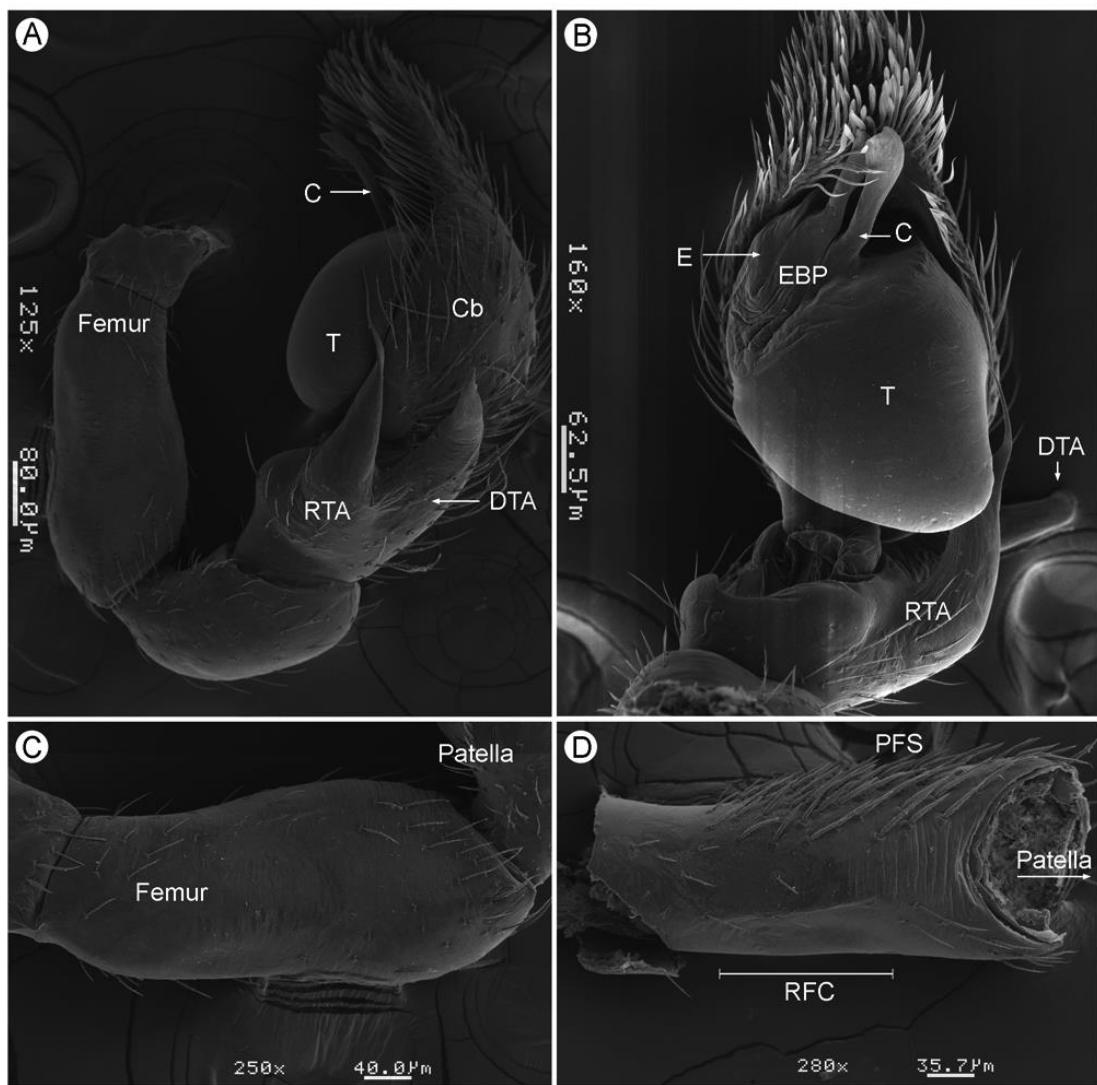


FIGURE 3. *Phonetimpus pennimani* sp. nov. A Left male palpus, retrolateral view; B Left male palpus, ventral view; C Left male palpus femur, retrolateral view; D Left male palpus femur, ventral view.

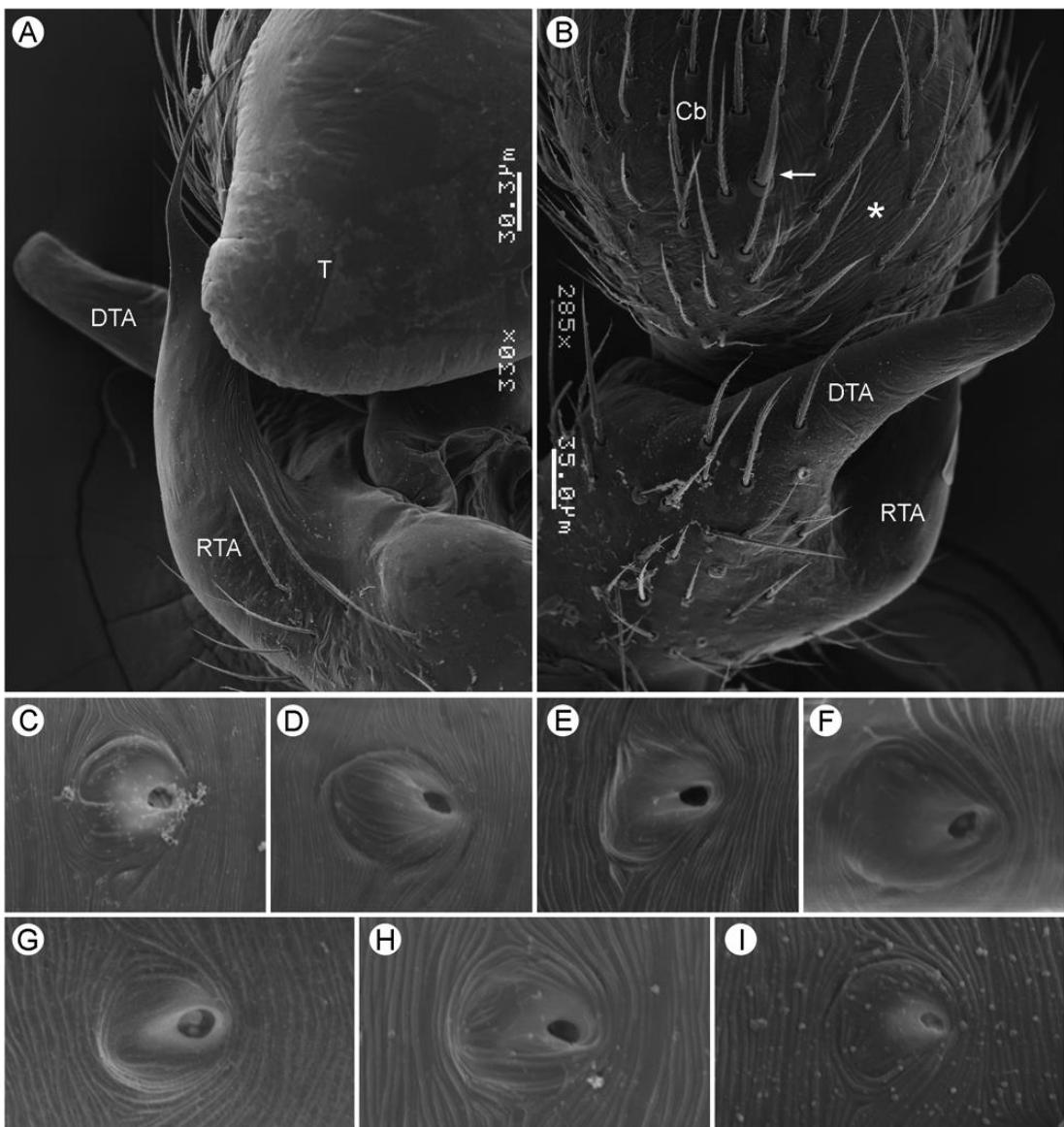


FIGURE 4. *Phonotimpus pennimani* sp. nov. A Right male palpus, RTA and DTA, ventral view; B Right male palpus, RTA and DTA, dorsal view (asterisk on a narrow area without setae in its basal half); C Male tarsal organ, leg I; D Male tarsal organ, leg II; E Male tarsal organ, leg III; F Male tarsal organ, leg IV; G Female tarsal organ, leg I; H Female tarsal organ, leg II; I Female tarsal organ, leg III.

Female allotype. Coloration similar to male, except thoracic region bordered with dark grey. Chelicerae yellowish, splattered with dark grey (Figs 2C–D). Total length 2.07; carapace 0.96 long, 0.91 wide, opisthosoma 1.11 long, 0.72 wide. Carapace, AER and PER as in male. Eye sizes and interdistances: AME 0.06, ALE 0.07, PME 0.05, PLE 0.07. AME-AME 0.03, AME-ALE 0.01, PME-PME 0.07, PME-PLE 0.03, ALE-PLE 0.06. MOA 0.17 long, front width 0.14, back width 0.18. Clypeus height 0.09. Cheliceral teeth and frontal spines on paturon as in male. Labium wider than long (0.15/0.10), endites longer than wide (0.27/0.18), sternum as long as wide (0.58/0.58). Dorsal scutum as in male. Legs measurements: I 3.77 (0.99, 0.38, 1.05, 0.93, 0.42), II 3.12 (0.83, 0.34, 0.76, 0.74, 0.45), III 2.77 (0.73, 0.31, 0.55, 0.73, 0.45), IV 3.87 (1.00, 0.34, 0.86, 1.06, 0.61). Leg formula and spination

as in male. Tarsal claw, onychium and tarsal organ (Figs 4G–I) as in male. Palpus: as in female of *P. separatus*, except tibia with one dorsal and one prolateral spine in its basal half, with small claw with few teeth. Epigynum: with two shallow atria separated by less than diameter of an atrium, depth of each atrium greater at CO, which are visible in ventral view (Figs 5A, 5C, 6C); B membranous, somewhat kidney-shaped in ventral view (Figs 5C, 6C). In dorsal view, oval S1 lie ectal to CD; B anterior to CO and slightly larger than S1 (Figs 5B, 5D); CD tube-like, slightly curved (Figs 5B, 5D); FD arise from mesal-posterior part of S1 (Fig. 5B).

Variation. Males (n=5) total length 1.93–2.27; carapace 0.95–0.97 long, 0.86–0.91 wide. The male scutum ranges from occupying roughly 3/5 to 4/5 of opisthosoma length. Females (n=11) total length 2.20–2.73; carapace 0.96–1.06 long, 0.85–0.97 wide. In females, the scutum ranges from almost 1/2 to 2/3 of the opisthosoma. Sometimes the same specimen (male or female) have one more or one less macrosetae on some of the anterior femora or metatarsi or both, but the leg in the opposite side has the number of macrosetae noted in the holotype. Some females have up to three slender white cream chevrons and one caudal spot above the anal tubercle.

Habitat. This species was collected from leaf litter in a shade-grown coffee plantation (*Coffea arabica* L.); the trees that provide shade are mostly *Inga* spp.

Distribution. Known only from the type locality in Chiapas, México (Fig. 12).

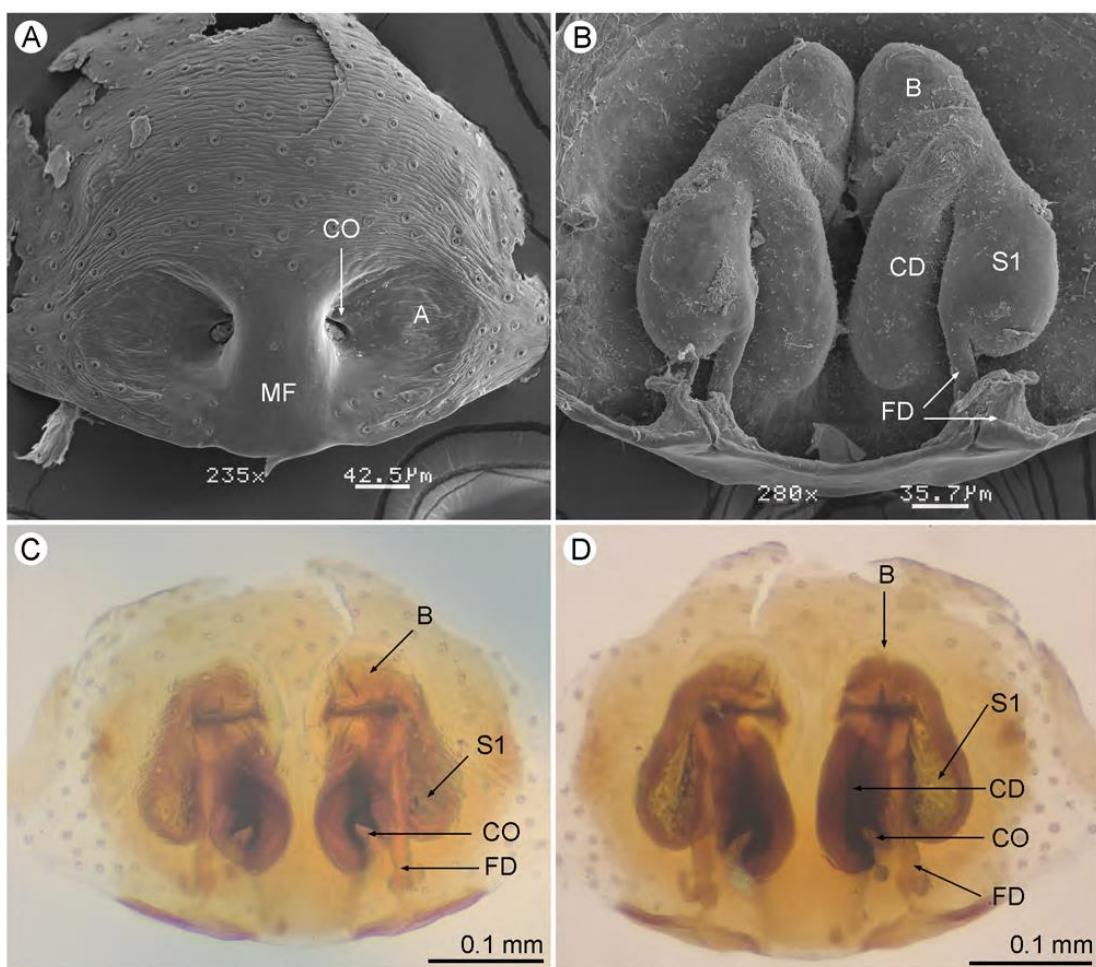


FIGURE 5. *Phonotimpus pennimani* sp. nov. A, C Epigynum, ventral view; B, D Epigynum, dorsal view.

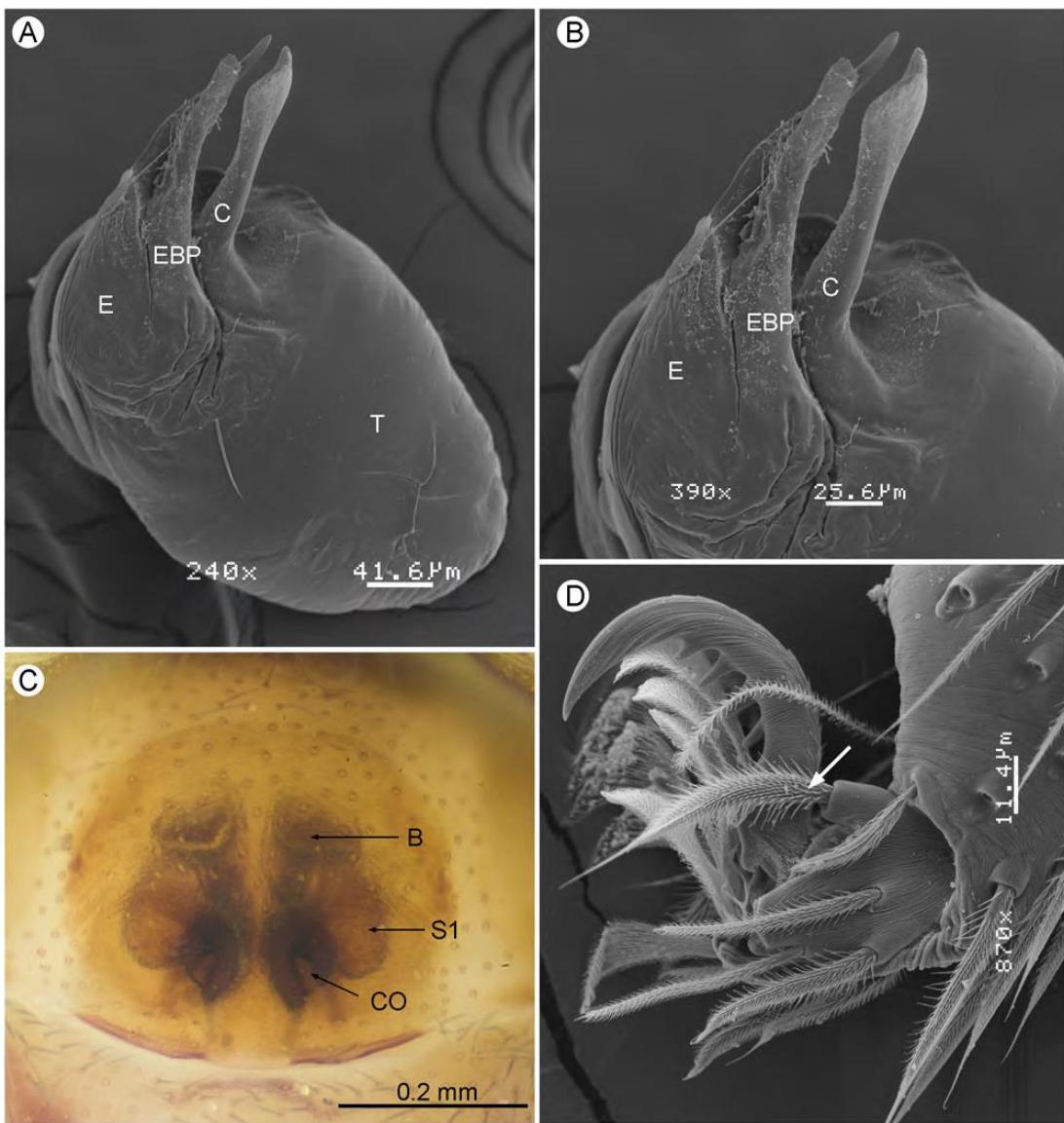


FIGURE 6. *Phonotimpus pennimani* sp. nov. A Left male palpus, apical-prolateral view of dissected bulb; B Left male palpus, apical-prolateral view of dissected bulb; C Epigynum intact, ventral view; D Left male tarsus IV, lateral view (arrow on tactile hair).

***Phonotimpus talquian* sp. nov.**

Figs 7–11

Piabuna sp1. Ibarra-Núñez et al. (2011): 1192, fig. 6a.

Type material. Holotype ♂: MEXICO: Chiapas, Municipio de Unión Juárez, Ejido Talquián ($15^{\circ}05'15.00''N$, $92^{\circ}05'56.00''W$, 2010 m), 10 March 2017, in leaf litter of cloud forest, leg. G. Angulo, D. Chamé, E. Chamé, H. Montaño, G. Suárez (ECOTAAR-8994).

Allotype ♀: same data except 7 March 2017 (ECOTAAR-8992).

Paratypes: 1♀, 1♂, same data as holotype (AMNH); 1♂, same data except 20 April 2016, D. Chamé, E. Chamé, H. Montaño, G. Suárez (CNAN-T1215); 1♀, same data except 25 May 2016 (CNAN-T1216); 1♂, same data except 20 April 2016 (CARCIB-208); 1♀, same data except 25 May 2016 (CARCIB-207); 2♂, same data except 23 February 2007, leg. D. Chamé, J.A. García (ECOTAAR-8225); 1♀, same data except 27 April 2007 (ECOTAAR-8251); 1♀, same data except 25 May 2007 (ECOTAAR-8267); 1♀, same data except (15°05'38.00"N, 92°06'06.00"W, 2044 m), 30 March 2007 (ECOTAAR-8244); 3♂, 3 juv., same data as holotype except 7 March 2017 (ECOTAAR-8993).

Etymology. The specific epithet is noun in apposition and refers to the type locality.

Diagnosis. The females of *P. talquian sp. nov.* differ from *P. eutypus* by having two oval atria (Fig. 10A) and the dorsal scutum covering more than half of the opisthosoma (Fig. 7C), while *P. eutypus* has two slit-like atria (Gertsch & Davis 1940, fig 27) and the dorsal scutum covers only the base of the opisthosoma. The females of *P. talquian sp. nov.* differ from *P. separatus* by having two large atria; S1 lie ectal to the CD, FD arise from the bottom of the S1 (Figs 10A–D), the carapace is almost as wide as long and the opisthosomal scutum is wide and long (Fig. 7C), while in *P. separatus* there is only one small atrium; S1 lie posterior to the CD, FD arise from the anterior part of the S1 (Figs 1E–H), the carapace is slightly longer than wide, and the opisthosomal scutum is narrow and short (Figs 1A, C). The females of *P. talquian sp. nov.* differ from *P. pennimani sp. nov.* by having an epigynum with deeper atria, CO not visible in ventral view (10A, 10C, 11C), S1 liver-shaped and with a small but evident S2 (Figs 10B, 10D), while in *P. pennimani sp. nov.* the atria are shallow, the CO visible in ventral view, the S1 oval, and they lack S2. Males differ from *P. pennimani sp. nov.* by the shape of the RTA, which is conical and tapering (Figs 8A, 9A), the DTA that is more slender than the RTA and S-shaped (Fig. 9B), and by the C with uniform width in ventral view (8B), while in *P. pennimani sp. nov.* the distal part of the RTA is very slender, the shape of DTA is finger-like and the C tip is clearly widened.

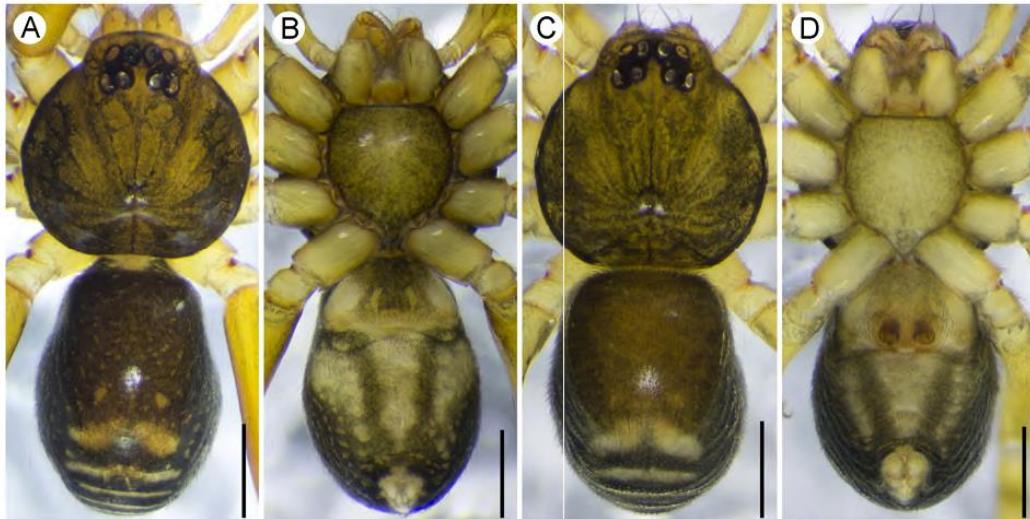


FIGURE 7. *Phonotimpus talquian sp. nov.* A Male habitus, dorsal view; B Male habitus, ventral view; C Female habitus, dorsal view; D Female habitus, ventral view. Scale bars: 0.5 mm.

Description. Male holotype. Carapace yellowish-brown, with black markings; endites and labium yellowish, sternum yellowish-brown. Legs yellowish splattered with dark markings, except metatarsi I–IV, which are lighter than other segments. Dorsum of opisthosoma black, with five clear chevrons decreasing in size near posterior margin, with bright dark brown scutum. Venter pale yellow, surrounded laterally with black and with two longitudinal black lines from epigastric furrow to spinnerets (Figs 7A–B). Total length 2.80; carapace 1.28 long, 1.22 wide; opisthosoma 1.52 long, 1.00 wide. Carapace, AER and PER as in *P. pennimani*. Eye sizes and interdistances: AME 0.08, ALE 0.10, PME 0.07, PLE 0.10. AME-AME 0.05, AME-ALE 0.01, PME-PME 0.11, PME-PLE 0.03, ALE-PLE 0.07. MOA 0.23 long, front width 0.21, back width 0.27. Clypeus height 0.09.

Chelicerae teeth as in *P. pennimani* sp. nov. and frontal spines on paturon as in *P. separatus*. Labium wider than long (0.19/0.13), endites longer than wide (0.37/0.25), sternum slightly longer than wide (0.79/0.71). Opisthosoma oval, with dorsal scutum covering 3/4 of the opisthosoma. Leg measurements: I 5.07 (1.33, 0.49, 1.41, 1.25, 0.59), II 4.25 (1.17, 0.47, 1.02, 0.99, 0.60), III 3.94 (1.07, 0.42, 0.81, 1.02, 0.62), IV 5.56 (1.47, 0.47, 1.27, 1.54, 0.81). Leg formula and spination: as in male of *P. pennimani* sp. nov. Tarsal claw, onychium and tarsal organ (Figs 9C–E) as in *P. pennimani* sp. nov. Palpus: femur with one dorso-distal spine, with a weak depression on distal third of ectal side, with cluster of setae on mesal side and inconspicuous ventral apophysis between those as a low ledge (Figs 8C–D). Patella with basal mesal spine. RTA long and tapering (Figs 8A, 9A), more sclerotized near the tip. DTA more slender than RTA, S-shaped in dorsal view (Figs 9B). Cb with few short thick setae on dorsal side (arrows in Figs 9A–B), bordering a longitudinal groove in its basal half (asterisk in Fig. 9A). T large, protruding ectally at its proximal side (Fig. 8B). Distal half of E and EBP hidden by C (Fig. 8B). E and C about same length, EBP pointed, slightly shorter than E, with some spines on its mesal side (arrows in Fig. 11B). Tip of C concave on its dorsal side (Fig. 11B).

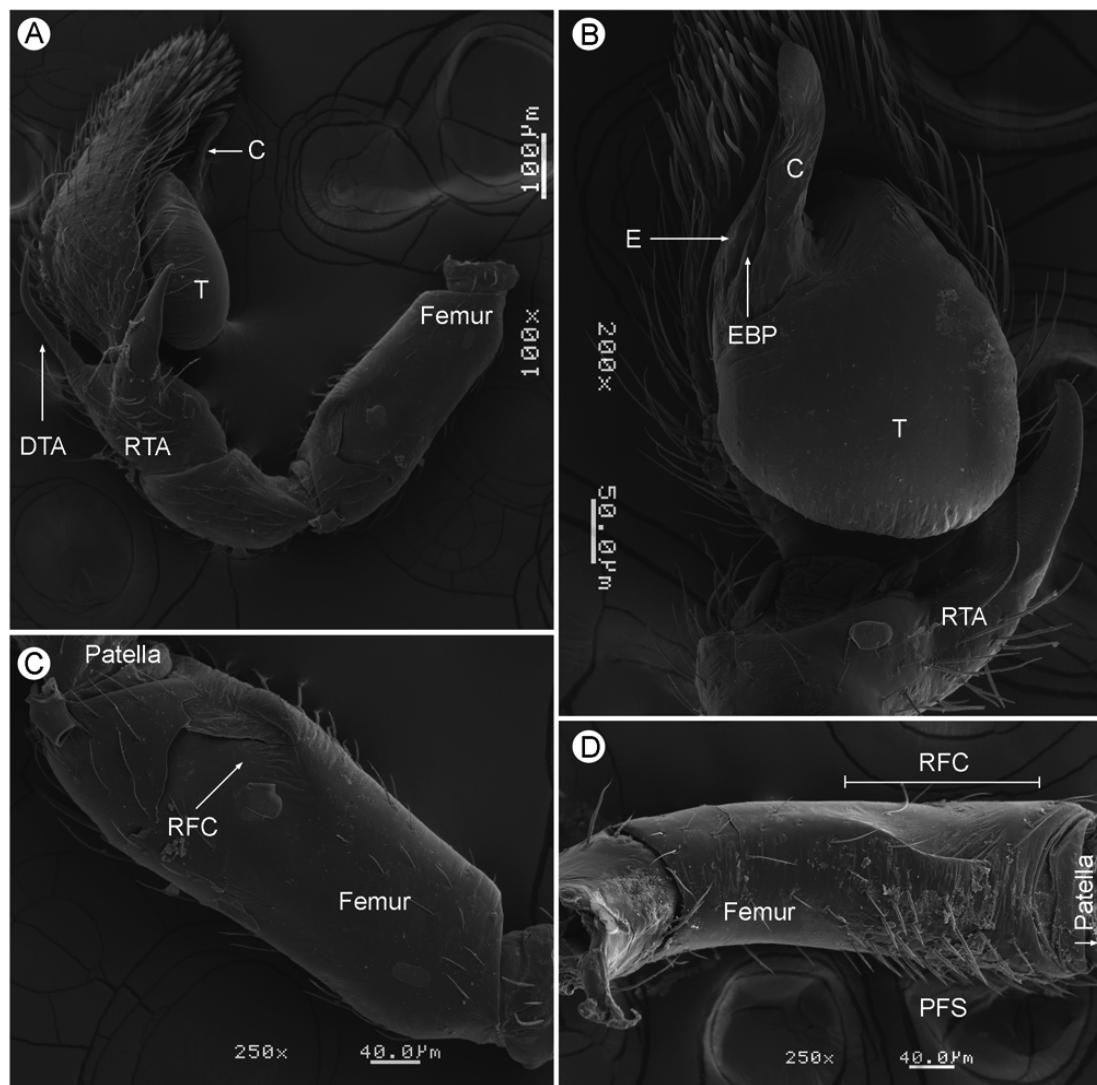


FIGURE 8. *Phonotimpus talquian* sp. nov. A Right male palpus, retrolateral view; B Left male palpus, ventral view; C Right male femur/patella, retrolateral view; D Same, ventral view.

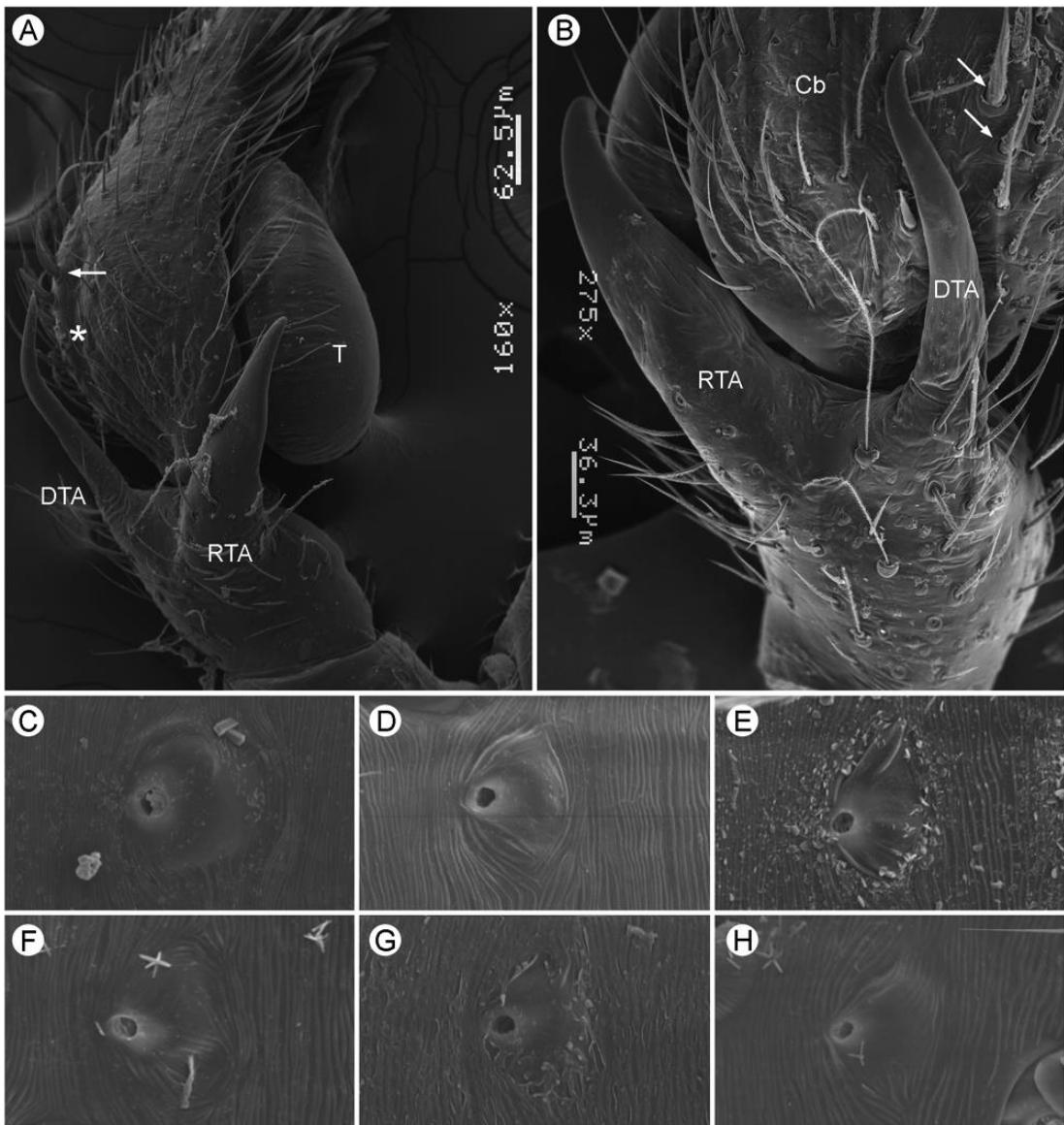


FIGURE 9. *Phonotimpus talquian* sp. nov. A Right male palpus, retrolateral view (arrow on short-thick seta, asterisk on groove of cymbium); B Left male palpus, RTA and DTA, dorsal view (arrows on short-thick setae); C Male tarsal organ, leg I; D Male tarsal organ, leg III; E Male tarsal organ, leg IV; F Female tarsal organ, leg II; G Female tarsal organ, leg III; H Female tarsal organ, leg IV.

Female allotype. Coloration similar to male, except thoracic region bordered with black (Figs 7C–D). Total length 2.78; carapace 1.28 long, 1.20 wide, opisthosoma 1.50 long, 1.00 wide. Carapace, AER and PER as in male. Eye sizes and interdistances: AME 0.08, ALE 0.07, PME 0.06, PLE 0.07. AME-AME 0.03, AME-ALE 0.01, PME-PME 0.10, PME-PLE 0.05, ALE-PLE 0.08. MOA 0.21 long, front width 0.20, back width 0.25. Clypeus height 0.09. Chelicerae teeth and frontal spines on paturon as in male. Labium wider than long (0.19/0.12), endites longer than wide (0.37/0.25), sternum longer than wide (0.78/0.69). Dorsal scutum covering slightly more than half of opisthosoma. Leg measurements: I 4.86 (1.30, 0.51, 1.36, 1.17, 0.52), II 4.06 (1.13, 0.46, 1.01, 0.93, 0.53), III 3.73 (1.01, 0.41, 0.76, 0.98, 0.57), IV 5.08 (1.33, 0.45, 1.20, 1.38, 0.72). Leg formula and spination as in male.

Tarsal organ (Figs 9F–H) and claw (Fig. 11D) as in *P. pennimani* sp. nov. Palpus: as in female of *P. pennimani* sp. nov. Epigynum: with pair of deep atria separated by roughly a diameter of an atrium, CO not visible in ventral view (Figs 10A, 10C, 11C); each atrium looks like an inverted cup (atrial hood) and is visible through integument (asterisk in Figs 10C, 11C). In dorsal view, S1 lie ectal to CD, liver-shaped and larger than S2 (Figs 10B, 10D). B membranous, oval-shaped, larger than S1 (Figs 10C–D). CO located deep on mesal side of atrial hood (Fig. 10D). FD arise from bottom of S1 (Figs 10B, 10D).

Variation. Males (n=8), total length 2.35–2.61; carapace 1.17–1.25 long, 0.98–1.17 wide. The male scutum ranges from occupying roughly 3/5 to 3/4 of opisthosoma length. Females (n=4), total length 2.97–3.37; carapace 1.27–1.42 long, 1.15–1.28 wide. In females, the scutum ranges from a half of the opisthosoma to slightly more. Some specimens have slightly different pigmentation on the opisthosoma venter: the pale-yellow lines between the black lines and black contour can be dotted, or the pair of black lines can be faded. As in *P. pennimani* sp. nov., some specimens of *P. talquian* sp. nov. have one more or one less macrosetae on the femur or metatarsus, or both, but the leg in the opposite side has the number of macrosetae noted in the holotype.

Habitat. All the specimens were captured in leaf litter of a montane cloud forest that is part of the Tacaná Volcano Biosphere Reserve.

Distribution. Known only from the type locality in Chiapas, México (Fig. 12).

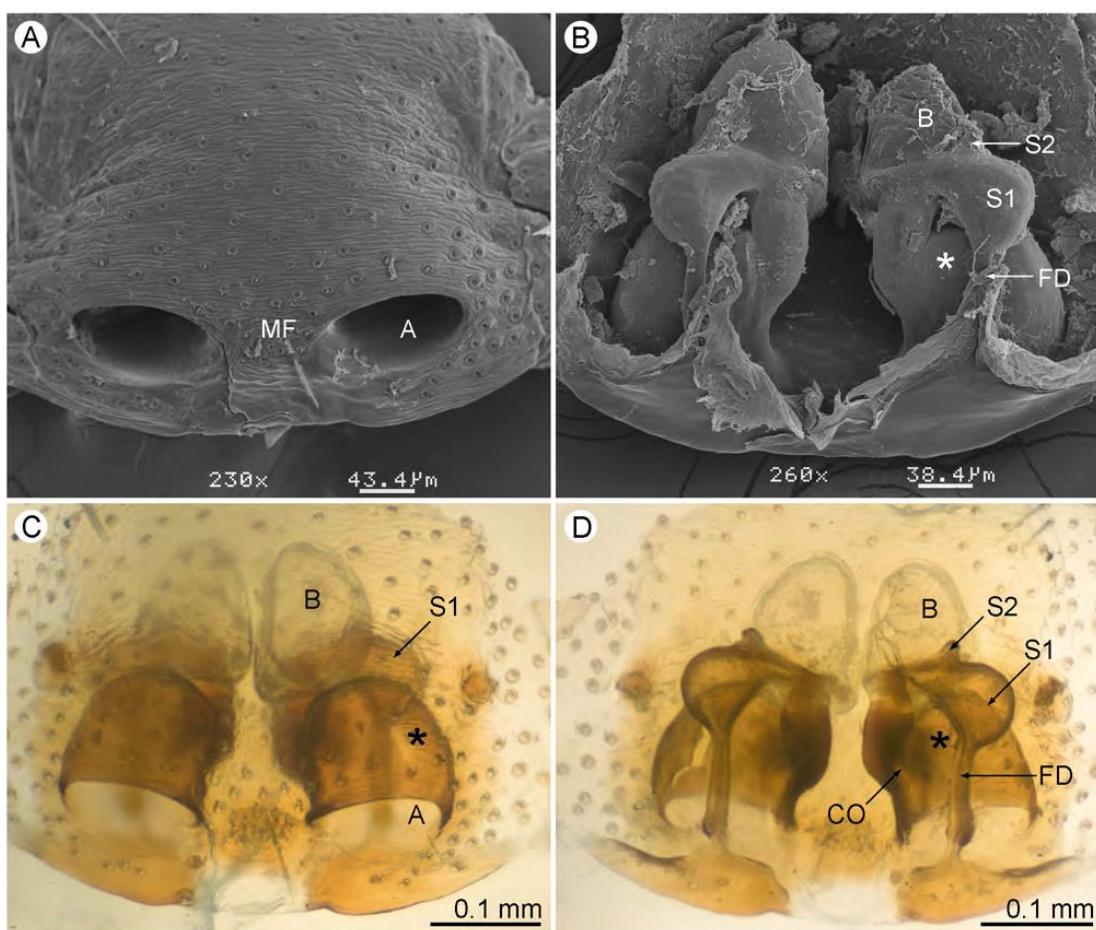


FIGURE 10. *Phonotimpus talquian* sp. nov. A, C Epigynum, ventral view; B, D Epigynum, dorsal view (asterisk on internal atrial hood).

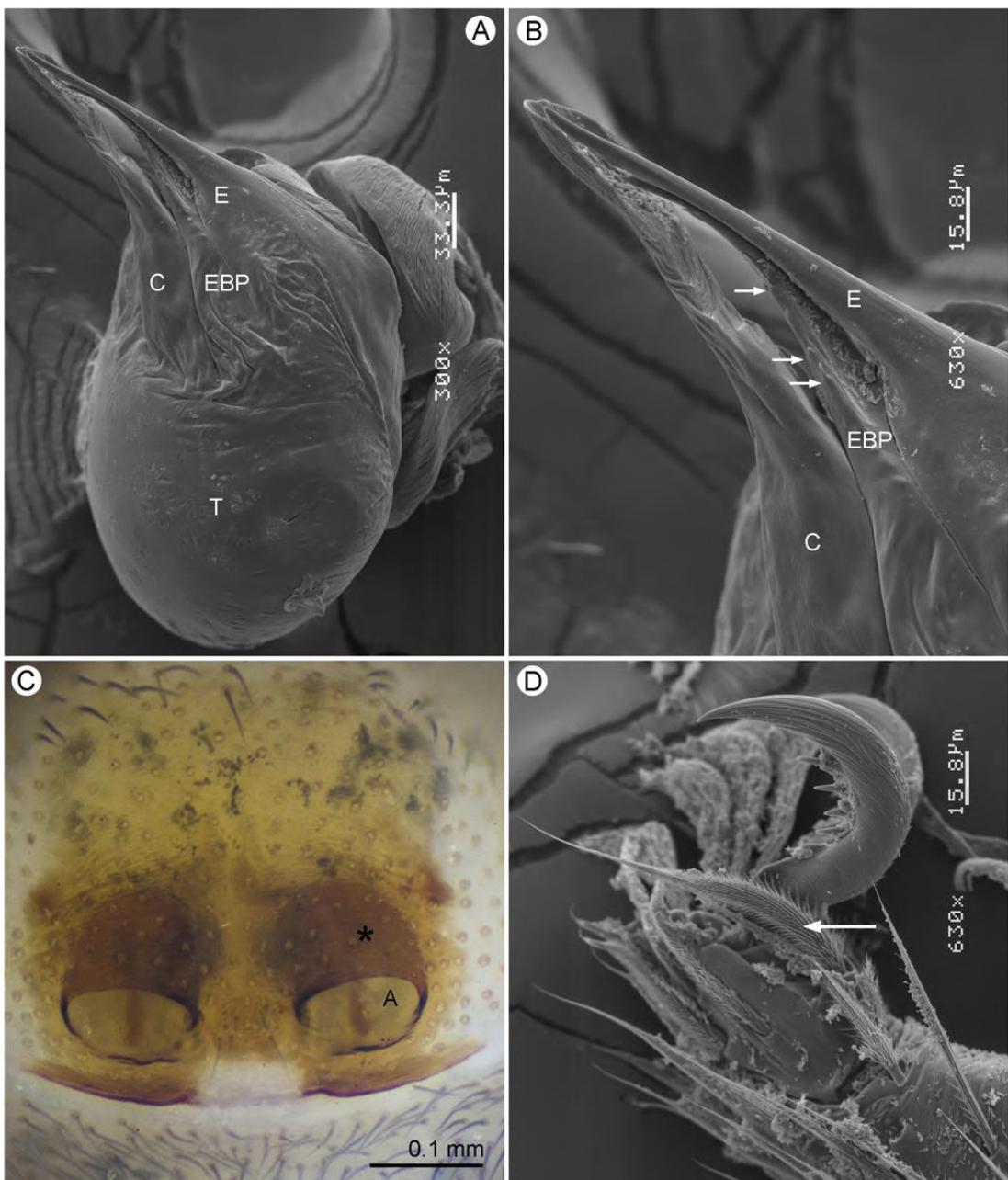


FIGURE 11. *Phonotimpus talquian* sp. nov. A Right male palpus, prolateral-apical view of dissected bulb; B Right male palpus, prolateral-apical view of dissected bulb (arrows on spines of EBP); C Epigynum intact, ventral view (asterisk on internal atrial hood); D Female left tarsus IV, lateral view (arrow on tactile hair).

Taxonomic comments

We place the two new species in the genus *Phonotimpus* based on the characters mentioned by Gertsch & Davis (1940) and Penniman (1985) for this genus: posterior eye sizes and their arrangement, the prolateral spine on

femora II, and the presence of a dorsal opisthosomal scutum in females. However, both new species described here share a set of characters that are different in *P. separatus*. The females of *P. pennimani* sp. nov. and *P. talquian* sp. nov. share the arrangement of the spermathecae, fertilization ducts, and bursae that differ clearly from those of *P. separatus*. In addition, both new species have a pair of oval atria near to the epigastric furrow. Gertsch & Davis (1940: 21) stated for *P. separatus* “the atrio-bursal orifices are widely separated whereas in *eutypus* they are closely approximated”. The epigynum of *P. separatus* illustrated here is similar to the drawing of Gertsch & Davis (compare Figs 1E–H vs Gertsch & Davis 1940: fig. 21). However, the interpretation made by them is partially inaccurate, because their “atrio-bursal orifices” are bursae and the copulatory openings are not widely separated. We assume the relatedness of *Phonotimpus* and *Piabuna*, following Penniman (1985), but he did not indicate which species of *Phonotimpus* he examined. Possibly both new species correspond to a distinct genus, but the lack of male descriptions and the absence of comprehensive diagnoses for the previously known species hinder us to elucidate the relationships among the species of *Phonotimpus*.



FIGURE 12. Distribution map of *Phonotimpus* spp.: Black square, *P. eutypus*; Black star, *P. separatus*; White triangle, *P. pennimani* sp. nov.; Black circle, *P. talquian* sp. nov.

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We thank G. Angulo, E.R. Chamé, H. Montaño and G.M. Suárez (ECOSUR) for their assistance in collecting spiders. R. Bautista and E.R. Chamé (ECOSUR) helped us with SEM images. Two anonymous reviewers, C. Haddad (subject editor of Zootaxa), A.L.J. Dor, L. Solís (ECOSUR) and especially N. Platnick (AMNH) contributed with valuable comments that helped improve this manuscript. N. Platnick kindly shared with us his observations on the types of *P. separatus* and *P. eutypus*. J.F. Gómez (Universidad Autónoma de San Luis Potosí) donated the specimen of *P. separatus*. Spiders were collected under government permits to G. Ibarra-Núñez (SGPA/DGVS/00034/09, SGPA/DGVS/00102/14 and SGPA/DGVS/05828/17). D. Chamé-Vázquez was supported by a graduate scholarship from Consejo Nacional de Ciencia y Tecnología (CONACYT).

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CAPITULO III. Life history of the neotropical spiders *Phonotimpus pennimani* and *P. talquian* (Araneae: Phrurolithidae). (Manuscrito sometido a Journal of Arachnology).



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**Life history of the neotropical spiders *Phonotimpus pennimani* and *P. talquian*
(Araneae: Phrurolithidae)**

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Abstract. *Phonotimpus pennimani* Chamé-Vázquez, Ibarra-Núñez & Jimenez, 2018 and *P. talquian* Chamé-Vázquez, Ibarra-Núñez & Jimenez, 2018 (Phrurolithidae) are two common spiders found in the leaf litter of tropical environments in Chiapas (Mexico), but little is known about their life history. Our research summarize field collecting and observations made with spiders reared under laboratory conditions. We found that juveniles and adults of both species co-occurred almost all the year in the field. This suggests that both species are eurychronous without a fixed period of reproduction, and several generations seem to overlap in the year. Females of both species are slightly larger than males, hence both species are sexually dimorphic. We observed that both species ambush and prey on springtails in the field and under laboratory conditions. First instars of *P. pennimani* are capable of subdue larger preys. Also, females of both species made a disk like egg sac and guarded it until emergence of their progeny, hence females of both species provide maternal care. *Phonotimpus pennimani* is an iteroparous species because the females laid up to four egg sacs. Juveniles and penultimate stages of both species usually made a retreat for the molting process. In addition, we observed the parasitism of a Scelionid wasp over eggs of *P. pennimani*.

Keywords: egg sac, ground spiders, maternal care, natural enemy, phenology.

Spiders are a megadiverse and abundant group of predators with over 48,000 species described (Wheeler et al. 2016; World Spider Catalog 2019). The order Araneae is one of the most important groups of natural enemies of arthropods because they kill an estimated of 400 to 800 million metric tons of preys per year (Nyffeler & Birkhofer 2017; Turnbull

1973). Moreover, spiders consume more preys in tropical than in temperate biomes, and the tropical spider biomass is roughly half of the estimated global spider biomass (Nyffeler & Birkhofer 2017). The importance of the spider over pest control in agroecosystems is controversial; some studies found that spiders suppress insect pest populations whereas other studies argued that spiders play a minor role as regulators (Riechert & Bishop 1990; Riechert 1999; Wise 1993). Nevertheless, they clearly play an important role in any terrestrial biome in terms of their diversity, abundance and biomass (Nyffeler & Birkhofer 2017; Wheeler et al. 2016).

Despite their importance, many spider families remain poorly studied. Moreover, for many of them all the information comes from the original taxonomic descriptions, which usually do not include data about their life history. Phrurolithids are small ground spiders that live under stones, fallen wood and leaf litter (Dondale & Redner 1982; Kaston 1948). These spiders eat springtails, booklice and true bugs (Angulo-Ordoñes et al. 2019; Pekár & Jarab 2011). The females build a scale-like egg sac, which is fastened to stones, and then they abandon it (Dondale & Redner 1982).

Phonotimpus Gertsch & Davis, 1940 is a small spider genus with distribution restricted to Mexico so far. Recently taxonomical studies described three new species from Mexico increasing the number of known species from two to five (World Spider Catalog 2019). However, no basic information about their life history was described for any of them. Recently, Angulo-Ordoñes et al. (2019) described the preference and predatory behavior of *Phonotimpus pennimani* and *P. talquian* Chamé-Vázquez, Ibarra-Núñez & Jimenez, 2018 under laboratory conditions. In this study, we obtained laboratory and field observations on the natural history of *P. pennimani* and *P. talquian*. We described the phenology, the egg

sac, the maternal care behavior and the retreat for molting of both species. Besides, we reported the interaction between a parasitoid wasp and *P. pennimani*.

METHODS

Studied species.—*Phonotimpus pennimani* and *P. talquian* are two small spiders (1.9–2.7 and 2.3–3.3 mm in total length, respectively), with allopatric geographic distributions in the southeast of Mexico (Chamé-Vázquez et al. 2018), and both species are considered the southernmost species of the genus *Phonotimpus* (World Spider Catalog 2019). *Phonotimpus pennimani* inhabits in leaf litter of shade coffee plantations at 920 m.a.s.l., whereas *P. talquian* inhabits in leaf litter of cloud forest at 2010 m.a.s.l. (Chamé-Vázquez et al. 2018). Both spiders are dominant species among the soil spider assemblages with high relative abundance (Chamé-Vázquez 2011; 2015).

Collection sites.—Samplings were carried out in the type localities of *P. pennimani* (Alpujarras 15°4'20.76"N, 92°9'57"W) and *P. talquian* (Talquián 15°05'15"N, 92°05'56"W); both sites are located in the slopes of Tacaná Volcano in Chiapas, Mexico.

Phenology.—In Talquián, samplings were made with 40 pitfall traps and 20 leaf litter samples (50 x 50 cm quadrat samples of leaf litter) per event. This site was bi-weekly sampled for December 2006-March 2007 (dry season) and April-May 2007 (rainy season). The spiders in Alpujarras were sampled with 20 pitfall traps and 12 leaf litter samples per event; this site was monthly sampled for February-March 2014 (dry season) and June and August 2014 (rainy season). The pitfall traps (10 cm in depth and 8 cm in diameter) were covered with a lid to exclude rain and litter; these traps were filled with a mixture of ethylene glycol and water, and all traps were removed after 72 hours. The spiders from leaf

litter samples were extracted with Berlese funnels for two or three days. In order to achieve a comprehensive overview of the phenology of both *Phonotimpus*, the previous data were pooled with records (date and development stage at the moment of the capture) from hand collecting (samplings from March 2016 to October 2019), which was the method used to capture spiders for laboratory rearing, by sprinkling leaf litter on a white fabric-sheet and using an aspirator to capture spiders. Specimens were deposited at Colección de Arácnidos del Sureste de México (ECOTAAR), El Colegio de la Frontera Sur, Tapachula, Chiapas, Mexico.

Laboratory rearing.—All spiders collected were housed individually in plastic containers (9 x 9 x 7 cm) with their bottom filled with a mixture of plaster of “Paris” and activated charcoal as substratum, which was moistened once a week. In addition, we added a moistened cotton ball and two translucent straws as shelter. Spiders were fed with reared springtails (Collembola) because they accepted springtails as prey in preliminary observations made in 2016. All spiders were maintained at $26 \pm 1.3^{\circ}\text{C}$, $57 \pm 4.3\%$ relative humidity, with 12 light:12 dark photoperiod regime.

Sexual size dimorphism and differences of body size between species were investigated with comparisons of prosoma length and prosoma width of adult individuals (Foellmer & Moya-Laraño 2007; Punzo & Farmer 2006).

Observations about predacious behavior were made while spiders were maintained in captivity. The shape of egg sac, the number of eggs, the number of egg sacs per female and the embryonic period were estimated with gravid females, which made their egg sac in the laboratory, and with females with egg sac captured in the field.

In order to assess if juveniles and penultimate individuals made retreat during the molting process, we recorded the presence or absence of retreat and date of molting.

Analysis.—Phenology of spiders have been assessed with pitfall traps (Buddle & Draney 2004); for comparison purposes, we first plotted pitfall and leaf litter data, then used the pooled data (which include hand collecting data) to make a phenological summary. For sexual dimorphism, we compared the body size between males and females of each species, and between species with paired Welch's t-test in R (R Core Team 2019). We followed the terminology of Alvarado-Castro & Jiménez (2016) with the subsequent modifications: “juvenile” to describe spiders from first instar (according to Wolff & Hilbrant 2011) to the antepenultimate stage prior to maturing molt; the term “penultimate” to refer the instar prior to maturing molt, penultimate males were identified by the swollen tarsi without sclerotized structures and penultimate females by the slightly sclerotized gonopore region but without vulva. The term “male” to refer to adult male with the pedipalpi modified (cymbium plus bulb sclerotized and associated sclerites, palpal tibia with apophyses), and “female” to refer to adult female with epigynum and vulva. The determination of the stage of development was based on external morphology.

RESULTS

We reared 34 males, 56 females (21 gravid, four with egg sac, and 33 not gravid), eight penultimate males, five penultimate females and 50 juveniles (plus 30 first instar spiderlings hatched in laboratory) of *P. pennimani*. For *P. talquian*, 11 males, 22 females (one gravid, and 21 not gravid), 15 penultimate males, seven penultimate females and 60 juveniles were reared.

Phenology.—Males and females of *P. pennimani* and *P. talquian* were collected in the rainy and dry season (Fig. 1A, B). However, more adults of *P. talquian* were caught in the rainy season, while juveniles were numerous in the dry season. Penultimate males of *P. talquian* were found only in dry season. Pooled data showed that juveniles and adults of both species occurred throughout the year. Moreover, males and females occurred most of the year although their abundance varied over time (Fig. 1C). Both sexes of *P. pennimani* were found from January to June, then in August and November, and only females occurred in October. *Phonotimpus talquian* showed a similar pattern as *P. pennimani*, both sexes were found in the rainy and dry season, from February to May, then in August. Males of *P. talquian* appeared in January and October whereas females occurred in September and December. Penultimate males of both species were found at irregular intervals in the first semester of the year, whereas penultimate females were predominant from January to April. Four females with egg sacs of *P. pennimani* were found in the field, one in January, two in April and one more in May.

Body size between species and sexual size dimorphism.—The prosoma length and width of *P. pennimani* was significantly smaller than *P. talquian* (Table 1). In addition, females of *P. pennimani* and *P. talquian* were larger than males of each species (Table 1). Therefore, our data showed a moderate sexual size dimorphism in both species.

Prey capture.—In the field, we observed and captured a female of *P. pennimani* (February 21, 2019) consuming an unidentified springtail of the family Tomoceridae (Collembola). Also, we collected a female of *P. talquian* (March 26, 2019) which was ingesting a *Pogonognathellus* sp. (Tomoceridae) springtail. In 2016, we made preliminary observations about prey acceptance, and both species of *Phonotimpus* preferred springtails

over booklice (Psocoptera) and ants (Formicidae). Indeed, both species accepted the following springtails (Figs. 2J–L, 3E–F): *Proisotoma* sp. (Isotomidae), *Pseudosinella* sp., *Lepidocyrtus* sp. (Entomobryidae) and *Cyphoderus* sp. (Cyphoderidae) in laboratory conditions. Moreover, *P. pennimani* and *P. talquian* were observed ambushing all the springtails that forage nearby. Furthermore, juveniles of both species are capable of capture springtails larger than themselves (Fig. 2L). In one event, we observed that a juvenile (first instar) of *P. pennimani* attacked a springtail with the ventral macrosetae of forelegs raised for a brief moment. The springtail attempted to escape by jumping but the spider grasped so tightly the prey that the escape mechanism was not effective even when the springtail jumped two times with the spider attached. In addition, we observed females of *P. pennimani* ambushing springtails while they were guarding their egg sac. Likewise, males of both species were prone to ambush springtails.

Retreat for molting.—We observed that juveniles and penultimate individuals of *P. pennimani* and *P. talquian* made a retreat for the molting process. The retreat was not elaborated, it was comprised by a loosely spun lower layer and a superior one making an enclosure of silk, all the silk threads were discernible in both layers. The basal layer was usually weaved denser than the superior one. The structure of retreat was variable (compare Figs. 2G–I, 3H–J); some retreats were tangled silk threads, whereas others were two denser layers. Juveniles and penultimate individuals of *P. pennimani* and *P. talquian* made a retreat although not all individuals of both species made a retreat (Table 2). Moreover, we recorded that the same individual made a retreat during one molting event but not in the following one. Retreats were found in the top of the container, within the straws, or in the bare substratum (Figs. 2G–I, 3H–J.). Several spiderlings died during or just

after the molting process. In one case, a spiderling could not release the legs and got trapped in the exuvium. We observed that some juveniles, which did not build retreat, just hold to the top or walls of the container with its legs and molted (Fig. 3G), no evidence of silk were found after a subsequent inspection of the area of molting.

Eggs sac, clutch size and maternal care.—The four females with egg sac of *P. pennimani* laid their egg sac in a dried leaf, while gravid females laid their eggs sac on the bare substratum, in the straw or in the corner of the container. The only gravid female of *P. talquian* chose to lay on a dried leaf in laboratory conditions. The egg sacs of both species were like disk with hue ranging from pinkish to whitish (Figs. 2D–F, 3D). The cover layer was very thin but dense and compact; individual silk's threads were not distinguishable (Figs. 4B–C). The basal layer was less dense than the upper one, and it was the substrate where the eggs were laid. The mean diameter of the egg sacs of *P. pennimani* was 5.62 ± 0.69 mm ($n = 16$), the mean number of eggs per sac was 8.93 ± 2.64 eggs ($n = 16$), with a range of six to 15 eggs, and the mean diameter of eggs was 0.49 ± 0.09 mm ($n = 14$). We observed a single instance of *P. talquian* with her egg sac (Fig. 3D), but we did not measure or count the number of eggs because the egg sac was lost while we awaited the emergence of the offspring. In both species, all females did not spin an extra layer or retreat to protect herself or the egg sac. Twenty-one gravid females of *P. pennimani* built at least one egg sac in laboratory, nine of those built their second egg sac, three of them made a third one and just one female made a fourth egg sac. Conversely, just one female of *P. talquian* made one egg sac. In laboratory, gravid females of *P. pennimani* laid their first egg sac in January ($n = 1$), March ($n = 1$), April ($n = 7$), May ($n = 6$), June ($n = 5$) or July ($n = 1$), whereas *P.*

talquian in April ($n = 1$). The female of *P. pennimani*, which laid four egg sacs in laboratory, built her last egg sac (with infertile eggs) in October (2019).

It was impossible to observe the complete process of egg sac construction by *P. pennimani* because the female abandoned the egg sac when it was disturbed. However, we observed first that the female spun the basal layer, then laid the eggs in the center and usually a viscous substance maintained all the eggs packed in the middle (Figs. 4D–E). Finally, the female sealed the eggs with the cover layer.

An unusual behavior was observed in laboratory, three females of *P. pennimani* weaved their second egg sac without eggs, and two of them were laid just over the first egg sac. The first egg sac had eggs, but no offspring emerged from them; the opening of the egg sac revealed that eggs were unfertilized.

The female of *P. pennimani* was not essential for the successful emergence of the offspring because in two events the females died earlier for unknown reasons, yet the offspring emerged from the egg sac. In a related event, a female built and guarded a second egg sac two days before her offspring emerged from the first egg sac; then the female built a third egg sac two days before her second clutch came out. Surprisingly, none spiderling emerged from this third egg sac.

In field and laboratory conditions, we observed that the females of both species guarded their egg sacs by staying over them (for *P. pennimani* $n = 21$ while for *P. talquian* $n = 1$); they always touched their egg sac with at least one leg (Figs. 2D–F, 3D). When the females were stressed, they ran fast to search a covert although they relocated again over their egg sac after several minutes, hours or they never returned. Nevertheless, the protection was not

infallible because we found in the field two egg sacs of *P. pennimani* with a parasite wasp (see further details below).

Embryonic period and survival in laboratory conditions. —The mean time of the embryonic development of *P. pennimani* was 22.66 ± 4.72 days ($n = 3$ egg sacs), whereas the embryonic period for *P. talquian* is unknown because just one female built one egg sac but none spiderling emerged. In laboratory conditions, the maximum number of molts of both species was three. For *P. pennimani*, the 60 % of juveniles molted one time, 30 % molted two times and 8 % molted three times (Table 2). Only three of eight penultimate males molted and reached maturity while all penultimate females reached maturity. For *P. talquian*, 76 % of juveniles molted one time, 38 % molted two times while 8 % molted three times and just three penultimate males and three penultimate females reached maturity (Table 2). Only six of 30 first instar spiderlings of *P. pennimani*, which emerged in laboratory conditions, molted to the second instar after roughly 36 days (Table 3). Then just one reached the third instar after nine days, the other spiderlings died for unknown reasons. The number of molts to reach maturity is unknown for *P. pennimani* and *P. talquian* because no specimen survived from eggs to adult stage, and the maximum number of molts observed in laboratory conditions was three (Table 2). Juveniles of *P. pennimani* molted every 18 to 26 days whereas juveniles of *P. talquian* molted every 24 to 26 days (Table 3). Females of both species survived longer than males, and females that were reared from the penultimate stage survived longer than males reared from penultimate stage (Table 3). Conversely, females of *P. talquian* reared from penultimate stage survived longer than females captured from the field. Also, penultimate females of both species survived longer than penultimate males.

Endoparasitoid of *Phonotimpis pennimani*.—Two females of *Phonotimpus pennimani* guarding their respective egg sacs were collected in the field (April 18, 2018 and January 14, 2019) and were taken to the laboratory for observations. Each egg sac was attached to a dried leaf, and none of them have visible perforations or damage in the surface of the cover layer. From the first egg sac, a male wasp emerged (four days after collection) leaving a small circular opening in the cover layer; inside of the egg sac we found five dead spiderlings (first instar), one female dead wasp and two wasps puparia (Figs. 4G–H). Inside of the second egg sac, we found an unbroken puparium, a male wasp (Fig. 4I), seven dead spiderlings (first instar) and two unfertilized spider eggs. All wasps were identified as *Idris* sp. Förster, 1856 (Platygastridae: Scelioninae; Figs. 4J–L).

DISCUSSION

Phenology.—Phenological studies and monitoring spiders in natural habitats are challenging because there are many logistical constraints. Both species of *Phonotimpus* are small spiders with cryptic colorations (see Figs. 2A–C, 3A–C) and they run fast when they are disturbed. Indeed, size and coloration may be the reasons of the scarce information that is known about phrurolithids.

Data from pitfalls traps and leaf litter samples showed that adults and juveniles of both species of *Phonotimpus* occurred in the dry and rainy season. The pooled data confirm that adults and juveniles are found almost all year. The occurrences indicate that these spiders are not restricted to one season or to a few months, hence both species are non-seasonal and seemingly there are overlapping generations. Our findings indicate that both species are eurychronous, which means that adults occur all seasons and the reproductive period can be

fixed or not to one period of the year (Aitchison 1984). Jackson (1978) defined the mating season as the period when adult males and females co-occurred. Our data showed that females and males of *P. pennimani* and *P. talquian* co-occurred in both seasons and almost all the year. Moreover, females can build egg sacs in dry and rainy season. Hence, it seems that there is not a fixed reproductive period restricted to a few months. Conversely, *Phrurotimpus borealis* (Emerton, 1911) (Phrurolithidae) was classified as eurychronous with a fixed period of reproduction in spring (May to July) (Aitchison 1984). Likewise, it seems that the mating season of the Nearctic *Phrurotimpus alarius* (Hentz, 1847) is in the spring since most male adults were trapped in April (Draney 1997), whereas *Scotinella fratrella* (Gertsch, 1935) mate in June and July because both sexes co-occurred in those months (Penniman 1978). The Palearctic *Phrurolithus nigrinus* (Simon, 1878) seems to mate from May to August (Blick et al. 2008). The majority of phenological studies on spiders were made in temperate zones (Aitchison 1984; Merret 1967; Schaefer 1977; Toft 1976) with seasons well defined, and with species well adapted to their habitats. For example, some spiders are winter active while others hibernate as adults or as egg stage, hence most of them are markedly seasonal (Aitchison 1984; Buddle & Draney 2004; Schaefer 1977; Toft 1976). Conversely, in the Neotropics just some phenological patterns have been identified. For example, in Brazil, Villanueva-Bonilla & Vasconcellos-Neto (2016) found that all stages of *Selenops cocheleti* Simon, 1880 (Selenopidae) occurred throughout all year except males; they concluded that *S. cocheleti* is a stenochronous species with reproductive period at summer. They also noticed the occurrence of males for several months and suggested that is a pattern in tropical species. In Mexico, almost all stages of *Peucetia viridans* (Hentz, 1832) were found from April to September but mating start in May with peaks between June and

August (Arango et al. 2000). The salticid *Psecas chapoda* (Peckham & Peckham, 1894) showed a phenological pattern like *P. pennimani* and *P. talquian*; all stages and both sexes co-occurred throughout the year. Moreover, it seems that mating season is not fixed because it was observed females with egg sacs and males displaying courtship behavior all the year (Romero & Vasconcellos-Neto 2005). We think that gaps in our phenological summary are more probably related with an undersampling bias than a phenological pattern for any of the *Phonotimpus* species studied here. A combination of pitfalls traps, leaf litter samples and hand collecting seems to be better approach to assess the phenology of small and cryptic spiders like *Phonotimpus* in tropical environments.

Body size between species and sexual size dimorphism.—Sexual size dimorphism (SSD) is ubiquitous among spiders; males are usually smaller than females. In some cases, the difference in size is extreme and males can be only a fraction of the female (Vollrath 1998; Foellmer & Moya-Laraño 2007). The difference in SSD in *P. pennimani* and *P. talquian* is small although it is significant. This difference can be a pattern in the genus (per. obs.) and in the family although more data are needed. Clubionidae and Gnaphosidae, which are related with Phrurolithidae, have variable SSD although the males, on average, are slightly smaller than their females (Austin 1984; Vollrath 1998; Vollrath & Parker 1992). The SSD bias toward females can be related with maximize energy intake hence females invested in fecundity (Pekár et al. 2011). The difference in body size between species can be explained by the difference in habitat temperature. A metanalysis showed that rearing temperature affects the body size in arthropods, such relation can be positive or negative, hence the body size can increase or decrease according to the rearing temperature (Atkinson 1994). In some species of Lycosidae the altitude is correlated with

the body size, spider populations of higher altitudes are slightly larger than their counterpart in lower elevations although not all species or populations followed such trend (Ameline et al. 2018). Elevation as a proxy of temperature can be one of several factors involved in the differences on body size observed between the two species of *Phonotimpus*.

Prey capture.—Recently, Angulo-Ordoñez et al. (2019) described the predatory behavior of *P. pennimani* and *P. talquian* against four types of prey. Among their results, they pointed out the preference for springtails (unidentified species) over true bugs (Hemiptera) or booklice (Psocoptera). Also, they showed that both species use the ambush or the active searching as hunting strategies. Even though we observed just two cases of predation over springtails in the field, the preference over springtails was also observed in the laboratory. This preference for springtails is shared with the phrurolithids *Liophrurillus flavitarsis* (Lucas, 1846) and *Phrurolithus festivus* (C. L. Koch, 1835) although they also accepted fruit flies (*Drosophila melanogaster* Meigen) and aphids (*Aphis fabae* Scopoli) as prey in laboratory conditions. Moreover, those phrurolithids preferred preys smaller than their body size (Pekár & Jarab 2011). The spider *Triaeris stenaspis* Simon, 1892 (Oonopidae) is a smaller species than *P. pennimani* and *P. talquian* and it is a specialist predator of springtails (Entomobryidae) because they preferred springtails among eleven prey types in laboratory conditions (Korenko et al. 2014). Larger wandering spiders like *Pardosa pseudoannulata* (Bösenberg & Strand, 1906) and *Pirata subpiraticus* (Bösenberg & Strand, 1906) (Lycosidae) preferred to eat hemipterans (*Nephrotettix cincticeps* (Uhler)) and dipterans (Chironomidae) (Ishijima et al. 2006) while some species of *Clubiona* Wagner, 1887 consume ants (Formicidae), Blattodea and Coleoptera (Austin 1984). None record of use of silk for prey capture was found for any phrurolithids nor was observed under laboratory

conditions. The spider *T. stenaspis* did not build a web for prey capture either, it just uses the grasp and hold tactic for prey catching (Korenko et al. 2014). Indeed, many hunting spider families as corinnids, lycosids and salticids do not use silk for prey catching, these spiders just jump, bite and hold with its chelicerae their prey (Nentwig & Wissel 1986; McGinley et al. 2015). Both *P. pennimani* and *P. talquian* ambush or approach quickly toward their prey, then they grasp and pull the prey with the forelegs to their chelicerae (Angulo-Ordoñez et al. 2019). The long ventral macrosetae on tibia and metatarsi of forelegs of *Phonotimpus pennimani* and *P. talquian* seems to be adaptations for prey catching and useful to handle large preys. The grasp and hold tactic seem to be effective since *T. stenaspis* jumps up attached in the back of their prey (“rodeo-riding”) in order to prevent the loss of the prey (Korenko et al. 2014) as we observed for a first instar of *P. pennimani* with a large springtail. The consumption of springtails by females of *P. pennimani* and *P. talquian* while they guarded their egg sac was unexpected. Some females of *Clubiona* spp. do not feed for up to three months, they stop prior the oviposition and resume their feeding habits when their spiderlings emerge from the nest (Austin 1984). Likewise, males of both *Phonotimpus* continue the feeding habits when they reach maturity, this can provide more energy for mate searching, while females can use them for oviposition and parental care.

Retreat for molting.—Not all spiders built a retreat for molting, differences among families or even among genus from the same family have been described (Austin 1984; Foelix 2011; Nentwig & Heimer 1987). Some families as Salticidae and Clubionidae use the retreat for optimal protection during the molting (Nentwig & Heimer 1987). Indeed, the salticids *Servaea incana* (Karsch, 1878) and *Phidippus johnsoni* (Peckham & Peckham, 1883) built a retreat for molting although they also use them when courtship occur and for

breeding (McGinley et al. 2015; Jackson 1979). In addition, juveniles of *Clubiona* spp. make a temporal retreat for molting; this structure can vary considerably within species (Austin 1984). The plasticity of the retreat made by both *Phonotimpus* is noticeable and can be associated with the condition of the individuals. For example, well-fed females of *Tigrosa helluo* (Walckenaer, 1837) are more likely to construct burrows than individuals with higher level of hunger because the construction of a burrow can be an energy expensive task (Walker et al. 1999). To our knowledge, there is not report of spiderlings building a molting retreat in Phrurolithidae. Moreover, this strategy is used by juveniles and penultimate individuals, hence it is not limited to early stages of development. Juveniles and penultimate individuals of both species of *Phonotimpus* seem to allocate resources to increase their safety during critical situations as the molting process, but experimental trials are needed in order to test this hypothesis.

Eggs sac, clutch size, embryonic period and maternal care.—A typical egg sac consists of a basal and a cover layer, which envelop the eggs. The shape and structure of the egg sac among spiders is highly variable, ranging from few silk threads enveloping the eggs to elaborated egg sacs made of several layers, and sometimes with the egg sac inside of a retreat or nest (Foelix 2011). Families related to phrurolithids construct egg sacs of different shapes although the shape of some of them are alike to *P. pennimani* and *P. talquian* egg sacs. For example, some species of the genera *Clubiona* (Clubionidae), *Agroeca* Westring, 1861 (Liocranidae), *Trachelas* L. Koch, 1872 (Trachelidae), *Callilepis* Westring, 1874, *Cesonia* Simon, 1893, *Herpyllus* Hentz, 1832, *Zelotes* Gistel, 1848, and *Drassodes* Westring, 1851 (Gnaphosidae) built a flattened oval or lenticular egg sac (Kaston 1948). Moreover, the egg sacs of most species of *Castianeira* Karsch, 1880 are a

flattened disc like covered with debris, which are fastened to a stone (Kaston 1948). Also, *Phrurotimpus* sp. Banks, 1892 (Phrurolithidae) laid a shiny red flattened and scale-like egg sac in stones (Kaston 1948). An undescribed species of *Phonotimpus* from central of Mexico (herein designated as *Phonotimpus* sp. A) built a pinkish disk-like egg sac over a dried leaf with the eggs clustered in the center as the egg sacs of *P. pennimani* and *P. talquian* (unpublished data). Therefore, the disk-like egg sacs seem to be a pattern among phrurolithids and related families as Trachelidae, Corinnidae or Liocranidae.

In spiders, the number of eggs laid, and the number of eggs sacs built by a female depends on the species, it ranges from a single egg to thousands (e.g., *Dolomedes vittatus* Walckenaer, 1837 laid up to 1,480 eggs) and from one to ten egg sacs (Kaston 1948). Families related with Phrurolithidae have diverse average numbers of eggs per egg sac, some species of *Clubiona* (Clubionidae) laid from 33 to 79 eggs per egg sac, *Trachelas* sp. (Trachelidae) laid 30 to 48, *Castianeira* spp. (Corinnidae) laid between 8 to 30, while *Micaria* spp. Westring, 1851 from 8 to 17, *Cesonia* sp. laid 57 eggs, *Gnaphosa* spp. Latreille, 1804 from 26 to 220, *Callilepis* sp. from 22 to 46, *Herpyllus* sp. laid 130, *Drassodes* spp. from 27 to 57, and *Zelotes* sp. from 40 to 60 eggs (Gnaphosidae) (Kaston 1948). The phrurolithids *L. flavitarsis* laid a mean of 4.7 eggs while *P. festivus* a mean of 4.1 eggs per clutch, and females of both species built more than one egg sac in laboratory conditions (Pekár & Jarab 2011). The average number of eggs in those Palearctic phrurolithids is lower than in *P. pennimani*. In contrast, the Nearctic *P. alarius* laid 13 eggs in one egg sac (Kaston 1948; Montgomery 1909). Moreover, we recorded that females of *Phonotimpus* sp. A built egg sacs with a mean diameter of 6.32 ± 1.25 mm ($n = 2$), and they

laid a mean of 14 eggs ($n = 2$) per egg sac (unpublished data); these values are similar to *P. pennimani* and *P. talquian*.

Across spider taxa, the body size is correlated with the number of eggs laid, larger species laid more eggs; likewise, the female body mass determine the clutch mass and the eggs mass (Marshall & Gittleman 1994). The available data suggest that *P. pennimani* lay a low number of eggs because it is a small spider; this can be a pattern among all *Phonotimpus* species since all of them are small spiders. Moreover, *P. pennimani* and probably *P. talquian* are iteroparous species because they laid up to four clutches. Likewise, the salticids *P. johnsoni* laid up to five batches while *S. incana* laid up to three clutches of eggs (McGinley et al. 2015; Jackson 1978). It is presumed that this reproductive strategy in spiders avoid the loss of the offspring by predators or by harsh environments (Jackson 1978). To our knowledge, the construction of egg sac without eggs was not observed in other spiders although the construction of an egg sac with infertile eggs alternate with a new egg sac with fertile eggs was observed in *P. johnsoni* (Jackson 1978). The empty egg sac laid over the first one also can be a strategy to avoid the predation or parasitism; the additional layers of silk of the empty egg sac can obstruct the easy access to the fertile eggs. Parental care is “any trait that enhances the fitness of a parent’s offspring...”; for instance, by protecting them from predators, cannibalism, parasitoids, fungal infections, food shortage, environmental harsh conditions, and so on (Santos et al. 2017; Smiseth et al. 2012; Tallamy 1984). The most common forms of care in spiders are the egg sac construction, egg sac guarding and brood care by the female (Yip & Rayor 2014). For example, some spiders grasp and carry the egg sac with their chelicerae or attach it to their spinnerets; other females aggressively deter predators whereas others carry their offspring

after the hatching (Kaston 1948; Yip & Rayor 2014). Another types of brood care are the food offering with preys, regurgitating fluids, trophic eggs (consumption of unfertilized eggs) or matryphagy (Ibarra-Núñez 1985; Kim & Roland 2000). In spiders, the female commonly abandons her egg sac after the completion (Foelix 2011). However, some females related with phrurolithids as clubionids, gnaphosids or salticids mount guard over the egg sac until the emergence of their offspring (Austin 1984; Kaston 1948; Jackson 1979). The guarding of the egg sacs by females of *P. pennimani* and *P. talquian* can deter natural enemies and reduce the parasitism by *Idris* wasps or other natural enemies. The maternal presence in the salticid *P. chapoda* increased the survival of the progeny because the mother deterred predators and parasitoids (Vieira & Romero 2008). However, in some cases such protection did not avoid parasitism (Barrantes & Weng 2007) or was useless against larger predators as mantispids (McGinley et al. 2015; Vieira & Romero 2008). In contrast to our observations, Dondale & Redner (1982) stated that females of *Phrurotimpus* abandon their egg sacs, but it is possible that they did not observe the female returns as we saw in *P. pennimani*, *P. talquian* and *Phnotimpus* sp. A. However, the way that the female recognizes the path to her egg sac is unknown since no traces of silk threads were observed. Chemical cues can be involved in such process although the shape and texture of the egg sac can be important.

Embryonic period and survival in laboratory conditions.—The time to reach maturity for *P. pennimani* or *P. talquian* is unknown but clearly both species molt more than three times. It is known that larger spiders need more molts to reach maturity than smaller ones; moreover, males usually reach adult stage before females (Austin 1984; Foelix 2011; Jackson 1978). For example, males of *P. johnsoni* matured at seven to nine

molts while females at instar ten (Jackson 1978); females of *Clubiona robusta* L. Koch, 1873 matured at seven to nine while males at instar six to eight (Austin 1984). Those species are larger than the species studied here; therefore, we hypothesize that both species of *Phonotimpus* need less molts to reach maturity. The variation in time to reach the maturity partially explains the occurrence of different stages at the same time of the year (Levy 1970). Furthermore, it is worthy of notice that one female of *P. pennimani* survived up to 156 days while some females of *P. talquian* survived more than two months. High longevity under laboratory conditions was observed in *P. johnsoni* (Salticidae); the females survived roughly four months while males survived roughly three (Jackson 1978). Likewise, high variation in the duration among stages was observed in *P. johnsoni* although later instars tended to be longer in days (Jackson 1978). Moreover, such variability in time could arise even with spiders reared with the same feeding regimes (Levy 1970). Adults females of both species of *Phonotimpus* survived longer than their males; since both sexes continue to feed after reaching maturity, females can use energy intake to endure during maternal care and therefore females allocate resources for the survival of their offspring.

Endoparasitoid of *Phonotimpus pennimani*.—Scelioninae (Hymenoptera: Platygastriidae) is a subfamily of endoparasitoid wasps specialized in using eggs of spiders or insects as host (Austin 1984; Austin et al. 2005; Loíacono & Margaría 2013). Prior of hatching, the larva of scelinoid wasp eats the content of the host egg and pupates inside it (Austin et al. 2005). The genera *Baeus* Haliday, *Ceratobaeus* Ashmead, *Idris* Förster and *Odontocolus* Kieffer (Baeini, Scelioninae) are specialized in exploiting eggs of spiders (Araneae) with high degree of host specificity (Austin 1984; Austin et al. 2005; Barrantes & Weng 2007; Loíacono & Margaría 2013).

This is the first record of an *Idris* sp. wasp parasiting eggs of Phrurolithidae, and it is a putative new species of *Idris* (Margaría 2019 *in litt.*). In the neotropical region, nine cases of parasitoidism by the genus *Idris* are known, in six of them their spider host were not identified. In Brazil, *Idris ovivorus* (Fouts) attack eggs of *Ctenus* sp. Walckenaer, 1805 (Ctenidae), an *Idris* sp. from Mexico attacks the eggs of *Pardosa* ca. *flavipalpis* F. O. Pickard-Cambridge, 1902 (Lycosidae) (Jiménez 1987), and an Argentinean *Idris* sp. attacks the eggs of *Sumampattus hudsoni* Galiano, 1996 (Salticidae) (Loiácono & Margaría 2013). The use of two eggs of all available eggs by the *Idris* sp. wasp can be strategy to avoid the depletion of the resources. For example, the mortality of eggs of some *Clubiona* sp. by *Ceratobaeus* spp. ranges from 10–30% of total eggs (Austin 1984), whereas the mortality of eggs in *Theridion evexum* Keyserling, 1884 by *Baeus* sp. range from 3-30% of total eggs (Barrantes & Weng 2007). The Baeini wasps can recognize their host by properties of the eggs or by cues from the silk of egg sac or retreat (Austin 1984). Furthermore, it is known that Baeini female wasps can go through the egg sac and gain access to the eggs or they can oviposit by piercing the chorion through the thin silk of the host egg sac (Austin et al. 2005; Loiácono & Margaría 2013). Nevertheless, we did not find any perforation in the cover layer of the two egg sacs studied; therefore, there is a probability that the *Idris* female wasp can oviposit while *P. pennimani* is laying her eggs, hence parasitizing the eggs before the female seal her egg sac. However, there is chance that we did not see such perforation because it was so small.

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Table 1. Measurements of prosoma length and width of *Phonotimpus pennimani* and *P. talquian* with the *t* statistic for the paired comparisons between species and males versus females of each species. Measurements are in millimeters.

Prosoma	Species	Sex	Mean	SD	n	t	degrees of freedom	P
Length	<i>P. pennimani</i>	-	0.998	0.0391	18	-11.51	18.091	<0.05
	<i>P. talquian</i>	-	1.26	0.0777	14			
Width	<i>P. pennimani</i>	-	0.909	0.0348	18	-11.046	17.016	<0.05
	<i>P. talquian</i>	-	1.157	0.0782	14			
Length	<i>P. pennimani</i>	M	0.970	0.0224	6	3.0013	15.347	<0.05
	<i>P. pennimani</i>	F	1.013	0.0382	12			
Width	<i>P. pennimani</i>	M	0.886	0.0187	6	2.7487	15.853	0.014
	<i>P. pennimani</i>	F	0.921	0.0356	12			
Length	<i>P. talquian</i>	M	1.202	0.0221	9	4.2606	4.581	<0.05
	<i>P. talquian</i>	F	1.339	0.0698	5			
Width	<i>P. talquian</i>	M	1.112	0.0681	9	2.7941	9.471	0.019
	<i>P. talquian</i>	F	1.216	0.0593	5			

Table 2. Number of individuals that molted and constructed a retreat per stage and per species; the percentages are in parentheses.

Species	Developmental Stage	Individuals reared (<i>n</i>)	Individual that molted (<i>n</i>)			Number of individuals that made a retreat during molting		
			One time	Two times	Three times	First molt	Second molt	Third molt
(Penultimates that reached maturity)								
<i>P. pennimani</i>	Juveniles	50	30 (60%)	18 (30%)	4 (8%)	4	3	1
	Penultimate	8	3	-	-	2	-	-
	males							
	Penultimate	5	5	-	-	3	-	-
	females							
<i>P. talquian</i>	Juveniles	60	46 (76.6%)	23 (38.3)	5 (8.3%)	20	7	1
	Penultimate	15	2			0	-	-
	males							
	Penultimate	7	3			1	-	-
	females							

Table 3. Duration in days of stages of *Phonotimpus pennimani* and *P. talquian*. In parentheses adults reared from penultimate stage under laboratory conditions. Spiders that died in the same day after collecting were excluded.

Species	Stage	Mean ± S.D.	Max	Min	n
<i>P. pennimani</i>	Juveniles 2 nd instar	36.66 ± 6.47	42	25	6
	Juveniles 3 rd instar	18.61 ± 7.08	34	7	18
	Juveniles 4 th instar	22.5 ± 3.41	27	19	4
	Penultimate females	14.4 ± 5.94	18	4	5
	Penultimate males	32.75 ± 26.64	89	5	8
	Females	47.82 ± 40.20	159	6 (7)	56 (5)
		(30.2 ± 21.34)	(53)		
	Males	30.56 ± 21.03	81 (31)	1 (11)	32 (3)
		(21.33 ± 10.01)			
<i>P. talquian</i>	Juveniles 3 rd instar	24.04 ± 5.13	34	13	23
	Juveniles 4 th instar	26.5 ± 4.12	31	21	4
	Penultimate females	13.16 ± 3.92	18	9	6
	Penultimate males	22.6 ± 10.10	35	3	15
	Females	23.5 ± 16.18	65 (45)	3 (27)	18 (4)
		(35.5 ± 8.06)			
	Males	21.77 ± 10.84	38 (24)	2 (11)	9 (2)
		(17.5 ± 9.19)			

Figure legends

Figure 1. A, B. Periods of capture (pitfall traps and leaf litter samples). C. Phenological summary (pooled data) of *Phonotimpus pennimani* (circles) and *P. talquian* (triangles). Occurrence and abundance are noted per stage and species for each month.

Figure 2 A–L. *Phonotimpus pennimani*. A. Habitus, female. B. Habitus, male. C. Habitus, preadult male. D–F. Female guarding their egg sac. G. Exuvium and retreat. H–I. Molted spiderling with retreat and exuvium. J. Female consuming a springtail. K. Same, male. L. Same, first instar.

Figure 3 A–J. *Phonotimpus talquian*. A. Habitus, female. B. Habitus, male. C. Habitus, spiderling. D. Female guarding her egg sac. E. Female consuming a springtail. F. Same, male. G. Spiderling molting. H. Exuvium and retreat. I–J. Molted spiderlings with retreat and exuvium.

Figure 4 A, D–E. Egg sac of *P. pennimani*. B–C. SEM image showing detail of cover layer of egg sac. F. Eggs with different embryonic stages. G–H. Egg sac with parasitoid wasp *Idris* sp. I. Parasitoid wasp with its puparium. J–L. Details of female parasitoid wasp of *Idris* sp.

Figure 1

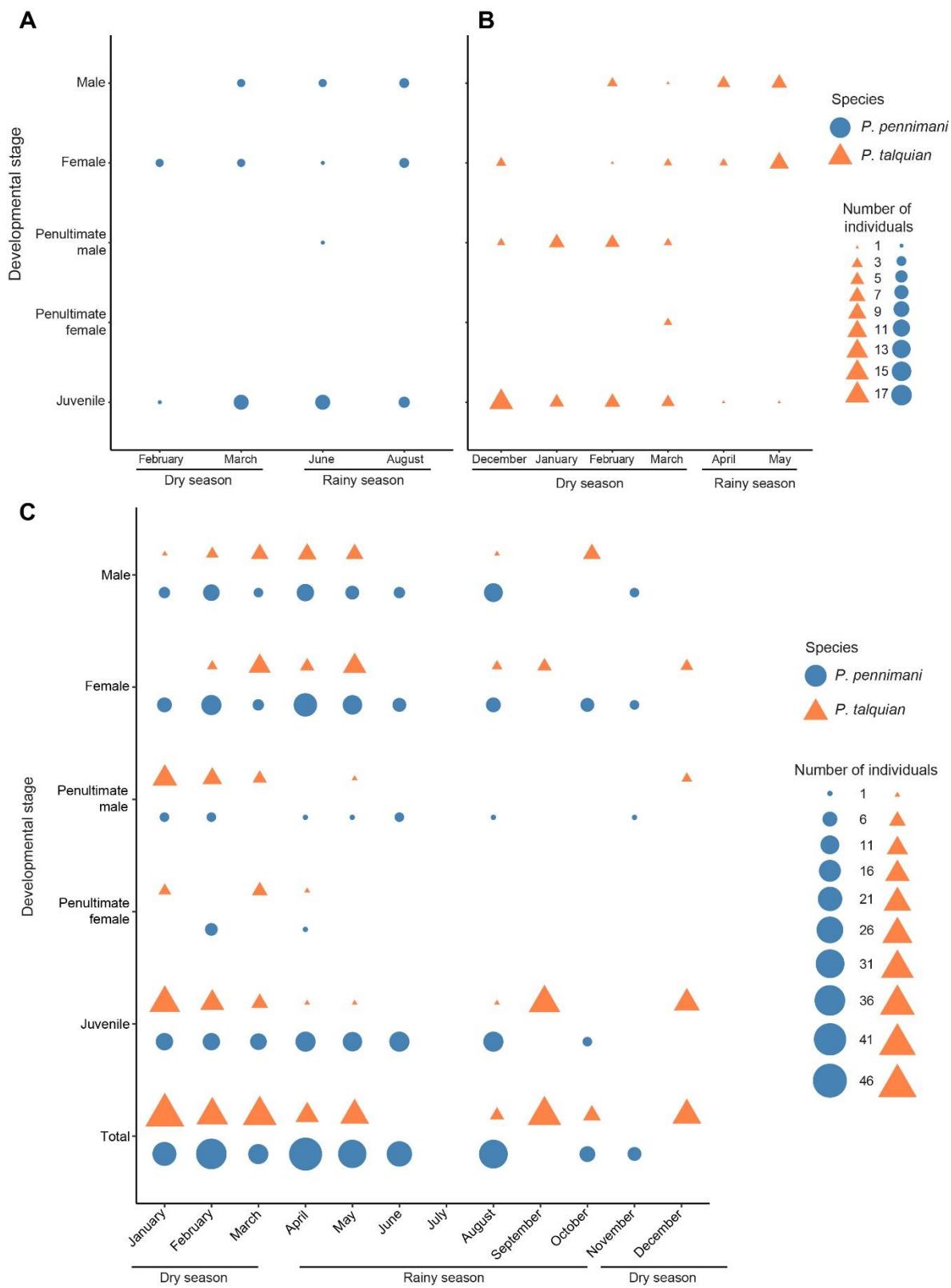


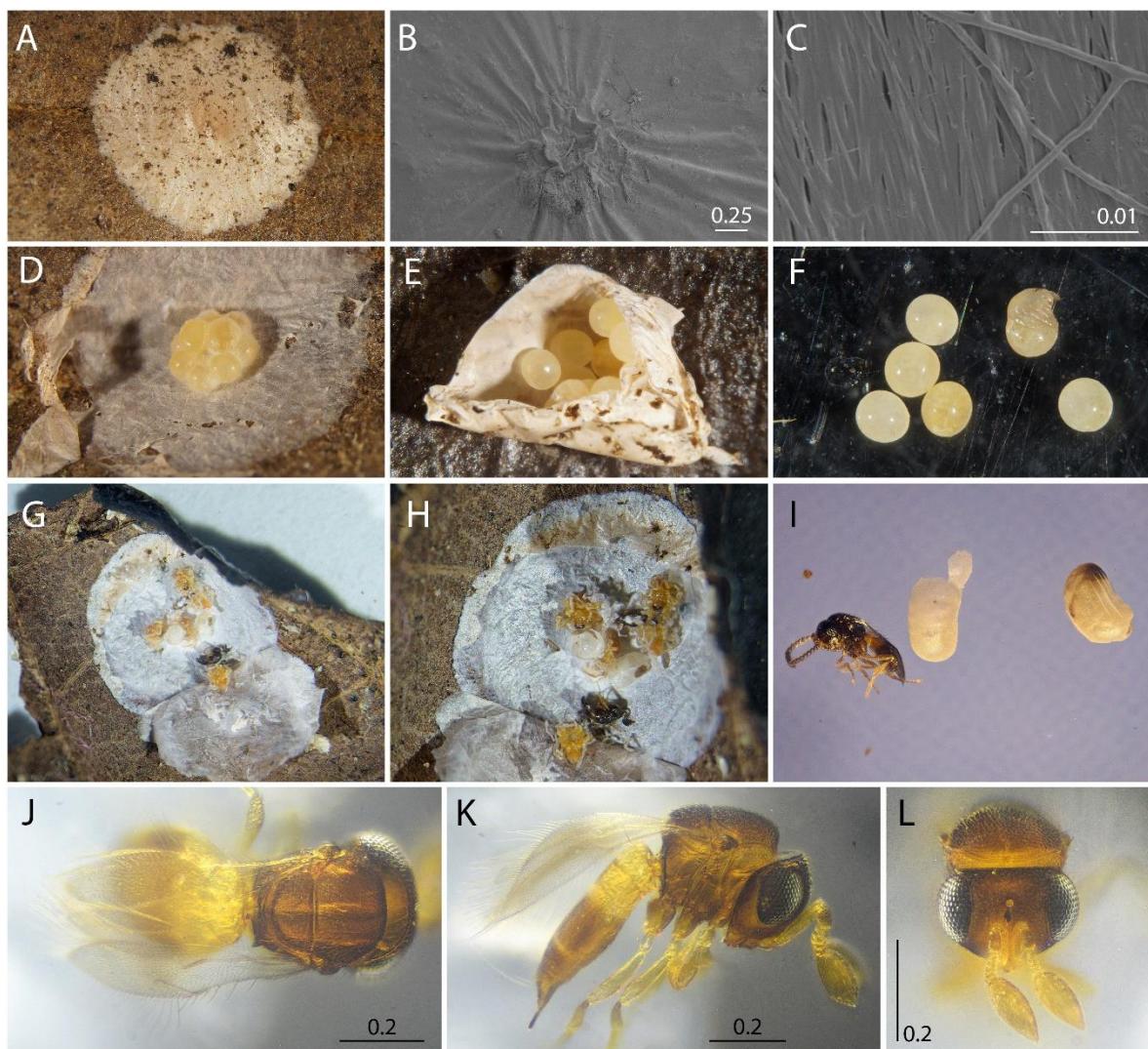
Figure 2



Figure 3



Figure 4



CAPITULO IV. CONCLUSIONES

Este trabajo de investigación se centró en el estudio taxonómico y biológico de dos especies de arañas (Phrurolithidae) endémicas de la parte alta del Volcán Tacaná, Chiapas. Mediante el análisis taxonómico se describieron las dos especies de arañas como nuevas para la ciencia y fueron denominadas *Phonotimpus pennimani* Chamé-Vázquez, Ibarra-Núñez & Jiménez, 2018 y *Phonotimpus talquian* Chamé-Vázquez, Ibarra-Núñez & Jiménez, 2018. Además, en la misma publicación se incluyó la redescricpción de la hembra de *Phonotimpus separatus* Gertsch & Davis 1940, la especie tipo del género (de la cual aún se desconoce el macho), la descripción realizada en este estudio aporta información sobre un conjunto de características taxonómicas importantes, y que no fueron incluidas en la descripción original.

La morfología de la genitalia de machos y hembras de *Phonotimpus pennimani* y *P. talquian* proveen evidencias de que dichas especies están estrechamente relacionadas entre sí y parecen conformar un grupo de especies que difiere de la especie tipo y de las dos especies restantes del mismo género. Sin embargo, sabemos que existen varias especies pertenecientes al mismo género (distribuidas desde el norte de México hasta Centroamérica) que aún no han sido descritas, por lo que se requiere incrementar los estudios taxonómicos de un mayor número de especies, con la finalidad de dilucidar el parentesco de las especies que residen en el Volcán Tacaná con las restantes especies del género *Phonotimpus*.

Los datos de las recolectas en el campo, indican que las dos especies estudiadas son eurícronas sin un periodo fijo de reproducción, es decir que estadios juveniles y adultos de ambas especies se pueden encontrar prácticamente durante todo el año en sus respectivas localidades. En contraste, existe poca información para otras especies de la misma familia. No obstante, los juveniles o adultos de muchas especies de arañas tienen una distribución estacional acentuada.

Las observaciones de campo y de laboratorio, junto con la información disponible en la literatura, sugieren que ambas especies de *Phonotimpus*, aun cuando son capaces de atacar y consumir otros tipos de insectos, prefieren como presas a los colémbolos (Hexapoda: Collembola).

Respecto a su reproducción, observaciones de campo y laboratorio mostraron que las hembras de ambas especies depositan un número comparativamente bajo de huevos (con relación a otras especies habitantes del suelo) en ovisacos con forma de disco y les proveen cuidado durante el periodo del desarrollo embrionario. El reducido número de huevos parece estar relacionado por una parte con su tamaño pequeño y por otra parte con la inversión en cuidado maternal. La forma del ovisaco que construyen las hembras de ambas especies, es un rasgo que comparten con otros géneros de su misma familia, pero también con especies de familias afines y que son habitantes del suelo.

A través de la cría en laboratorio se observó que, durante su crecimiento, las arañuelas de ambas especies usualmente construyen un refugio hecho de seda, fabricado *ex profeso* al momento de realizar la muda. La estructura de este refugio es muy simple y variable, tal estructura va de unos pocos hilos hasta una envoltura de seda, al punto que en algunas de las mudas no fue posible detectar esta estructura. Este refugio y la fabricación del ovisaco, parecen ser de los pocos usos de la seda que hacen estas especies, ya que no fabrican redes de caza. Algunos de los comportamientos anteriores parecen ser habituales en el género, pero se requieren más datos de otras especies para establecer patrones.

Se registró por primera vez el parasitismo de avispas del género *Idris* (Platygastridae) atacando huevos de *Phonotimpus pennimani*, siendo el primer registro de parasitoides que atacan huevos de arañas de la familia Phrurolithidae.

Mediante los resultados obtenidos con este trabajo se amplía el conocimiento taxonómico y biológico de la familia Phrurolithidae y en particular del género *Phonotimpus*, grupos cuyos estudios previos, aunque limitados, se habían centrado en los aspectos taxonómicos, con muy escasas aportaciones a su biología.

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