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REVISIÓN TAXONÓMICA Y ANÁLISIS FILOGENÉTICO DE LA FAMILIA STYGNOPSIDAE SØRENSEN, 1932 (OPILIONES: LANIATORES: GRASSATORES)

TESIS

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Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día 3 de abril de 2017, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **CRUZ LÓPEZ JESÚS ALBERTO** con número de cuenta **511010352** con la tesis titulada: **"REVISION TAXONOMICA Y ANALISIS FILOGENETICO DE LA FAMILIA STYGNOPSIDAE SORENSEN, 1932 (OPILIONES: LANIATORES: GRASSATORES)"**, realizada bajo la dirección del **DR. OSCAR FEDERICO FRANCKE BALLVÉ:**

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
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A los que ya no se encuentran entre nosotros: José Cruz† y Mamagude†, ejemplos de fortaleza.

A mi compañera de vida: Catalina.

A los que vienen: Santi y Sofi, el futuro.

Do not go gentle into that good night,
old age should burn and rave at close of day;
rage, rage against the dying of the light.

Though wise men at their end know dark is right,
because their words had forked no lightning they
do not go gentle into that good night.

Good men, the last wave by, crying how bright
their frail deeds might have danced in a green bay,
rage, rage against the dying of the light.

Wild men who caught and sang the sun in flight,
and learn, too late, they grieved it on its way,
do not go gentle into that good night.

Grave men, near death, who see with blinding sight
blind eyes could blaze like meteors and be gay,
rage, rage against the dying of the light.

And you, my father, there on the sad height,
curse, bless, me now with your fierce tears, I pray.
do not go gentle into that good night.
rage, rage against the dying of the light.

Do not go gentle into that good night – Dylan Thomas.

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RESUMEN

La familia Stygnopsidae es un grupo de opiliones armados (Opiliones: Laniatores), el cual se distribuye principalmente en la Sierra Madre Oriental de México. El grupo está actualmente conformado por 17 géneros y 56 especies. Filogenéticamente es el grupo más tempranamente divergente dentro de la superfamilia Gonyleptoidea. Salvo por escasos y dispersos trabajos taxonómicos, la monofilia de la familia, así como de los taxones supra-específicos dentro de ella, no han sido puestos a prueba. En el presente trabajo se propuso la primera hipótesis filogenética de la familia Stygnopsidae, Para lo cuál se han integrado información morfológica y molecular, conjuntando 72 caracteres morfológicos, el gen mitocondrial codificante citocromo oxidasa 1 (CO1), el gen mitocondrial no codificante 16S y tres dominios del gen nuclear 28S. Los árboles filogenéticos fueron inferidos utilizando Máxima Verosimilitud e Inferencia Bayesiana. De acuerdo a las topologías obtenidas, se propuso un re-arreglo taxonómico de Stygnopsidae en dos subfamilias: Stygnopsinae y Karosinae subfam. nov. Tres géneros conflictivos fueron redescritos: *Hoplobunus*, *Serrobunus* stat. rev., y *Stygnopsis*. Adicionalmente los siguientes taxones fueron descritos: *Iztlina venefica* gen. nov., sp. nov., y *Tonalteca* gen. nov. Los siguientes cambios taxonómicos fueron propuestos: *Serrobunus queretarius* comb. nov., *Stygnopsis apoalensis* comb. nov., *Stygnopsis oaxacensis* comb. nov., y *Tonalteca spinooculorum* comb. nov. Se analizó la evolución de los genitales masculinos, detectándose convergencia entre *Hoplobunus* y *Tampiconus*. De acuerdo a la examinación de genitales masculinos y el análisis filogenético, la estructura del pene en Stygnopsidae es plesiomórfico en relación con los restantes integrantes de Gonyleptoidea, y también se refutó la noción de que el glande en Stygnopsidae sea convergente con familias asiáticas de Assamioidea y Epedanoidea. Finalmente se discutió la convergencia de algunas condiciones morfológicas como los pedipalpos desarmados, el patrón genital "Paramitraceras" y los tubérculos ventrales glandulares en machos, los cuáles se encuentran presentes en algunas especies de *Paramitraceras*, *Philora*, *Sbordonia* y *Troglostygnopsis*.

ABSTRACT

The family Stygnopsidae is a neglected group of armored harvestmen (Opiliones: Laniatores), which is distributed mainly in the Sierra Madre Oriental in Mexico. The family is formed by 16 genera and 56 species. Also is the earliest divergent group among Gonyleptoidea. A number of scattered taxonomic works dealing with the family are known, but the monophyly of the family and/or either supraspecific groups have never been tested. In the present work, the first phylogenetic hypothesis of the Stygnopsidae was proposed, integrating total evidence data from 72 morphological characters, the mitochondrial protein-coding cytochrome oxidase 1 (CO1) gene, mitochondrial non-coding 16S gene, and three domains of the nuclear 28S. The phylogenetic tres were inferred using Maximum Likelihood and Bayesian Inference. According to the results, a new taxonomic arrangement in two subfamilies was proposed: Stygnopsinae and Karosinae subfam. nov. Three genera were redescribed: *Hoplobunus*, *Serrobunus* stat. rev., y *Stygnopsis*. Additionally, the following taxa were described: *Iztlina venefica* gen. nov., sp. nov., y *Tonalteca* gen. nov. The following taxonomic changes were proposed: *Serrobunus queretarius* comb. nov., *Stygnopsis apoalensis* comb. nov., *Stygnopsis oaxacensis* comb. nov., y *Tonalteca spinooculorum* comb. nov. Also, the evolution of male genitalia was discussed, detecting morphological convergence in *Hoplobunus* and *Tampiconus*. According to the examination of male genitalia and the phylogenetic analysis, the general structure on penis in Stygnopsidae is a plesiomorphic structure with respect to remaining members of Gonyleptoidea, as well as, the previous hypotheses of convergence in penises among Assamioidea and Epedanoidea with Stygnopsidae were refuted. Finally, convergence in some characters as unarmed pedipalps, "Paramitraceras" male genitalia pattern and ventral glandular tubercles on males, present on some species of *Paramitraceras*, *Philora*, *Sbordonia* and *Troglostygnopsis*, were discussed.

INTRODUCCIÓN GENERAL

Sistemática en Opiliones, breve historia

El Orden Opiliones Sundevall, 1833 es el tercer grupo más diverso de arácnidos (Arthropoda: Arachnida), con aproximadamente 6,500 especies descritas, después de los ácaros (Acari) y arañas (Araneae) (Giribet y Sharma, 2015). El Orden se divide en cuatro subórdenes vivientes: Cyphophthalmi, Dyspnoi, Eupnoi y Laniatores. El suborden Laniatores abarca más del 60% de la diversidad de Opiliones, con un aproximado de 4,100 especies (Kury, 2013).

El auge de los estudios sistemáticos enfocados en Laniatores se llevó a cabo durante inicios del siglo XX, en donde predominó una tendencia tipológica. Como consecuencia se propusieron numerosos géneros monotípicos con base en pocos caracteres provenientes de la morfología externa. Esta percepción estuvo fuertemente promulgada por C. F. Roewer, quien consideró que dentro de Laniatores sólo se reconocían seis familias, y que Phalangodidae Simon, 1879 incluía la mayor diversidad (Roewer, 1923).

Posteriormente, surgió una tendencia reduccionista en la taxonomía de Opiliones, la cual se caracterizaba por la propuesta de sinonimias injustificadas. Respecto a la taxonomía de Opiliones en el Continente Americano, los principales exponentes fueron C. J. y M. L. Goodnight. Entre las publicaciones de estos autores destaca el trabajo Goodnight y Goodnight (1953), dónde sinonimizaron 82 géneros del sur de México, Guatemala y Belice, en ocho géneros.

La tercera tendencia fue propuesta por J. Martens (Martens, 1976, 1986), quién postuló la examinación de la morfología genital, principalmente de los genitales masculinos. En la actualidad esta tendencia es de gran importancia en trabajos taxonómicos y filogenéticos, debido a que estas estructuras aportan información desde nivel específico hasta nivel de suborden en Opiliones.

Estás tres tendencias mencionadas anteriormente han estado en conflicto debido a que no existe acuerdo común en las propuestas taxonómicas. Diferentes autores han demostrado que las dos primeras propuestas han generado grupos poli- y parafiléticos. En este sentido, el uso exclusivo de genitales masculinos debe tomarse con precaución porque se han descubierto con evidencia molecular, genitales convergentes entre linajes que no comparten un ancestro común (Pérez-

González, 2006; Kury *et al*., 2007; Sharma y Giribet, 2011; Sharma *et al*., 2011a, 2011b; Cruz-López, 2014; Cruz-López y Francke, 2015, en prensa; Cruz-López *et al*., 2016).

Debido a la controversia y el reciente interés en el grupo, en los últimos 20 años se han aplicado herramientas filogenéticas a diferentes niveles dentro de Opiliones con el objetivo de reconocer grupos monofiléticos. A partir del año 2002 a la fecha, se han descrito o elevado al menos 11 grupos a nivel de familia con base en: a) la examinación de genitales masculinos, b) análisis filogenéticos inferidos a través de caracteres morfológicos, c) análisis inferidos de caracteres moleculares, y d) bajo el supuesto de "grupos morfológicamente diferentes" (Kury y Pérez-González, 2002; Kury y Pérez-González en Kury, 2003; Pérez-González y Kury, 2007; Sharma y Giribet, 2011; Sharma *et al*., 2011b; Kury, 2012, 2014; Pinto-da-Rocha, 2014; Bragagnolo *et al*., 2015; Kury y Villarreal, 2015).

Actualmente, el uso de datos moleculares ha cobrado mayor importancia en la generación de hipótesis filogenéticas descartando la información morfológica. Los trabajos que incorporan la información morfológica sobre topologías obtenidas previamente con datos moleculares son escasas, y no se han reportado trabajos que combinen ambas fuentes de información en las reconstrucciones filogenéticas en grupos dentro de Opiliones (Giribet *et al*., 2010; Hedin y Thomas, 2010; Sharma y Giribet, 2009; Sharma *et al*., 2011b, 2016; Wolff *et al*., 2016a, 2016b).

Por lo anterior, en este trabajo se realizó la revisión sistemática de la familia Stygnopsidae Sørensen, 1932 utilizando datos combinados de la morfología externa y genital, y tres marcadores moleculares, dos mitocondriales (COI y 16S) y uno nuclear (28S).

Sistemática de la familia Stygnopsidae

La familia Stygnopsidae tiene una historia taxonómica confusa, siendo varios de sus géneros y especies descritos antes del reconocimiento de la familia, como parte de Phalangodidae o Assamiidae Sørensen, 1884. Sørensen (1932) describió originalmente a Stygnopsidae como aquellos Laniatores con distitarso I con dos segmentos y ausencia de lóbulos maxilares sobre la coxa II. Todos los géneros que actualmente se incluyen en la familia pasaron por la tendencia

tipológica de Roewer, y posteriormente por la tendencia reduccionista de Goodnight y Goodnight. Kury (1997, 2003), Kury y Cokendolpher (2000), Cokendolpher (2004) y Mendes y Kury (2007) fueron quienes redefinieron a la familia como aquellos Laniatores con una morfología genital plesiomórfica en comparación con Gonyleptoidea, Epedanoidea y Assamiioidea. Estos autores reconocieron nueve géneros y 36 especies dentro de la familia.

Actualmente, las hipótesis filogenéticas con base en información morfológica y molecular soportan que Stygnopsidae es grupo hermano de las restantes familias de Gonyleptoidea, siendo el grupo más tempranamente divergente. Por lo tanto, la morfología genital se ha considerado como un atributo plesiomórfico dentro de esa superfamilia, y convergente con la morfología de algunas familias asiáticas (*e.g.* Epedanidae y Pyramidopidae), (Kury, 1994, 1997). Sin embargo, se han incluido pocos taxones de la familia Stygnopsidae en diferentes trabajos filogenéticos, los cuales son insuficientes para inferir las relaciones filogenéticas dentro de la familia (Kury, 1994, 1997; Giribet *et al*., 2002, Sharma y Giribet, 2011; Cruz-López y Francke, 2015; Kury y Villarreal, 2015; Cruz-López *et al*., 2016).

Estudios enfocados en Stygnopsidae comenzaron con Cokendolpher (2004), quién revalidó el género *Chinquipellobunus* Goodnight y Goodnight, 1944 de su sinonimia bajo *Hoplobunus* Banks, 1900, sinonimia propuesta por Goodnight y Goodnight (1953). Adicionalmente, Cokendolpher confirmó la importancia de los genitales masculinos para el reconocimiento genérico en la familia. Posteriormente, Cruz-López y Francke (2012, 2013a) describieron tres especies de *Paramitraceras* Pickard-Cambridge, 1905, además rediagnosticaron al género e ilustraron por primera vez los genitales masculinos mediante microscopia electrónica de barrido.

Como parte de la revisión sistemática del género *Karos* Godnight y Goodnight, 1944,Cruz-López y Francke (2015) refutaron las sinonimias de Goodnight y Goodnight (1953), revalidando cuatro géneros, además de la adición de tres géneros y nueve especies nuevos. Además, se concluyó que la taxonomía del grupo estaba fuertemente influenciada por el criterio taxonómico de Goodnight y Goodnight (1953), por lo que era probable la existencia de grupos para- y/o polifiléticos. Lo anterior influyó significativamente en el desarrollo de la revisión sistemática de la familia.

La presente tesis está compuesta por tres artículos científicos que fueron generados de menor a mayor complejidad de acuerdo al conocimiento acumulado sobre las relaciones filogenéticas dentro de la familia Stygnopsidae. En esta tesis, los artículos son presentados a modo de capítulos, como se menciona a continuación:

Capítulo 1. Artículo: Cruz-López, J. A. y Francke, O. 2013b. On the enigmatic genus *Philora*: familial assignment and taxonomic revision (Opiliones: Laniatores: Stygnopsidae). *The Journal of Arachnology*, 41: 291-305. En este trabajo se revisó el género *Philora* Goodnight y Goodnight, 1954, que se encontraba sin asignación familiar. Los autores determinaron que *Philora* pertenece a Stygnopsidae con base en la examinación de los genitales masculinos, y propusieron un patrón genital único en la familia, el cual se encuentra solamente en los géneros *Paramitraceras*, *Philora* y *Troglostygnopsis sensu stricto*. Este patrón llamado "Paramitraceras" podría tener un solo origen, por lo que estos tres géneros podrían estar relacionados entre sí. Dos años después, Cruz-López y Francke (2015) mediante un análisis filogenético con base en información morfológica, demostraron que dicho patrón genital se originó una sola vez en estos tres géneros, formalizándose así el grupo genérico monofilético "Paramitraceras".

Capítulo 2. Artículo: Cruz-López, J. A., Proud, D. y Pérez-González, A. 2016. When troglomorphism dupes taxonomists: morphology and molecules reveal the first pyramidopid harvestman (Arachnida, Opiliones, Pyramidopidae) from the New World. *Zoological Journal of the Linnean Society*, 177: 602-620. En este trabajo los autores se enfocaron en la especie originalmente descrita como *Stygnomma pecki* Goodnight y Goodnight, 1977, dentro de Samooidea: Stygnommatidae. Pérez-González (2006) en la revisión de Stygnommatidae, detectó que *S. pecki* no compartía ninguna afinidad con los miembros de Stygnommatidae, incluso con ningún miembro de Samooidea. Debido a la morfología genital, el anterior autor consideró que *S. pecki* podría tratarse de un estygnópsido tempranamente divergente, con una morfología externa inusual como consecuencia de la vida cavernícola. Durante la revisión de ejemplares de Stygnopsidae, otros Gonyleptoidea, Epedanoidea y Assamiioidea, más la generación de secuencias de tres marcadores moleculares (COI, 18S y parcial 28S), los autores detectaron que en realidad *S. pecki* pertenece a Pyramidopidae, familia conocida solamente de África Tropical. También en este trabajo se examinó detalladamente la morfología externa y genital mediante microscopía electrónica de barrido. Además se realizaron estudios anatómicos del movimiento de los órganos

copuladores masculinos, con esto se generó información para el reconocimiento de Pyramidopidae y Assamiioidea. También en este trabajo se proporcionó la primera evidencia para considerar que los genitales masculinos de Stygnopsidae no son convergentes con Epedanidae ni con Pyramidopidae.

Capítulo 3. Artículo de requisito: Cruz-López, J. A. y Francke, O. En prensa Total evidence phylogeny of the North American harvestman family Stygnopsidae (Opiliones: Laniatores: Grassatores) reveals hidden diversity. *Invertebrate Systematics*. En este trabajo se propuso la primer hipótesis filogenética de Stygnopsidae con base en evidencia total, en el cual se incluyeron la mayor cantidad de representantes posibles. Los resultados apoyan a Stygnopsidae como un grupo monofilético conformado por dos clados: Stygnopsinae Sørensen, 1932 y Karosinae subfam. nov. Los géneros *Hoplobunus*, *Stygnopsis* Sørensen, 1902 y *Serrobunus* Goodnight y Goodnight, 1942 stat. rev. fueron rediagnosticados. Adicionalmente se describieron los siguientes taxones: *Iztlina venefica* gen. nov. *et* sp. nov., y *Tonalteca* gen. nov. También se propusieron los siguientes cambios taxonómicos: *Serrobunus queretarius* (Šilhavý, 1974) comb. nov., *Stygnopsis apoalensis* (Goodnight y Goodnight, 1973) comb. nov., *Stygnopsis mexicana* (Roewer, 1915) comb. nov., *Stygnopsis oaxacensis* (Goodnight y Goodnight, 1973) comb. nov. y *Tonalteca spinooculorum* (Goodnight y Goodnight, 1973) comb. nov. La evolución de la morfología genital, así como la evolución de caracteres convergentes en los genitales del grupo "Paramitraceras" fueron analizados. También se discutió la convergencia de poros glandulares en los machos y de los pedipalpos desarmados en Stygnopsinae. Finalmente, se abordó la posición filogenética de *Mexotroglinus* Šilhavý, 1977, un género monotípico que presenta características morfológicas de ambas subfamilias, pero que se anida dentro de Stygnopsinae.

OBJETIVOS

GENERAL

- Investigar la Sistemática de la familia Stygnopsidae empleando evidencia morfológica y molecular.

PARTICULARES

- Proponer una hipótesis filogenética para poner a prueba la monofilia de la familia Stygnopsidae.
- Proponer un nuevo arreglo taxonómico de acuerdo a los resultados del análisis filogenético.

Capítulo 1. Artículo: Cruz-López, J. A. y Francke, O. 2013b. On the enigmatic genus *Philora*: familial assignment and taxonomic revision (Opiliones: Laniatores: Stygnopsidae). *The Journal of Arachnology*, 41: 291-305.

2013. The Journal of Arachnology 41:291–305

On the enigmatic genus *Philora*: familial assignment and taxonomic revision (Opiliones: Laniatores: Stygnopsidae)

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Abstract. The harvestman genus *Philora* Goodnight & Goodnight 1954 and the type species *P. tuxtlae* are redescribed, and *Philora quetzalzin* new species is described. The genus is newly assigned to the family Stygnopsidae Sørensen 1932 based on external morphology and male genitalia, which are described herein for the first time. The genus is compared with the morphologically similar genera *Paramitraceras* Pickard-Cambridge 1905, *Sbordonia* Šilhavý 1977, and *Troglostygnopsis* Šilhavý 1974 sensu stricto. *Philora* is unique within the family in having a scutum completum. The presence of a scutum completum in *Philora* and others laniatoreans is discussed. The male genitalia of the genera *Paramitraceras*, *Philora*, *Troglostygnopsis* and presumably the genus *Sbordonia*, are very similar and share a morphological pattern described here as the Paramitraceras-pattern.

Keywords: Mexico, Stygnopsidae, new species, scutum completum, male genitalia

There are 66 genera and 92 species without familial assignment (incertae sedis) within the harvestman suborder Laniatores Thorell 1876, representing 4.8% and 2.2% of the total diversity of the suborder (Kury 2011). Recently, some genera listed as incertae sedis or with predetermined familial assignment have been transferred to different families, based on morphological characters (particularly male genitalia) or based on cladistic analyses (Pinto-da-Rocha & Hara 2009; Pérez-González 2011; Kury 2012; Villareal & Kury 2012). The monotypic genus *Philora* Goodnight & Goodnight 1954 and its type species *P. tuxtlae* was described from material collected near the San Martin Volcano, Los Tuxtlas, Veracruz in Mexico. The authors indicated that this genus is related to *Paramitraceras* Pickard-Cambridge 1905, differing only by a lower tarsal count of 2(1):2(1):4:4 in *Philora* versus 3(2):4(2):5:5 in *Paramitraceras*. Initially, this genus was assigned to the subfamily Phalangodinae Simon 1879 of the family Phalangodidae Simon 1879, a familial assignment based on few, poorly understood external morphological characters, and the genus was later regarded as incertae sedis until adequately reviewed in a modern context (Kury & Cokendolpher 2000; Kury 2003).

Recently we made several collecting trips to the rainforests of the Los Tuxtlas region, and have collected adult specimens of *P. tuxtlae* from the type locality. In addition, specimens of a second species of the genus, described herein, were collected in the western region of the state of Veracruz. The male genitalia of the two species assigned to *Philora* have an internal capsule forming a follis on the ventral side in dorsal view of the pars distalis, with a few distal espiniform projections and with several setae on the pars distalis; this morphology corresponds to the general pattern of the family Stygnopsidae Sørensen 1932, and also shows great similarity to the male genitalia of the genus *Paramitraceras* (Pérez-González 2006; Cruz-López & Francke 2012, 2013).

Using the external morphology and male genitalia of the two species, we revise the diagnosis of the genus, newly transfer the genus to the family Stygnopsidae, and discuss and describe the Paramitraceras-pattern of the male genitalia, present in the genera *Paramitraceras*, *Philora*, the type species of the genus *Troglostygnopsis* Šilhavý 1974, and probably in the genus *Sbordonia* Šilhavý 1977.

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METHODS

The material examined is deposited in the Colección Nacional de Arácnidos (CNAN), Instituto de Biología, Universidad Nacional de México (UNAM), Mexico. We made photos using a Hitachi SU1510 Scanning Electronic Microscope (SEM) and a Nikon Coolpix S10 VR camera. Photographs were edited using PhotoShop CS5 software. Male genitalia nomenclature follows Cruz-López & Francke (2013).

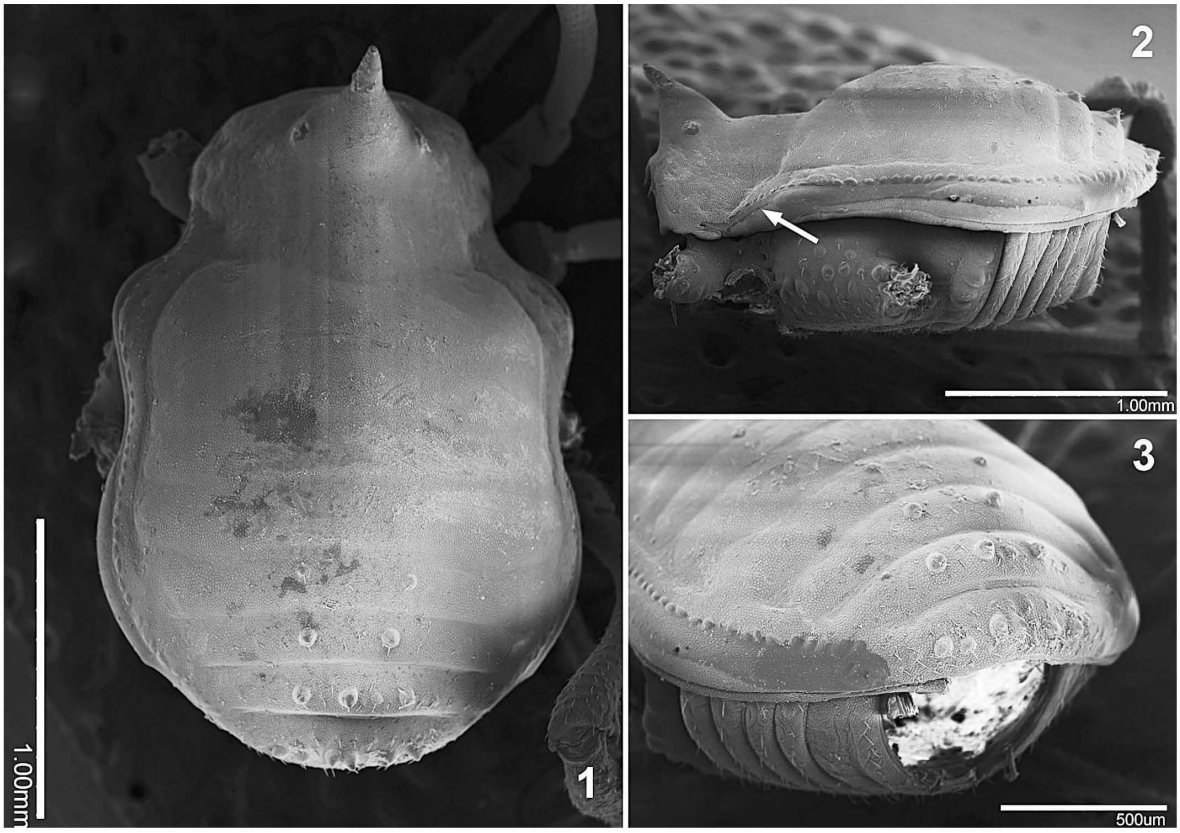
TAXONOMY

Family Stygnopsidae Sørensen 1932
Genus *Philora* Goodnight & Goodnight 1954

Philora Goodnight & Goodnight 1954:345; Kury & Cokendolpher 2000:154; Kury 2003:27.

Type species.—*Philora tuxtlae* Goodnight & Goodnight 1954, by original designation

Emended diagnosis.—Small stygnopsids, 3 mm maximum length. Scutum completum with numerous light-colored areas on sides (Figs. 1, 17, 33–36). Setiferous tubercles on pedipalps with bases conical, setae inserted basally (Figs. 8, 9, 43). Metatarsus IV dorsally with one prominent setiferous tubercle distally, with one or two apical setae (Figs. 44, 46). Pars distalis with Paramitraceras-pattern (as defined herein), with 6 to 10 pairs of lateral setae, arranged in two groups; these setae originating basally or laterally to follis. Pars distalis ventroapically with two pairs of setae, paramedian pair are represented by two microsetae close to each other; lateral pair large, pointing basally. Lobes of the dorsal bilobular projection wing-shaped, apex points basally; ventroapical margin of pars distalis with two lateral spiniform projections (Figs. 12–14, 28–32). Tarsal count low, 2:2:4:4, distitarsi I and II with one subarticle only. Males with four light-colored, pointed areas in the stigmatic region (Figs. 37–40).



Figures 1–3.—*Philora tuxtlae* Goodnight & Goodnight 1954, male. 1. Habitus dorsal view; 2. Habitus lateral view (arrow points to anterior lateral light-colored areas); 3. Habitus dorso-posterior view.

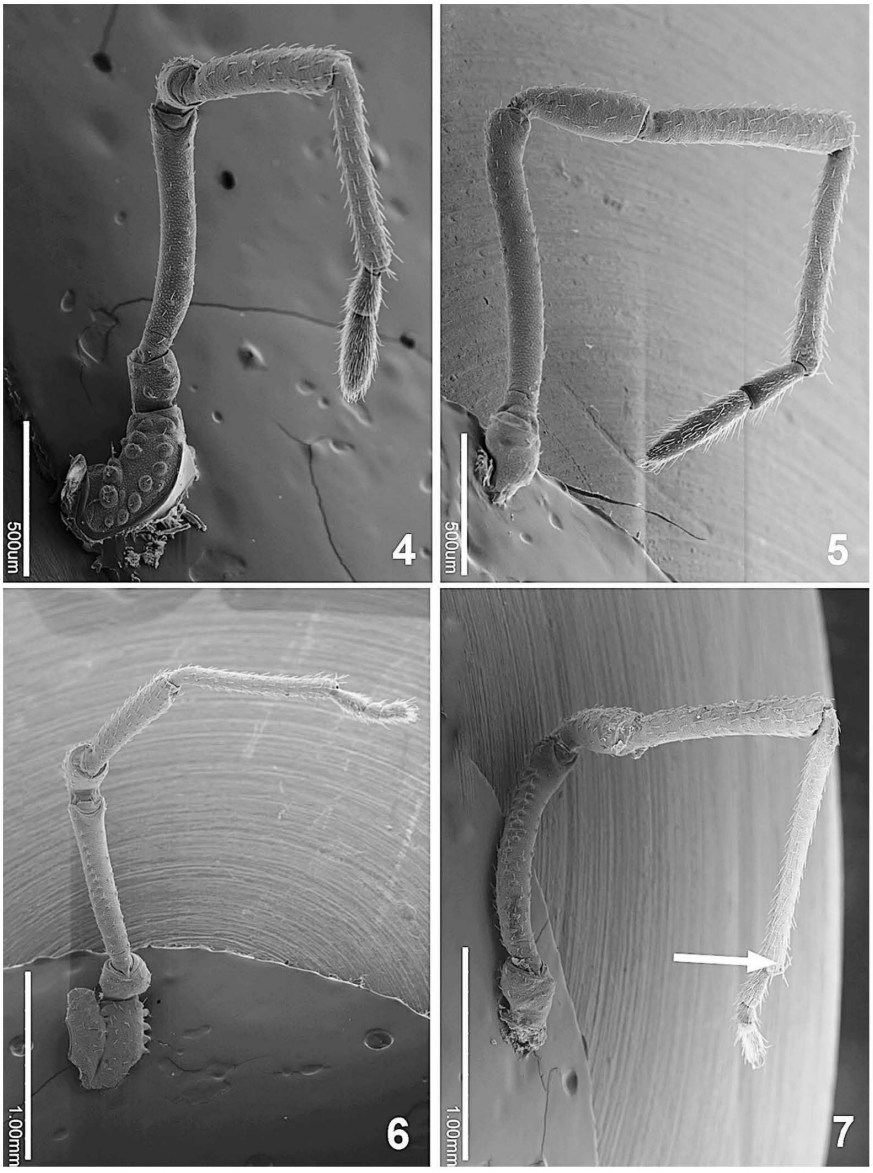
Philora tuxtlae Goodnight & Goodnight 1954
(Figs. 1–16, 33, 36–38, 41–44)

Philora tuxtlae Goodnight & Goodnight 1954:346, Figs. 1, 2; Kury & Cokendolpher 2000:154; Kury 2003:27.

Type data.—MEXICO: *Veracruz*, Holotype male?, and paratypes males or females? (see Remarks), San Martín volcano, 1050 m, 12 km N of San Andrés Tuxtla, Municipio San Andrés Tuxtla (deposited in American Museum of Natural History, New York; not examined).

Material examined.—MEXICO: *Veracruz*, 1 ♀, Estación Biológica Tropical de "Los Tuxtlas", UNAM, Municipio San Andrés Tuxtla (18°34′47.399″N, 95°04′53.399″W, 429 m.), 27 August 2005, O. Francke, A. Valdez, H. Montaño, M. Córdoba, A. Jaimes (CNAN); 1 ♂, same data, 11 January 2012, O. Francke, G. Montiel, J. Cruz, R. Monjaraz (CNAN); 8 ♂, 9 ♀, 6 juveniles, same data, 10 November 2012, O. Francke, G. Montiel, A. Valdez, J. Cruz, R. Monjaraz (CNAN); 5 ♂, 10 ♀, 5 juveniles, 1 km SE. of Díaz Ordaz, Municipio San Andrés Tuxtla (18°31′39.899″N, 95°05′12.875″W, 480 m), 10 November 2012, O. Francke, G. Montiel, A. Valdez, J. Cruz, R. Monjaraz (CNAN); 3 ♀, 2 juveniles, 1.5 km E of Ejido "La Perla de San Martín", Municipio Catemaco (18°33′19.800″N, 95°07′16.103″W, 749m), 11 November 2012, O. Francke, G. Montiel, A. Valdez, J. Cruz, R. Monjaraz (CNAN); 2 ♀, 1 juvenile, 3 km W of Ejido Ruíz Cortines, Municipio Catemaco (18°31′24.852″N, 95°08′27.780″W, 1,152 m), 11 November 2012, O. Francke, G. Montiel, A. Valdez, J. Cruz, R. Monjaraz (CNAN).

Diagnosis.—*Philora tuxtlae* differs from *P. quetzalzin* in having a narrow ocularium, with a noticeably pointed apex. The dorsal ornamentation is composed of minute tubercles in *P. tuxtlae* (Fig. 1), but has larger tubercles in *P. quetzalzin* (Fig. 17); the posterior tergites with the medial spiniform tubercles markedly larger than the rest of the dorsum in *P. tuxtlae* (Figs. 1–3), whereas they are uniform in size in *P. quetzalzin* (Fig. 17–19). The sexual dimorphism in *P. tuxtlae* is only in the coloration and shape of the stigmatic region (Figs. 37, 38); whereas in *P. quetzalzin*, the sexual dimorphism is in the coloration and the shape of stigmatic region and the cheliceral size (scutum/cheliceral hand ratio: 2.8 in males, vs. scutum/cheliceral hand ratio: 3.1 in females), and the shape of ocularium (Figs. 33, 34, 39, 40). Males of *P. tuxtlae* have a small dorsodistal tubercle on metatarsus IV (Figs. 7, 44), which is larger and mesally in *P. quetzalzin* (Figs. 23, 46). The 12 setae of the pars distalis originate lateral to the follis, and are in two distinctive groups of three setae (basal and lateral) on each side in *P. tuxtlae* (Figs. 12–14); whereas they number 20, with 10



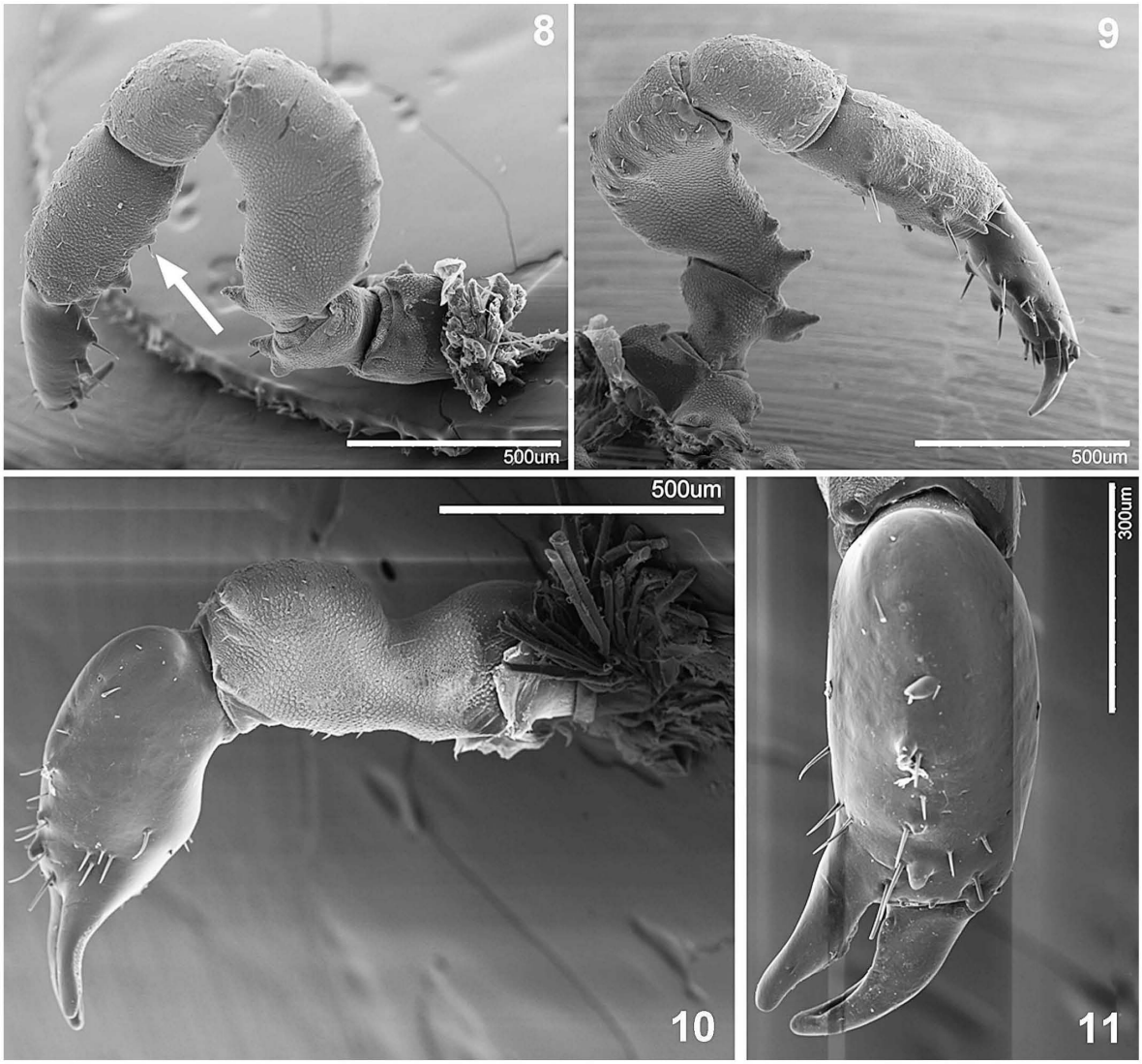
Figures 4–7.—*Philora tuxtlae* Goodnight & Goodnight 1954, male. 4. Leg I mesal view; 5. Leg II mesal view; 6. Leg III mesal view; 7. Leg IV mesal view (arrow points to dorsodistal setiferous tubercle).

scattered setae on each side in *P. quetzalzin* (Figs. 28–32). The ventroapical macrosetae of the pars distalis is stouter in *P. quetzalzin* (Figs. 31, 32), than in *P. tuxtlae* (Figs. 14, 15).

Redescription.—*Male:* Measurements (based on a male from Estación Biológica Tropical "Los Tuxtlas"): Scutum length: 2.3, scutum width: 1.3. Dorsum: Scutum covered by very small tubercles, equally sized on all dorsum, with few setae. Posterior tergites with medial tubercles noticeably developed, rounded. Ocularium conical, basal area small, pointed distally, without posterior bulge (Figs. 1–3).

Venter: Densely covered by spiniform setae. Coxa I with 1 median, irregular row of small, setiferous tubercles. Free sternites with setae similar to the rest of ventral region, but more densely covered. Stigmatic area with 4 differentiated light-colored areas, 2 posterior areas slightly closer to each other than anterior pair (Fig. 37). Anal plate with some rounded tubercles.

Chelicera: Scutum/cheliceral hand ratio: 4, with 3 to 4 setiferous spiniform tubercles on the frontal side, slightly developed. Cheliceral teeth present only on fixed finger,



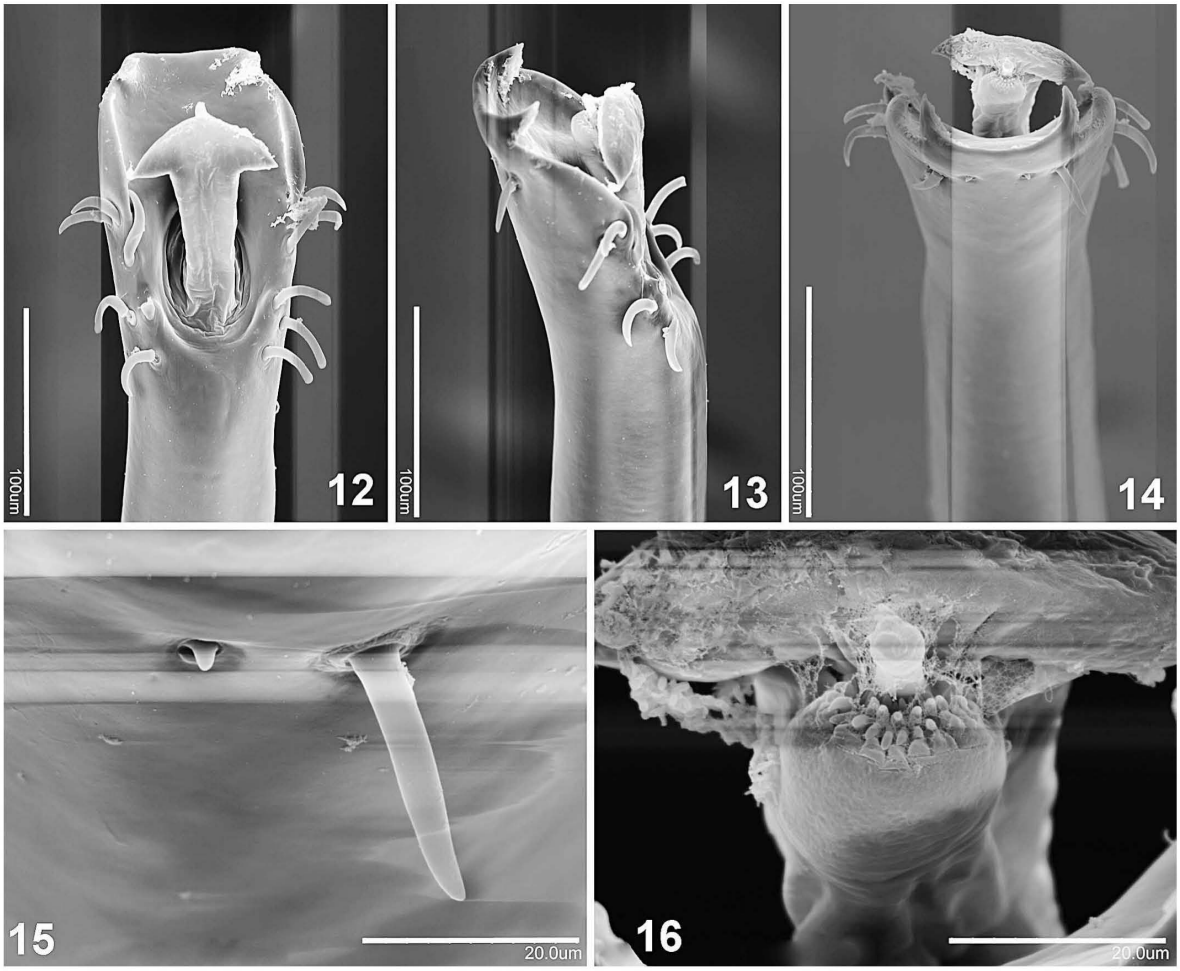
Figures 8–11.—*Philora tuxtlae* Goodnight & Goodnight 1954, male. 8. Pedipalp ectal view (arrow points to setiferous tubercle on pedipalpal tibia); 9. Pedipalp mesal view; 10. Chelicera ectal view; 11. Chelicera frontal view.

composed by 2 low and contiguous teeth; movable finger with medial concavity (Figs. 10, 11).

Pedipalp: Coxa with median irregular row of tubercles. Trochanter globular, with 2 prominent spiniform tubercles ventrally. Femur slightly concave mesally, with few spiniform tubercles dorsally; ventrally with 3 noticeable, spiniform tubercles, 2 basal, the basalmost larger than the others; the third one distally displaced. Patella unarmed, covered only by setae. Tibia and tarsus with 3 spiniform tubercles on both sides, the bases of theses tubercles are conical, with the setae displaced basally (Figs. 8, 9).

Legs: Measurements: I: 0.35/0.20/0.70/0.55, II: 1.00/0.36/0.85/0.85, III: 0.45/0.25/0.69/0.80, IV: 1.00/0.35/0.70/1.00. All legs similar in ornamentation, covered by small setae, denser distally; posterior legs without remarkable sexual dimorphism, covered by small setae, denser distally. Metatarsus IV with dorsodistal tubercle, small and inconspicuous, with a small, curved apical seta (Figs. 4–7, 44).

Genitalia: Setae of pars distalis filiform, rounded apically, without grooves; grouped into 2 distinct sets, 1 basal and 1 mesal, of 3 setae each. Ventroapical region of pars distalis with 2 submedial microsetae and 2 lateral macrosetae pointing basally, similar to the others setae of pars distalis; ventroapical margin with 2 pointed apices. Base of follis excavated; bilobular dorsal projections of the follis contiguous with it, apices robust, pointed distally. Stylus short and hidden within



Figures 12–16.—*Philora tuxtlae* Goodnight & Goodnight 1954, male genitalia. 12. Dorsal view; 13. Lateral view; 14. Dorso-ventral view; 15. Detail of one ventroapical microsetae and one ventroapical macrosetae on pars distalis; 16. Dorsal view of bilobular projection of follis.

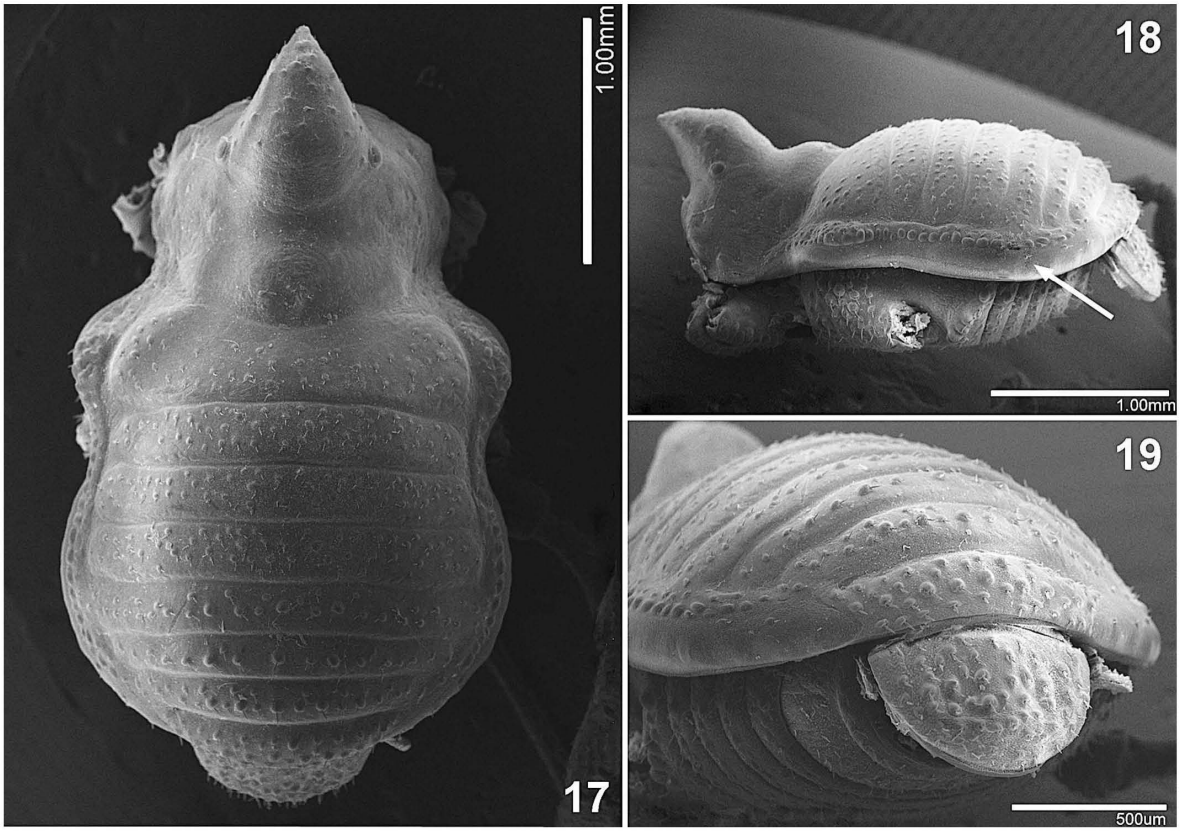
the apical portion of follis, spiniform projections only visible on the ventral side of glans. (Figs. 12–16).

Color: Scutum and venter dark brown, boundaries between dorsal areas lighter. Lateral margins of scutum and anterior portion of dorsal areas slightly darker. Ocularium and prosoma reticulated, background color brown, with black grid. Chelicera and pedipalps are very similar in coloration to ocularium, but lighter. Legs light brown, distal articles dark yellow. Stigmatic area with four light-colored pointed areas, almost white (Figs. 35, 36).

Female: Very similar to male, differing only in slightly larger size, and the shape and coloration of the stigmatic region. Females with lateral margins of stigmatic area shorter than on males, without 4 light-colored areas ventrally (Figs. 37, 38).

Variation: There is minimal morphological variation among males and females; the following variation in size was observed [ranges in mm (males/females) $n = 10$]: scutum length 2.3–2.5/2.5–2.7, pedipalpal femur length 0.6–0.7/0.7–0.8, femur II length 1.0–1.1/1.1–1.2, femur IV length 1.2–1.4/1.2–1.3.

Remarks.—The type material of this species was not studied, but we consider that the material examined corresponds to *P. tuxtlae* because in the original description the authors mentioned the following characters: small size, low tarsal count, dorsal ornamentation; which match the specimens redescribed here. Further, the material examined comes from localities within the "Reserva Especial de la Biosfera del Volcán San Martín", which includes the type locality (Fig. 53). We question the sex of the types, as indicated by the original authors, because males and females are very similar and we have examined some stygnopsids of the genera *Hoplobunus* Banks 1900, *Karos* Goodnight & Goodnight 1944 and *Paramitraceras*, which were identified and labeled by Goodnight and Goodnight, and in most of them the sexual and life-stages (adult vs. juvenile) determinations are erroneous. These errors in determining the sex by the Goodnights



Figures 17–19.—*Philora quetzalzin* new species, male. 17. Habitus dorsal view; 18. Habitus lateral view (arrow points to posterior lateral light-colored areas); 19. Habitus dorso-posterior view.

have been corroborated by other authors (e. g., Vázquez & Cokendolpher 1997; Cokendolpher 2004; Shear, 2010; Cruz-López & Francke 2013), and thus we do not trust their determinations without examining the types.

Distribution.—*Philora tuxtlae* is only known from the tropical rainforest of the Reserva Especial de la Biósfera, Volcan San Martín, Los Tuxtlas, Veracruz (Fig. 53).

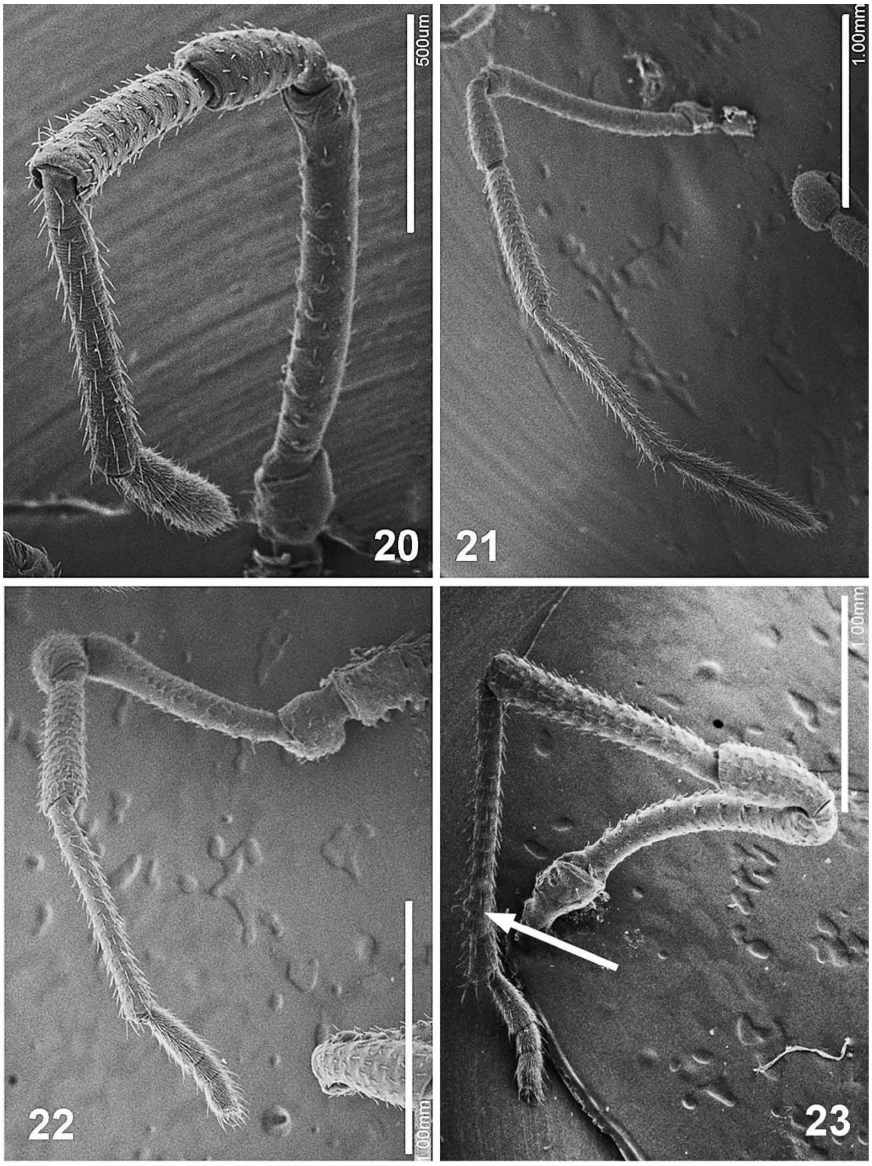
Natural history.—The specimens collected in August 2005 and January 2012 were located by actively searching in appropiate microhabitats and were found inside decomposing tree stumps. Using this collecting method we also found many laniatorean specimens of the genera *Flaccus* Goodnight & Goodnight 1947 of the family Biantidae Thorell 1889 [we decided not to follow the synonymy of *Flaccus* under *Stygnomma* Roewer 1912, proposed by Goodnight & Goodnight (1951), according to unpublished data of Pérez-González (2006)]; *''Cynorta''* Koch 1839 (Kury et al. 2007), *Erginulus* Roewer 1912, *Eucynortula* Roewer 1912, and *Paecilaema* Koch 1839 of the family Cosmetidae Koch 1839; *Hoplobunus*, *Paramitraceras*, and an undetermined genus of the family Stygnopsidae; and *Pachylicus* Roewer 1923 of the family Zalmoxidae Sørensen 1886. However, active searching was a poor method to collect *Philora* specimens. In November 2012, we collected by sifting leaf litter over a white sheet, obtaining contrasting results, and many more specimens of *Philora* were collected. This species showed thanatosic behavior, remaining stationary for several minutes, and resembling small pieces of dirt on the white sheet (making visual search difficult). However, after a few minutes, they started crawling away and their identification and capture became much easier. *Philora tuxtlae* was found in both well-preserved and disturbed rainforest (mostly cleared to make pastures for cattle) where there was leaf-litter accumulation.

Philora quetzalzin new species
(Figs. 17–32, 33, 35, 39, 40, 45, 46)

Type material.—MEXICO: *Veracruz*, holotype male, 5 km E of Tlaquilpa, Municipio Tlaquilpa (18°38′30.228″N, 97°06′26.495″W, 2,233 m), 22 January 2010, O. Francke, A. Valdez, C. Santibañez, J. Cruz (CNAN-T0743). Paratypes: 1 male, same data as holotype (CNAN-T0744); 1 male, 1 female, same locality, 23 March 2007, O. Francke, A. Valdez, C. Santibañez, A. Ballesteros, H. Montaño (CNAN-T0745).

Etymology.—The specific name is derived from ''quetzalzin'', which in Nahuatl means ''small beauty''. The name is used as a noun in apposition.

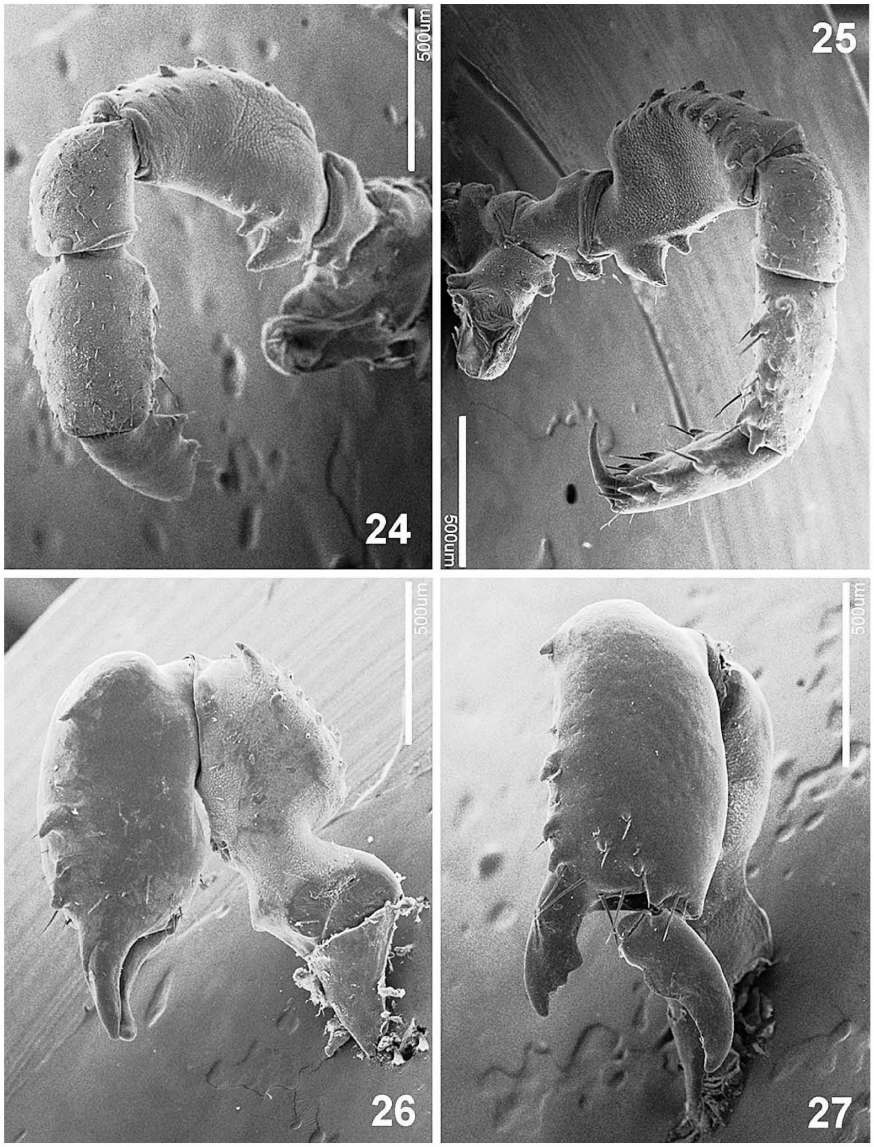
Diagnosis.—*Philora quetzalzin* differs from *P. tuxtlae* in having a moderately dense, noticeable dorsal ornamentation; a



Figures 20–23.—*Philora quetzalzin* new species, male. 20. Leg I frontal mesal view; 21. Leg II mesal view; 22. Leg III mesal view; 23. Leg IV mesal view (arrow points to dorsodistal setiferous tubercle).

strong ocularium with a marked posterior bulge; and tubercles of posterior tergites similar in size and shape to those on the dorsum (Figs. 17–19, 33, 34). It exhibits notable sexual dimorphism, with males having a strongly developed cheliceral hand (scutum/cheliceral hand ratio: 2.8 in males, vs. scutum/cheliceral hand ratio: 3.1 in females), and the base of the ocularium is wider in males than in females; whereas in *P. tuxtlae* there is almost no sexual dimorphism. The two species also differ in cheliceral dentition: the fixed finger has 2 teeth in *P. tuxtlae* and 3 teeth in *P. quetzalzin*; the movable finger has no teeth in *P. tuxtlae* and 2 teeth in *P. quetzalzin* (Figs. 10, 11, 26, 27). The dorsal tubercle on metatarsus IV is distinctive and meso-distal (Figs. 23, 46), whereas on *P. tuxtlae* it is inconspicuous and distal. The setae of the pars distalis number 10 pairs, are disorganized in the basal portion, originating basally to the follis, with medial grooves, and are distally pointed rather than rounded. The ventroapical macrosetae are considerably swollen and quite distinctive (Figs. 28–32).

Description.—*Male (holotype):* Measurements: Scutum length: 2.9, scutum width: 1.9. Dorsum: scutum densely covered with small, rounded setiferous tubercles, slightly larger posteriorly. Prosoma rugose. Base of ocularium broad,



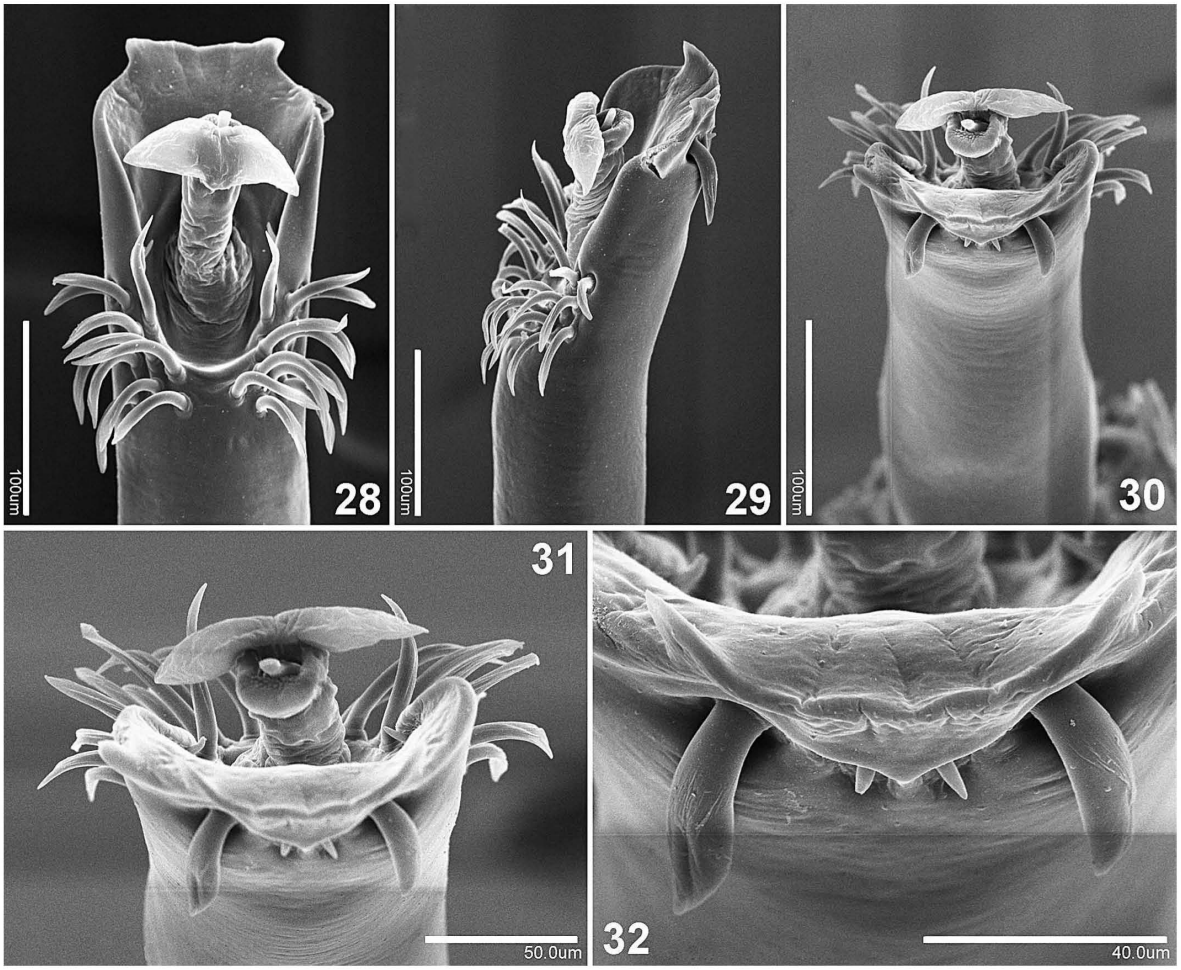
Figures 24–27.—*Philora quetzalzin* new species, male. 24. Pedipalp frontal ectal view; 25. Pedipalp mesal view; 26. Chelicera ectal view; 27. Chelicera frontal view.

occupying over half of prosoma, dorsally covered with anteriorly directed small tubercles, apex of ocularium robust, ocularium with prominent posterior bulge (Figs. 17–19).

Venter: Uniformly ornate with small setiferous tubercles, smaller than on dorsum, except in coxa I where the tubercles are spiniform and slightly developed. Stigmatic area with lateral margins straight, short. Posterior light-colored pointed areas somewhat fused (Fig. 39). Free sternites covered by small setiferous tubercles.

Chelicera: Cheliceral hand swollen (scutum/cheliceral hand ratio: 2.8). Basichelicerite covered dorsally by spiniform tubercles, the largest on meso-distal face. Cheliceral hand inserted dorsally on the basichelicerite; in frontal view covered with 3 spiniform tubercles distally pointed. Cheliceral dentition heterogeneous: fixed finger with 3 teeth, the basal most slightly larger; movable finger with 2 teeth, bulge-shaped, rounded (Figs. 26, 27).

Pedipalp: Coxa with median irregular row of setiferous tubercles. Trochanter globular with two blunt, larger spiniform tubercles. Femur concave on mesal side, with 2 irregular rows of spiniform setiferous tubercles ventrally; mesal row with 2 large tubercles, basal most largest; ectal row with 4



Figures 28–32.—*Philora quetzalzin* new species, male genitalia. 28. Dorsal view; 29. Lateral view; 30. Dorso-ventral view; 31. Dorsal view of bilobular projection of glans; 32. Details of ventroapical pairs of micro- and macrosetae on pars distalis.

smaller ones. Femur covered dorsally by 2 rows of small spiniform tubercles, increasing in size distally. Patella unarmed, covered only by setae. Tibia with 3 setiferous spiniform tubercles on each margin. Tarsal armature similar to tibia, setiferous tubercles with the setae at the base (Figs. 24, 25).

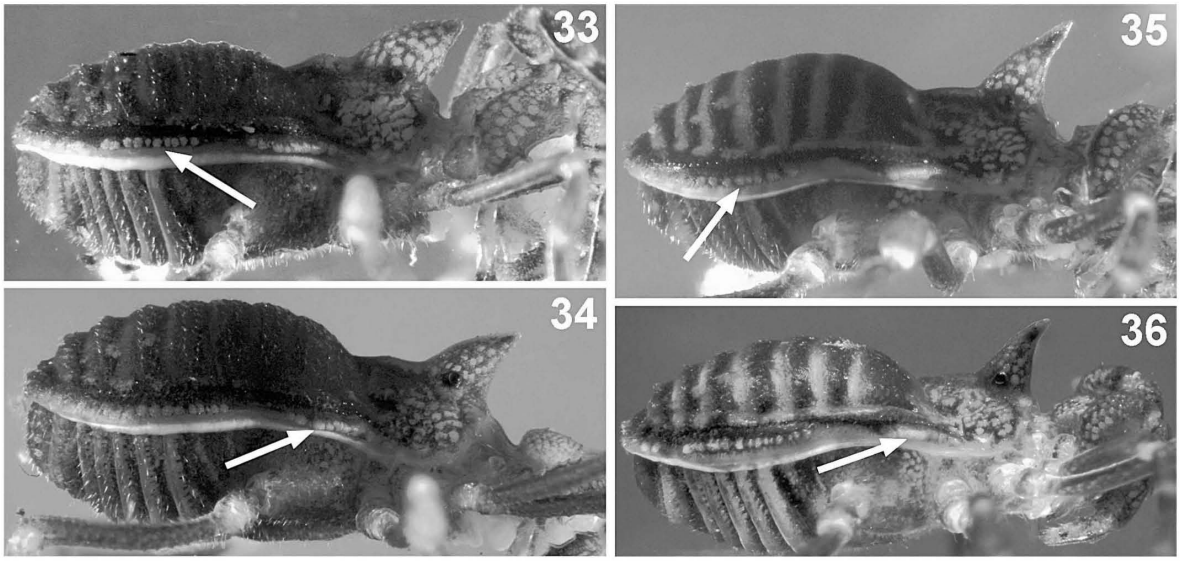
Legs: Measurements: I: 0.55/0.40/0.95/0.75, II: 1.40/0.55/1.05/1.00, III: 0.65/0.40/0.80/1.00, IV: 1.25/0.45/0.90/1.25. All legs similar in ornamentation, covered by numerous small setae. Femora III and IV curved. Leg IV without sexually dimorphic ornamentation. Metatarsus IV with strong spiniform setiferous tubercle mesodistally, with 1 or 2 apical setae (Figs. 20–23, 46).

Genitalia: Pars distalis with 10 pairs of setae, basal to follis, without distinct groupings, all setae with distal median groove. Lateral margins of pars distalis in dorsal view curved towards the follis, with a pair of minute setae on the lateral margins hidden by curls. Apex of distal ventroapical margin with two small lateral projections. Two pairs of ventroapical setae, the middle pair formed by two microsetae, very close between them; the lateral setae slightly spoon-shaped distally, with an apical median groove. Follis narrower than the maximum width of pars distalis, base of follis excavate; bilobular dorsal projection widespread, apices rounded distally; stylus short and hidden within the apical portion of follis. Spiniform projections small and only present in the ventral side of apical follis (Figs. 28–32).

Color: Similar to *P. tuxtlae*, but the boundaries between dorsal areas of scutum almost as dark as the rest of dorsum (Figs. 33, 34).

Female (paratype): Differs from the male in having a narrower ocularium, chelicera noticeably smaller (scutum/cheliceral hand ratio: 3.1), setiferous tubercles of pedipalps less developed and having lateral margins of stigmatic area shorter than the males (Figs. 33, 34, 39, 40).

Distribution.—This species is known only from the type locality (Fig. 53).



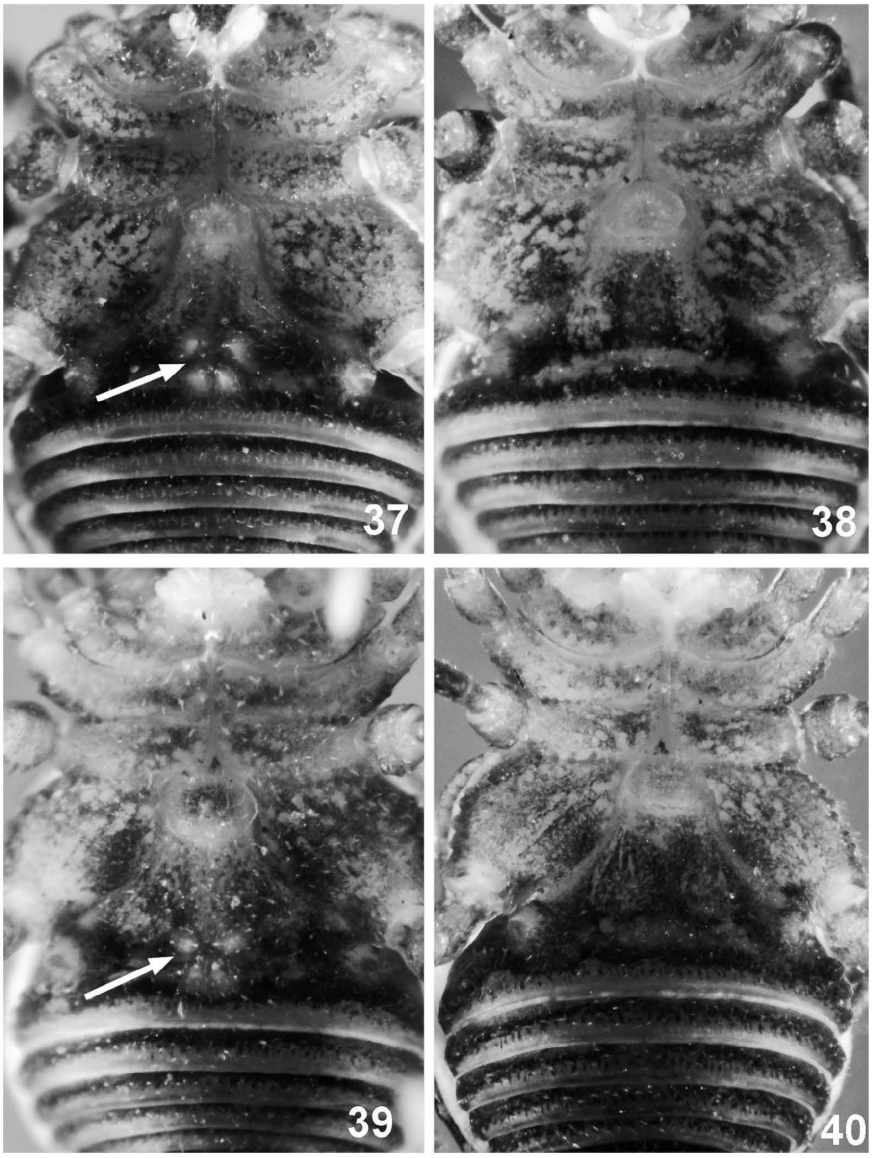
Figures 33–36.—*Philora* species, male and female lateral view. 33. *Philora quetzalzin* new species, male; 34. *P. quetzalzin*, female; 35. *P. tuxtlae* Goodnight & Goodnight 1954, male; 36. *P. tuxtlae* female. Arrows indicate anterior (females, lower illustrations) and posterior (males, upper illustrations) light-colored areas.

Natural history.—Similar to *P. tuxtlae*, the specimens collected in 2010 showed thanatosic behavior, and were found among the roots of decomposing tree stumps, forming a small aggregation with specimens of *Flaccus* sp. *Philora quetzalzin* inhabits a pine-oak forest, above 2,000 m, unlike *P. tuxtlae* which lives in the rainforest of Los Tuxtlas region at a lower altitude of less than 1,200 m.

DISCUSSION

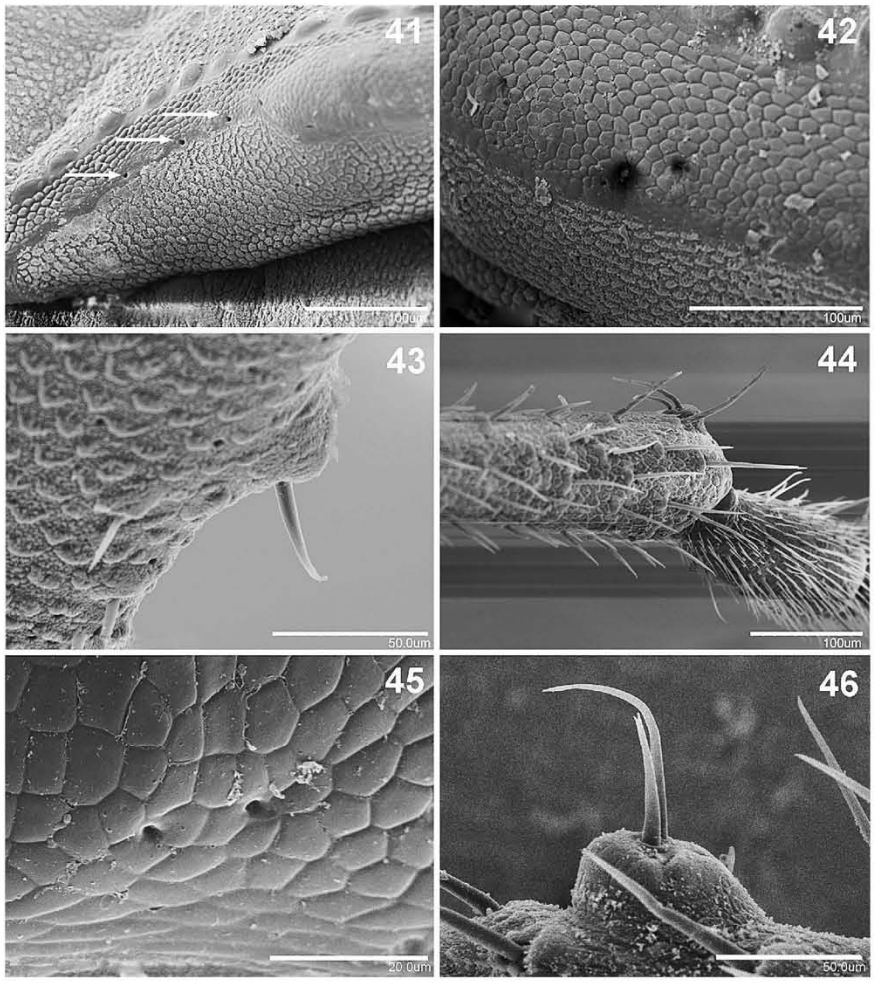
Goodnight & Goodnight (1954) argued that tarsal counts alone were sufficient to differentiate the genus *Philora* from its close relative *Paramitraceras*. It is surprising that those authors did not mention the presence of a scutum completum in the generic diagnosis of *Philora*, because this character is quite distinctive. The fusion of all dorsal tergites forming a scutum completum was previously known only in the suborder Cyphophthalmi Simon 1879; in the families Dicranolasmatidae Simon 1879, Nemastomatidae Simon 1872 and Trogulidae Sundevall 1833 within the suborder Dyspnoi Hansen & Sørensen 1904 (Shear 2006; Sharma & Giribet 2011). Regarding the suborder Laniatores, the scutum completum is present in the family Sandokanidae Özdikmen & Kury 2007 (formerly Oncopodidae Thorell 1876), in the males of *Heteropachylus inexpectabilis* (Soares & Soares 1946) of the family Gonyleptidae Sundevall 1833, and presumably in *Paralola buresi* Kratochvíl 1951 of the family Phalangodidae Simon 1879 (Schwendinger 2007; Ubick 2007; Mendes 2011). This morphological condition was considered plesiomorphic in the order, but this hypothesis is inconsistent with recent outgroup comparison and with the retention of primitive dorsal longitudinal muscles in higher Opiliones (Shultz & Pinto-da-Rocha 2007); and the scutum completum appears to have evolved convergently in several Opiliones lineages (Sharma & Giribet 2009). Moreover, reciprocally in Cyphophthalmi, Sandokanidae and *Philora*, this character is matched by low tarsal counts and could reflect adaptations to similar ecological niches, but this hypothesis has not been tested (Sharma & Giribet 2009, 2011). The recent hypothesis of phylogenetic relationships, using molecular data, of the families with all or one member with scutum completum is: the family Sandokanidae is considered the sister group of the non-phalangodid Grassatores Kury 2002, whereas the family Stygnopsidae is considered the sister group of the superfamily Gonyleptoidea; and finally, the family Gonyleptidae is within the Gonyleptoidea (Giribet et al. 2010; Sharma & Giribet 2011).

The phylogenetic and taxonomic status of Gonyleptidae and Sandokanidae has been well studied, wherein the external morphology and the male genitalia of the majority of the genera and species of the family are well known (e.g., Schwendinger & Martens 2002; Schwendinger 2006, 2007; DaSilva & Gnaspini 2009; Yamaguti & Pinto-da-Rocha 2009; DaSilva & Pinto-da-Rocha 2010; Mendes 2011). In contrast, within the family Stygnopsidae, external morphology and male genitalia are well known for the genera *Chinquipellobunus* Goodnight & Goodnight 1944 (Cokendolpher 2004) and five of six species of *Paramitraceras* (Cruz-López & Francke 2012, 2013). There are published drawings of the male genitalia of the *Hoplobunus boneti* (Goodnight & Goodnight 1942), *H. queretarius* Šilhavý 1974, *Karos rugosus* Goodnight & Goodnight 1971, *Mexotroglinus sbordonii* Šilhavý 1977, *Sbordonia armigera*, both known species of the genus *Stygnopsis* Sørensen 1902, both known species of the genus *Troglostygnopsis* Šilhavý 1974, and SEM photos of *Karos* sp. and *Stygnopsis valida* (Sørensen 1884) (Šilhavý 1974, 1977; Mendes & Kury 2007). Mendes & Kury (2007) described the male genitalia of the family Stygnopsidae, but in the majority of species the male genitalia are unknown.



Figures 37–40.—*Philora* species, male and female ventral views. 37. *Philora tuxtlae* Goodnight & Goodnight 1954, male; 38. *P. tuxtlae* female; 39. *Philora quetzalzin* new species, male; 40. *P. quetzalzin* female. Arrows indicate the four ventral light-colored pointed areas on the males of *Philora* species.

We have observed the male genitalia of some stygnopsids using a scanning electronic microscope and have noted that the male genitalia of the type species of *Troglostygnopsis*, along with the known male genitalia of the genera *Paramitraceras*, *Philora*, and presumably the genus *Sbordonia* (based on the drawing by Šilhavý 1977), share a similar and unique genital pattern, herein called the Paramitraceras-pattern. This pattern is recognizable by having 1) setae of pars distalis generally forming two rows or groups, one dorsolaterally or mesal, and the other, laterobasal and ventrally; 2) numerous pairs of setae in these two rows, from three to fourteen pairs; 3) pars distalis very wide, follis narrow compared with it; 4) presence of a bilobular dorsal projection of the follis; and 5) presence of a unique pair of micro-ventral setae in the meso or meso-distal region of ventral plate (Figs. 47–52). Regarding the other described species of *Troglostygnopsis*, *T. inops* (Goodnight & Goodnight 1971), we have observed that it does not share this male genitalic pattern, and possibly this species should be transferred out of the genus. A phylogenetic analysis of these and other stygnopsid genera would clarify



Figures 41–46.—*Philora* species, details of lateral pores, setiferous tubercle of pedipalp and dorsal distal tubercles of femur IV; 41. *Philora tuxtlae* Goodnight & Goodnight 1954, male, antero-lateral pores (arrows, see also arrow in Figure 2); 42. *P. tuxtlae* male, detail of a pore; 43. *P. tuxtlae* male, setiferous tubercle of pedipalpal tibia (see arrow in Figure 8); 44. *P. tuxtlae* male, detail of dorsal distal spiniform setiferous tubercle on metatarsus IV (see arrow in Figure 7); 45. *Philora quetzalzin* new species, details of latero-posterior pores (arrow in Figure 18); 46. *P. quetzalzin*, detail of dorso meso-distal spiniform setiferous tubercle on metatarsus IV (see arrow in Figure 23).

whether this pattern is due to common ancestry or due to homoplasy. Those three genera can be differentiated by combinations of external and genital characters (Table 1).

The "lateral projections" (Šilhavý 1974, 1977) are present in both species of the genus *Philora*; these structures and the light-colored lateral areas on the sides of the scutum were observed under SEM, and there are numerous micropores in those areas (Figs. 33–36, 41, 42, 45). Šilhavý (1974) proposed that these lateral projections, present in the stygnopsid genera *Karos*, *Paramitraceras*, *Sbordonia* and *Troglostygnopsis* could be glandular openings similar to those reported on other Laniatores (Eisner et al. 2004; Machado et al. 2005; Willemart et al. 2010). A detailed examination using SEM of these light-colored areas on those other genera will contribute to a better knowledge about glandular openings in the family Stygnopsidae.

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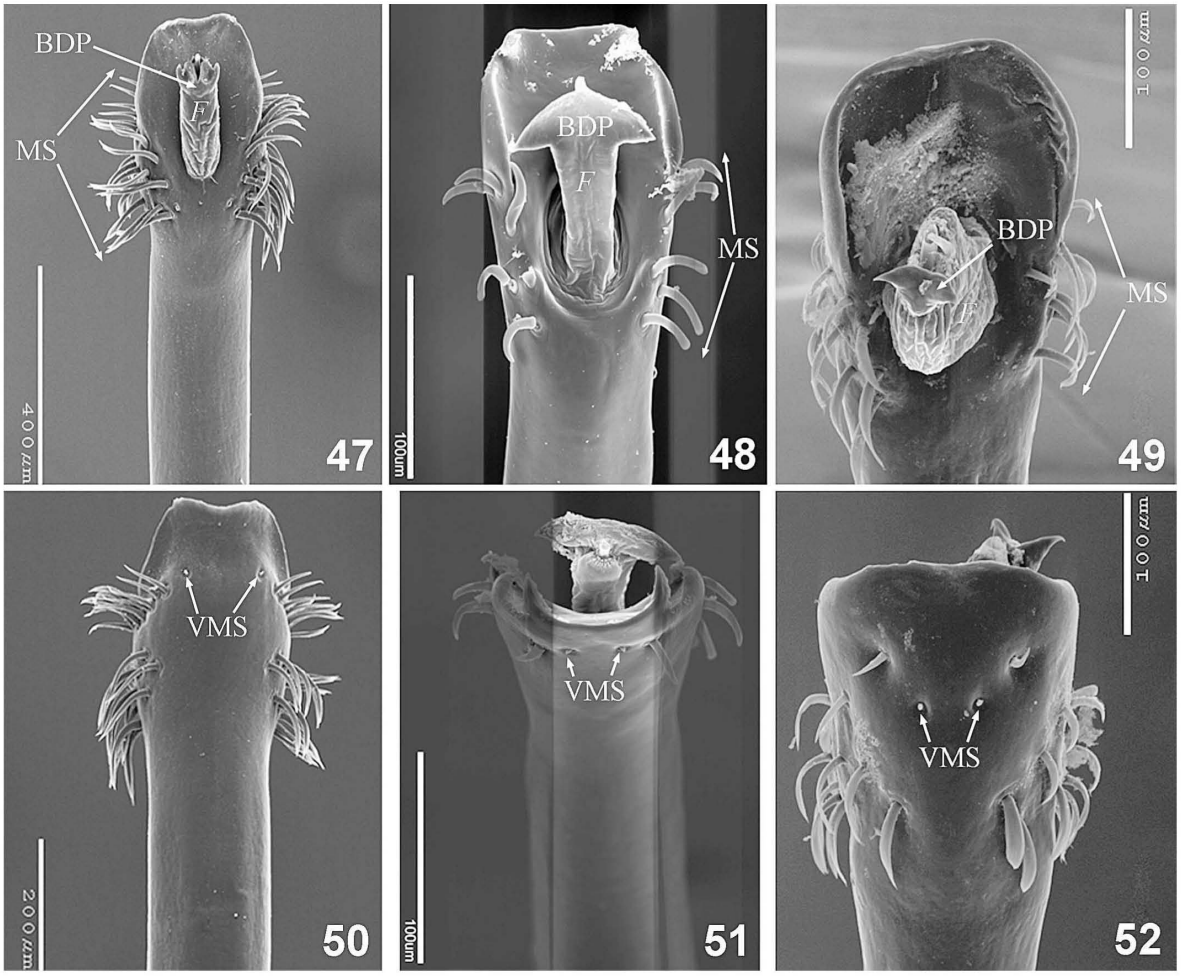

Figures 47–52.—Male genitalia of the genera having the Paramitraceras-pattern. 47 & 50. *Paramitraceras granulatum* Pickard-Cambridge 1905; 47. Dorsal view; 50. Ventral view. 48 & 51. *Philora tuxtlae* Goodnight & Goodnight 1954; 48. Dorsal view; 51. Ventral view. 49 & 52. *Troglostygnopsis anophthalma* Šilhavý 1974; 49. Dorsal view; 52. Ventral view. Abbreviations: BDP = bilobular dorsal projection, *F* = follis, MS = macrosetae, VMS = ventral microsetae.

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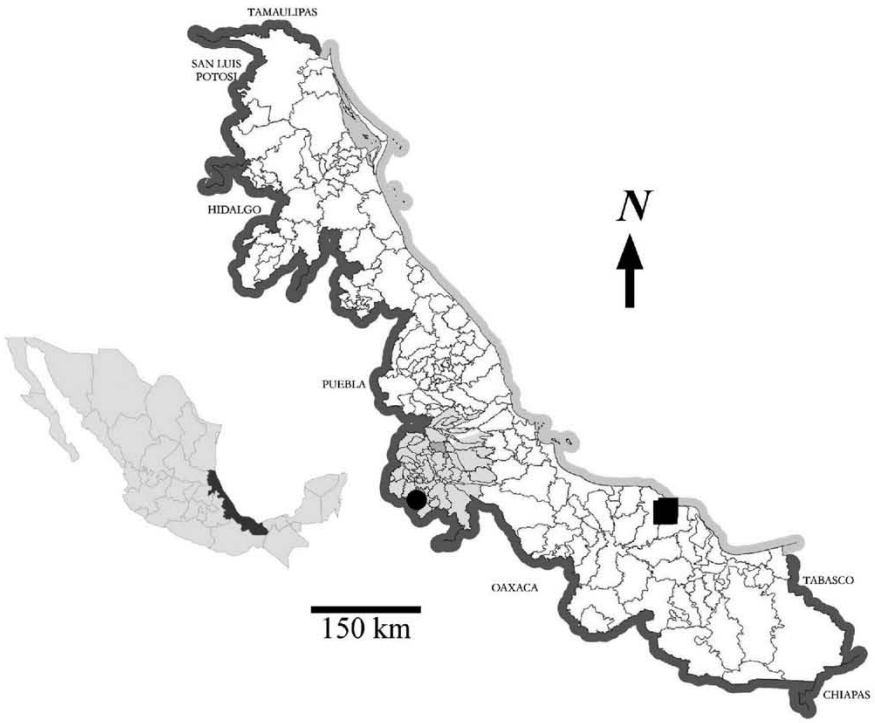

Figure 53.—Distribution of the species of *Philora*. State of Veracruz enlarged. Circle: *Philora quetzalzin* new species. Squares: *Philora tuxtlae* Goodnight & Goodnight 1945, including the type locality.

Table 1.—Differences in morphological characters between the stygnopsid genera *Paramitraceras* Pickard-Cambridge 1905, *Philora* Goodnight & Goodnight 1954, *Sbordonia* Šilhavý 1977, and *Troglostygnopsis anophthalma* Šilhavý 1974.

	Paramitraceras	*Philora*	*Sbordonia*	*T. anophthalma*
Scutum	*magnum*	*completum*	*magnum*	*magnum*
Eyes	Present	Present	Present	Absent
Body, lateral view	Opisthosoma convex	Opisthosoma convex	Opisthosoma convex	Opisthosoma flattened
Pedipalpal armature	Absent	Present	Present	Present
Pedipalpal armature on the tibia	-	Entire length	Distally only	Entire length
Setae and base of setiferous tubercles of the pedipalpi	-	Not contiguous	Contiguous	Contiguous
Length of the setiferous tubercles of pedipalpi	-	Not greater than respective segments	Not greater than respective segments	Greater than respective segments
Ventral armature of the femur IV	*P. femorale* only with a basal ventro-distal bulge	Absent	With conspicuous spiniform tubercles	Absent
Lenght of femur IV	Less than or equal to scutum	Less than or equal to scutum	Less than or equal to scutum	Longer than scutum
Distitarsus I and II	2/2–3	1/1	2/2	3/3
Origin of lateral setaes of pars distalis	Lateral to follis	Basal and lateral to follis	unknown	Lateral to follis
Ventral microsetae	Distant from each other	Close between them	unknown	Close between them
Position of the ventral microsetae respect to apical pair of dorsal lateral setae row	At the same level or slightly apical	Basal to them	unknown	Basal to them
Apical pair of the dorsal lateral setae row	Contiguous with the rest	Separated from the rest, close to ventral microsetae	unknown	Separated from the rest, close to ventral microsetae

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When troglomorphism dupes taxonomists: morphology and molecules reveal the first pyramidopid harvestman (Arachnida, Opiliones, Pyramidopidae) from the New World

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Cavernicolous species that exhibit a high degree of troglomorphism often provide some of the most intriguing evolutionary riddles. For such taxa, the correct systematic arrangement is difficult to determine and becomes problematic when based solely on highly convergent external morphological characters, leading to exaggerated support of spurious relationships. For the arachnid order Opiliones, examination of male genitalia morphology often aids in determining the family to which a particular taxon belongs. However, many taxa described prior to the 1990s lack detailed descriptions or drawings of this important character and, for highly-derived species, it is may still be necessary to seek support from additional sources of characters (e.g. molecular data) to accurately assess systematic placement. The enigmatic species *Stygnomma pecki* Goodnight & Goodnight, 1977 from a cave in Belize proved to be especially difficult to place based on morphological characters alone. Thus, using a previously published dataset for laniatorean harvestmen, we carried out a robust phylogenetic analysis aiming to determine the evolutionary relationship of this Neotropical troglomophic species. Informed by the results of the molecular phylogenetic analysis of 88 terminals representing Laniatores, we describe ***Jarmilana* gen. nov**. and provide a redescription of the type species *Jarmilana pecki* (Goodnight & Goodnight, 1977) **comb. nov**. Morphological evidence, including male genitalia morphology, supports the inclusion of *J. pecki* in the family Pyramidopidae. This represents the first record for the family Pyramidopidae in the New World, raising the question of whether this represents transoceanic dispersal or a relict of an ancient widespread tropical Gondwanan distribution.

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ADDITIONAL KEYWORDS: biogeography – molecular phylogeny – new genera – phylogenetic position – taxonomy.

INTRODUCTION

Systematics of laniatorean harvestmen (Opiliones: Laniatores) has received increasingly more attention in the last decade (Giribet & Sharma, 2015) and recent major revisions have resulted in many new systematic arrangements and descriptions of supraspecific taxa (Kury & Pérez-González, 2002; Kury, 2003; Pinto-da-Rocha & Hara, 2009; Sharma & Giribet, 2011, 2014; Sharma, Prieto & Giribet, 2011; Kury, 2012, 2014; Pinto-da-Rocha *et al.*, 2014). This has been greatly facilitated by the inclusion of a detailed description of male genitalic morphology, a structure that has played an increasingly important

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role in defining natural groups in harvestmen (Macías-Ordóñez *et al.*, 2010; Pérez-González, 2011; Pinto-da-Rocha *et al.*, 2012). Additionally, molecular data are rapidly advancing our understanding of evolutionary relationships of harvestmen, particularly within and among diverse Laniatores groups, often providing important insights about the systematic position of odd or poorly known taxa (Giribet *et al.*, 2010; Sharma & Giribet, 2011; Sharma, Prieto & Giribet, 2011; Pinto-da-Rocha *et al.*, 2014; Bragagnolo, Hara & Pinto-da-Rocha, 2015). The datasets produced by these studies have become a powerful resource for testing the affinities of taxa that are difficult to place based only on morphological traits, especially when character homology is masked by strong convergent evolution; for example, as observed in some cavernicolous species that exhibit a high degree of troglomorphism.

Despite recent advances in our understanding of harvestmen systematics (Giribet & Sharma, 2015), within Laniatores, there are still many non-natural groups consisting of multiple diverse lineages that require major systematic revision. This is partly a result of the typological approach engendered by early classification systems (e.g. the Roewerian system) in which a restricted number of convergent morphologies (e.g. the presence of tarsal scopula, tarsal formula, armature of ocularium) were used in combination to create many non-natural groups or, in some cases, to create a 'wastebasket taxon' into which species were 'dumped' based on a lack of characters. Among laniatorean harvestmen, the family Stygnommatidae is the epitome of wastebasket taxa because it contains species without a common ocularium that also lack a tarsal scopula. The family currently comprises one genus and 33 species (Kury, 2013b), although several studies have indicated that this is a non-monophyletic assemblage (Pérez-González, 2006, 2007; Pérez-González & Kury, 2007; Sharma & Giribet, 2011).

Within the genus *Stygnomma* Roewer, 1912, one of the most remarkable and enigmatic species is *Stygnomma pecki* Goodnight & Goodnight, 1977, a troglobite from Belize. The species authors recognized the unusual morphology of this species and indicated their uncertainty regarding relationships with other species of the genus by stating that 'It is unusual in appearance ... It bears no obvious relationships to any forms we have previously observed.' (Goodnight & Goodnight, 1977: 148). In an unpublished thesis, Pérez-González (2006) recognized that the male genitalia of this species did not match that of the Stygnommatidae *s.s.* (as subsequently defined in Pérez-González, 2007), nor any of the families belonging to the clade Samooidea + Zalmoxoidea. Pérez-González (2006) considered that the male genitalic morphology related this species with a group formed by Stygnopsidae, Epedanidae, 'Pyramidopidae', and Assamiidae (but, for current superfamilial concepts, see also Giribet & Sharma, 2015) and suggested that it was most likely related to Stygnopsidae because this was the only one of the four known from the New World.

Recent field expeditions in Belize have provided fresh material that enabled us to carry out a detailed study of *S. pecki*. In the present study, we investigate the systematic position of *S. pecki* using a molecular phylogenetic approach. Based on results of our analysis, we propose new familial and generic assignments. We provide a diagnosis for ***Jarmilana* gen. nov**. and a redescription of the species ***Jarmilana pecki* comb. nov.** based on detailed observations of morphological characters that strongly support the new taxonomic changes.

MATERIAL AND METHODS

Material examined

The material examined has been deposited in the Colección Nacional de Arácnidos (CNAN) UNAM, Mexico; American Museum of Natural History (AMNH), New York, USA; Texas Memorial Museum (TMM), Texas, USA, and Museo Argentino de Ciencias Naturales (MACN), Buenos Aires, Argentina. We adopted the terms alpha and beta male commonly used for Opiliones (Kury, 2008, 2013a; Ferreira & Kury, 2010; Kury & Ferreira, 2012; Ázara, DaSilva & Ferreira, 2013) and equivalent to Major/Minor males (Zatz *et al.*, 2011; Buzatto & Machado, 2014) to describe the dimorphic male condition in which larger, more strongly armed males (= alpha) are distinct from smaller, weakly armed males (= beta). One beta male of ***J. pecki* comb. nov.** was dissected and prepared for scanning electron microscopy (SEM) as described by Acosta, Pérez-González & Tourinho (2007). For SEM preparation, the specimens were dehydrated in a series of increasing concentrations of ethanol (85, 90, 95 and 100%), and dried using hexamethyldisilazane (Brown, 1993). After drying, they were mounted on adhesive copper tape (EMS 77802; Electron Microscopy Sciences) affixed to a stub and sputter coated with Au-Pd. Specimens were examined at accelerating voltages of 10–20 kV under high vacuum with a FEI XL30 TMP (at the MACN) and a Hitachi SU1510 (at the Instituto de Biología, UNAM). Photographs of ethanol preserved specimens were obtained with a DFC 290 digital camera (Leica) attached to a M165C stereomicroscope (Leica), and the focal planes were combined using HELICON FOCUS PRO (www.heliconsoft.com). Male genitalia were temporarily mounted in glycerol and drawn using a camera lucida attached to a BH-2 compound microscope (Olympus). To

expand the glans, the male genitalia was immersed in a hot, saturated solution of KOH for 2 min, and afterwards transferred to distilled water. All images were edited using Photoshop CS5 software (Adobe Systems Inc.).

Taxon sampling

We used a subset of data from Sharma & Giribet (2011) to include a broad sampling of 81 species of Grassatores plus five outgroup taxa represented by Triaenonychoidea and Travunioidea. Additionally, '*Stygnomma* sp.' (MCZ DNA 106176; Sharma & Giribet, 2012) was included as an additional representative of the South American fauna of Samooidea (although it is not *Stygnomma* or Stygnommatidae *s.s.* as defined in Pérez-González, 2007). We added sequence data for ***J. pecki* comb. nov.** (MACN-DNA-Op024) to these previously sequenced taxa for a total of 88 terminals in our molecular phylogenetic analysis.

Molecular methods

Sequence data were retrieved from GenBank via Batch Entrez for 87 species of Laniatores. GenBank files were parsed using the perl script parseGB.pl (https://sites.google.com/site/shannonhedtke/Scripts). Reconstruction of the Laniatores phylogeny utilized eight of the ten markers employed by Sharma & Giribet (2011), including three mitochondrial genes (i.e. for *12S* rRNA, *16S* rRNA, and cytochrome *c* oxidase subunit I) and five nuclear genes (i.e. for *18S* rDNA, *28S* rDNA, histones *H3* and *H4*, and *U2* snRNA). We excluded cytochrome *b* and elongation factor-1α from our analysis because a large number of taxa (> 70%) in the dataset lacked sequence data for the appropriate genes.

Total DNA was extracted from one adult female ***J. pecki* comb. nov.** (MACN-DNA-Op024) using DNEasy tissue kits (Qiagen) by soaking two legs in lysis buffer overnight (approximately 14 h) as described in Boyer, Karaman & Giribet (2005). Genomic DNA was used as a template for amplification by a polymerase chain reaction (PCR) of three gene fragments (*COI*, complete *18S*, and partial *28S*). *COI* was amplified using the primer pair LCO1490-HCOoutout (Folmer *et al.*, 1994; Prendini, Weygoldt & Wheeler, 2005). *18S* was amplified using three primer pairs that produce overlapping regions, including *18S* 1F-5R, *18S* 3F-bi, and *18S* a2.0-9R (Giribet *et al.*, 1996; Whiting *et al.*, 1997). For *28S*, the region amplified was bounded by the primer pair *28S* rd4.8a-rd7b1 (Schwendinger & Giribet, 2005). More information about primer sequences is provided in Sharma & Giribet (2011). Reactions were carried out in 15-μL volumes consisting of 0.5 μM each primer, 200 μM dNTPs, 1 × PCR buffer, 1.5 mM $MgCl_2$, 1.5 U of Taq DNA Polymerase (Thermo Scientific), and 1–2 μL of DNA template. For *28S* and *18S*, cycles were run using a step-down protocol (Evans & Paulay, 2012) that involved an initial denaturation step (95 °C for 5 min), 15 high-specificity cycles (95 °C for 30 s, 51 °C for 45 s, 72 °C for 45 s), and 20 standard-specificity cycles (95 °C for 30 s, 49 °C for 45 s, 72 °C for 45 s). For *COI*, annealing temperatures were modified to 45 °C, stepped down to 42–43 °C.

PCR products were visualized by agarose gel electrophoresis (1.2% agarose) and later purified by adding 0.5 μL of Exonuclease I and 1.0 μL of FastAP Thermosensitive Alkaline Phosphatase (Thermo Scientific) and running reactions at 37 °C for 30 min followed by 85 °C for 15 min. Products were sequenced using the forward primers, carried out at the Instituto Nacional de Tecnología Agropecuaria (Buenos Aires, Argentina) or Macrogen (Seoul, South Korea).

Chromatograms were viewed and automated sequence reads were edited using SEQUENCHER (Gene Codes). Most sequences were aligned using MUSCLE (Edgar, 2004). Sequences for *28S* and *12S* were aligned using Q-INS-i and L-INS-i algorithms, respectively, implemented in MAFFT (Katoh, 2013) through the online CBRC portal using the parameters: 200 PAM/k = 2 scoring matrix, gap opening penalty of 1.53, and an offset value of 0.1. Alignments were inspected and manually adjusted, and were treated with GBLOCKS, version 0.91b (Castresana, 2000) to identify and remove ambiguous sites with the allowed gap positions parameter set to 'with half', the minimum number of sequences for a flanking position set to 75% of the total number of sequences in a partition, and the remaining parameters at their default setting. Lengths of the original sequence alignment and final selected blocks are provided (Table 1). Sequences were concatenated, and file types were converted, using the perl script BeforePhylo.pl (https://github.com/qiyunzhu/BeforePhylo) customized to generate relaxed phylip format.

We assessed the substitution saturation in the third-position of codons for protein-coding genes (*COI*, *H3*, *H4*) using a test for substitution saturation (Xia *et al.*, 2003; Xia & Lemey, 2009) implemented in DAMBE5 (Xia, 2013). The third-position of *COI* was highly saturated by substitutions; thus, the phylogenetic signal was obscured, which is an expected outcome for a broad sampling of taxa across diverse lineages of Laniatores. Therefore, we partitioned *COI* by codon position, retained positions 1 and 2 as separate partitions, and excluded position 3 from our

Table 1. Selection of conserved blocks for each gene sequence after treatment with GBLOCKS

Gene	Number of sequences	Original sequence length	Length of selected blocks	Number of selected blocks
12S	42	387	143	8
16S	26	490	374	13
18S	88	1828	1728	10
28S	88	3761	2332	22
COI	56	814	642	1
H3	71	327	321	1
H4	74	159	159	1
U2	40	131	131	1

analysis. We retained all three codon positions for *H3* and *H4*.

Four errors were discovered among the sequence data available for Laniatores and we indicate those errors here so that future studies that utilize this dataset may take these changes into account. Sequence accession numbers are from GenBank, and we refer to accession numbers listed in Sharma & Giribet (2011). GenBank accession number FJ796492 refers to a *COI* sequence that belongs to *Caenocopus* sp. MCZ DNA102593, and thus *COI* sequence data for *Cynortula granulata* MCZ DNA100332 do not exist at this time. Additionally, we discovered that *16S* sequence data available for *Pellobunus insularis* MCZ DNA101421 (GenBank# JF786469) was identical to *Pyramidops* sp. MCZ DNA101432 (GenBank# JF786468), which is implausible. We determined that the sequence belongs to *Pyramidops* sp. and thus we omitted the *16S* sequence data for *P. insularis*. Similarly, we discovered that *H4* sequence data for *Glysterus* sp. MCZ DNA101422 (GenBank# FJ475957) were identical to *Icaleptes* sp. MCZ DNA101420 (GenBank# FR850199) and determined that the sequence belongs to the latter species. Finally, sequence data for *Neopygoplus siamensis* were previously only available in GenBank for three genes (*COI*, *18S*, and *28S*); however, sequences for three additional genes were presumably included in the analysis of Sharma & Giribet (2011) but never published. Sequence data have been made available for histone *H3* (KU049766), histone *H4* (KU049767), and *U2* snRNA (KU049768) from *N. siamensis* (MCZ DNA104858).

Phylogenetic methods

Phylogenetic trees were reconstructed using maximum likelihood (ML) and Bayesian inference. ML analysis was conducted using RAXML, version 8.1.11 on XSEDE (Stamatakis, 2014) through the online CIPRES portal. Data were partitioned by gene, with *COI* partitioned into first and second codon positions, resulting in nine data partitions for the ML analysis. We inferred trees using a GTR + GAMMA model of sequence evolution for each data partition and estimated support values with 1000 bootstrap replicates.

Bayesian inference analysis was conducted using MrBayes, version 3.2.3 (Ronquist *et al.*, 2012) on XSEDE through the online CIPRES portal. Data were partitioned by gene, and protein coding genes *H3* and *H4* were further partitioned by codon position, resulting in a 13 partition scheme. Best-fit models of molecular evolution were specified for each partition (Table 2) as selected under the Bayesian information criterion using PARTITIONFINDER, version 1.1.1 (Lanfear *et al.*, 2012). The analysis consisted of two simultaneous runs each with four chains for 20 000 000 generations sampling every 1000 trees. The initial 25% of sampled trees were discarded as burn-in. The average SD of split frequencies between runs was < 0.01. Stationarity of parameters was visually confirmed in TRACER, version 1.6 (Rambaut *et al.*, 2014) and stationarity of tree topologies was confirmed using compare plots generated by AWTY (Nylander *et al.*, 2008). To investigate whether missing data had an effect on the placement of the taxon of interest, we analyzed a dataset consisting of only the genes available for ***J. pecki* comb. nov.** in a four partition scheme (i.e. *18S*, *28S*, and *COI* codon positions 1 and 2). There was no change in the nodal support for taxa relevant to our study; thus, we proceeded to use the eight gene dataset that provided better resolution of deep

Table 2. Best-fit models for sequence evolution for each partition selected under Bayesian information criterion using PARTITIONFINDER

Partition	Model
12S	GTR + I + G
16S	GTR + I + G
18S	GTR + I + G
28S	GTR + I + G
COI, first codon position	GTR + I + G
COI, second codon position	GTR + I + G
H3, first codon position	GTR + I + G
H3, second codon position	JC
H3, third codon position	GTR + G
H4, first codon position	GTR + I + G
H4, second codon position	JC
H4, third codon position	GTR + G
U2	GTR + I + G

phylogenetic relationships and facilitated direct comparisons with previous studies.

RESULTS AND DISCUSSION

Phylogenetic analysis

New sequences for ***J. pecki* comb. nov.** have been submitted to GenBank for three genes: *COI* (KU049765), complete *18S (*KU049764), and partial *28S* (KU049763). The tree topology obtained by Bayesian inference was generally in agreement with the previous analyses of Sharma & Giribet (2011) with respect to the monophyly of families and some major superfamilial clades (Fig. 1). However, in our analysis, utilizing a subset of genes from Sharma & Giribet (2011), making several corrections to sequence data, and employing a different partitioning scheme had some impact on family level relationships (Fig. 1). The implications for these findings are discussed below. The phylogenetic tree obtained by ML (see Supporting information, Fig. S1) was generally congruent with Bayesian analyses (Fig. 1).

Familial assignment in Pyramidopidae: molecular and morphological evidence

The African family Pyramidopidae, represented in our analysis by *Conomma oedipus* Roewer, 1949 and *Pyramidops* sp. is recovered as monophyletic [bootstrap support (BS) = 100%, posterior probability (PP = 1.00)]. ***Jarmilana pecki* comb. nov.** was recovered as sister to African pyramidopids with strong support in both analyses (BS = 99%, PP = 1.00).

The external morphology of ***J. pecki* comb. nov.** is extremely misleading because it is highly convergent with other troglobitic species, as demonstrated by the strongly developed pedipalps, the loss of eyes, and the dubious limits of an ocularium (Fig. 3). These troglomorphic characteristics, combined with the hourglass-shaped *scutum magnum* and the disregard for examining penis morphology, erroneously led the species authors to conclude that it belonged to Stygnommatidae.

Detailed examination of the male genitalic morphology provides supporting evidence with respect to placement of ***J. pecki* comb. nov.** in Pyramidopidae. Pyramidopids typically exhibit complex and aberrant penis morphologies. The pars distalis is armed with characteristic large paired macrosetae (with exceptions) and the glans lacks prominent parastylar conductors (Sharma *et al.*, 2011). The penis of ***J. pecki* comb. nov.** does not have a strongly developed par distalis, as is found in many pyramidopids (Sharma *et al.*, 2011), although it does exhibit the characteristically large macrosetae, a simple glans with a follis ending in two large dorsoapical lobes, and a simple stylus without parastylar conductors (Figs 10, 11). The penis morphology of ***J. pecki* comb. nov**. shares similarities with other pyramidopids that possess a shorter, less complex and slightly swollen pars distalis; compare Fig. 10A to fig. 5n in Sharma *et al.* (2011). The large dorsoapical lobes of the follis are strikingly similar to *Conomma* sp. from Cameroon (Sharma *et al.*, 2011: fig. 5a) and *Pyramidops pygmaeus* Loman, 1902 from Nigeria (for which the genitalia was illustrated and homology of setae was interpreted by Kury & Villarreal, 2015: fig. 22d–f). Also, the mode of hydraulic expansion shows the affinities between ***J. pecki* comb. nov**. and the pyramidopid *C. oedipus*. When expanded, the movement of the glans is very similar in both species. The base of the follis inflates and moves dorsally, whereas the dorsoapical lobes of the follis inflate, separate slightly, and curl apically. The stylus projects apically and is exposed between the tips of the two lobes (Fig. 11). Another striking similarity between ***J. pecki* comb. nov.** and *P. pygmaeus* is the dorsal pair of macrosetae adjacent to the glans (referred to as D1 in Kury & Villarreal, 2015). The placement of a large pair of setae next to a mobile and expandable glans may serve a proprioceptive function, and may therefore be conserved across closely-related taxa with similar penis morphologies. However, tracing the homology of the macrosetae, defining species groups and delimiting genera in Pyramidopidae will require a better understanding of the diverse penis morphologies. Studying the penis morphology in the expanded state will also be important with respect to future studies of this group.

An interesting morphological character that we observed is the presence of microtrichia on the distal half of the setae of the major setiferous tubercles on the pedipalps (Fig. 7D, F) herein termed 'plumose setae'. These plumose setae also have a smooth base and small pores located near the socket on the tubercle (Fig. 7E). This type of major setiferous tubercle with plumose setae is also present in *C. oedipus*, widely exhibited throughout Samooidea, and absent in Gonyleptoidea (J. Cruz-López, pers. observ.). However, this character is poorly surveyed in the remaining laniatorean families and thus its potential phylogenetic utility remains unknown.

Elusive interfamilial relationships for Pyramidopidae

Previous molecular phylogenetic studies have indicated a close relationship between Pyramidopidae + Assamiidae, together forming the Assamioidea

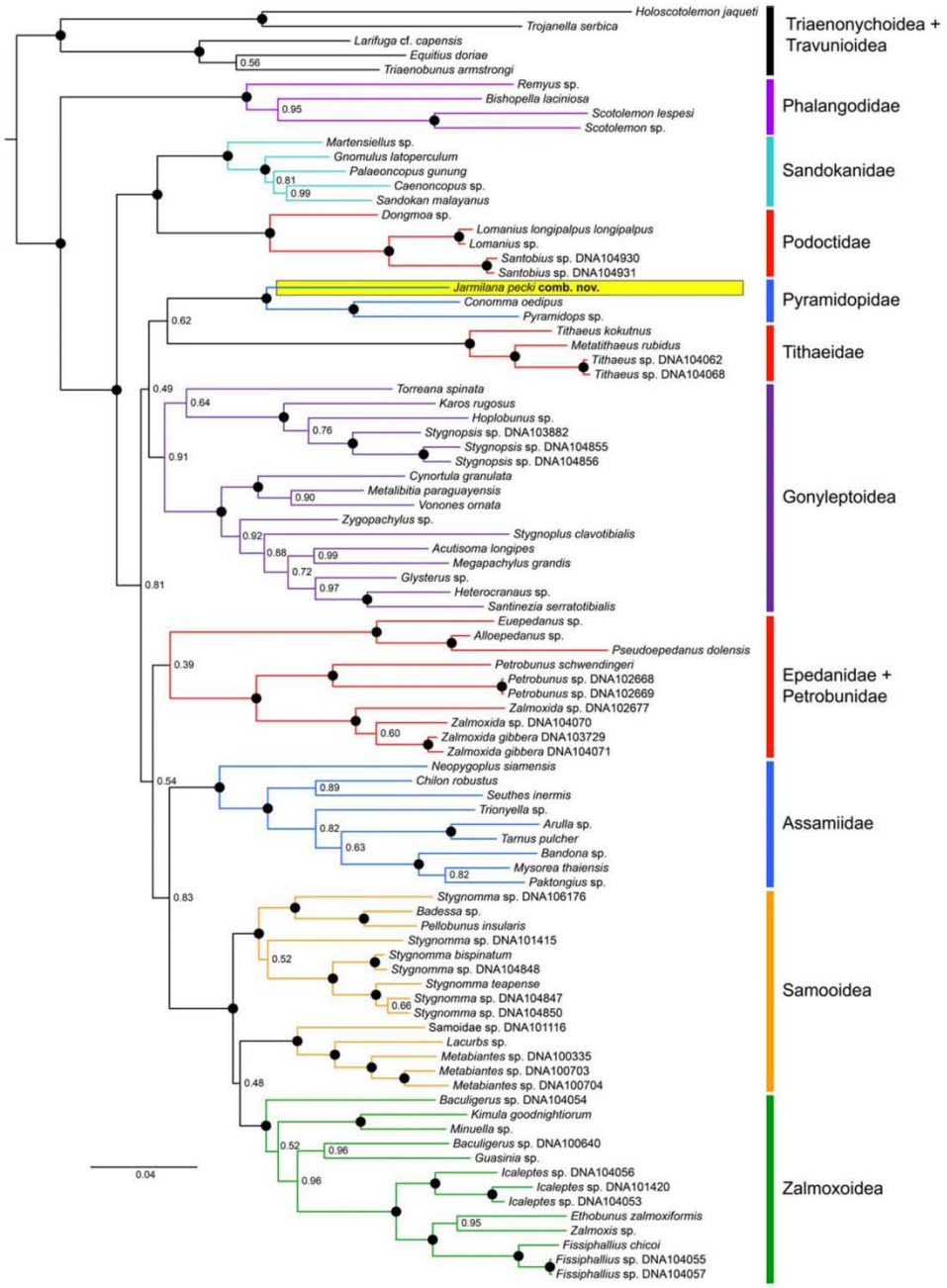

Figure 1. Phylogenetic relationships based on Bayesian inference analysis revealing the relationship of the Neotropical troglobite *Jarmilana pecki* comb. nov. (highlighted) with the African family Pyramidopidae. Numbers on nodes correspond to posterior probabilities; black circles at nodes indicate posterior probability of 1.00. Branch colours correspond to higher taxa (families or superfamilies) and reflect the same colour scheme used by Sharma & Giribet (2011) to facilitate direct comparison. The superfamilies Assamioidea (blue) and Epedanoidea (red) are recovered as polyphyletic.

(*sensu* Sharma & Giribet, 2011) and later Pyramidopidae was formalized and the family rank completed with a diagnosis for this diverse group (Sharma *et al.*, 2011). In the latter study, it was concluded that Pyramidopidae should be considered a separate family, sister to Assamiidae, rather than being included within Assamiidae. Inclusion in Assamiidae would have created a group without clear synapomorphies, thus making it difficult to diagnose (Sharma *et al.*, 2011). This was a sensible decision, given that the clade Pyramidopidae + Assamiidae was partially justified based on the exclusion of Pyramidopidae from other superfamilies rather than clear synapomorphies that unite these families under Assamioidea.

In the Bayesian analysis, we recovered Assamiidae as sister to Zalmoxoidea + Samooidea, although with only moderate support (PP = 0.83), agreeing with the previous analysis of the full Laniatores dataset (i.e. Sharma & Giribet, 2011). Interestingly, however, we

Figure 2. *Jarmilana pecki*, comb. nov. alpha male MACN_Ar 35555, habitus. A, dorsal view. B, dorsolateral view. Scale bars = 2 mm.

did not recover Pyramidopidae + Assamiidae as a clade. Instead, we recovered Pyramidopidae as sister to Tithaeidae (PP = 0.63), casting doubt on the sister-group relationship of Pyramidopidae + Assamiidae. Although this analysis does not offer well-supported alternatives to the sister-group of Pyramidopidae, it clearly demonstrates that the evolutionary history of these lineages is much more complex than the current taxonomic sampling depicts, and the elusive relationships will only be resolved with broader taxonomic sampling for the African and South-east Asian harvestmen fauna.

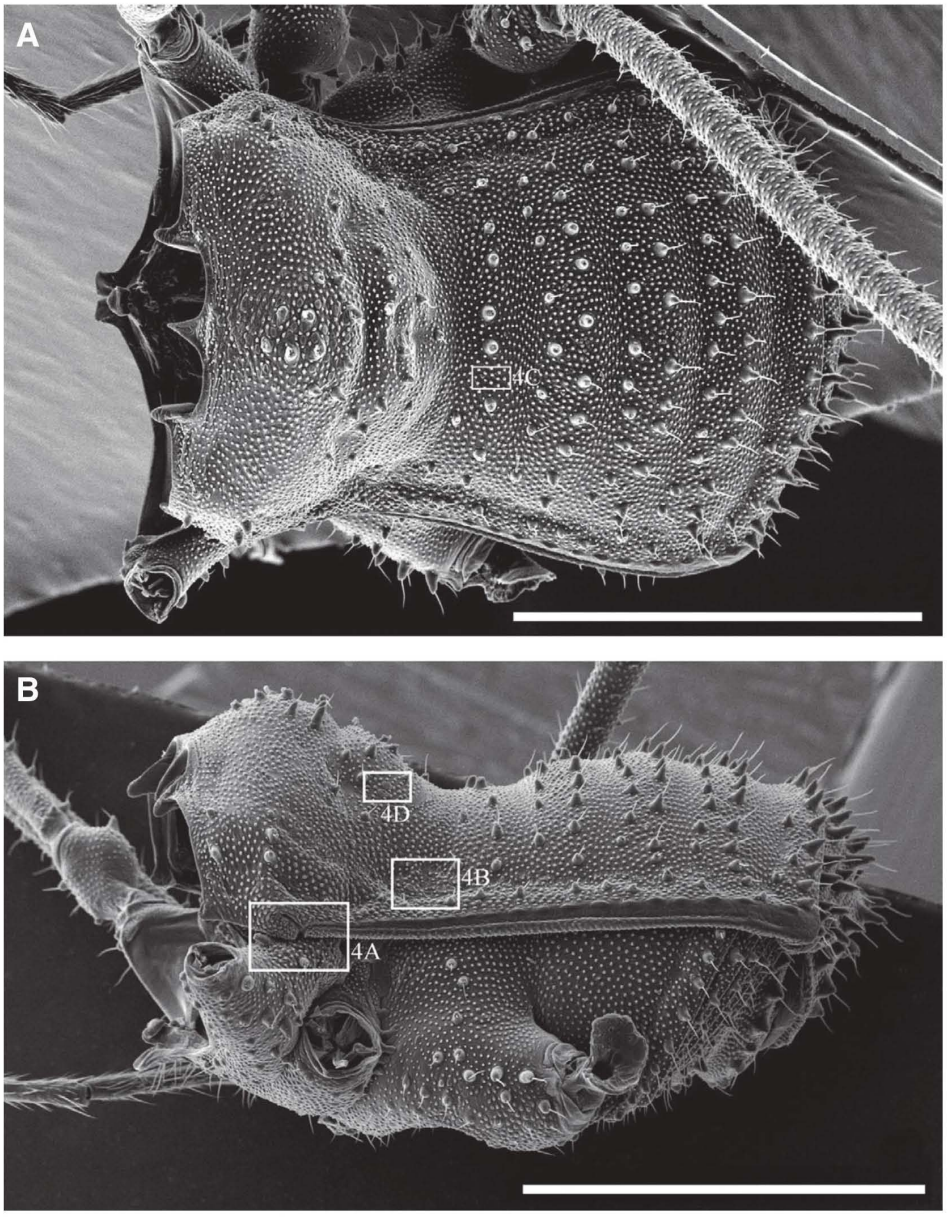

Figure 3. *Jarmilana pecki*, comb. nov. beta male MACN_Ar 35557, habitus. A, dorsal view. B, lateral view. Boxes indicate areas shown in detail in Fig. 4. Scale bars = 1 mm.

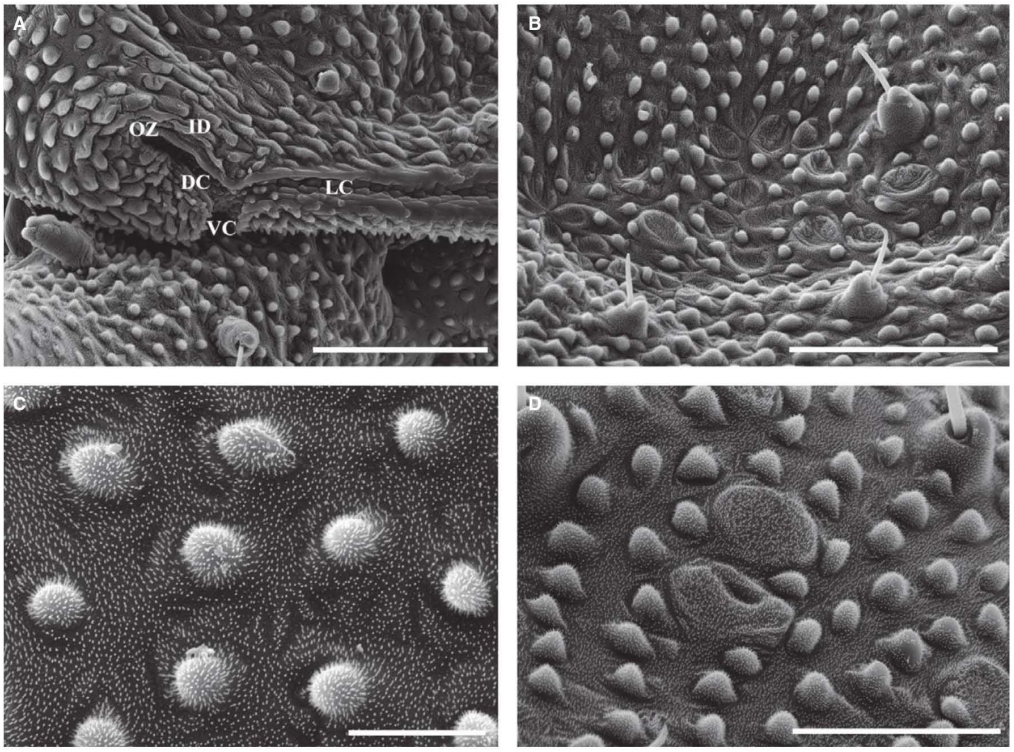

Figure 4. *Jarmilana pecki*, comb. nov. beta male MACN_Ar 35557, enlargements of Fig. 3 boxed areas. A, ozopore, lateral view. B, concentration of rough pit glands in depressed area adjacent to sulcus I, lateral view. C, microanatomy of the mesotergum showing verrucose cuticle with rounded granules covered in abundant hair-like microtrichia. D, rough pit glands concentrated in depressed area lateral to the position of sulcus I. Scale bars: (A, B) 100 μm; (C) 20 μm; (D) 50 μm. DC, descending channel; ID, integumentary dome; LC, lateral channel; OZ, ozopore; VC, vertical channel.

Implications for neotropical Pyramidopidae

Prior to this work, Pyramidopidae was formed by 45 species grouped in 12 genera with a geographical distribution restricted to central and western Africa (Sharma *et al.*, 2011). With the addition of ***J. pecki* comb. nov.** from the Cayo area in Belize, the family now consists of 46 species in 13 genera and shows a remarkable transoceanic distribution, spanning both Afrotropical and Neotropical regions. For sufficiently old lineages, this distribution is often explained by ancient vicariant events related to the break up of Gondwana, such as has been inferred for Ricinulei, Onychophora, Myriapoda, and other lineages of Opiliones (San Mauro *et al.*, 2004; Giribet & Edgecombe, 2006; Murienne *et al.*, 2013, 2014; Fernández & Giribet, 2015). On the other hand, some disjunct biogeographical distributions for harvestmen families have been explained by transoceanic dispersal, as demonstrated by Zalmoxidae (Sharma & Giribet, 2012) and some Cyphophthalmi (Boyer *et al.*, 2007; Giribet *et al.*, 2012).

With respect to Pyramidopidae, either hypothesis may explain the transoceanic Gondwanan distribution. Previous estimates indicate that the Pyramidopidae lineage diverged from Assamiidae approximately 232 Mya and, within African pyramidopids (between *Conomma* and *Pyramidops*), the divergence dates to approximately 140 Mya (Sharma & Giribet, 2011); thus, the family appears to be sufficiently old. However, given that we have sequence data available for only three species of Pyramidopidae, we did not estimate divergence times using our dataset. Thus, it remains for future studies to determine whether ***J. pecki* comb. nov.** is an ancient relict from a widespread Gondwanan distribution or whether this is a case of transoceanic dispersal out of Africa.

Revisiting Sandokanidae + Podoctidae

The relationship of Sandokanidae with other families within Grassatores has long been a challenge. Sharma & Giribet (2009) provided strong support for

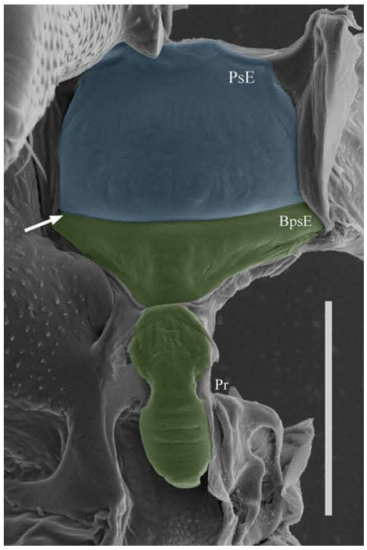

Figure 5. *Jarmilana pecki*, comb. nov. beta male MACN_Ar 35557, epistome, anterior view. Blue, post-sulcal epistome (PsE); green, pre-sulcal epistome consisting of two regions: a basal pre-sulcal epistome (BpsE) and pre-sulcal epistome process (Pr); arrow indicates the sulcus. Scale bar = 200 μm.

the monophyly of Sandokanidae and the first molecular phylogenetic evidence to support a sister group relationship with Podoctidae. Subsequently, the first Laniatores phylogeny of Giribet *et al.* (2010), which represented many more families but utilized fewer markers, suggested that Phalangodidae, Sandokanidae, and Podoctidae form a grade near the base of the Laniatores tree and found only weak support for Sandokanidae + Podoctidae in the ML analysis. However, in both of those studies, Podoctidae was represented by only a single species. Adding a number of Laniatores taxa, including four more podoctids, and utilizing data from ten molecular markers, Sharma & Giribet (2011) clarified many important laniatorean relationships, although placement of Sandokanidae was still not well-resolved. They recovered Sandokanidae as either sister to all nonphalangodid Grassatores, or as sister to Podoctidae nested within other Epedanoidea. Given that we used a large subset of the data (including all Grassatores) from Sharma & Giribet (2011), it is interesting to note that we consistently recovered the clade Sandokanidae + Podoctidae with high nodal support in both analyses (BS = 88, PP = 1.00) and, together, they are recovered as sister to all nonphalangodid Grassatores (BS = 18; PP = 0.81). With respect to the basal placement of Sandokanidae, this outcome is consistent with the original analysis of this dataset (i.e. Sharma & Giribet, 2011), although the newfound strong support for Sandokanidae + Podoctidae reiterates the idea that the relationship of this group with other Grassatores is sensitive to the analytical methods employed (Sharma & Giribet, 2009, 2011; Giribet & Sharma, 2015). As is the case for Pyramidopidae, resolving these relationships awaits a broader taxonomic sampling of African and Southeast Asian lineages.

SYSTEMATICS

PYRAMIDOPIDAE SHARMA, PRIETO & GIRIBET, 2011

JARMILANA GEN. NOV.

Stygnomma (partim):. Goodnight & Goodnight, 1977: 148; Reddell, 1981: 166; Rambla & Juberthie, 1994: 219; Kury, 2003: 235.

Type species:. *Stygnomma pecki* Goodnight & Goodnight, 1977.

Etymology:. The genus name is a tribute to Dr Jarmila Kukalová-Peck, recognized paleontologist and collector of the type series, who, in company with her husband, Dr Steward Peck, made important collections of cave dwelling animals across the Central American and Caribbean countries. Gender feminine.

Diagnosis:. Eyeless harvestman (Fig. 2). Carapace highly elevated with a large anterior hump and smaller posterior hump (Fig. 3B). Male pedipalps very strong with palpal femur laterally compressed and high (Figs. 7A, C, 8). Male basichelicerite armed with two dorsal apophyses, cheliceral hand with one dorsal apophysis (Fig. 6A, B). Trochanter IV without sexually dimorphic spurs. Pars distalis of male genitalia slightly swollen and bulbous, without a marked ventral plate as in Gonyleptoidea, apical margin terminating in a small lip, curled ventrally. Pars distalis armed with six pairs of macrosetae, with one lateral pair in close proximity to the follis. Stylus subapical, long and curved, arising from the mid-follis, concealed below two huge dorsoapical lobes of the follis (Figs 10, 11). Several morphological features clearly separate this genus from other Pyramidopidae genera, such as the cheliceral and pedipalpal armature and the absence of an inflated dorsodistal bulla in the basiquelicerite. The male genitalic morphology is also distinctive of this genus. The combination of a pars distalis swollen with one small and rounded lamina apicalis and a follis with dorsoapical portion modified into two large lobes that conceal (when retracted) a stylus ending with a dorsal barb appears to be unique to *Jarmilana* and not presented in any other know genera of Pyramidopidae.

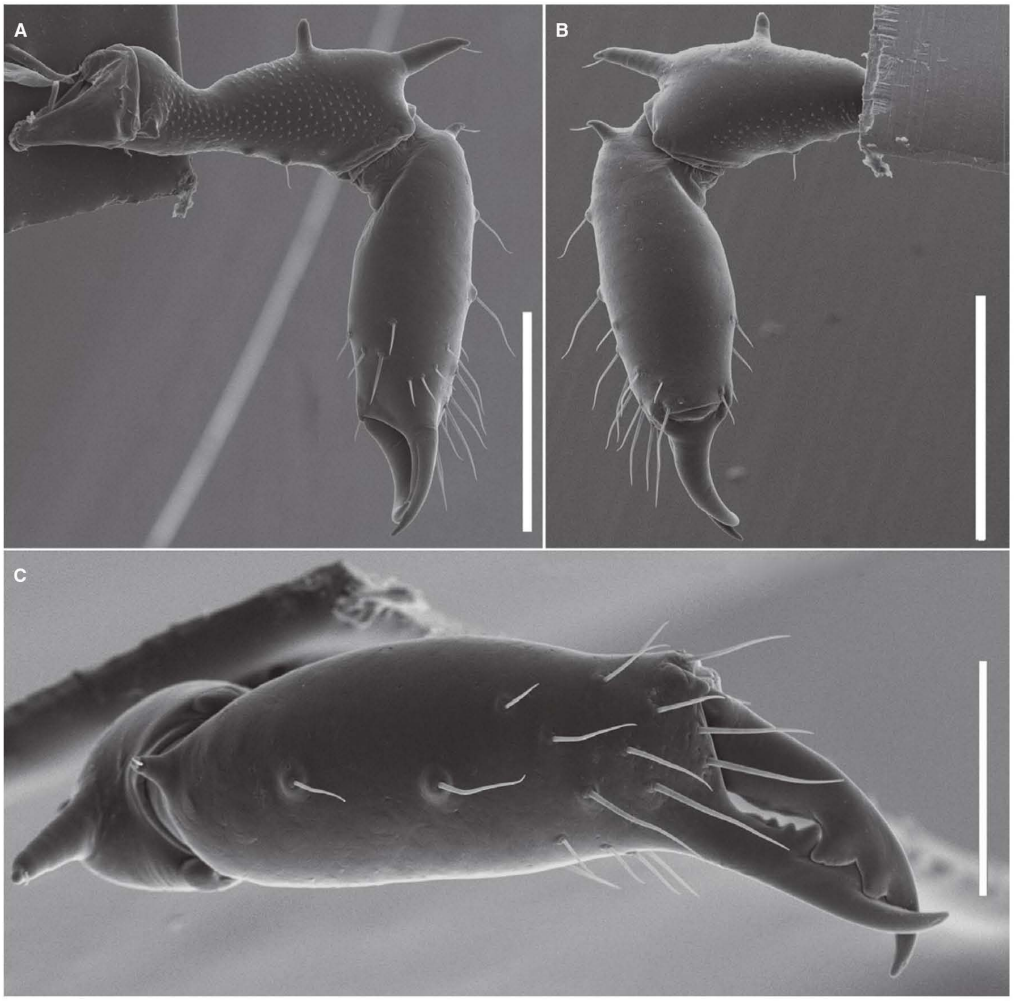

Figure 6. *Jarmilana pecki*, comb. nov. beta male MACN_Ar 35557, left chelicera. A, mesal view. B, ectal view. C, frontal view. Scale bars: (A, B) 500 μm; (C) 250 μm.

Jarmilana pecki (Goodnight & Goodnight, 1977) **comb. nov.** (Figs 2–11)

Stygnomma pecki Goodnight & Goodnight, 1977: 148; fig. 11; Reddell, 1981: 166; Rambla & Juberthie, 1994: 219; Kury, 2003: 235.

Type material:. One male holotype from Belize, Distrito de Cayo, Cave Branch, St Herman's Cave, 23 July to 21 August 1972, S. & J. Peck (AMNH, examined). One male and one female paratypes from Belize, Distrito de Cayo, Caves Branch, Mountain Cow Cave, 5 August 1972, S. & J. Peck (AMNH, examined).

Other material examined:. One male, one female, and one juvenile (CNAN-Op1702), one alpha male (MACN_Ar 35555), one beta male (MACN_Ar 35557, SEM voucher) and one female (MACN_Ar 35556, DNA voucher, extraction code Op024) from the same locality as the holotype, Belize, Distrito de Cayo, Caves Branch, St Herman's Cave, 6 November 2013, 17°08′48.76′N, 88°40′29.06′W, R. Monjaraz & C. Santibáñez. Two females from Belize, Distrito de Cayo, Caves Branch, St Herman's Cave, August 1972, S. & J. Peck (TMM-33.316, examined).

Diagnosis:. See diagnosis of the genus.

Redescription:. Based on one alpha male (MACN_Ar 35555). Body measurements: total body length 2.50,

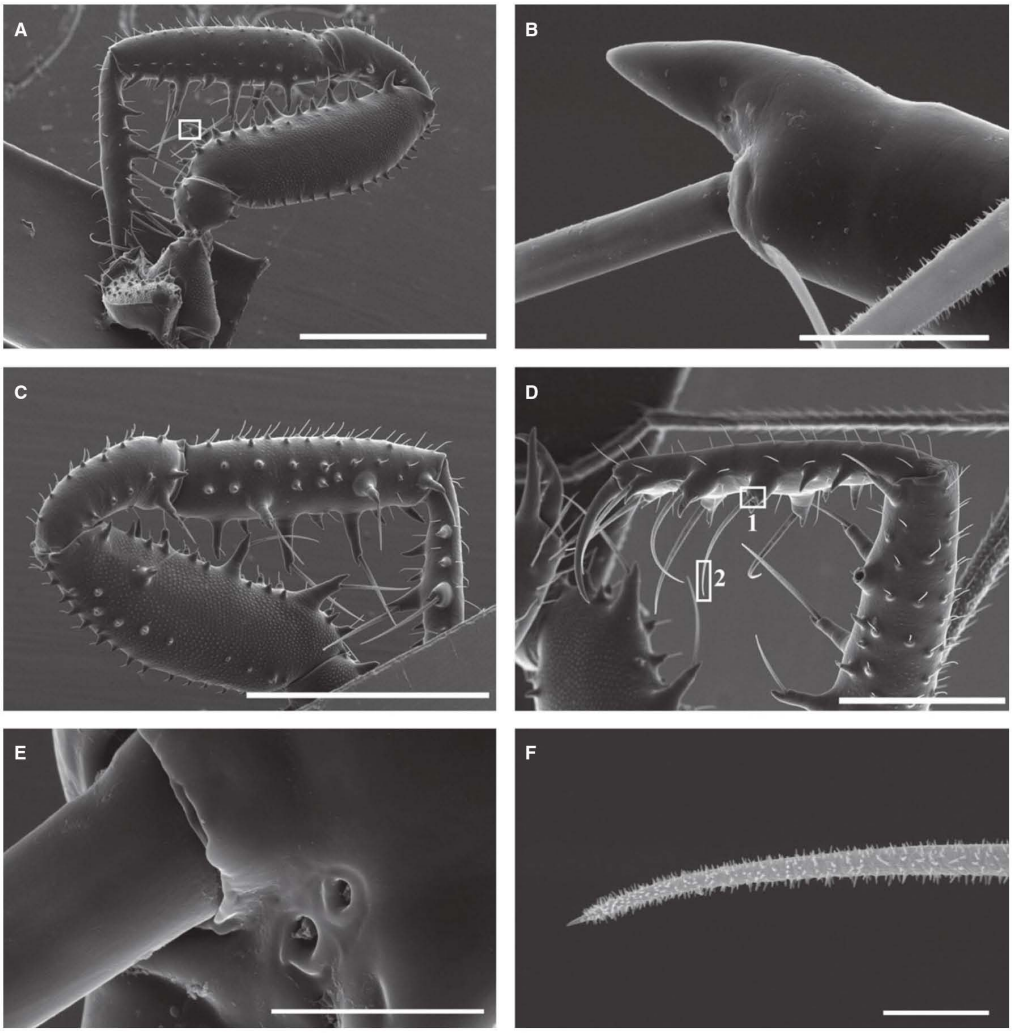

Figure 7. *Jarmilana pecki*, comb. nov. beta male MACN_Ar 35557, pedipalp. A, left pedipal, ectal view. B, enlargement of box in (A), smooth base of plumose seta inserted on major setiferous tubercle. C, left pedipalp, mesal view. D, right pedipalpal tarsus, mesal view. E, enlargement of box 1 in (D), small pores at base of plumose seta inserting on major setiferous tubercle. F, enlargement of box 2 in (D), microtrichia on the distal part of a plumose seta associated with major setiferous tubercle. Scale bars: (A, C) 1 mm; (D) 500 μm; (B) 50 μm; (E, F) 20 μm.

scutum magnum length 2.14, carapace length 1.00, carapace maximum width 1.37, mesotergal scute maximum width 1.60.

Dorsum:. Completely lacks eyes. *Scutum magnum* hourglass shaped with the constriction between prosoma and opisthosoma slightly pronounced (Figs 2, 3). Posterior margin of the *scutum* slightly convex, almost straight. Carapace with anterior margin straight, cheliceral sockets narrow but well marked (Fig. 3). Carapace and mesotergum in lateral view convex, sulcus I not marked. Carapace highly elevated with a large anterior hump and smaller posterior hump, ornamented with small setiferous tubercles (Figs 2, 3). The absence of a cornea (or any evidence of eye position) makes it impossible to recognize whether one of these humps represents a vestigial ocularium. Mesotergal scutum with five recognizable, slightly convex areas. Sulci between mesotergal areas are not well marked. Areas I–V with transverse rows of setiferous tubercles: area I

with one row, II–IV with two rows, and V with one row. Lateral margins of mesotergum with a row of setiferous tubercles from sulcus I to sulcus V that increase slightly in size from anterior to posterior. Free tergites each with one transverse row of tubercles (Fig. 3). Ozopore region with well-marked descending, vertical and lateral channels, and a rounded integumentary dome covering the anteriodorsal area of ozopore (Fig. 4A). Lateral pegs (*sensu* Gnaspini & Rodrigues, 2011) present (Fig. 3B). Lateral to the sulcus I position, there is a depressed area that forms a wide trough (Figs 3, 4B). *Venter*. Coxa IV visible in dorsal view, terminating adjacent to sulcus II. Free sternites each with a transverse row of setiferous tubercles (Fig. 3). Spiracles crescent-shaped, with a mass of granules and tubercles protruding from the posterior border (Fig. 9D); not concealed by coxa IV. Anal operculum covered by many large, scattered setiferous tubercles. *Epistome*. Epistome with sulcus well marked. Post-sulcal epistome wider than tall, appearing subrectangular, arched dorsally. Basal pre-sulcal epistome wide and short, almost triangular. Pre-sulcal epistome process hourglass-shaped, with remarkable median constriction (Fig. 5). *Chelicera*. Chelicera normal, neither swollen, nor obviously hypertelic. Basichelicerite slightly elongated, without well-marked bulla, dorsally with two strong spiniform setiferous tubercles, the subdistal tubercle oriented dorsally and curved, and the distal tubercle larger, straight and pointed anteriorly (Fig. 6). Cheliceral hand with a proximodorsal setiferous tubercle oriented anteriodorsally. Mobile finger of cheliceral hand with two wide teeth, fixed finger with two small teeth proximally and one distally (Fig. 6). *Pedipalp*. Coxa almost as long as the basichelicerite, without remarkable armature. Trochanter globular, with a large ventral and small dorsal setiferous tubercle, among other scattered tubercles. Femur strong, distinctly widened dorsoventrally. Femur armed with three ventral and one subdistal mesal major setiferous tubercles, and with one dorsal, one mesal, and two ventral rows of setiferous tubercles; ventral ectal row terminates distally with one curved spiniform apophysis (Figs 7, 8). Patella cylindrical, armed with one major setiferous tubercle ventrodistally; with several rows of small setiferous tubercles on dorsal and mesal surfaces. Tibia armed ventrally with two ectal and three mesal major setiferous tubercles, and multiple apophyses interspersed in ectal row; with several rows of small setiferous tubercles on mesal, dorsal, and ectal surfaces. Tarsus armed ventrally with three ectal and three mesal major setiferous tubercles; with multiple apophyses interspersed in mesal and ectal rows (Figs 7, 8). All major setiferous tubercles possess a 'plumose seta' that inserts subapically in a socket on the tubercle. Plumose setae are defined

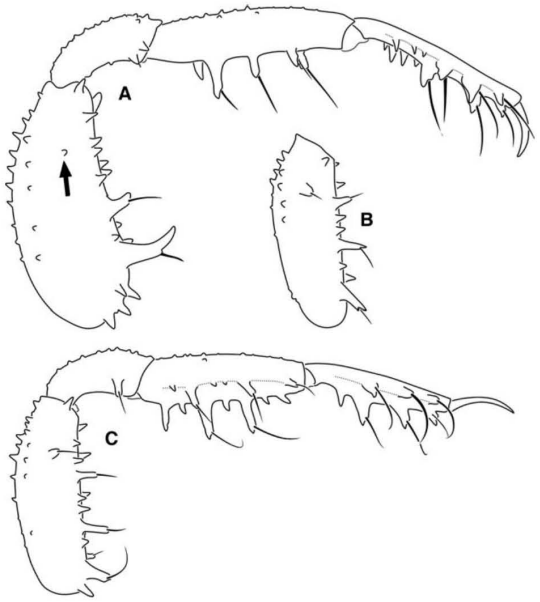

Figure 8. *Jarmilana pecki*, comb. nov. comparison of left pedipalps. A, entire palp, alpha male MACN_Ar 35555, mesal view. B, palpal femur of beta male MACN_Ar 35557, mesal view. C, entire palp, female MACN_Ar 35556, mesal view. All drawings are to same scale. Arrow indicates the mesal subdistal major setiferous tubercle.

Table 3. Length of appendages (in mm) for *Jarmilana pecki*, comb. nov. alpha male MACN_Ar 35555

	Coxa	Trochanter	Femur	Patela	Tibia	Metatarsus	Tarsus
Leg I	0.70	0.25	1.75	0.55	1.15	1.80	0.75
Leg II	0.90	0.30	2.72	0.75	2.20	2.30	3.20
Leg III	0.70	0.32	2.05	0.50	1.40	1.95	0.95
Leg IV	1.00	0.45	2.55	0.67	1.85	2.40	1.15

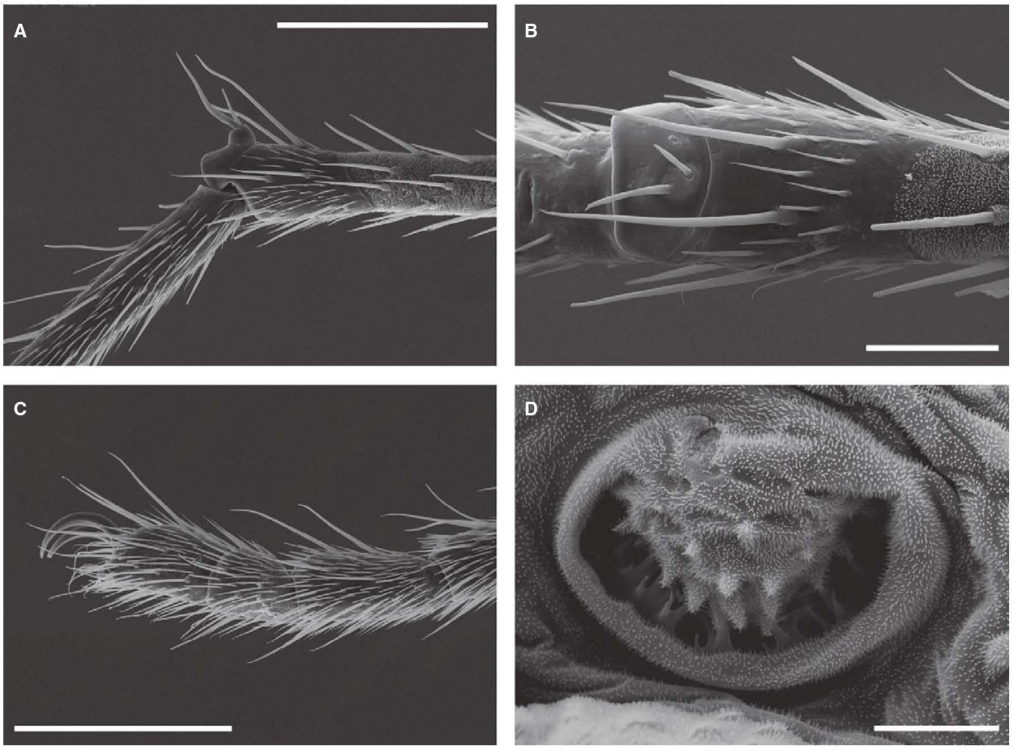

Figure 9. *Jarmilana pecki*, comb. nov. beta male MACN_Ar 35557, details of legs and spiracle. A, B, right metatarsus IV showing the division between calcaneous and astragalus, and the dorsodistal tubercle with two large setae, from (A) prolateral view and (B) dorsal view. C, distitarsus of leg IV, prolateral view. D, spiracle. Scale bars: (A, C) 200 μm; (B) 50 μm; (D) 20 μm.

here as setae with microtrichia covering the majority of the shaft (Fig. 7F) but with a smooth base (Fig. 7B, E); small pores are associated with plumose setae, found near the socket on the tubercle (Fig. 7B, E). *Legs*. Measurements in Table 3. Legs I–IV slender, cylindrical, equal in diameter, without remarkable armature. Calcaneus restricted to the distal portion of legs (Fig. 9A, B), not expanded throughout the ventral portion of the metatarsus in leg III (as in many samooid harvestmen; e.g. Pérez-González & Kury, 2007, fig. 4.37 d). Without scopula (Fig. 9C). Tarsal count: 3(2):9(4):4:5, the first tarsomere on legs III and IV is very long compared to the remaining tarsomeres, more than three times the length of the second tarsomere. Metatarsus IV has a large dorsodistal tubercle with two large setae inserted (Fig. 9A, B). *Microanatomy of cuticle*. Cuticle of entire body and coxa to metatarsus (calcaneus only) of legs I–IV covered in small rounded granules (i.e. verrucose) that are < 10 μm in diameter and height (Figs 3, 4). Cuticle is further modified with dense microtrichia (Fig. 4C). Femur of pedipalps verrucose but with few microtrichia. Palpal patella, tibia, and tarsus relatively smooth, although some flattened granules are visible. On the pedipalps, plumose setae of the major setiferous tubercles possess microtrichia on the medial and distal portion (Fig. 7F), with smooth base (Fig. 7E). Rough pit glands (*sensu* Murphree, 1988; see also Willemart, Chelini & Gnaspini, 2007; Rodriguez *et al.*, 2014) are distributed on the entire carapace, along the lateral margins of the mesotergal scutum, and along sulcus V of the mesotergum; these structures are especially concentrated within a

Figure 10. *Jarmilana pecki*, comb. nov. genitalia of beta male MACN_Ar 35557, non-expanded. A, dorsal view. B, lateral view. C, ventral view. D, detail of stylus and apical lobes of follis. Scale bars: (A, B, C) 100 μm; (D) 50 μm. D1, macrosetae D1; Fo, follis; Lb, lobe of follis; St, stylus.


A
Fo
B
D1
C
D
St
Lb
Lb

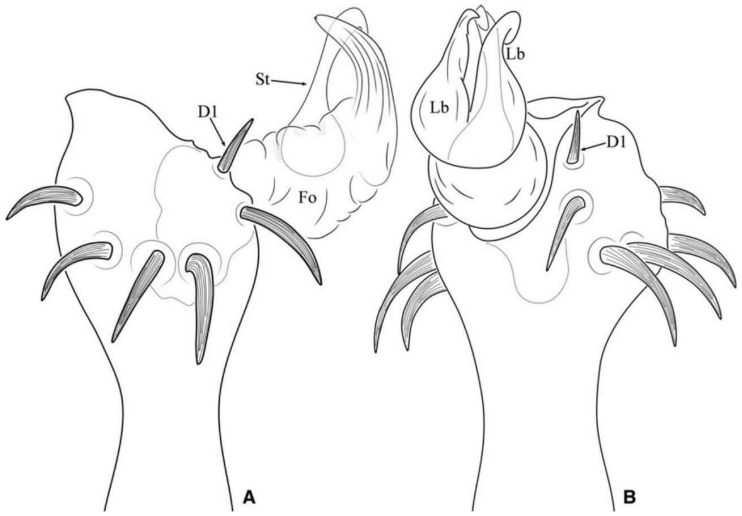

Figure 11. *Jarmilana pecki*, comb. nov. genitalia of alpha male MACN_Ar 35555, expanded. A, lateral view. B, dorsolateral view. D1, macrosetae D1; Fo, follis; Lb, lobe of follis; St, stylus.

Table 4. Comparative size of the pedipalps between alpha male (MACN_Ar 35555), beta male (MACN_Ar 35557), and female (MACN_Ar 35556) for *Jarmilana pecki* comb. nov.

	Femur length	Femur width	Femur length/width	Patella length	Tibia length	Tarsus length
Alpha male	2.10	0.84	2.5	1.05	1.77	1.55
Beta male	1.42	0.47	3.02	0.72	1.23	1.10
Female	1.41	0.46	3.06	0.67	1.21	1.00

depressed area lateral to the position of sulcus I (Fig. 4B, D). *Male genitalia*. Pars distalis swollen, with slight constriction at base. Ventral plate not differentiated, as in Gonyleptoidea, although with one small and rounded lamina apicalis. Follis with dorsoapical portion modified into two lobes that conceal the stylus when retracted. Capsula interna without accessory sclerites (e.g. parastylar conductors). Stylus arising subapically from follis (i.e. at base of lobes), long and curved, tip of stylus ending with a dorsal barb. Pars distalis armed with two dorsal and four lateral pairs of macrosetae, with rounded tips and numerous longitudinal striae along the entire length. One pair of dorsal setae (D1 setae *sensu* Kury & Villarreal, 2015) insert directly adjacent to the follis, projecting dorsoapically; the second dorsal pair is inserted basolaterally to the glans and directed dorsobasally (Figs 10, 11). When the genitalia is expanded, the follis unfolds and inflates dorsally, whereas the lobes inflate, separate and curl apically; the stylus is directed apically between the tips of the two lobes (Fig. 11).

Beta male (MACN_Ar 35557). Body measurements:. Total body length 1.70, *scutum magnum* length 1.61, carapace length 0.70, carapace maximum width 1.12, mesotergal scute maximum width 1.28. Similar to the alpha male but with the differences: smaller body size; pedipalps not strongly developed, and more similar in shape and size to the palps of the female (Table 4); palpal femur with mesal subdistal setiferous tubercle more strongly developed (Fig. 8B); cheliceral armature slightly reduced in size.

Female (MACN-35556). Body measurements:. Total body length 2.00, *scutum magnum* length 1.76, carapace length 0.70, carapace maximum width 1.15, mesotergal scute maximum width 1.36. Tarsal formula same as males. Similar in general appearance to males but with less developed sexual dimorphic characters, such as the size and armature of pedipalps (more similar to the beta male) (Fig. 8C, Table 4) and chelicerae.

Distribution:. Known only from two caves: Mountain Cow Cave and St Herman's Cave – located in Caves Branch, Cayo District, Belize.

Natural history:. Individuals were observed in the twilight zone of the cave, actively walking and climbing on the floor and walls of the cave. When disturbed, they exhibited thanatosis.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Phylogenetic relationships based on Maximum Likelihood revealing the relationship of the Neotropical troglobite *Jarmilana pecki* comb. nov. (highlighted) with the African family Pyramidopidae. Numbers on nodes correspond to bootstrap support; black circles at nodes indicate bootstrap values of 100. Branch colors correspond to higher taxa (families or superfamilies) and reflect the same color scheme used in Figure 1, and by Sharma & Giribet (2011). The superfamilies Assamioidea (blue) and Epedanoidea (red) are recovered as polyphyletic.

Capítulo 3. Artículo de requisito: Cruz-López, J. A. y Francke, O. 2017. Total evidence phylogeny of the North American harvestman family Stygnopsidae (Opiliones: Laniatores: Grassatores) reveals hidden diversity. *Invertebrate Systematics*. 31: 317-360.

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Total evidence phylogeny of the North American harvestman family Stygnopsidae (Opiliones : Laniatores : Grassatores) reveals hidden diversity

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Abstract. Systematic relationships among Laniatores have received considerable attention during the past few years. Many significant taxonomic changes have been proposed, particularly in the superfamily Gonyleptoidea. As part of this superfamily, the basalmost Stygnopsidae is the least known family. In order to propose the first total evidence phylogeny of the family, we produced four datasets: three molecular markers – partial nuclear *28S*, mitochondrial ribosomal *16S*, mitochondrial protein-encoding cytochrome *c* oxidase subunit I; and 72 morphological characters. With these data, we performed three different phylogenetic analyses: (1) Bayesian Inference with molecular data, and (2) Bayesian Inference and (3) Maximum Likelihood using combined data. Our results are congruent: a monophyletic Stygnopsidae subdivided into two major clades: Stygnopsinae and Karosinae, subfam. nov. The following genera are redefined: *Stygnopsis*, *Hoplobunus* and *Serrobunus* stat. rev. The following taxa are described: *Iztlina venefica*, gen. nov., sp. nov. and *Tonalteca*, gen. nov. Additionally, the following changes are proposed: *Serrobunus queretarius* (Šilhavý, 1974), comb. nov., *Stygnopsis apoalensis* (Goodnight & Goodnight, 1973), comb. nov., *Stygnopsis mexicana* (Roewer, 1915), comb. nov., *Stygnopsis oaxacensis* (Goodnight & Goodnight, 1973), comb. nov., and *Tonalteca spinooculorum* (Goodnight & Goodnight, 1973), comb. nov. We also discuss the status of the genera *Isaeus* stat. rev. and *Mexotroglinus*. Finally, we discuss the evolution of male genitalia and convergence of selected homoplastic diagnostic characters.

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Introduction

The order Opiliones Sundevall, 1833, with ~6500 species, is the third most diverse group in Arachnida, after Acari and Araneae (Giribet and Sharma 2015). The group comprises conspicuous arachnids from humid habitats in both tropical and temperate zones, but mostly in the Neotropical region (Pinto-da-Rocha *et al*. 2014). Four major lineages are recognised in the order: (1) the mite-like harvestmen Cyphophthalmi Simon, 1879; (2) the daddy-longlegs Eupnoi Hansen and Sørensen, 1904; (3) the thread-like palpi Dyspnoi Hansen and Sørensen, 1904; and (4) the armoured harvestmen Laniatores Thorell, 1876 (Wolff *et al*. 2016). This last lineage is the most diverse, encompassing more than two-thirds of the diversity in Opiliones (Sharma and Giribet 2011).

During the last two decades, the systematics of Laniatores has received special attention (Sharma and Giribet 2014; Giribet and Sharma 2015). For example, 11 family-group taxa have been described or re-assigned, many of these previously considered as part of the 'waste-basket' Phalangodidae Simon, 1879 under Roewer's criterion (revisited in part for selected taxa by Pinto-da-Rocha *et al*. (2012), Bragagnolo *et al*. (2015) and Cruz-López *et al*. (2016). These taxa have been erected or re-assigned based on three general criteria: (1) the re-examination of male genitalia as in Escadabiidae Kury and Pérez-González, 2003, Icaleptidae Kury and Pérez-González, 2002 and Kimulidae Pérez-González *et al*., 2007 (Kury and Pérez-González 2002; Kury and Pérez-González in Kury 2003; Pérez-González and Kury 2007); (2) morphology-based phylogenies as in Cranaidae Roewer, 1013, Cryptogeobiidae Kury, 2014, Globibuninae Kury, 2012, Manaosbiidae Roewer, 1943 and Nomoclastidae Roewer, 1943 (Kury 2012, 2014; Kury and Villarreal 2015); and (3) molecular-based phylogenies as in Gerdesiidae Bragagnolo *et al*., 2014, Metasarcidae Kury, 1994, Petrobunidae Sharma and Giribet, 2011, Pyramidopidae Sharma *et al*., 2011 and Tithaeidae Sharma and Giribet, 2011 (Sharma and Giribet 2011; Sharma *et al*. 2011; Pinto-da-Rocha *et al*. 2014; Bragagnolo *et al*. 2015).

Among Laniatores, the superfamily Gonyleptoidea Sundevall, 1833 is one of the most controversial groups. Phylogenetically,

relationships have been open to discussion, depending on the data source and taxon sampling, as in the status of Cranaidae/nae and Manaosbiidae/nae. Using morphological evidence, these groups have been considered to form a grade with Gonyleptidae and preserved their familial status (Kury and Villarreal 2015). Conversely, based on multi-locus phylogenetic research, these two families are nested within Gonyleptidae, and are considered subfamilies (Pinto-da-Rocha *et al*. 2014).

Currently, both data sources, morphology and molecules, support Stygnopsidae Sørensen, 1932 (although only a few representatives of the group have been sampled) as sister-group of the other families of Gonyleptoidea (Giribet *et al*. 2002, 2010; Sharma and Giribet 2011; Kury and Villarreal 2015). However, the monophyly of the family has never been tested using a strict phylogenetic approach, either with morphological or molecular data, and the internal relationships remain unclear. Complementary to the phylogenetic position of Stygnopsidae, Kury (2003), Pérez-González (2006), Mendes and Kury (2007) and Sharma *et al*. (2011) considered that the glans penis formed by an exposed multifolded follis with small apical spines could be a synapomorphic feature for the family, although similar genital structures are present in Epedanidae Sørensen, 1886, Assamiidae Sørensen, 1884 and Pyramidopidae Sharma *et al*., 2011.

The taxonomic history of Stygnopsidae is very complex, with isolated descriptions of genera and species in different families and many synonymies and transfers. Many of these taxonomic problems were generated by Roewer (1912, 1915) and Goodnight

Table 1. Taxa used in the phylogenetic analysis, including GenBank accession numbers

Taxa	Family	DNA voucher	*28S*	*16S*	*COI*
Zalmoxida sp.	Petrobunidae	DNA104070	JF786583	JF786462	JF786435
Conomma oedipus	Pyramidopidae	DNA101051	GQ912801.2	GQ912853	GQ912882
Cynortula granulata	Cosmetidae	DNA100332	GQ912809.2	JF786464	–
Glysterus sp.	Gonyleptidae, Ampycinae	DNA101422	GQ912814.2	FJ796472	FJ796493
Zygopachylus sp.	Nomoclastidae, Nomoclastinae	DNA101425	GQ912818.2	GQ912855	GQ912889
Chapulobunus asper	Stygnopsidae, Karosinae	CNAN-DNA-0043	KY042066	–	–
Chapulobunus poblano	Stygnopsidae, Karosinae	CNAN-DNA-0072	KY042067	–	–
Chapulobunus psilocybe	Stygnopsidae, Karosinae	CNAN-DNA-0069	KY042068	KY042047	KY097807
Chapulobunus unispinosus	Stygnopsidae, Karosinae	CNAN-DNA-0042	KY042069	KY042048	KY097808
Chinquipellobunus aff. *madlae*	Stygnopsidae, Stygnopsinae	CNAN-DNA-0067	KY042070	–	–
Chinquipellobunus aff. *russelli*	Stygnopsidae, Stygnopsinae	CNAN-DNA-0065	KY042071	KY042049	KY097809
Chinquipellobunus osorioi	Stygnopsidae, Stygnopsinae	CNAN-DNA-0068	KY042072	KY042050	KY097810
Crettaros valdezi	Stygnopsidae, Karosinae	CNAN-DNA-0073	KY042073	KY042051	KY097811
Hoplobunus barretti	Stygnopsidae, Stygnopsinae	CNAN-DNA-0090	KY042074	KY042052	KY097812
Hoplobunus sp.	Stygnopsidae, Stygnopsinae	CNAN-DNA-0002	KY042075	KY042053	KY097813
'*Hoplobunus*' sp.	Stygnopsidae, Stygnopsinae	CNAN-DNA-0033	KY042076	KY042054	KY097814
'*Hoplobunus*' aff. *planus*	Stygnopsidae, Karosinae	CNAN-DNA-0029	KY042082	–	KY097820
'*Hoplobunus*' *zullinii*	Stygnopsidae, Stygnopsinae	CNAN-DNA-0170	KY042065	KY042046	KY097806
Huasteca gratiosa	Stygnopsidae, Karosinae	CNAN-DNA-0020	KY042077	KY042055	KY097815
Huasteca rugosa	Stygnopsidae, Karosinae	CNAN-DNA-0004	KY042078	–	KY097816
Huasteca sp.	Stygnopsidae, Karosinae	CNAN-DNA-0060	KY042079	KY042056	KY097817
Iztlina venefica	Stygnopsidae, Stygnopsinae	CNAN-DNA-0057	KY042080	KY042057	KY097818
Karos barbarikos	Stygnopsidae, Karosinae	CNAN-DNA-0031	KY042081	–	KY097819
Mexotroglinus aff. *sbordonii*	Stygnopsidae, Stygnopsinae	CNAN-DNA-0051	KY042083	KY042058	KY097821
Mictlana inops	Stygnopsidae, Karosinae	CNAN-DNA-0063	KY042084	–	KY097822
Paramitraceras aff. *granulatum*	Stygnopsidae, Stygnopsinae	CNAN-DNA-0009	KY042085	–	KY097823
Paramitraceras aff. *hispidulum*	Stygnopsidae, Stygnopsinae	CNAN-DNA-0152	KY042086	–	KY097824
Paramitraceras tzotzil	Stygnopsidae, Stygnopsinae	CNAN-DNA-0035	KY042087	–	KY097825
Paramitraceras veracruz	Stygnopsidae, Stygnopsinae	CNAN-DNA-0007	KY042088	–	KY097826
Philora mazateca	Stygnopsidae, Stygnopsinae	CNAN-DNA-0046	KY042089	–	–
Philora tuxtlae	Stygnopsidae, Stygnopsinae	CNAN-DNA-0045	KY042090	–	KY097827
Potosa sp.	Stygnopsidae, Karosinae	CNAN-DNA-0089	KY042091	KY042059	KY097828
Sbordonia aff. *parvula*	Stygnopsidae, Stygnopsinae	CNAN-DNA-0163	KY042092	KY042060	KY097829
Sbordonia sp.	Stygnopsidae, Stygnopsinae	CNAN-DNA-0055	KY042093	–	KY097830
Serrobunus boneti	Stygnopsidae, Stygnopsinae	CNAN-DNA-0005	KY042094	KY042061	KY097831
Stygnopsis apoalensis	Stygnopsidae, Stygnopsinae	CNAN-DNA-0064	KY042095	KY042062	KY097832
Stygnopsis mexicana	Stygnopsidae, Stygnopsinae	CNAN-DNA-0071	KY042096	–	KY097833
Stygnopsis oaxacensis	Stygnopsidae, Stygnopsinae	CNAN-DNA-0083	KY042097	–	KY097834
Stygnopsis robusta	Stygnopsidae, Stygnopsinae	CNAN-DNA-0036	KY042098	KY042063	KY097835
Stygnopsis valida	Stygnopsidae, Stygnopsinae	CNAN-DNA-0044	KY042099	–	KY097836
Tonalteca spinooculorum	Stygnopsidae, Stygnopsinae	CNAN-DNA-0084	KY042100	KY042064	KY097837
Troglostygnopsis sp.	Stygnopsidae, Stygnopsinae	CNAN-DNA-0049	KY042101	–	–
Troglostygnopsis sp.	Stygnopsidae, Stygnopsinae	CNAN-DNA-0050	KY042102	–	KY097838

and Goodnight (1953). Sørensen (1932) described the family Stygnopsidae as those Laniatores with distitarsus I with two segments and without maxillary lobes on coxae II. Sørensen (1932) included three genera in the family: *Stygnopsis* Sørensen, 1902, *Tachus* Sørensen, 1932 (currently *Tibangara* Mello-Leitão, 1940 in Cryptogeobiidae Kury, 2014) and *Isaeus*

Table 2. Molecular markers, primers sequences and original references

28S		
28S D1F	5′-GGG ACT ACC CCC TGA ATT TAA GCA T-3′	Park and Ó Foighil (2000)
28Srd4b	5′-CCT TGG TCC GTG TTT CAA GAC-3′	Edgecombe and Giribet (2006)
28Sa	5′-GAC CCG TCT TGA AAC ACG GA-3′	Whiting *et al.* (1997)
28Srd5b	5′-CCA CAG CGC CAG TTC TGC TTA C-3′	Schwendinger and Giribet (2005)
28Srd4.8a	5′-ACC TAT TCT CAA ACT TTA AAT GG-3′	Schwendinger and Giribet (2005)
28Srd7b1	5′-GAC TTC CCT TAC CTA CAT-3′	Schwendinger and Giribet (2005)
16S		
16Sa	5′-CGC CTG TTT ATC AAA AAC AT-3′	Xiong and Kocher (1991)
16Sb	5′-CTC CGG TTT GAA CTC AGA TCA-3′	Edgecombe *et al.* (2002)
COI		
LCO1490	5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′	Folmer *et al.* (1994)
HCOoutout	5′-GTA AAT ATA TGR TGD GCT C-3′	Prendini *et al.* (2005)
Vf1d_t1	5′-TGT AAA ACG ACG GCC AGT TCT CAA CCA ACC ACA ARG AYA TYG G-3′	Ivanova *et al.* (2007)
Vr1d_t1	5′-CAG GAA ACA GCT ATG ACT AGA CTT CTG GGT GGC CRA ARA AYC A-3′	Ivanova *et al.* (2007)

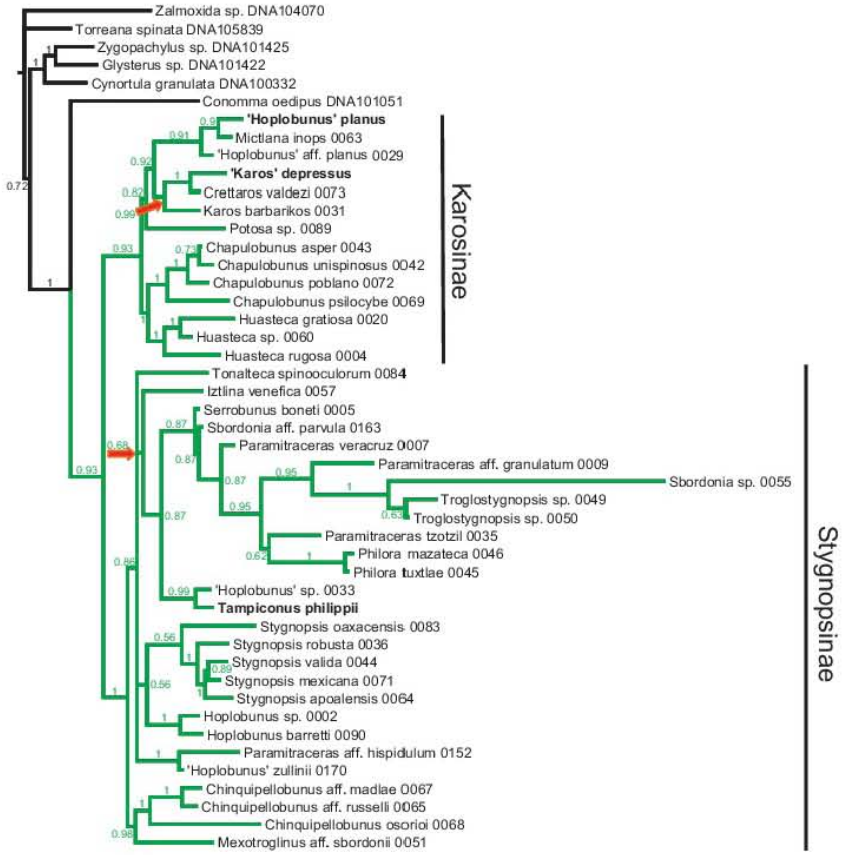

Fig. 1. Phylogenetic relationships of the family Stygnopsidae based on Bayesian Inference (BI) using combined data. Numbers on nodes correspond to posterior probabilities. Terminals in bold black correspond to taxa with only morphology data available from females only.

Sørensen, 1932, a monotypic genus described in the same work. It is remarkable that at the same time, other genera currently placed in Stygnopsidae were allocated to Phalangodidae or Assamiidae (Banks 1900; Sørensen 1902; Pickard-Cambridge 1905).

Mello-Leitão (1938) revised the familial classification of Sørensen and adopted proposal of Roewer (1923). Mello-Leitão (1938) considered Stygnopsinae Sørensen, 1932 as subfamily within Stygnopsidae with only two genera, *Stygnopsis* and *Tachus*, and erected the subfamily Isaeinae Mello-Leitão, 1938 for *Isaeus*, this last proposal without any justification.

Goodnight and Goodnight (1942, 1944) described four monotypic genera: *Serrobunus* Goodnight & Goodnight, 1942, *Chinquipellobunus* Goodnight & Goodnight, 1944, *Karos* Goodnight & Goodnight, 1944, and *Monterella* Goodnight & Goodnight, 1944; all of them in Phalangodinae. Later, Goodnight and Goodnight (1945, 1946) transfered *Chinquipellobunus*, *Hoplobunus* Banks, 1900 and *Serrobunus* to Stygnopsinae, and described the monotypic genera *Montabunus* Goodnight & Goodnight, 1945 in Phalangodinae and *Chapulobunus* Goodnight & Goodnight, 1946 in Stygnopsinae. In subsequent publications, Goodnight and Goodnight (1947*b*, 1953, 1954, 1967, 1971, 1973, 1977) again ignored Stygnopsidae/nae, and described more monotypic genera, *Potosa* Goodnight & Goodnight, 1947 and *Philora* Goodnight & Goodnight, 1954, in Phalangodinae. Among the several papers by the Goodnights, Goodnight and Goodnight (1953) stands out, because the authors made many unjustified synonymies in laniatorean genera, and reduced almost all of the monotypic genera previously described by them to only three genera: *Hoplobunus*, *Karos* and *Paramitraceras* Pickard-Cambridge, 1905.

Šilhavý (1974) considered Stygnopsidae with two subfamilies: Stygnopsinae with *Hoplobunus* and *Stygnopsis*, and a new subfamily, Troglostygnopsinae Šilhavý, 1974, for the monotypic *Troglostygnopsis* Šilhavý, 1974, a genus described in the same work. The last action was justified by the high tarsal count in legs I, with more than two segments in distitarsus I. It is also remarkable that Šilhavý (1974) considered *Karos* and *Paramitraceras*, placed at the time in Phalangodinae, with presence of 'lateral projections' on either side of scutum, as 'related' to *Troglostygnopsis*, which has similar lateral projections.

On the basis of male genitalic morphology, Kury (1994, 1997, 2003) and Kury and Cokendolpher (2000) rediagnosed and restricted the family to *Hoplobunus*, *Karos*, *Mexotroglinus* Šilhavý, 1977, *Paramitraceras*, *Sbordonia* Šilhavý, 1977, *Stygnopsis*, *Tampiconus* Roewer, 1949 and *Troglostygnopsis*, without any subfamilial groupings.

Recently, Cokendolpher (2004) revalidated *Chinquipellobunus* from its synonymy under *Hoplobunus* on the basis of male genitalia of selected North American stygnopsids. Cruz-López

Fig. 2. Dorsal habitus of *Stygnopsis*. (*A*) *Stygnopsis valida* male. (*B*) *Stygnopsis valida* female. (*C*) *Stygnopsis robusta* male. (*D*) *Stygnopsis robusta* female. (*E*) *Stygnopsis oaxacensis* male. (*F*) *Stygnopsis oaxacensis* female. Scale bars: A, B, C, D = 4.0 mm, E, F = 3.0 mm.

and Francke (2013*b*) revised *Philora* and transferred this genus from *incertae sedis* to Stygnopsidae. They also described a unique male genital pattern present only in the Neotropical stygnopsid genera *Paramitraceras* and *Philora*, the type species of *Troglostygnopsis*, and presumably in *Sbordonia*.

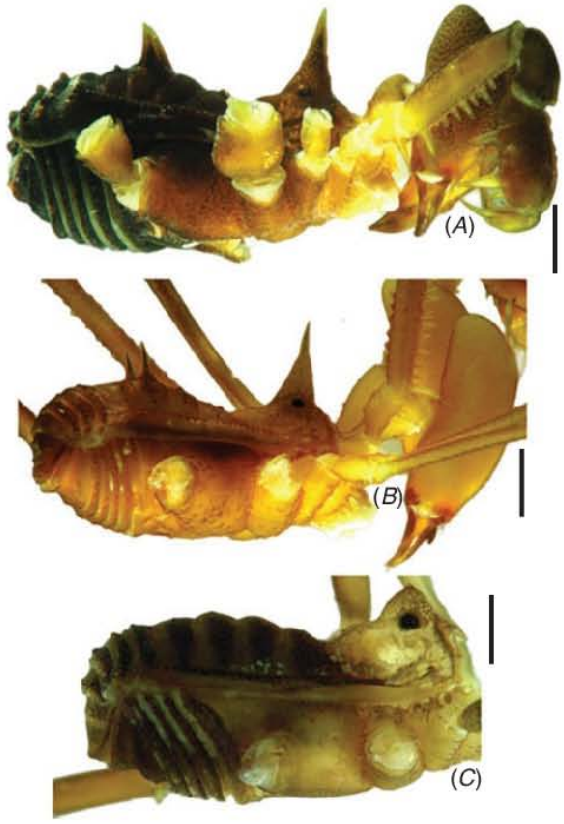

Fig. 3. Lateral habitus of *Stygnopsis*. (*A*) *Stygnopsis valida* male. (*B*) *Stygnopsis robusta* male. (*C*) *Stygnopsis oaxacensis* male. Scale bars: A, B, C = 2.00 mm.

Cruz-López and Francke (2015) performed a cladistic analysis of the genus *Karos* using morphological data. They found that the Goodnights' concept of *Karos* represented a paraphyletic group, because *Troglostygnopsis inops* (Goodnight and Goodnight 1971) is nested within it with high support. They also proposed the revalidation of all genera currently in synonymy with *Karos*, because all of them exhibit sufficient synapomorphies and diagnostic characters to be considered valid (Cruz-López and Francke 2015). In addition, Cruz-López and Francke (2015) proposed two monophyletic genus-groups within Stygnopsidae: the *Paramitraceras*-group, diagnosable according to Cruz-López and Francke (2013*b*), and the *Karos*-group, comprising those stygnopsids with armature on the meso-apical and mesal surfaces of the pedipalpal femur and patella, the ocularium located in the middle of the prosoma, males and females without sexual dimorphism in dentition and cheliceral size, and penis flattened apically, with lateral macrosetae forming a longitudinal row.

Currently, Stygnopsidae is composed of 17 genera and 56 species. This family is distributed mainly in the Sierra Madre Oriental in Mexico, inhabitating pine forest, pine-oak forest, rainforest and/or caves. However, *Chinquipellobunus* occurs in caves in Southern Texas, USA, and *Paramitraceras* extends to tropical regions in Guatemala, Belize, El Salvador and Honduras.

Here, we propose the first total evidence phylogenetic hypothesis of Stygnopsidae relationships, based on two mitochondrial markers, *COI* and *16S*, the almost entire nuclear *28S*, and 72 morphological characters, and sampling the largest ever number of representative taxa of the family. Our results support the recognition of two subfamilies in Stygnopsidae: Stygnopsinae and Karosinae, subfam. nov. Additionally, we discuss the evolution of male genitalia, the convergence of some diagnostic morphological characters, the polyphyly of the genera *Hoplobunus* and *Paramitraceras*, and the taxonomic status of selected taxa, including the description of the following taxa: *Tonalteca*, gen. nov. and *Iztlina venefica*, gen. nov., sp. nov.

Fig. 4. Chelicera of *Stygnopsis* males. (*A*) Frontal view of *Stygnopsis valida*. (*B*) Mesal view of *Stygnopsis valida*. (*C*) Frontal view of *Stygnopsis robusta*. (*D*) Mesal view of *Stygnopsis robusta*. (*E*) Frontal view of *Stygnopsis oaxacensis*. (*F*) Mesal view of *Stygnopsis oaxacensis*. Arrows indicate the basal blunt tooth. Scale bars: A = 2.0 mm, B, C = 1.5 mm.

Materials and methods

Morphological data and taxon sampling

Diverse material of described and undescribed Stygnopsidae and additional Laniatores was examined from the following collections and museums: American Museum of Natural History, New York, USA (AMNH); the Natural History Museum, London, UK (NHM); Colección Nacional de Arácnidos, Mexico City, Mexico (CNAN); Laboratorio de Acarología 'Anita Hoffmann', Facultad de Ciencias, Universidad Autónoma de México (UNAM), Mexico City, Mexico (LAAH); Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN); Naturmuseum Senckenberg Sektion Arachnologie, Frankfurt, Germany (SMF); Texas Memorial Museum, Texas, USA (TMM); and The Museum, Texas Tech University, Texas, USA (TTU). Types of new taxa described here and DNA vouchers of ingroup are deposited in CNAN. For a complete list of material examined, see Supplementary Materials 1 and 2 (available as Supplementary material to this paper).

We attempted to include the greatest representation of stygnopsid taxa in our analyses, but it was not possible to obtain DNA from '*Hoplobunus*' *planus* Goodnight & Goodnight, 1973, '*Karos*' *depressus* Goodnight & Goodnight, 1971 and *Tampiconus philippi* Roewer, 1949, species where only the female types are known. Even so, we included them in the combined analyses because they are problematic taxa. The types of *P. granulatum* Pickard-Cambridge, 1905, *P. hispidulum* Pickard-Cambridge, 1905 (both sexes), and *Sbordonia parvula* (Goodnight & Goodnight, 1953) (female), and an additional male of *S. parvula* (MACN) were examined, but it was not possible to obtain fresh tissue for DNA extraction for these species. However, DNA and morphological data of three closely related species (aff.) were included in the analyses.

We selected six taxa from Sharma and Giribet (2011) as outgroups (Table 1). The selection was based on the availability of both morphological and molecular data of some Gonyleptoidea, and of two more distant groups, Pyramidopidae and Petrobunidae. Only one male of *Conomma oedipus* Roewer, 1949 (Pyramidopidae) was examined for morphology. With respect to the remaining outgroups, the morphological data were obtained as complete as possible from Goodnight and Goodnight (1947*a*), Avram (1977) and Kury and Villarreal (2015). The ingroup is formed by 41 species (Supplementary Materials 1 and 2). For the most diverse genus, *Hoplobunus*, we included eight of the 10 species known, plus two undescribed species 'similar' to the type species *Hoplobunus barretti* Banks, 1900. We focused on this genus, because it is currently the most diverse, although this diversity is an artefact due to its complex taxonomic history based on some of the Goodnight's unjustified synonymies. This problem has been corroborated for some other Mexican taxa, as reported by Cruz-López and Francke (2013*a*, 2015) in *Paramitraceras* and *Karos*, respectively.

To collate the morphological data, the specimens were examined under a Nikon SMZ 625 microscope. Colour photographs were taken with Nikon Coolpix S10 camera with adaptor for the microscope. Electronic photographs were taken using two differents SEMs: Hitachi S-2460N and Hitachi SU1510, both in the Instituto de Biología, UNAM, Mexico. All figures were edited using Adobe Illustrator CC and PhotoShop CS5. We coded 72 morphological characters, some of which were taken and modified from Kury and Villarreal (2015) and Cruz-López and Francke (2015). To see

Fig. 5. Mesal view of pedipalps of *Stygnopsis* males. (*A*) *Stygnopsis robusta*. (*B*) *Stygnopsis valida*. (*C*) *Stygnopsis oaxacensis*. Scale bars: A = 2.5 mm, B = 2.0 mm, C = 1.5 mm.

the list and description of all characters and how these were coded, see Supplementary Materials 3 and 4.

Taxonomic nomenclature

For the description of morphological characters and new taxa, we adopted different nomenclatural sources, including the scutum shape from Kury and Medrano (2016), the morphology of the chelicera, pedipalp and ornamentation of dorsum and legs from Cruz-López and Francke (2015, 2016*a*), and the pedipalpal armature from Acosta *et al.* (2007). To describe the male genitalia, we adopted the penial setation nomenclature recently proposed by Kury and Villarreal (2015), with modifications as treated in Cruz-López and Francke (2016*a*, 2016*b*), and additional modifications proposed here. For morphology of the capsula externa and interna, we follow Pérez-González (2006).

Molecular data

All outgroups sequences were obtained from GenBank (Table 1). Total DNA of the ingroup was extracted from legs or complete juveniles using DNeasy tissue kit (Qiagen, Mexico City, Mexico) following supplier procedure with modifications proposed by Boyer *et al.* (2005). Total DNA was used as a template for amplification of partial nuclear ribosomal *28S* obtained from assembly of three fragments, the mitochondrial ribosomal *16S* and the mitochondrial protein-encoding cytochrome *c* oxidase subunit I (*COI*). Primer sequences and their original references are indicated in Table 2.

PCR reactions were carried out in 12.5 µL volumes, consisting of 0.2 µM each primer, 0.8 µM deoxynucleotides, 1 × PCR buffer, 4 mM $MgCl_2$, 1.25 U of *Taq* DNA polymerase (TaKara LA *Taq*, CA, USA) and 1–2 µL of DNA template for *COI* and *16S*. Similarly, we carried out PCR reactions using Green Master Mix Polymerase (WI, USA) for *28S*, with the following mix: 0.5 × of the mix, 0.2 µM each primer and 1–2 µL of DNA template. For all markers, the cycles were according to Sharma and Giribet (2009), except annealing temperature of 46°C for *COI*. For the primer pairs Vf1d_t1-Vr1d_t1, the cycles were: 5 initial cycles of 94°C × 2 min, 94° × 30 s, 50° × 40 s, 72° × 1 min; plus 30 cycles of 94° × 30 s, 55° × 40 s, 72° × 1 min, with a final extention of 72° × 5 min. PCR products were visualised by agarose gel electrophoresis (1.5% agarose). Unpurified products were sequenced in the Instituto de Biología (UNAM), Mexico City, and by High Throughput Sequencing (htSEQ), in the University of Washington, Seattle, USA. Chromatograms and sequences were viewed and edited in Geneious ver. 9.1.2 (Kearse *et al.* 2012) and BioEdit ver. 7.2.5 (Hall 1999). The fragments of *28S* were assembled in Geneious. Finally, we obtained 99 sequences of the ingroup (Table 1). To see the complete collection data of vouchers, see Supplementary Material 2.

The *16S* and *COI* markers were aligned using MAFFT (Katoh 2013), with default parameters through the interface Mesquite ver. 3.0.4 (Maddison and Maddison 2015). The *28S* marker was aligned using the L-INS-i algorithms implemented in

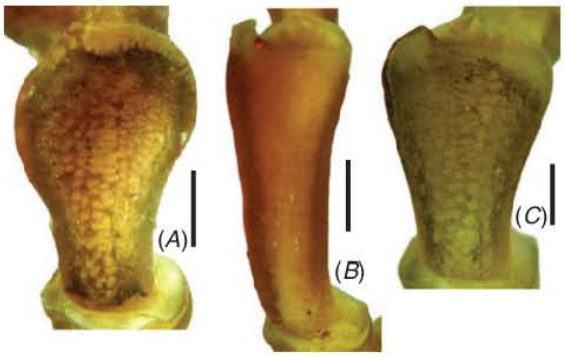

Fig. 6. Dorsal view of pedipalp patella of *Stygnopsis* males. (*A*) *Stygnopsis valida*. (*B*) *Stygnopsis robusta*. (*C*) *Stygnopsis oaxacensis*. Scale bars: A, B = 0.5 mm, C = 0.25 mm.

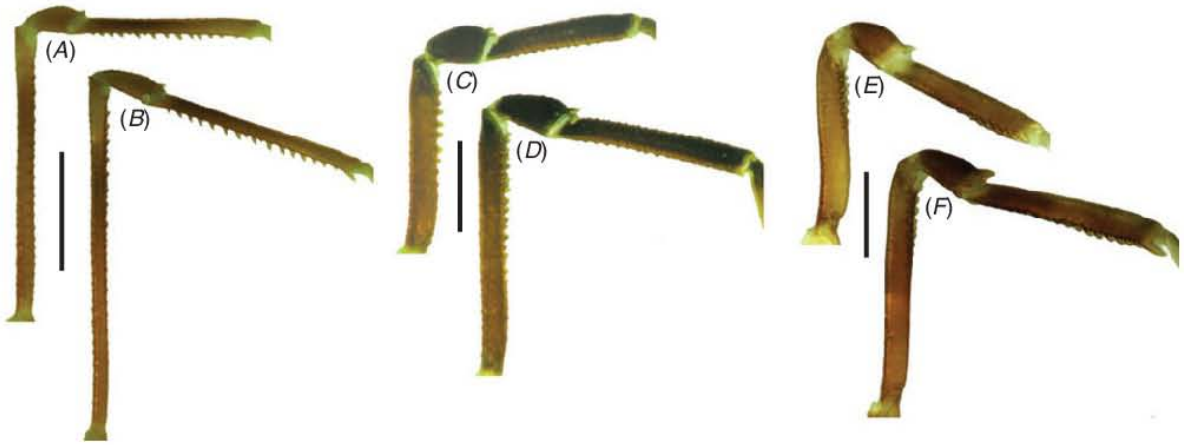

Fig. 7. Retrolateral views of legs III and IV of *Stygnopsis* males. (*A*) Leg III of *Stygnopsis robusta*. (*B*) Leg IV of *Stygnopsis robusta*. (*C*) Leg III of *Stygnopsis valida*. (*D*) Leg IV of *Stygnopsis valida*. (*E*) Leg III of *Stygnopsis oaxacensis*. (*F*) Leg IV of *Stygnopsis oaxacensis*. Scale bars: A = 5.0 mm, B = 4.5 mm, C, D, F = 3.00 mm, E = 2.5 mm.

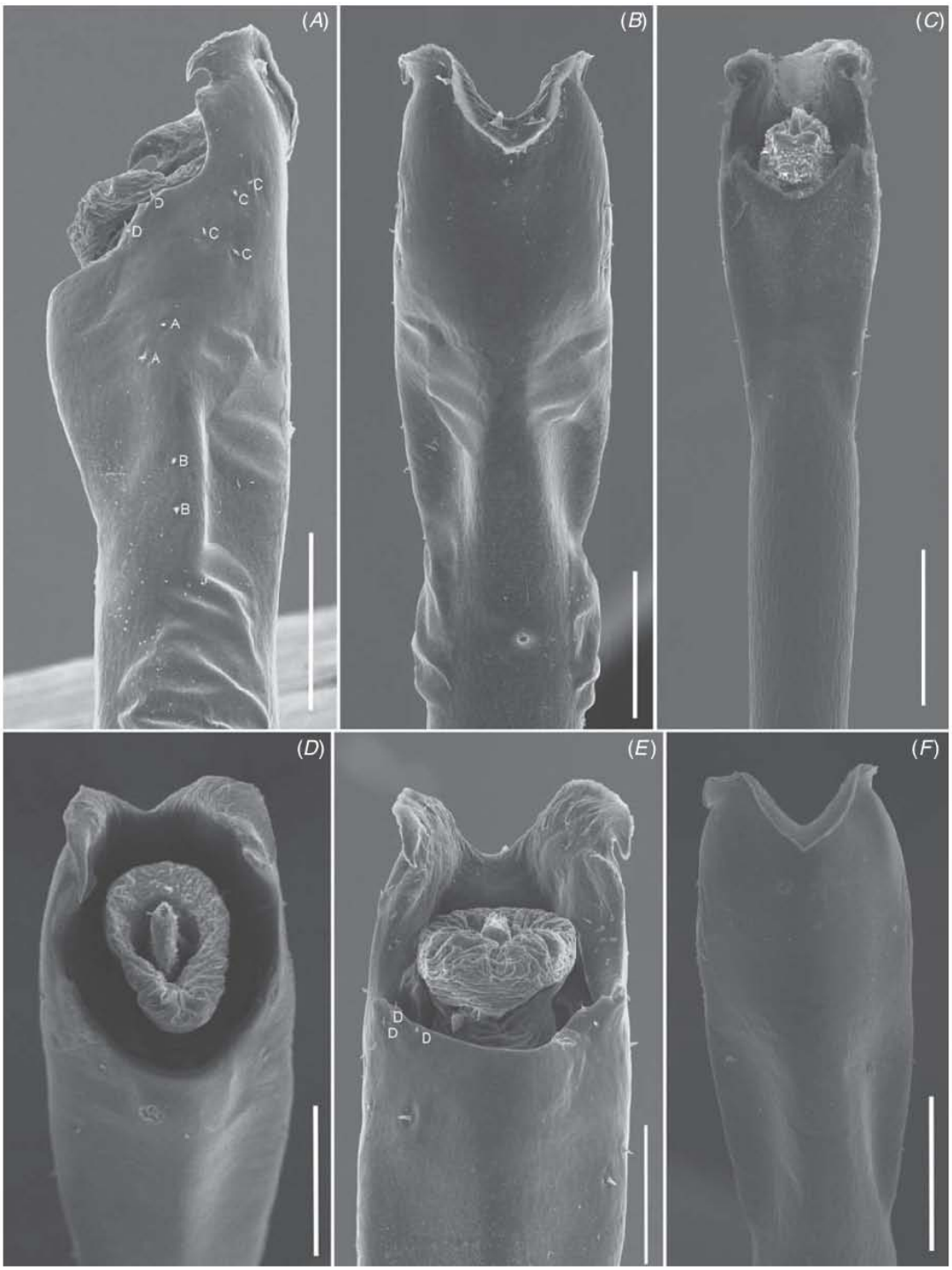

Fig. 8. Male genitalia of *Stygnopsis*. (*A*) Lateral view of *Stygnopsis robusta*. (*B*) Ventral view of *Stygnopsis robusta*. (*C*) Dorsal view of *Stygnopsis oaxacensis*. (*D*) Dorsal view of *Stygnopsis valida*. (*E*) Dorsal view of *Stygnopsis robusta*. (*F*) Ventral view of *Stygnopsis valida*. Small letters A, B, C and D indicate setal groups. Scale bars: A, B, C, F = 250 µm, D, E = 200 µm.

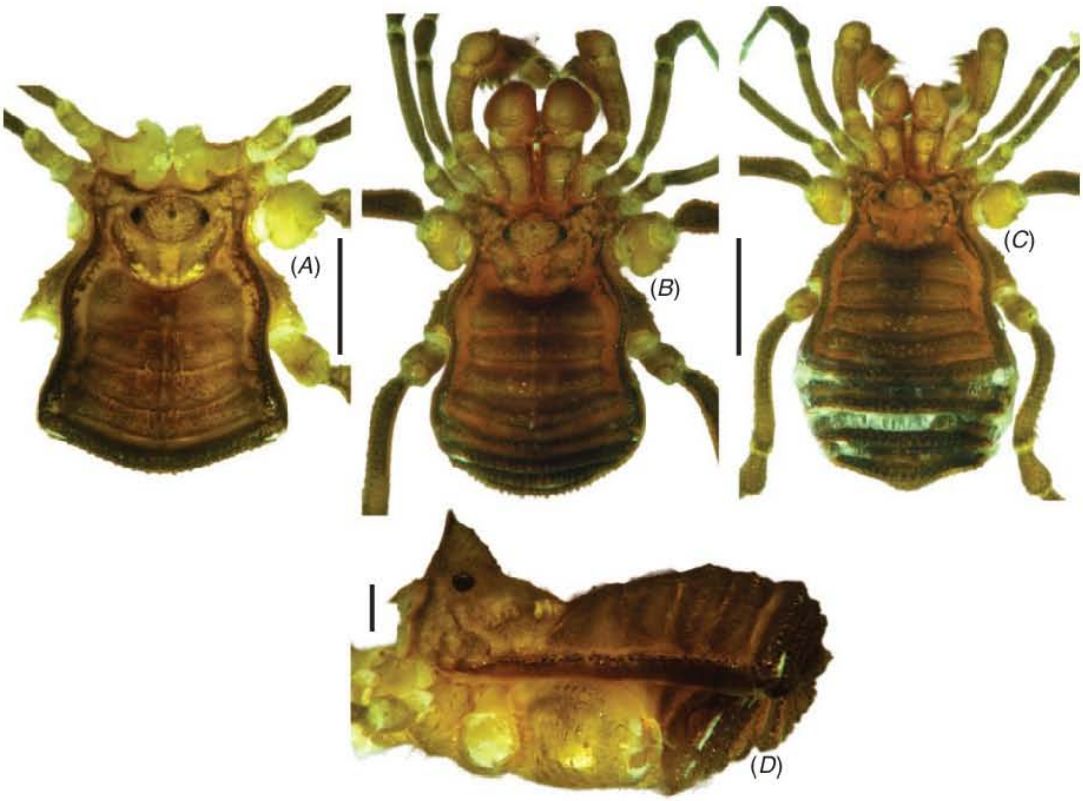

Fig. 9. Habitus of *Hoplobunus*. (*A*) Dorsal view of *Hoplobunus barretti* male. (*B*) Dorsal view of *Hoplobunus* sp. 0002 male. (*C*) Dorsal view of *Hoplobunus* sp. 0002 female. (*D*) Lateral view of *Hoplobunus barretti* male. Scale bars: A = 1.5 mm, B, C = 2.0 mm, D = 0.5 mm.

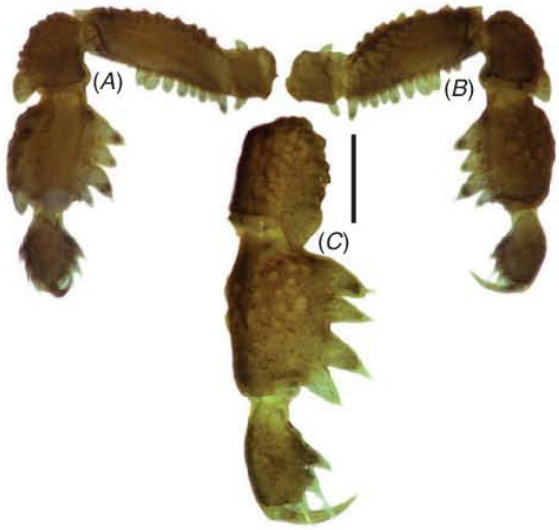

Fig. 10. Pedipalp of *Hoplobunus barretti* male. (*A*) Mesal view. (*B*) Ectal view. (*C*) Frontal view. Scale bars: A, B = 1.0 mm, C = 0.7 mm.

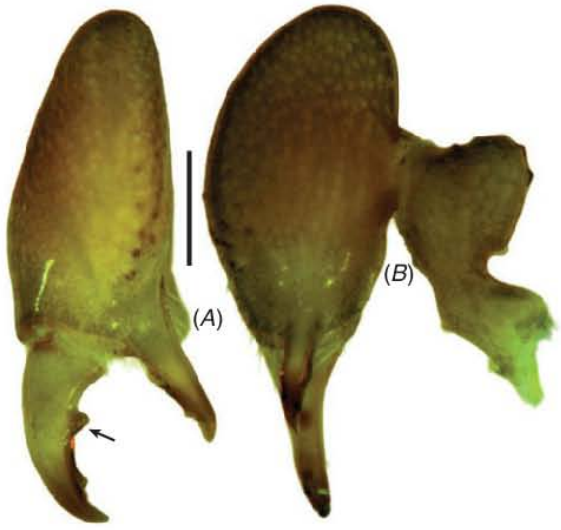

Fig. 11. Chelicera of *Hoplobunus barretti* male. (*A*) Frontal view. (*B*) Mesal view. Arrow indicates the basal blunt tooth. Scale bars: A, B = 0.7 mm.

MAFFT. Aligned sequences were concatenated and file types modified in Mesquite. Three different matrices were generated: (1) molecular Nexus file with 44 terminal taxa; (2) total evidence Nexus file with 47 terminal taxa; and (3) total evidence Phylip file with 47 terminal taxa (Supplementary Materials 5–7). These matrices were partitioned for each molecular marker and for morphological data, respectively.

To select the evolutionary model for each molecular partition, we used jModelTest ver. 2.1.6 (Darriba *et al.* 2012). We compared the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) to choose the best model for each molecular marker. The evolutionary models chosen were: general time reversible (GTR) + proportion of invariable sites (I) + gamma distribution (G) for both *28S* and *COI* sets, and Hasegawa–Kishino–Yano (HKY) + G for the *16S* set. For the total evidence matrices, the model applied to the morphological dataset was MkV (Markov model for variable characters) (Lewis 2001), with Lewis correction for Maximum Likelihood analysis (Lewis 2001), as previously used in other studies (e.g. Monjaraz-Ruedas *et al.* 2016). The models were specified for the MrBayes block in both molecular and total evidence matrices, and a partition.txt file and in morphological specific command line for Maximum Likelihood analysis.

Phylogenetic methods

Phylogenetic trees were reconstructed using Bayesian Inference (BI) and Maximum Likelihood (ML). BI analyses on molecular

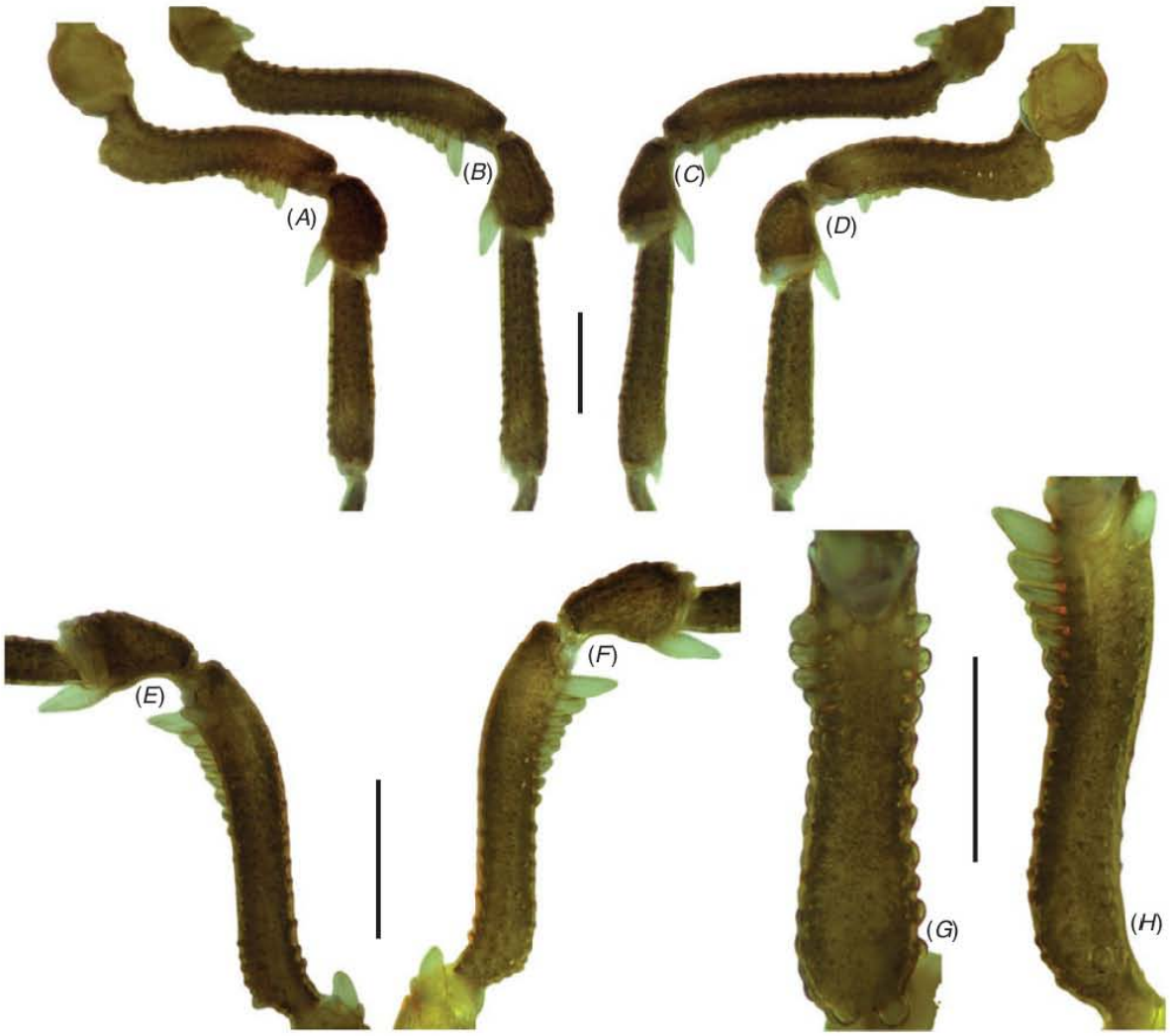

Fig. 12. Legs III and IV of *Hoplobunus barretti* male. (*A*) Leg III prolateral view. (*B*) Leg IV prolateral view. (*C*) Leg IV retrolateral view. (*D*) Leg III retrolateral view. (*E*) Femur IV prolateral view. (*F*) Femur IV retrolateral view. (*G*) Femur III ventral view. (*H*) Femur IV ventral view. Scale bars: A, D, G = 1.0 mm, B, C = 1.1 mm, E, F, H = 1.5 mm.

and total evidence matrices were conducted with MrBayes ver. 3.2.6 on XSEDE (Ronquist and Huelsenbeck 2003) through the online portal CIPRES gateway (Miller *et al.* 2010). The ML analysis for total evidence was conducted using RaxML HPC-AVX ver. 8.2.7 (Stamatakis 2014) on a Dell XPS 8900 desktop computer. The BI analyses consisted of two simultaneous runs each, with four chains defaults for 10 000 000 generations sampling every 2000 trees. The initial 25% of sampled trees were discarded as burn-in. Stationarity parameters were viewed in TRACER ver. 1.6 (Rambaut *et al.* 2014). The ML analysis consisted of 1000 bootstrap replicates, with 500 hits to find the tree with the best value of ML.

Results

Phylogenetic analyses

We obtained similar topologies in the three matrices analysed under BI and ML approaches, with high support values for major clades (Fig. 1, Figs S1 and S2). In all analyses, Stygnopsidae was recovered as monophyletic, as sister-group of *C. oedipus* (Pyramidopidae). Gonyleptoidea was not recovered as a clade, which could be due to the use of a different subset of molecular markers than those used to generate previous laniatorean phylogenies (see Sharma and Giribet 2011; Cruz-López *et al.* 2016). However, the support values for Stygnopsidae in both BI analyses are high, and are considerably higher in the ML analysis.

Phylogenetic relationships among Stygnopsidae

The BI analysis with the molecular data (Fig. S1) generated high support values for the family, subfamilies and some genera. This analysis produced the following major monophyletic relationships: (Karosinae (*Paramitraceras*-group (Stygnopsinae + *P.* aff. *hispidulum*))). The BI analysis using combined data obtained similar general topology to that for molecular data

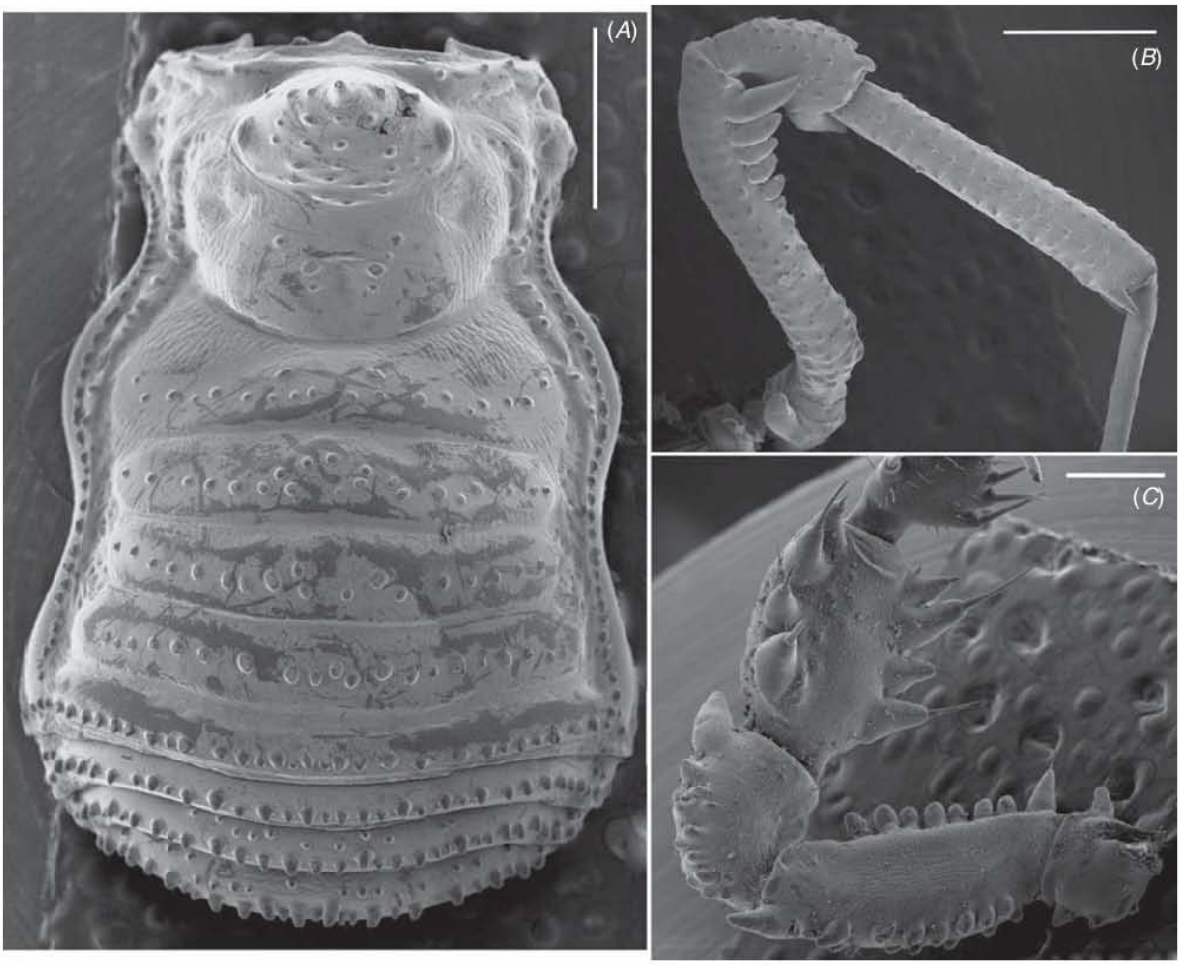

Fig. 13. Scutum, leg IV and pedipalp of *Hoplobunus barretti* male. (*A*) Dorsal view of scutum. (*B*) Prolateral view of leg IV. (*C*) Mesal view of pedipalp. Scale bars: A = 1 cm, B, C = 0.5 cm.

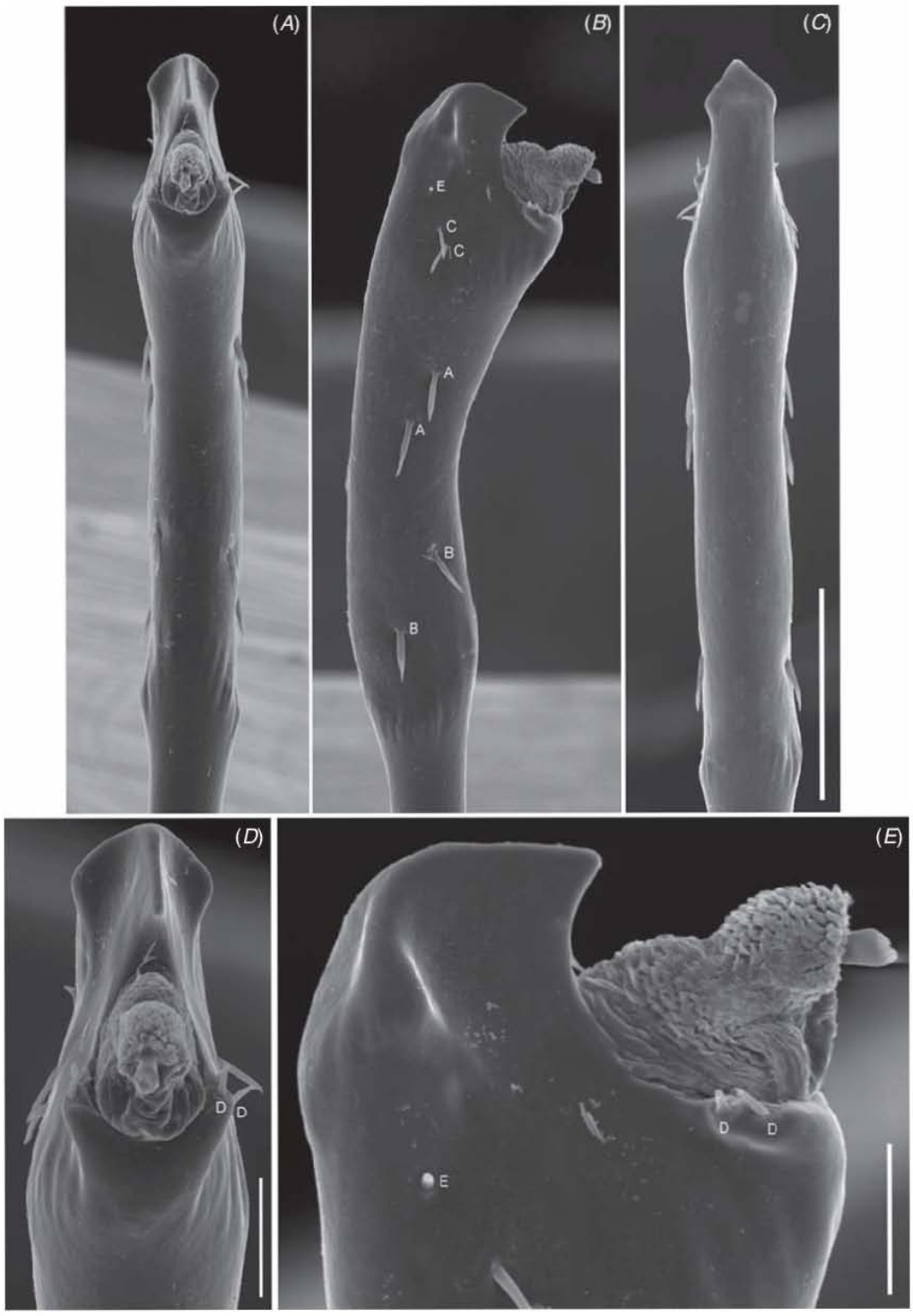

Fig. 14. Male genitalia of *Hoplobunus barretti*. (*A*) Dorsal view. (*B*) Lateral view. (*C*) Ventral view. (*D*) Dorsal view. (*E*) Lateral view. Small letters A, B, C, D and E indicate setal groups Scale bars: A, B, C = 200 µm, D, E = 50 µm.

only, but with the *Paramitraceras*-group nested within Stygnopsinae (Fig. 1). Also, the BI analysis of combined data generated support values slighly lower than the BI analysis of molecular data, which may be caused by the high number of homoplastic morphological characters. The ML analysis of combined data yielded considerable support values for some clades (Fig. S2).

Both BI and ML analyses using combined data nested the *Paramitraceras*-group in Stygnopsinae, with the surprising inclusion of *Serrobunus* as sister-group of the remaining members of the *Paramitraceras*-group. Another surprising result is the exclusion of *Paramitraceras* aff. *hispidulum* from *Paramitraceras*, but forming the clade (*P.* aff. *hispidulum* + '*Hoplobunus*' *zullinii*), with high support values in the three analyses. Despite the similar external appareance in the known *Paramitraceras* species (Fig. 35), the presence of ventral glandular tubercles on males (Figs 38, 39), and the unarmed pedipalp (Figs 44, 45), the analyses did not recover a monophyletic *Paramitraceras*. However, the male genitalia of *P. hispidulum* and of *P.* aff. *hispidulum* (Fig. 41*A–C*) do not share the genital pattern present in the remaining *Paramitraceras*

Fig. 15. Habitus of '*Hoplobunus*' sp. 0033. (*A*) Dorsal view of male. (*B*) Dorsal view of female. (*C*) Lateral view of male. Scale bars: A, B = 2.0 mm, C = 1.0 mm.

Fig. 16. Chelicera of '*Hoplobunus*' sp. 0033 male. (*A*) Frontal view. (*B*) Mesal view. Scale bars: A, B = 1.0 mm.

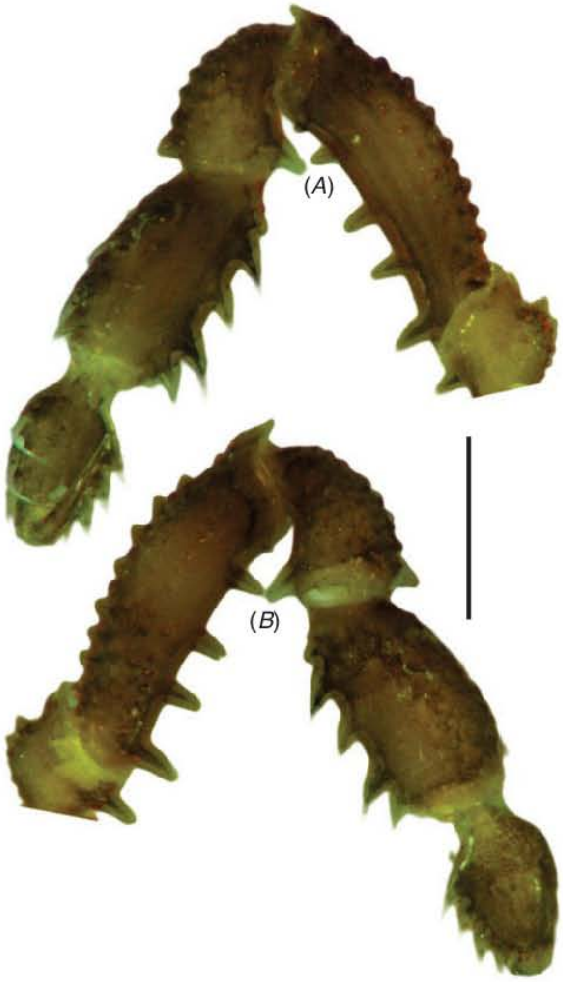

Fig. 17. Pedipalp of '*Hoplobunus*' sp. 0033 male. (*A*) Mesal view. (*B*) Ectal view. Scale bars: A, B = 0.9 mm.

and, unfortunately, the male genitalia of '*Hoplobunus*' *zullinii* Šilhavý, 1977 remains unknown.

In all three analyses, we recovered *Hoplobunus* as a polyphyletic group. It is remarkable that only the type species, *H. barreti* and *Hoplobunus* sp. 0002 form a clade, sharing uniform external and male genital morphology (Figs 9–14). The voucher '*Hoplobunus*' sp. 0033 was recovered as sister-group of *T. philippi* (with high support values) in both BI and ML analyses using combined data. These specimens plus an undescribed *Tampiconus*-like taxon are slightly similar to *Hoplobunus*, with the following differences: (1) ventral armature of pedipalpal femur formed by cylindrical, strong almost fused setiferous tubercles in *Hoplobunus*, and formed by scattered spiniform setiferous tubercles in *Tampiconus*-like clade (Figs 10, 17); (2) mesotergal area III unarmed in *Hoplobunus*, armed with two small paramedian spines in *Tampiconus*-like clade (Figs 9, 15); (3) pedipalp patella with dorsal crest formed by strong setiferous tubercles ending in a prominent tubercle in *Hoplobunus*, absent in *Tampiconus*-like clade (Figs 10, 17); (4) two ventral rows of rounded tubercles, increasing in size apically in legs III and IV in *Hoplobunus*, legs III and IV without remarkable rows of tubercles in *Tampiconus*-like clade (Figs 12, 18); (5) presence of E setae on penis in *Hoplobunus* and absence of these setae in *Tampiconus*-like clade (Figs 14, 19); and (6) presence of basal blunt tooth on movable cheliceral finger in *Hoplobunus* and absence of this tooth in *Tampiconus*-like clade (Figs 11, 16). Also, *Hoplobunus* is found in pine-forest at relatively high elevations in central and Northern Mexico, and members of the *Tampiconus*-like clade are found in lowland rain-forest in Eastern Mexico. However, without available males of *T. philippii*, the type species of this genus, it is difficult to determine the true identity of this genus and its related taxa. The'not-true' *Hoplobunus* are discussed in the taxonomic treatments below.

Taxonomy

Family **STYGNOPSIDAE** Sørensen

Phalangodidae (in part): Roewer, 1923: 69; Mello-Leitão, 1938: 137; Goodnight & Goodnight, 1942: 1; Goodnight & Goodnight, 1944: 1.
Stygnopsidae Sørensen, 1932: 272; Šilhavý, 1974: 176; Šilhavý, 1977: 220; Rambla & Juberthie, 1994: 218.
Included subfamilies: Stygnopsinae Sørensen, 1932, and Karosinae, subfam. nov.

Emended diagnosis

Harvestmen with scutum type zeta (ζ) (Figs 2, 9, 15, 20, 24, 28), with the mid-bulge tending to be almost absent or type gamma (γ) in several taxa (Figs 35*A*, *C*, 46*A*). Shape and size of ocularium varying over a wide range, from small, almost absent, to large, conical, and armed with long median spine. Chelicera ranging

Fig. 18. Legs III and IV of '*Hoplobunus*' sp. 0033 male. (*A*) Prolateral view of leg III. (*B*) Ventral view of femur III. (*C*) Ventral view of femur IV. Scale bars: A = 1.5 mm, B = 1.0 mm, C = 0.7 mm.

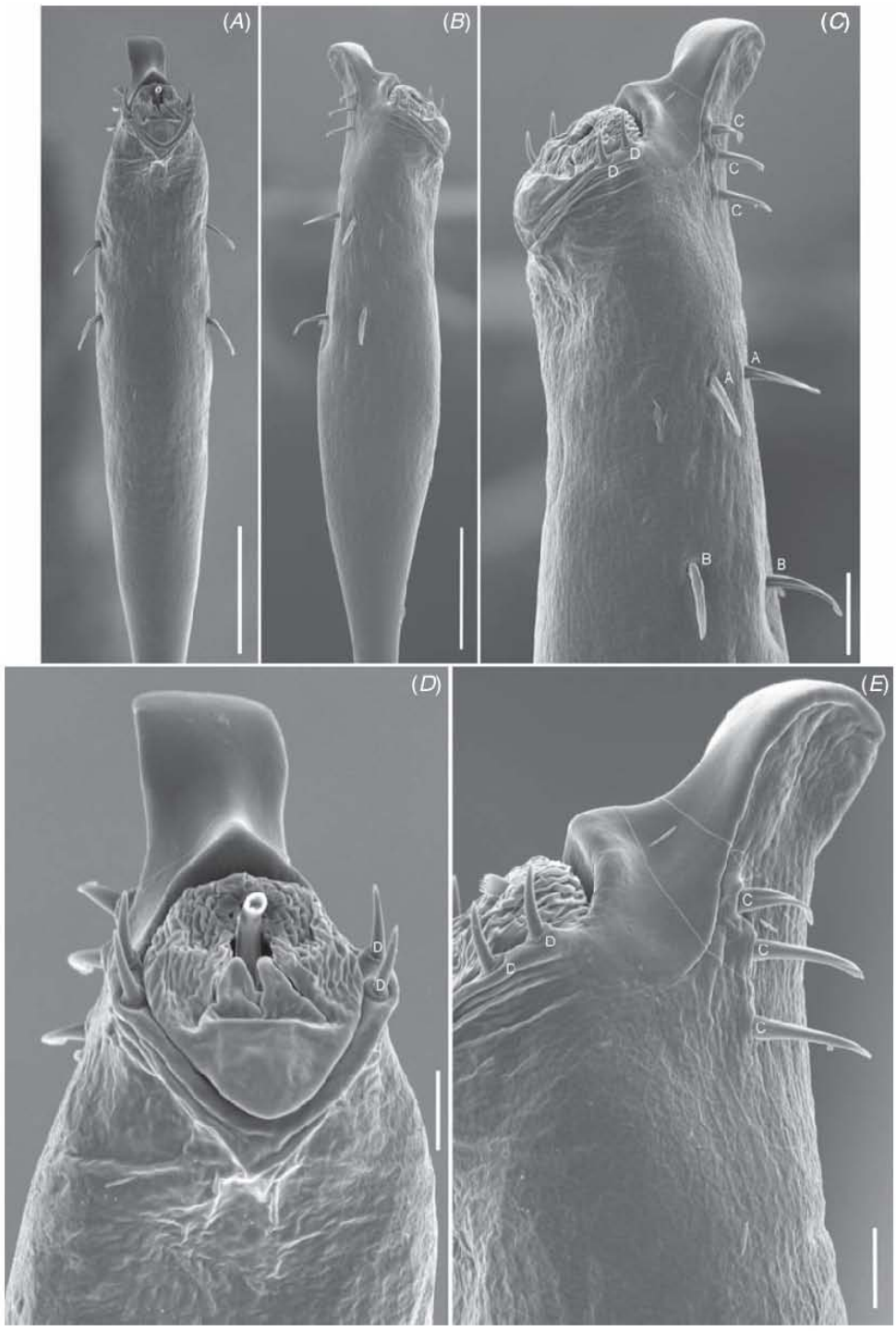

Fig. 19. Male genitalia of '*Hoplobunus*' sp. 0033. (*A*) Frontal view. (*B*) Lateral view. (*C*) Detail of follis in lateral view. (*D*) Detail of follis in dorsal view. (*E*) Detail of setae D and C, lateral view. Small letters A, B, C, and D indicate setal groups. Scale bars: A, B = 150 µm, C = 50 µm, D, E = 25 µm.

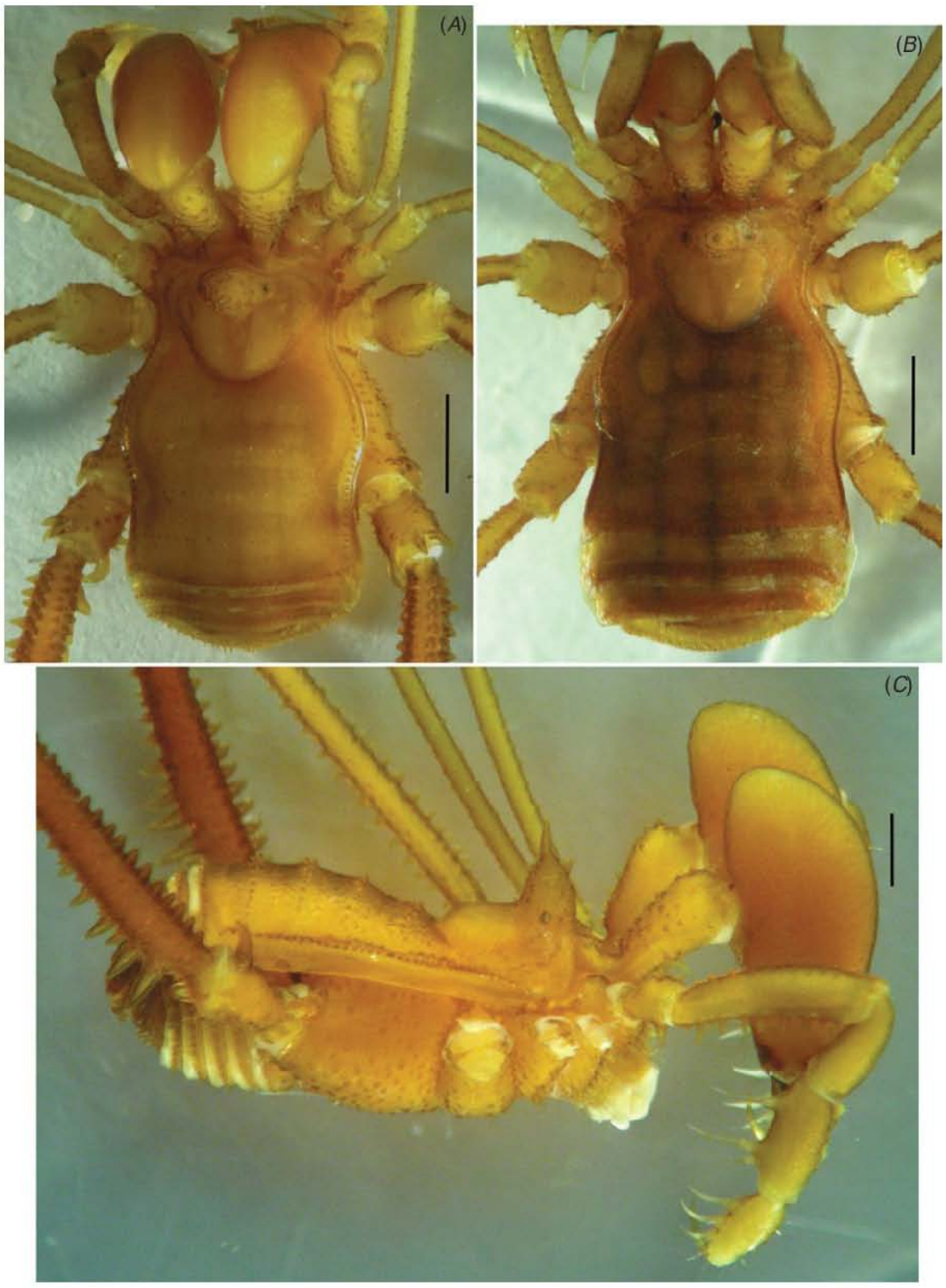

Fig. 20. Habitus of *Serrobunus boneti*. (*A*) Dorsal view of male. (*B*) Dorsal view of female. (*C*) Lateral view of male. Scale bars: A, B = 1.5 mm, C = 1.0 mm.

from small-sized in Karosinae and *Mexotroglinus*, to slightly swollen in *Paramitraceras*, and large in *Hoplobunus* and *Stygnopsis*. Cheliceral dentition formed by many similar-sized teeth in non-sexually-dimorphic species (Fig. 32); prominent basal and/or medial teeth on movable finger in sexually dimorphic species (Figs 4, 43). Pedipalps armed with setiferous tubercles, unarmed or with only spiniform setae in *Paramitraceras* and *Sbordonia* (Figs 44, 45). Sexual dimorphism on legs occurs in many different ways within the family: presence of glandular opening in males (*Potosa*); males with legs longest (*Karos*); modified articles on males, possibly with glandular pores (*Huasteca* Cruz-López & Francke, 2015, *Mexotroglinus*, Fig. 46*C*, *G*); male legs strongly armed (*Chapulobunus*, *Chinquipellobunus*, *Hoplobunus*, *Sbordonia*, *Stygnopsis*); or without sexual dimorphism (*Crettaros* Cruz-López & Francke, 2015, *Mictlana* Cruz-López & Francke, 2015, *Montabunus*, *Monterella*, *Paramitraceras*, *Philora* and *Troglostygnopsis*). Calcaneous covering apical portion of metatarsus. Tarsi without scopulae or pseudonychium, claws non-pectinate. Penis without well defined ventral plate, truncus generally cylindrical, ventral portion elongated, forming a flimsy lamina (Figs 8, 14, 19, 23, 27, 31, 34, 40, 41, 47). Three major penial macrosetal patterns are found in the family: (1) *Paramitraceras*-pattern: with several macrosetae C forming a row along lateral margins; macrosetal complex A+B latero-basally to follis, sometimes extending to ventral portion; two ventral pairs of setae E, the inner micro and the external macro; 1–3 pairs of microsetae D near lateral margins (Fig. 40); (2) *Karos*-pattern: setal complex A+B+C forming longitudinal rows along the lateral margins, sometimes setae B can be recognised by small size; ventral microsetae E in two pairs or forming two longitudinal rows of several setae; 2–4 pairs of macrosetae D near to base of follis (Fig. 34); and (3) *Stygnopsis*-pattern: macrosetae (micro in *Stygnopsis*) setal groups A, B and C recognisable and separated, each formed by two or three pairs; one pair of small setae E, absent or only vestigial socket; two pairs of small or microsetae D (Figs 8, 14, 19, 31). Capsula externa formed by an exposed and rigid multi-folded follis, apical portion covered by small spines (except in *Stygnopsis*). Capsula interna formed by internal stylus, slightly evertible, cylindrical, with small apical bristles (Figs 14*E*, 23, 27, 34, 40).

Fig. 21. Chelicera of *Serrobunus boneti* male. (*A*) Frontal view. (*B*) Mesal view. Arrow indicates the basal blunt tooth. Scale bars: A, B = 1.5 mm.

Subfamily **STYGNOPSINAE** Sørensen

Phalangodinae (in part): Roewer, 1912: 108; Roewer, 1923: 69; Goodnight & Goodnight, 1942: 1; Goodnight & Goodnight, 1944: 1.
Isaeinae (in part): Mello-Leitão, 1938: 137.
Troglostygnopsinae (in part): Šilhavý, 1974: 182.
Stygnopsinae: Mello-Leitão, 1938: 137; Šilhavý, 1974: 176; Šilhavý, 1977: 220; Rambla & Juberthie, 1994: 218.
Included taxa. Hoplobunus Banks, 1900, *Stygnopsis* Sørensen, 1902, *Paramitraceras* Pickard-Cambridge, 1905, *Serrobunus* Goodnight & Goodnight, 1942 stat. rev., *Chinquipellobunus* Goodnight &

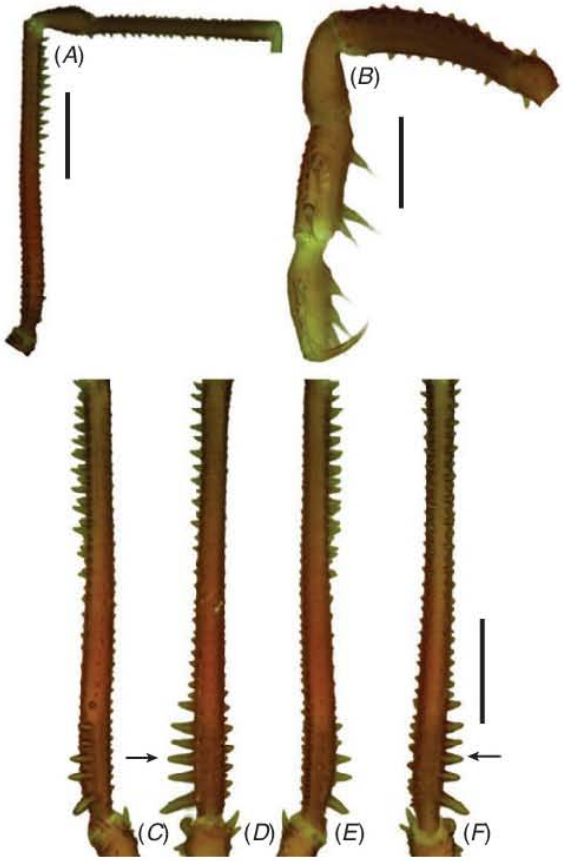

Fig. 22. Leg IV and pedipalp of *Serrobunus boneti* male. (*A*) Retrolateral view of leg IV. (*B*) Mesal view of pedipalp. (*C*) Retrolateral view of femur IV. (*D*) Dorsal view of femur IV. (*E*) Prolateral view of femur IV. (*F*) Ventral view of femur IV. Arrows indicate tubercles of ventral retrolateral row. Scale bars: A, C, D, E, F = 3.0 mm, B = 1.5 mm.

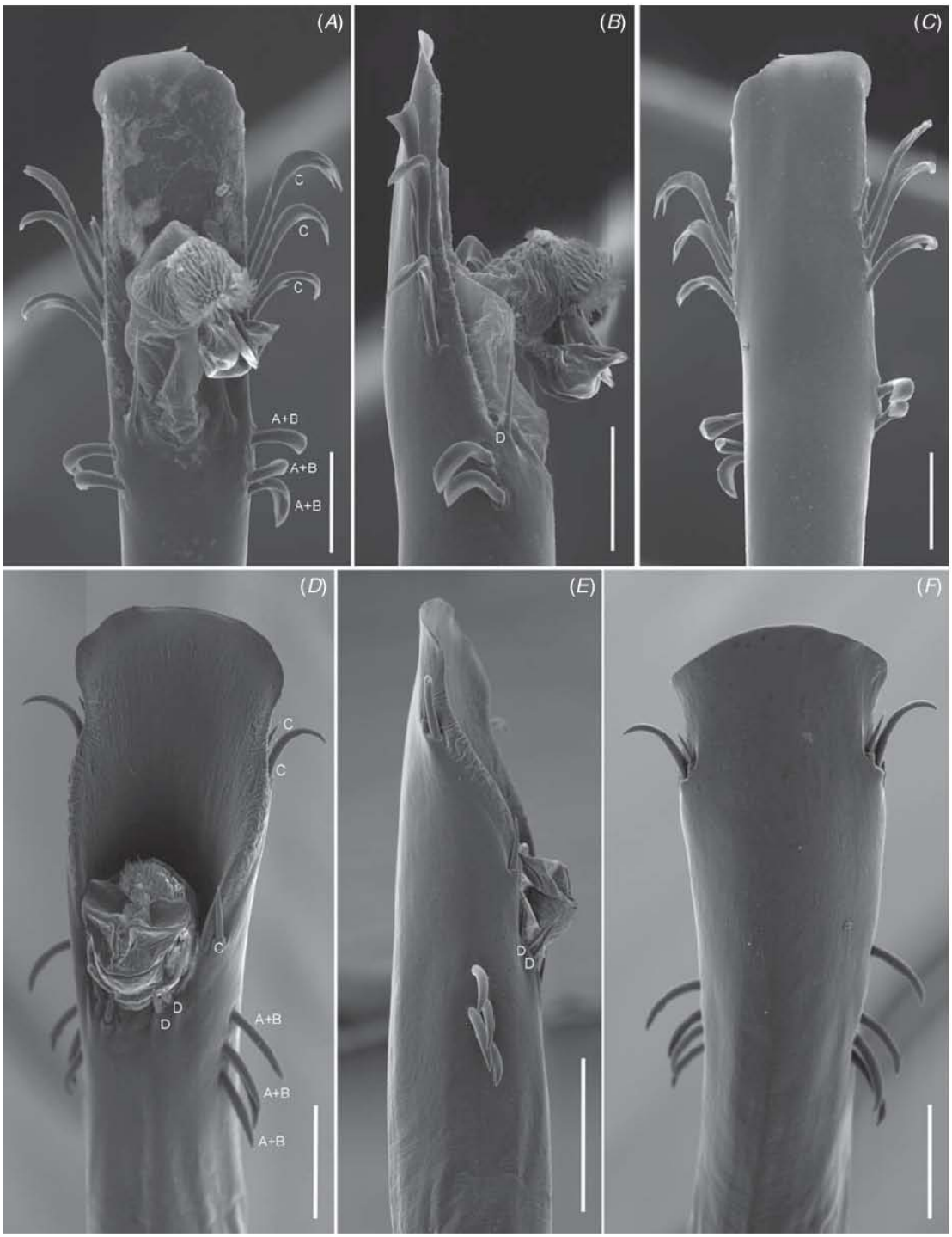

Fig. 23. Male genitalia of *Serrobunus*. (*A*) Dorsal view of *Serrobunus boneti*. (*B*) Lateral view of *Serrobunus boneti*. (*C*) Ventral view of *Serrobunus boneti*. (*D*) Dorsal view of *Serrobunus queretarius*. (*E*) Lateral view of *Serrobunus queretarius*. (*F*) Ventral view of *Serrobunus queretarius*. Small letters A+B, C, and D indicate setal groups. A, B, C, D, *F* = 100 µm, E = 150 µm.

Fig. 24. Habitus of *Iztlina venefica*. (*A*) Dorsal view of male holotype. (*B*) Dorsal view of female paratype. (*C*) Lateral view of male holotype. Scale bars: A, B, C = 2.0 mm.

Goodnight, 1944, *Tampiconus* Roewer, 1949, *Philora* Goodnight & Goodnight, 1954, *Troglostygnopsis* Šilhavý, 1974, *Mexotroglinus* Šilhavý, 1977, *Sbordonia* Šilhavý, 1977, *Iztlina*, gen. nov., *Tonalteca*, gen. nov., and the uncertain '*Hoplobunus*' *zullinii* Šilhavý, 1977.

Type genus: *Stygnopsis* Sørensen, 1902.

Emended diagnosis

Large and medium-sized harvestmen (scutum length ~6 or >8 mm), except the small *Mexotroglinus*, *Philora* and some *Sbordonia* (<3 mm). Ocularium at frontal margin of prosoma (Figs 3, 9, 15, 20, 35*D–H*, 46*A*), medium-sized and rounded in *Chinquipellobunus* and *Mexotroglinus*, very large, usually with an apical spine in the remaining members. Mesotergal sulci straight (Figs 13*A*, 35*D–H*, 46*A*, *E*). Chelicera usually large, movable finger with prominent basal teeth (Figs 4, 11, 21); usually with sexual dimorphism in cheliceral size and dentition. *Mexotroglinus* exhibits Karosinae-type chelicera (Fig. 46*D*). Pedipalpal femur and patella without mesal setiferous tubercles, except in *Mexotroglinus*. Penis with setal patterns *Stygnopsis*, *Paramitraceras* and an unrecognisable pattern (Figs 8, 14, 31, 40). Pars distalis forming an angle of 40° or more with respect to flimsy ventral lamina (Figs 14*E*, 31*B*). *Mexotroglinus* is the only member of the subfamily that exhibits many convergences with Karosinae in male genitalia, such as: apical projection of pars distalis contiguous with truncus; macrosetae D near to follis and similar size of macrosetae A+B+C complex; and setal complex A+B+C forming a longitudinal row (Fig. 47). *Iztlina*, gen. nov., exhibits a unique and unrecognisable setal pattern within the subfamily, which is described below.

Remarks

Because the polyphyletic *Hoplobunus* has created much confusion in some taxonomic determinations, we put special emphasis on the taxonomy of selected stygnopsine taxa previously considered as *Hoplobunus* according to Goodnight and Goodnight (1953): the type *Stygnopsis*, *Hoplobunus*, *Serrobunus* stat. rev. and the new genera *Tonalteca*, gen. nov. and *Iztlina*, gen. nov.

Genus ***Stygnopsis*** Sørensen

Stygnus (in part): Sørensen, 1884: 644.

Stygnopsis Sørensen, 1902: 4; Roewer, 1912: 153; Roewer, 1923: 116; Mello-Leitão, 1926: 329; Roewer, 1927: 272; Sørensen, 1932: 273 (=*Haehnelia* Roewer 1915); Šilhavý, 1974: 176; Šilhavý, 1977: 220.

Included taxa. *Stygnopsis valida* (Sørensen, 1884), *Stygnopsis mexicana* (Roewer, 1915), comb. nov., *Stygnopsis robusta* (Goodnight & Goodnight, 1971), *Stygnopsis apoalensis* (Goodnight & Goodnight, 1973), comb. nov., *Stygnopsis oaxacensis* (Goodnight & Goodnight, 1973), comb. nov.

Type species: *Stygnus validus* Sørensen, 1884, by subsequent designation.

Emended diagnosis

Large harvestmen (scutum length >6 mm). Ocularium high, usually with strong median spine. Chelicera large and sexually dimorphic in α males, but there are β males with chelicera similar to those of females. Cheliceral dentition heterogeneous, basal tooth on movable finger blunt (Fig. 4). Pedipalpal patella smooth, roundly swollen apically, with small mesal apophysis (Figs 5, 6). Femora to tibiae III and IV armed with two ventral rows of spiniform tubercles, increasing in size apically (Fig. 7). Penis setal *Stygnopsis*-pattern, with all setae of penis are microsetae. Three to four pairs of setae C, two pairs of setae A and B, and two or three pairs of setae D, the last on dorsal margin (Fig. 8). Pars distalis with apical depression, follis inserted inside it. Latero-apical apices of pars distalis rolled ventrally, pointed, ventral margin concave (Fig. 8). Follis without small apical spines.

Remarks

Sørensen (1932) synonymised the monotypic *Haehnelia* Roewer, 1915 under *Stygnopsis*, forming the new combination *Stygnopsis mexicana* (Roewer, 1915). However, Goodnight and Goodnight (1953) ignored this synonymy, and considered *Haehnelia* a synonym of *Hoplobunus*.

Šilhavý (1974) was the first to rediagnose the genus and illustrated for the first time the male genitalia of *Stygnopsis valida* (Sørensen, 1884) and *Stygnopsis robusta* (formerly *Hoplobunus robustus* Goodnight & Goodnight, 1971). Šilhavý mentioned that the main character to differentiate between *Hoplobunus* and *Stygnopsis* is the presence of one pair of paramedian long spines in mesotergal area III in the latter (Fig. 3*A*, *B*). These spines are present in *S. valida*, *S. mexicana* and *S. robusta*. It is remarkable that Šilhavý did not mention anything about *Haehnelia mexicana*, a species redescribed as *Hoplobunus mexicanus* by Goodnight and Goodnight (1971), with well developed dorsal spines (Goodnight and Goodnight 1971: fig. 20). Additionally, Goodnight and Goodnight (1971) reported several additional records for *H. mexicanus*; however, the record labelled as: 'Cueva Arriba del Presidente, 1½ km N

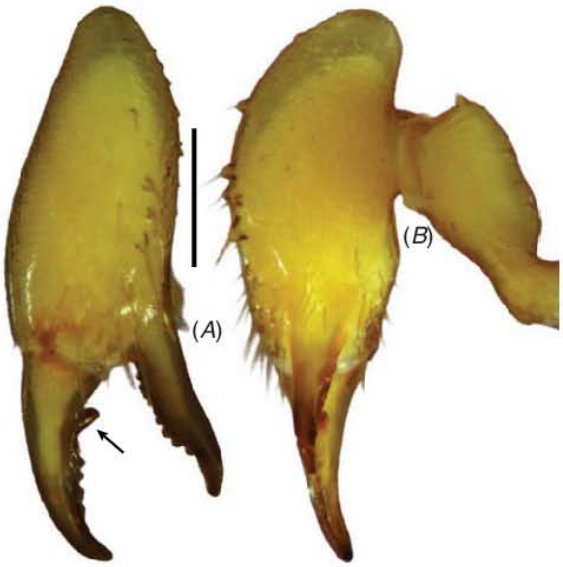

Fig. 25. Chelicera of *Iztlina venefica* male paratype. (*A*) Frontal view. (*B*) Mesal view. Arrow indicates the basal blunt tooth. Scale bars: A, B = 1.0 mm.

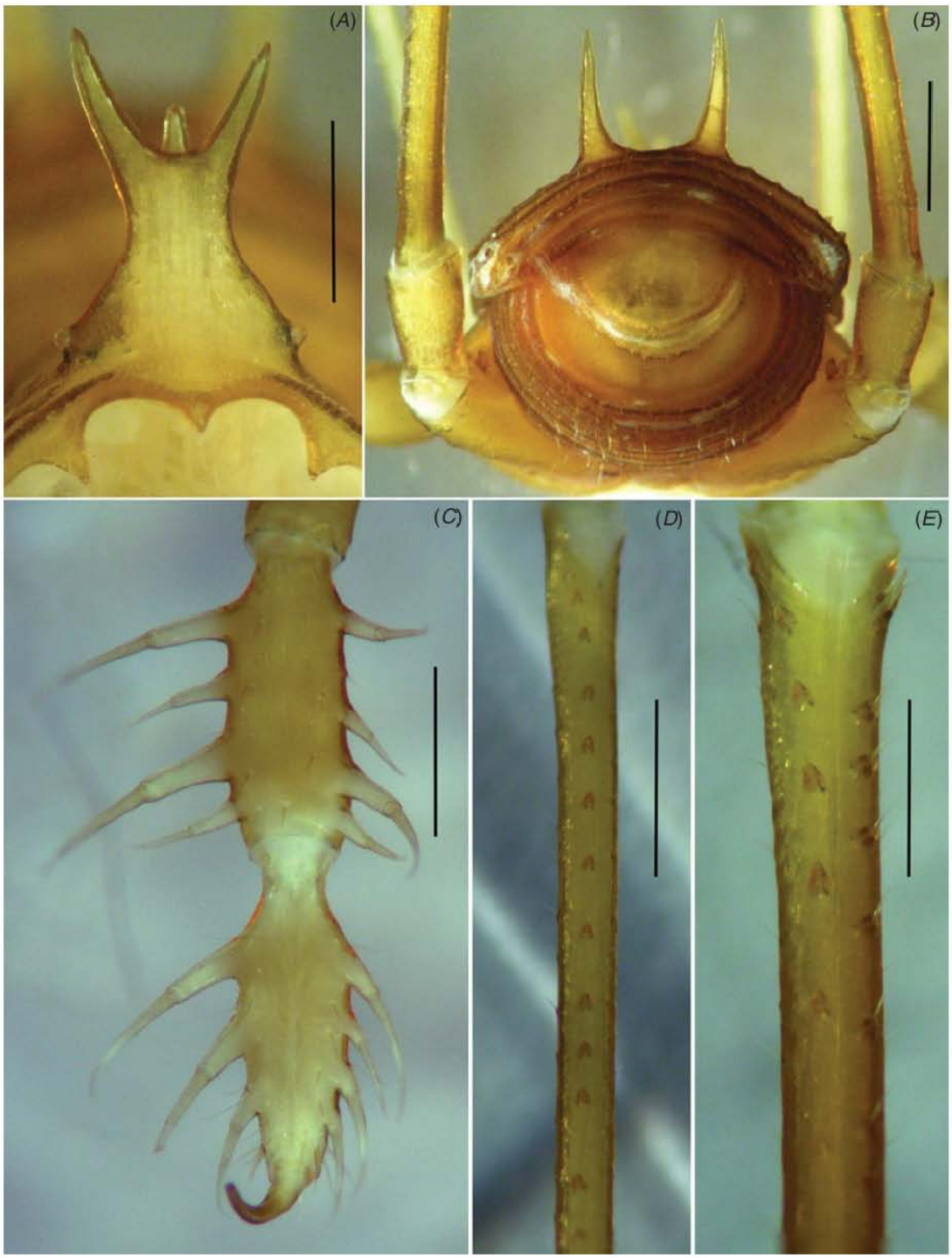

Fig. 26. Ocularium, pedipalp, legs III and IV, and posterior habitus of *Iztlina venefica*. (*A*) Ocularium frontal view of male paratype. (*B*) Posterior view of habitus of holotype. (*C*) Ventral view of pedipalp tibia and tarsus. (*D*) Ventral view of femur III. (*E*) Ventral view of femur IV. Scale bars: A = 1.5 mm, B = 2.0 mm, C, D = 1.0 mm, E = 0.5 mm.

of Huautla, Oaxaca, August 12, 1967 (one female), collected by J. Reddell and J. Fish' corresponds to an undescribed species.

Like Sørensen (1932), we consider that *S. mexicana* could be a junior synonym of *S. valida*, but with incomplete locality data for the types, and the great similarities among male genitalia in the five known species of the genus, it is impossible to corroborate the proposed synonymy at this time. Maybe further molecular studies from specimens from a range of localities would help clarify this situation.

Genus ***Hoplobunus*** Banks

Hoplobunus Banks, 1900: 200; Pickard-Cambridge, 1905: 585; Roewer, 1912: 149; Roewer, 1923: 112; Roewer, 1927: 272; Goodnight & Goodnight, 1942: 1; Goodnight & Goodnight, 1945: 3; Goodnight & Goodnight, 1953: 19; Goodnight & Goodnight, 1967: 1, Goodnight & Goodnight, 1971: 38; Goodnight & Goodnight, 1973: 86; Šilhavý, 1974: 176; Šilhavý, 1977: 220; Edgar, 1990: 548; Rambla & Juberthie, 1994: 218.

Included taxa: *Hoplobunus barretti* Banks, 1900, by monotypy.

Emended diagnosis

Medium-size harvestmen (scutum length ~5 mm). Ocularium very high, conical, with small apical spine (Fig. 9). Posterior margin of scutum wider than mid-bulge width (Fig. 9). Chelicera large and sexually dimorphic. Cheliceral dentition heterogeneous, basal tooth on movable finger blunt (Fig. 11). Pedipalpal femur compressed laterally, with two dorsal longitudinal rows of spiniform tubercles, ending in a spiniform apical apophysis (Figs 10, 13*C*). Pedipalpal patella with dorsal crest of contiguous, procurved spiniform tubercles (Figs 10, 13*C*). Sockets of pedipalpal tibia, tarsus and ventral femur cylindrical, very wide and contiguous (Figs 10, 13*C*). Femora to tibiae III and IV armed with two ventral rows of spiniform tubercles, increasing in size apically and ending in spiniform apophysis (Figs 12, 13*B*). Trochanter III globose, basal-most portion of femur III dorsally curved abruptly (Fig. 12*E*, *F*). Penis setal patterns *Stygnopsis*-pattern, two pairs of small setae D on dorsal projection of truncus, latero-dorsal to follis base (Fig. 14*D*), one pair of microsetae E, over setal group C (Fig. 14*B*, *E*), setal groups A, B and C formed by two or three macrosetae (Fig. 14*A–C*). Pars distalis compressed laterally in almost one-half the length of penis, slightly curved dorsally (Fig. 14*A–C*). Surface of follis rugose (Fig. 14*E*).

Remarks

Since the description of the genus and type species by Banks (1900), the diagnosis of the genus was revised only once by Goodnight and Goodnight (1953). They proposed a brief rediagnosis based on ambiguous characters, the reason they synonymised *Haehnelia*, *Isaeus*, *Serrobunus* and *Chinquipellobunus* under *Hoplobunus*. Recently, Cokendolpher (2004) revalidated *Chinquipellobunus* from its synonymy under *Hoplobunus* on the basis of the male genitalia. He also transferred *Hoplobunus madlae* Goodnight & Goodnight, 1967 and *Hoplobunus russelli* Goodnight & Goodnight, 1967 to *Chinquipellobunus*. Before this study, *Hoplobunus* included 10 species under the diagnosis of Goodnight and Goodnight (1953). It is remarkable that after the phylogenetic analyses based on combined data, the genus now becomes monotypic (but some undescribed species are known). As mentioned earlier, three species were transferred to *Stygnopsis*. *Hoplobunus spinooculorum* Goodnight & Goodnight, 1973 is here transferred to *Tonalteca*, gen. nov., *H. boneti* is restored as a valid species of *Serrobunus*, and *Hoplobunus queretarius* Šilhavý, 1974 is transferred to *Serrobunus*. Finally, '*H.*'

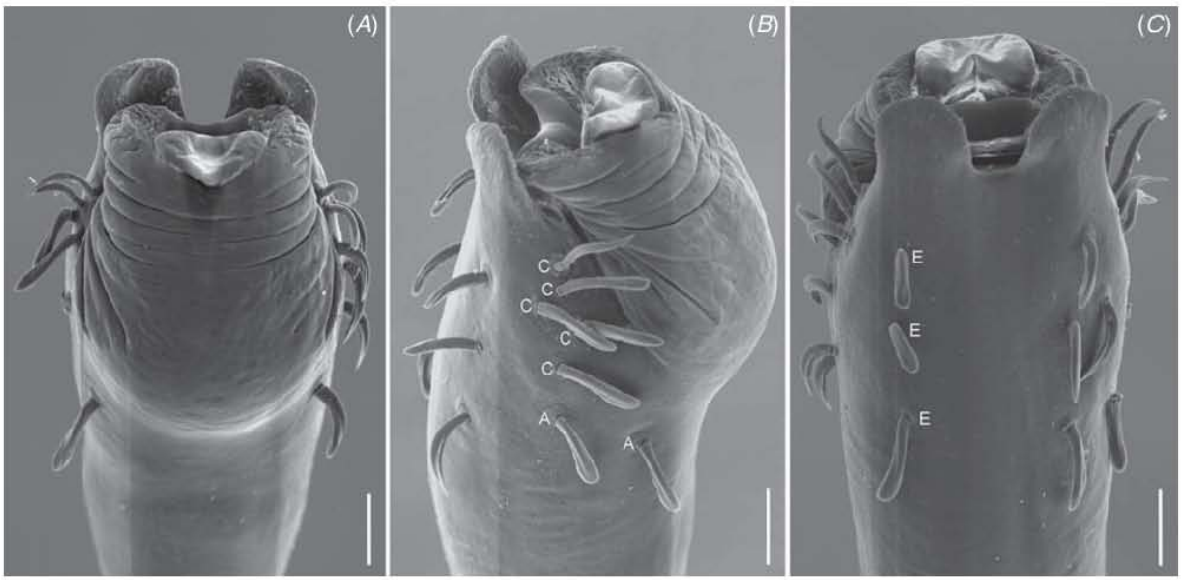

Fig. 27. Male genitalia of *Iztlina venefica* male paratype. (*A*) Dorsal view. (*B*) Lateral view. (*C*) Ventral view. Small letters A, C, and E indicate setal groups. Scale bars: A, B and C = 50 µm.

Fig. 28. Habitus of *Tonalteca spinooculorum*. (*A*) Dorsal view of male. (*B*) Ventral view of female. (*C*) Lateral view of male. Scale bars: A, B = 1.0 mm, C = 1.5 mm.

planus and '*H.*' *zullinii* remain as incertae sedis in Karosinae and Stygnopsinae, respectively. These new taxonomic proposals are described below.

Genus ***Serrobunus*** Goodnight & Goodnight, stat. rev.

Serrobunus Goodnight & Goodnight, 1942: 2.
Hoplobunus (in part): Goodnight & Goodnight, 1953: 19.
Included taxa: *Serrobunus boneti* Goodnight & Goodnight, 1942 stat. rev., *Serrobunus queretarius* (Šilhavý, 1974), comb. nov.

Emended diagnosis

Large harvestmen (scutum length ~6 mm), troglomorphic. Ocularium very high, conical, with long apical spine (Fig. 20). Chelicera large and sexually dimorphic. Cheliceral dentition heterogeneous, basal tooth on movable finger blunt (Fig. 21). Legs very long, femur IV longer than scutum, straight. Femur IV ornate with longitudinal rows of spiniform tubercles, all tubercles of the rows increasing in size apically, except on the ventral retrolateral row, which decrease in size (Fig. 22*C–F*). Trochanter III slightly globular. Trochanter IV with both dorsal and ventral apophyses (Fig. 22*C–F*). Penis setal *Paramitraceras*-pattern, with the following modifications: setae C formed by three or four macrosetae, the apical-most small, three or four setae A+B, laterally on truncus, slightly below of follis base, one or two pairs of setae D, slightly shorter than other macrosetae, lateral to follis, without setae E (Fig. 23). Apical margin of pars distalis rounded. Follis with bilobular dorsal projection and apically covered by acute spines (Fig. 23*A*, *D*).

Remarks

Kury and Villarreal (2015) examined two males of *S. boneti* labelled 'Mexico, SL Potosí, Cueva de los Sabinos, near Valles, underground waterway to Devil's Hole, 26.iii.1946, EJ Dontzin & E Ruda leg.'. These authors mentioned the presence of two median pairs of microsetae E forming a rectangle (Kury and Villarreal 2015: fig. 1B, C). Examining material from different localities of *S. boneti* (Supplementary Material 3), we did not find evidence of the presence of these setae. Therefore, it is possible that Kury and Villarreal (2015) examined a different taxon.

Despite not including *H. queretarius* in the molecular analyses, we have transferred it to *Serrobunus* because it shares external and male genital morphology with *S. boneti* (Fig. 23*D–F*).

Genus ***Iztlina***, gen. nov.

(Figs 24–27)

http://zoobank.org/NomenclaturalActs/urn:lsid:zoobank.org:act:A6450531-D49F-46F9-BD91-0202703BA758
Type species: *Iztlina venefica*, sp. nov.

Diagnosis

Medium-size harvestmen (scutum length <5 mm), troglomorphic. Ocularium very high, conical, apex divided into two divergent tips (Fig. 26*A*). Mesotergal area IV with two long paramedian spines (Fig. 26*B*). Chelicera large and sexually dimorphic. Cheliceral dentition heterogeneous, basal tooth on movable finger blunt (Fig. 25). Legs very long, femur IV longer than scutum, straight. Femora III and IV almost smooth, femur III with one ventral longitudinal row of spiniform tubercles increasing in size distally (Fig. 26*D*), femur IV with two ventral rows apically (Fig. 26*E*). Trochanter III slightly globose. Setation of penis unique for subfamily: five or six setae C laterally to follis, two pairs of setae A below setae C, two ventral longitudinal rows of three pairs of setae E, setae D absent (Fig. 27). All penial setae are uniform in size and shape. Truncus cylindrical, almost contiguous with ventral projection, ventro-apical margin with U-shaped

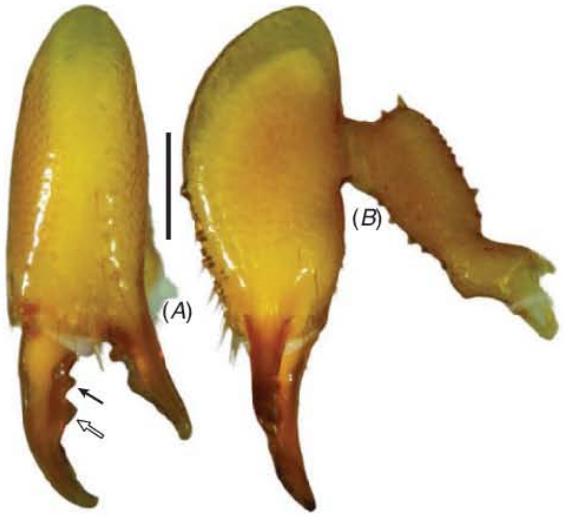

Fig. 29. Chelicera of *Tonalteca spinooculorum* male. (*A*) Frontal view. (*B*) Mesal view. Black arrow indicates the basal tooth, white arrow indicates the median tooth. Scale bars: A, B = 1.0 mm.

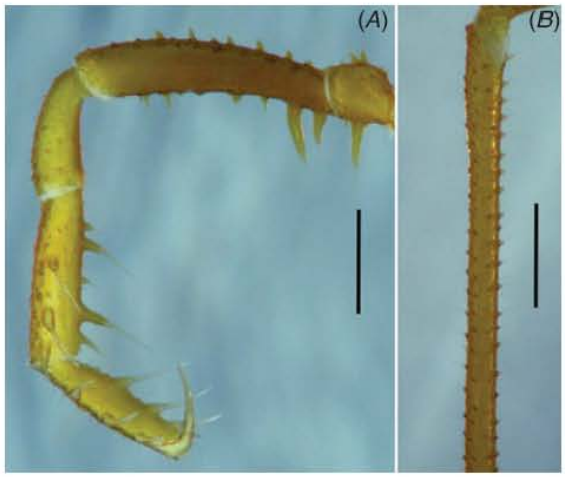

Fig. 30. Pedipalp and femur IV of *Tonalteca spinooculorum* male. (*A*) Mesal view of pedipalp. (*B*) Ventral view of femur IV. Scale bars: A = 1.0 mm, B = 1.5 mm.

concavity (Fig. 27*C*). Follis globose, with dorsal lobular projection (Fig. 27*A*, *B*).

Remarks

This genus can be easily distinguished from other genera of Stygnopsinae by the unique presence of two long paramedian spines on mesotergal area IV and apex of ocularium divided in two tips and general shape of male genitalia.

Etymology

'Iztli' is the name of a god of sacrifice and stone knives in the Mexica culture. This god is associated with the deities of death and darkness. The name was modified to feminine ending.

Iztlina venefica, sp. nov.

(Figs 24–27)

http://zoobank.org/NomenclaturalActs/urn:lsid:zoobank.org:act:0E780459-A572-41C2-B7A3-F0DB9A279862

Material examined

Holotype. MEXICO: *Chiapas*: Municipio de Cintalapa: male, Cueva del Arco, 16°50′51.6″N, 93°43′04.5″W, 19.xi.2011, coll. K. Zárate, male (CNAN-T1092).

Paratypes. MEXICO: *Chiapas*: Municipio de Cintalapa: 2 males, collected with holotype (CNAN-T1093); 1 male, 1 female, Cueva Ejidal, Ejido López Mateos, 16°51′54.1″N 93°42′45.3″W, 23.iv.2013, coll. K. Zárate (CNAN-T1101).

Diagnosis

As for the genus.

Description

Male (*holotype*)

Scutum length 4.5 mm, scutum width 3.7, femur II 9.5 mm, femur IV 11.7 mm.

Dorsum. Scutum type ζ, mid-bulge gently rounded, both constrictions 1 and 2 shallow (Fig. 24*A*, *B*). Ocularium at frontal margin of prosoma, very high and conical shape, with the

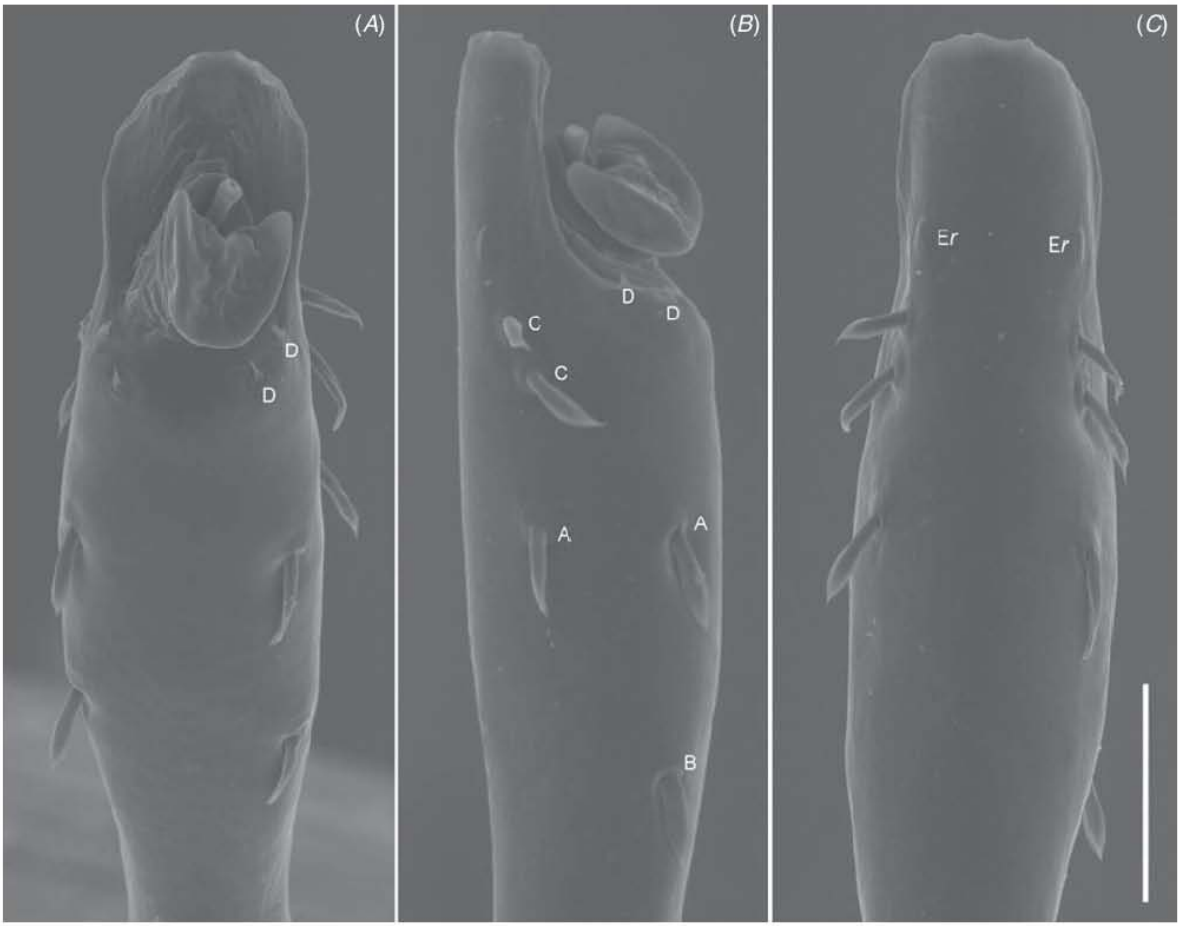

Fig. 31. Male genitalia of *Tonalteca spinooculorum*. (*A*) Dorsal view. (*B*) Lateral view. (*C*) Ventral view. Small letters A, B, and C indicate setal groups, Er indicates vestigial insertion bases of E setae. Scale bars: A, B and C = 100 μm.

apex divided in two diverging tips (Fig. 26*A*). Eyes well marked but small-sized, at the base of ocularium. Dorsum smooth, mesotergal sulci wide and shallow. Mesotergal areas I–III with transverse row of minute and scattered setiferous tubercles, area IV with one pair of long paramedian spines (Fig. 26*B*). Lateral pegs forming a continuous and distintive row.

Venter. Coxae I and II ornate with long spiniform setiferous tubercles, coxae III and IV with small ones and setae. Length of coxa IV similar to length of coxa III. Lateral margins posterior to genital operculum parallel.

Chelicera. Basichelicerite elongated, bulla softly marked. Cheliceral hand swollen, dorsal portion elevated, frontal face covered by small tubercles and spiniform setae (Fig. 25*B*). Fixed finger with a row of six teeth, from the base to almost the end, increasing in size slightly apically. Movable finger with basal blunt tooth and four flat teeth medially (Fig. 25*A*).

Pedipalp. All segments almost rectangulgar in cross-section. Trochanter and basal femur with one long spiniform setiferous tubercle ventrally (Fig. 24*C*). Ventrally femur with longitudinal row of five scattered tubercles. Patella unarmed. Tibia and tarsus armed with long spiniform setiferous tubercles as follows: both margins of tibia IiIi (3 >1 >4 >2), ectal margin of tarsus IIII (1 = 2 = 3 = 4), mesal margin of tarsus III (1 = 2 = 3) (Fig. 26*C*). Claw elongated.

Legs. All segments long and slenders, anterior legs covered with few small spiniform setae. Posterior legs covered with small tubercles. Femur III with two ventral rows of scattered spiniform tubercles. Femur IV with two ventral rows of tubercles confined only to apical portion (Fig. 26*D*, *E*). Tarsal count: 8(3):20(4):8:9/10.

Penis. Truncus cylindrical, flimsy lamina slightly projected, contiguous with the truncus, with apical concavity U-shaped (Fig. 27*C*). All macrosetae of penis of the same size and shape, with longitudinal sulcus and rounded apices (Fig. 27). Setation of penis: five or six setae C laterally to follis, two pairs of setae A basal to setae C, two ventral longitudinal rows of three pairs of setae E, setae D absent (Figs 27). Follis with dorsal lobe projection (Fig. 27*A*).

Female (*paratype*)

Similar to male, but with chelicera slightly smaller (Fig. 24*A*, *B*).

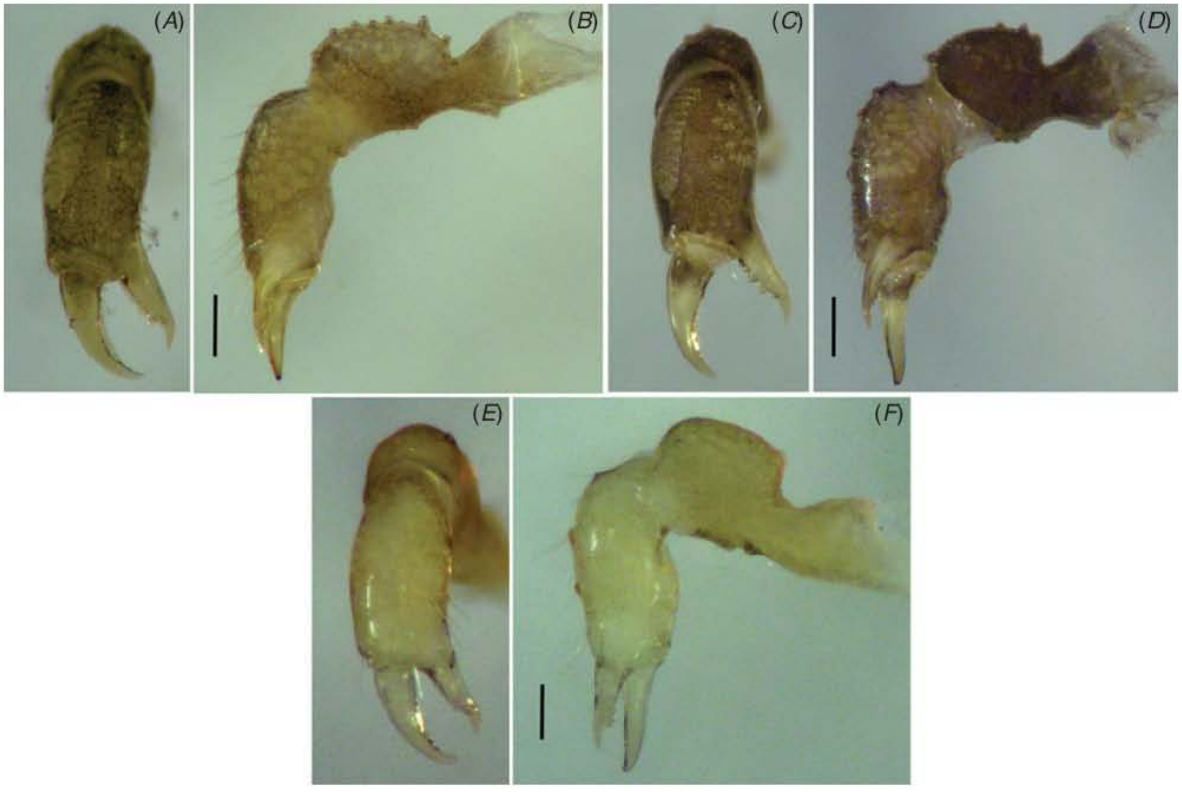

Fig. 32. Chelicera of Karosinae males. (*A*) Frontal view of *Karos barbarikos*. (*B*) Mesal view of *Karos barbarikos*. (*C*) Frontal view of *Chapulobunus unispinosus*. (*D*) Mesal view of *Chapulobunus unispinosus*. (*E*) Frontal view of *Huasteca gratiosa*. (*F*) Mesal view of *Huasteca gratiosa*. Scale bars: A, B, E, F = 0.2 mm, C, D = 0.3 mm.

Etymology

From Latin '*venefica*', which means 'a female who poisons' in reference to a sorceress who used poisons and potions for various reasons.

Genus ***Tonalteca***, gen. nov.

(Figs 28–31)

http://zoobank.org/NomenclaturalActs/urn:lsid:zoobank.org:act:7DECBCBC-5A22-4E6D-89A9-286AFF240825

Hoplobunus (in part): Goodnight & Goodnight, 1973: 86.

Type species: *Hoplobunus spinooculorum* Goodnight & Goodnight, 1973.

Diagnosis

Medium-size harvestmen (scutum length ~5 mm), troglomorphic. Ocularium very high, conical, with long apical spine (Fig. 28*C*). Chelicera large and sexually dimorphic. Basal tooth on movable finger blunt (Fig. 29*A*). Legs long, femur IV slightly longer than scutum, straight. Ornamentation of all legs formed by longitudinal rows of small, scattered spiniform setiferous tubercles (Fig. 30*B*). Penis setal *Stygnopsis*-pattern, two longitudinal pairs of setae C, two transversal pairs of setae A, one basalmost pair of setae B, and two pairs of small setae D, near to follis base (Fig. 31). With one ventral pair of vestigial insertion bases of setae E (Fig. 31*C*). Pars distalis forming an angle of 90° at the base of ventral projection. Pars distalis slightly compressed laterally (Fig. 31*A*). Follis with dorsal lobe rounded (Fig. 31*A*).

Remarks

Tonalteca can be distinguished from the following epigean stygnopsin genera (*Hoplobunus*, *Paramitraceras*, *Philora*, *Tampiconus* and *Sbordonia*) in having femur IV straight and longer than the scutum. It can be separated from the troglomorphic *Chinquipellobunus*, *Mexotroglinus* and *Troglostygnopsis* by the ocularium with a long apical spine. *Tonalteca* can be distinguished from the troglomorphic *Iztlina* by the absence of two paramedian spines on mesotergal area IV. It can be separated from *Serrobunus* by legs III and IV without remarkable rows of spiniform tubercles, and finally, from *Stygnopsis* by pedipalpal patella covered with few small tubercles and the absence of a mesal apophysis.

Etymology

The 'Tonalteca' is the initial waltz of a folkloric dance named 'Flor de Piña' from Oaxaca, Mexico. This dance is an emblematic cultural reference to Oaxaca, specially the Northern region of Papaloapan, where this genus occurs. The name is feminine.

Subfamily **KAROSINAE**, subfam. nov.

http://zoobank.org/NomenclaturalActs/urn:lsid:zoobank.org:act:B6392819-5994-4F15-9EEB-409F3BB5C4B1

Phalangodinae (in part): Roewer, 1912: 108; Roewer, 1923: 69; Goodnight & Goodnight, 1944: 1; Goodnight & Goodnight, 1947*b*: 3; Goodnight & Goodnight, 1953: 13; Goodnight & Goodnight, 1971: 33; Goodnight & Goodnight, 1973: 83; Šilhavý, 1974: 185; Šilhavý, 1977: 227; Rambla & Juberthie, 1994: 218.

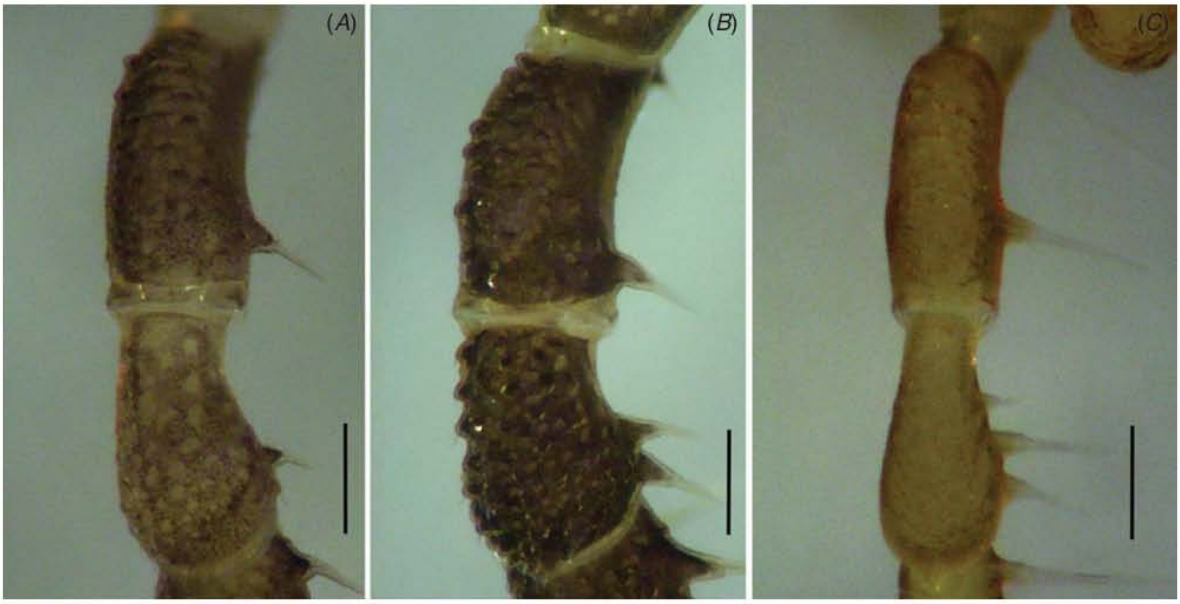

Fig. 33. Dorsal views of pedipalp femur and patella of Karosinae males. (*A*) *Karos barbarikos*. (*B*) *Chapulobunus unispinosus*. (*C*) *Huasteca gratiosa*. Scale bars: A, B, C = 0.3 mm.

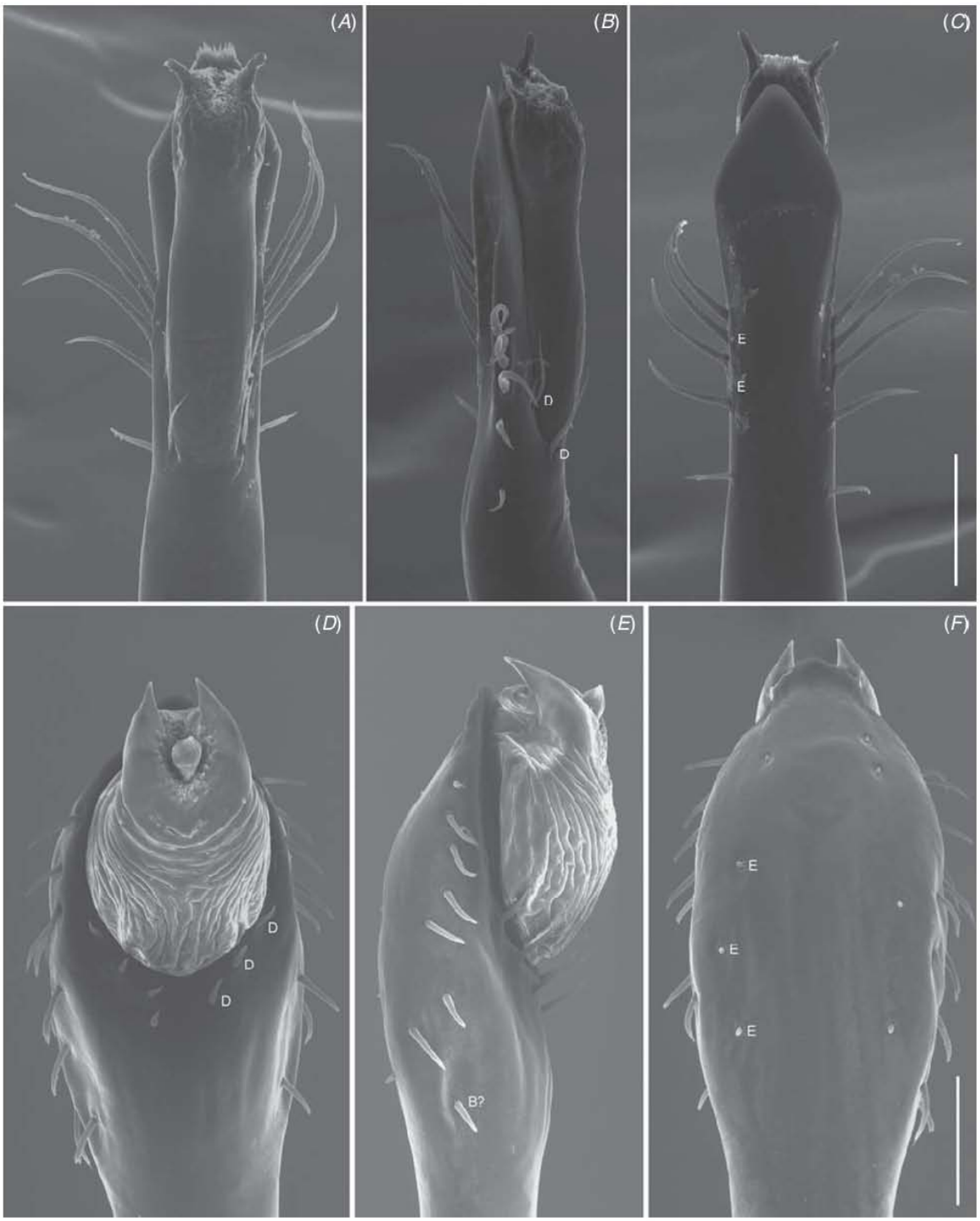

Fig. 34. Male genitalia of Karosinae. (*A*) Dorsal view of *Karos barbarikos*. (*B*) Lateral view of *Karos barbarikos*. (*C*) Ventral view of *Karos barbarikos*. (*D*) Dorsal view of *Chapulobunus asper*. (*E*) Lateral view of *Chapulobunus asper*. (*F*) Ventral view of *Chapulobunus asper*. Small letters D and E indicate setal groups, B? indicates possibly B setae. Scale bars: A, B, C, D, E, *F* = 100 μm.

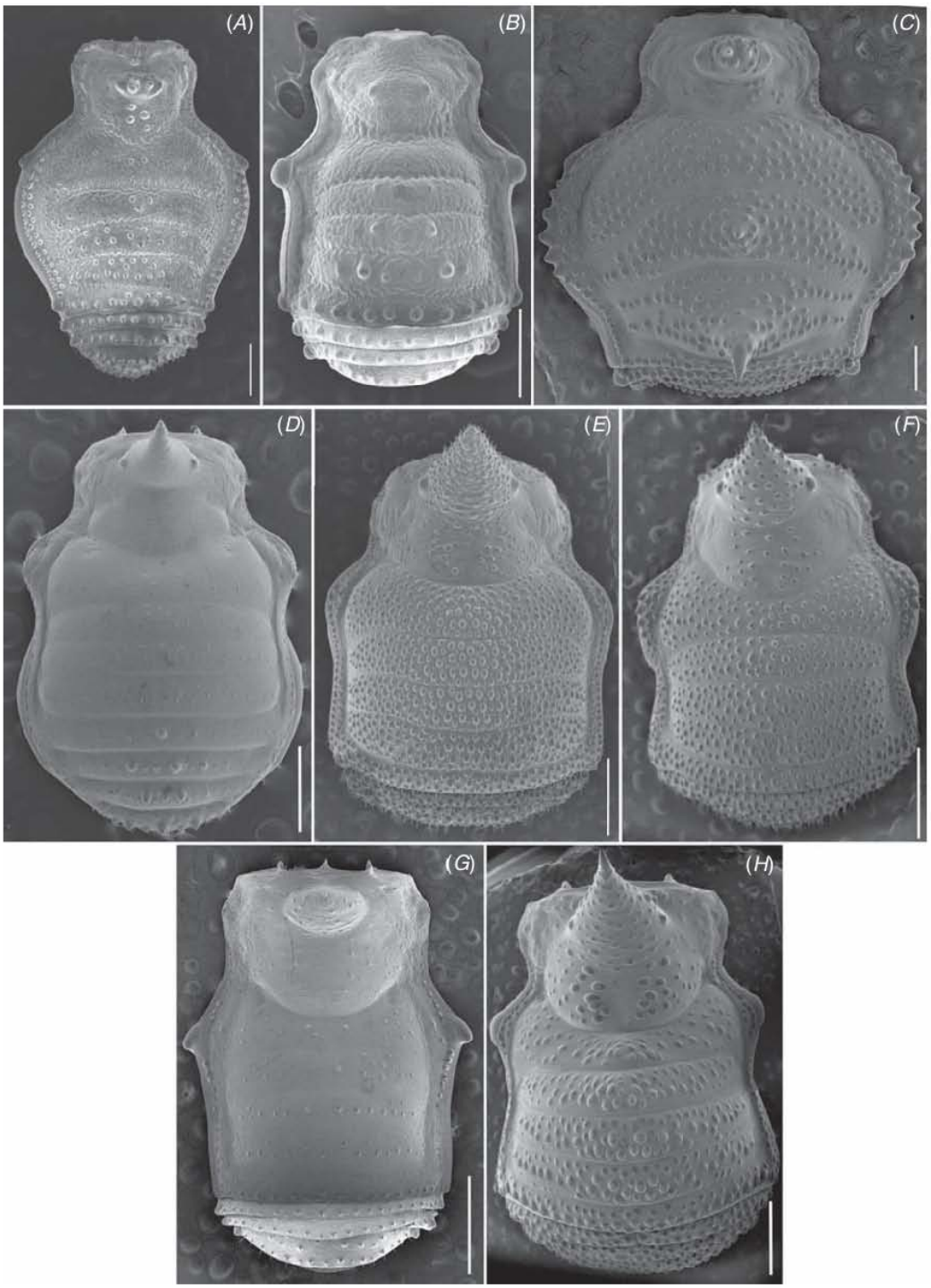

Fig. 35. Dorsal habitus of Karosinae and Paramitraceras-group. (*A*) *Karos barbarikos*. (*B*) *Huasteca gratiosa*. (*C*) *Chapulobunus unispinosus*. (*D*) *Philora tuxtlae*. (*E*) *Paramitraceras veracruz*. (*F*) *Paramitraceras* aff. *hispidulum*. (*G*) *Troglostygnopsis* sp. 0049. (*H*) *Paramitraceras* aff. *granulatum*. Scale bars: A, B, C, D = 0.5 cm, E, F, G, H = 1 cm.

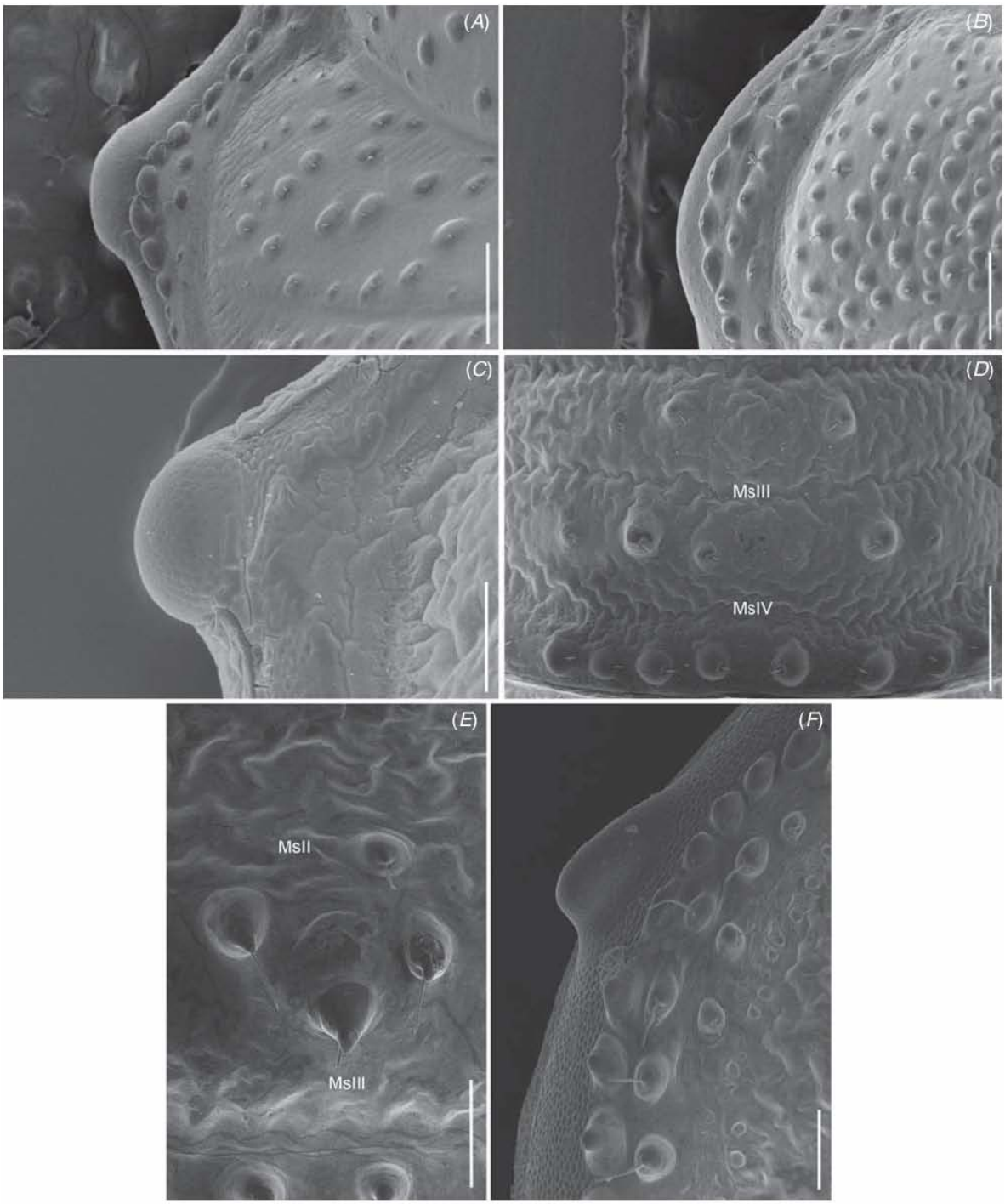

Fig. 36. Lateral projections of scutum and mesotergal sulci of Karosinae and *Paramitraceras*-group. (*A*) Lateral projection of *Paramitraceras* aff. *granulatum*. (*B*) Lateral projection of *Paramitraceras veracruz*. (*C*) Lateral projection of *Huasteca gratiosa*. (*D*) Mesotergal sulci III and IV of *Huasteca gratiosa*. (*E*) Detail of mesotergal sulci II and III of *Karos barbarikos*. (*F*) Lateral projection of *Karos barbarikos*. MsII to MsIV indicate mesotergal sulcus II, III and IV respectively. Scale bars: A = 0.5 mm, B = 250 μm, C, E, F = 100 μm, D = 200 μm.

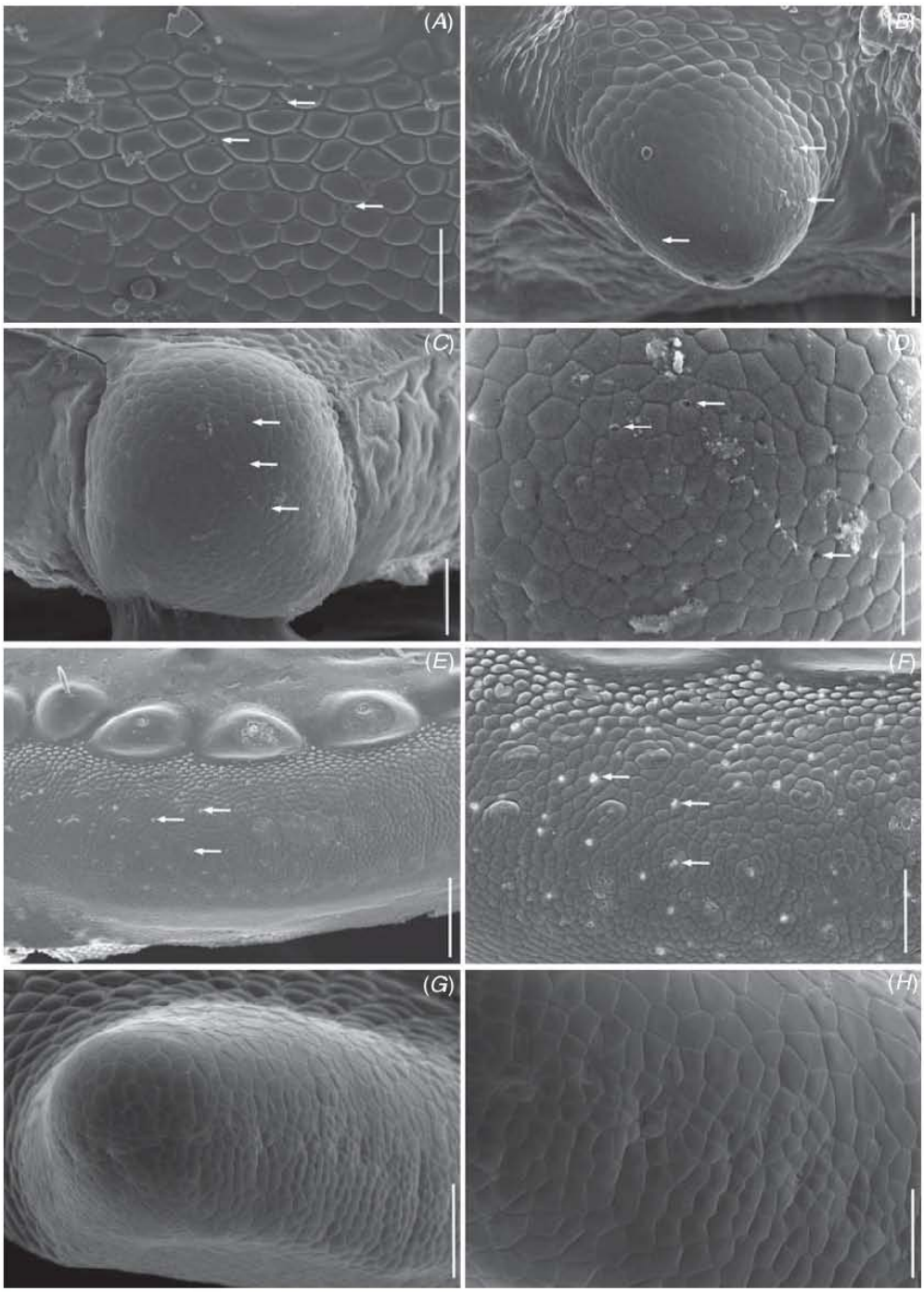

Fig. 37. Details of lateral projections and associated pores in Karosinae and *Paramitraceras*-group. (*A*) Pores at level of mesotergal area I in *Karos barbarikos*. (*B*) Projection of corner on mesotergal area V in *Karos barbarikos*. (*C*) Lateral projection of *Huasteca gratiosa*. (*D*) Pores on lateral projection in *Huasteca gratiosa*. (*E*) Lateral projection of *Paramitraceras veracruz*. (*F*) Pores on lateral projection in *Paramitraceras veracruz*. (*G*) Lateral projection in *Troglostygnopsis* sp. 0049. (*H*) Detail of lateral projection in *Troglostygnopsis* sp. 0049. Arrows indicate some pores. Scale bars: A, D, H = 25 µm, B, C, F, G = 50 = µm, E = 100 µm.

Stygnopsinae (in part): Goodnight & Goodnight, 1945: 1; Goodnight & Goodnight, 1946: 1.
Karos-group (in part): Cruz-López & Francke, 2015: 838.
Type genus: *Karos* Goodnight & Goodnight, 1944.
Included taxa: *Karos* Goodnight & Goodnight, 1944, *Monterella* Goodnight & Goodnight, 1944, *Montabunus* Goodnight & Goodnight, 1945, *Chapulobunus* Goodnight & Goodnight, 1946, *Potosa* Goodnight & Goodnight, 1947, *Crettaros* Cruz-López & Francke, 2015, *Huasteca* Cruz-López & Francke, 2015, *Mictlana* Cruz-López & Francke, 2015, and the uncertain '*Karos*' *depressus* Goodnight & Goodnight, 1971 and '*Hoplobunus*' *planus* Goodnight & Goodnight, 1973.

Diagnosis

Modified from Cruz-López and Francke (2015). Small to medium harvestmen (< to ~6 mm). Ocularium in the middle of prosoma,

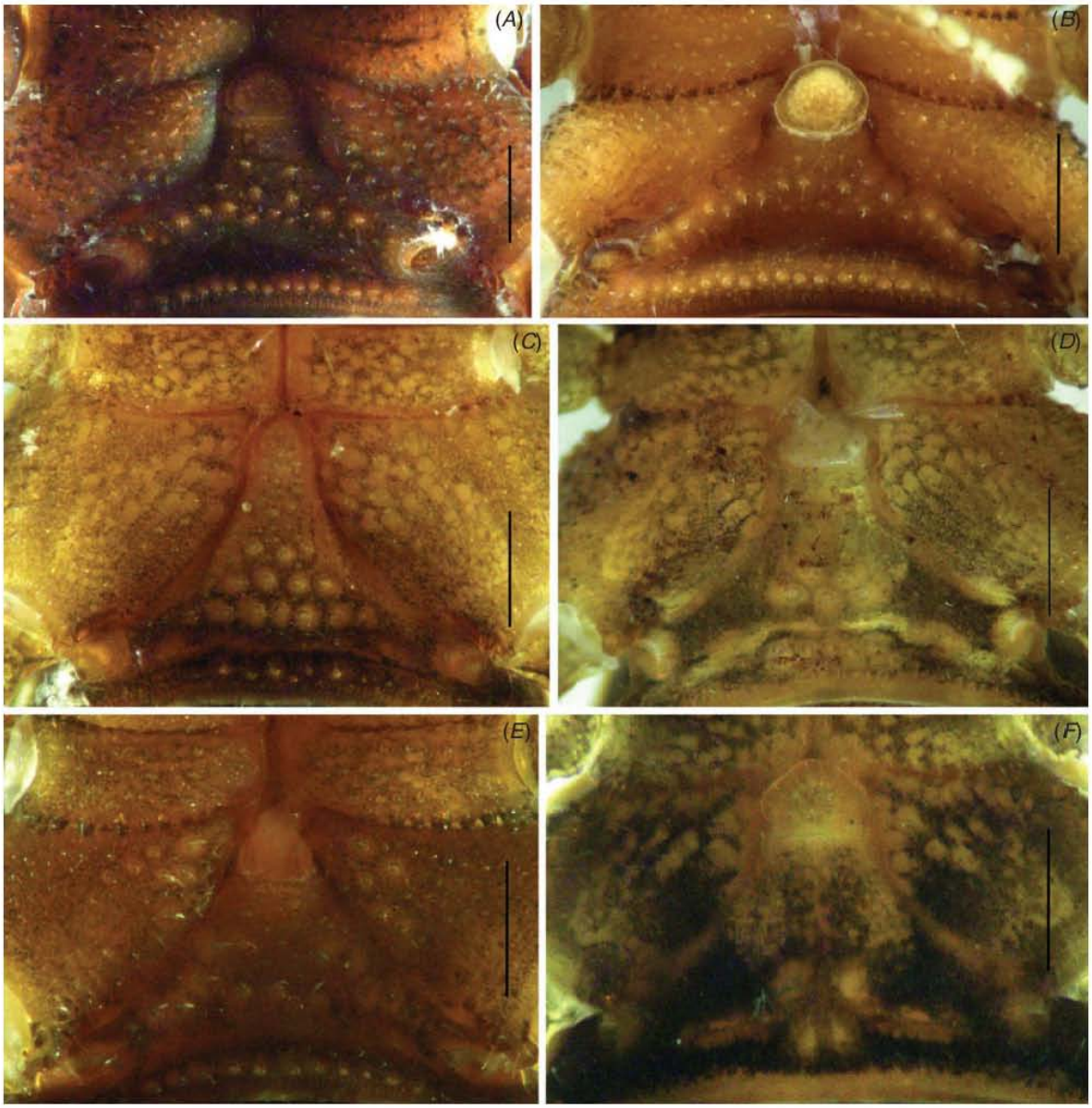

Fig. 38. Colour detail of ventral glandular tubercles on stigmatic area in *Paramitraceras*-group males. (*A*) *Paramitraceras* aff. *hispidulum*. (*B*) *Paramitraceras tzotzil*. (*C*) *Paramitraceras* aff. *hispidulum*. (*D*) *Sbordonia* aff. *parvula*. (*E*) *Paramitraceras veracruz*. (*F*) *Philora tuxtlae*. Scale bars: A = 1.3 mm, B, E = 0.8 mm, C, D = 0.7 mm, F = 0.4 mm.

small to medium size, generally unarmed (Fig. 35*A–C*). Usually with spiniform bulge anterior to ocularium (Fig. 35*A–C*). Mesotergal sulci generally sinuous (Figs 35*A–C*, 36*D*, *E*). Lateral channels at level of mesotergal areas I, II, V and usually in free tergites forming rounded projections, these projections have the surface covered by small pores (Figs 35*A–C*, 36*C*, *F*, 37*A–D*). Chelicera small, both fingers with similar, small and uniform dentition (Fig. 32). Meso-apical surface of pedipalp femur and patela armed with spiniform setiferous tubercles (Fig. 33). Penis setation *Karos*-pattern. Pars distalis contiguous with ventral projection, not forming an angle (Fig. 34).

Remarks

Karosinae exhibits more uniform diagnostic characters than Stygnopsinae. The ocularium in the middle of prosoma and mesal armature of pedipalpal femur and patella are consistent also in '*H.*' *planus* and '*K.*' *depressus*, species known from females only. The spiniform bulge anterior to the ocularium is an inconspicuous character present in almost all Karosinae examined (Fig. 35*A–C*). *Mictlana inops* and '*H.*' *planus* exhibit two dorsal bulges on the prosoma. Cruz-López and Francke (2015) considered the anterior bulge in *M. inops* as the ocularium; a similar structure is present in '*H.*' *planus*. In this work, we are not sure which of the two bulges is the ocularium because without evidence of eyes, retina or eye-spots, we are uncertain, as occurs in *Jarmilana pecki* (Goodnight and Goodnight 1977), as indicated by Cruz-López *et al.* (2016).

Conflictive taxa, the case of Mexotroglinus *and* Isaeus

The genus *Mexotroglinus* is the most controversial taxon within the family. This genus has small chelicerae without sexual

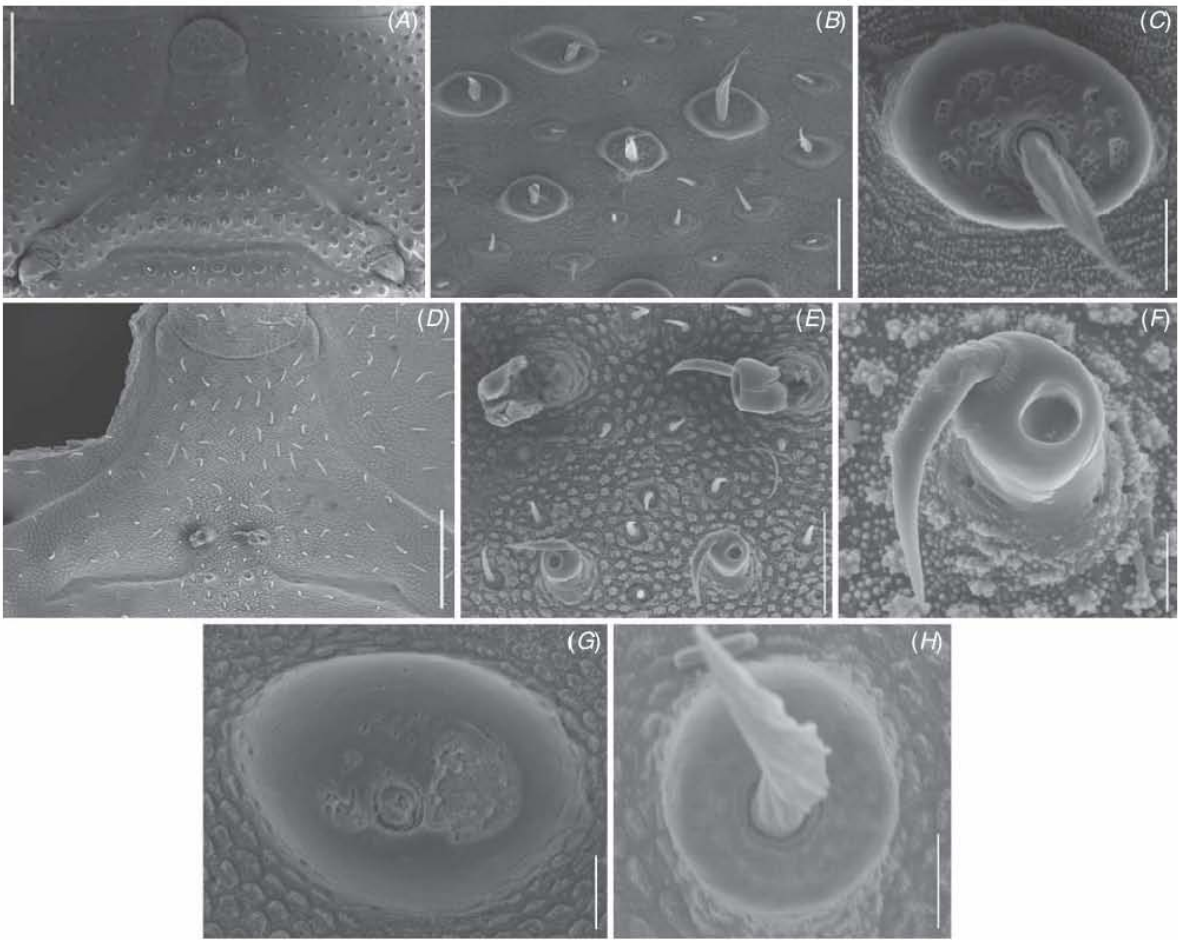

Fig. 39. Detail of ventral glandular tubercles on stigmatic area in *Paramitraceras*-group males. (*A*) Stigmatic area of *Paramitraceras* aff. *hispidulum*. (*B*) Glandular tubercles of *Paramitraceras* aff. *hispidulum*. (*C*) Detail of one glandular tubercle of *Paramitraceras* aff. *hispidulum*. (*D*) Stigmatic area of *Philora tuxtlae*. (*E*) The four glandular tubercles of *Philora tuxtlae*. (*F*) Detail of one glandular tubercle of *Philora tuxtlae*. (*G*) Detail of one glandular tubercle of *Paramitraceras* aff. *granulatum*. (*H*) Detail of one glandular tubercle of *Paramitraceras veracruz*. Scale bars: A = 1 mm, B = 100 μm, C, G = 25 μm, D = 200 μm, E = 50 μm, F = 10 μm, H = 20 μm.

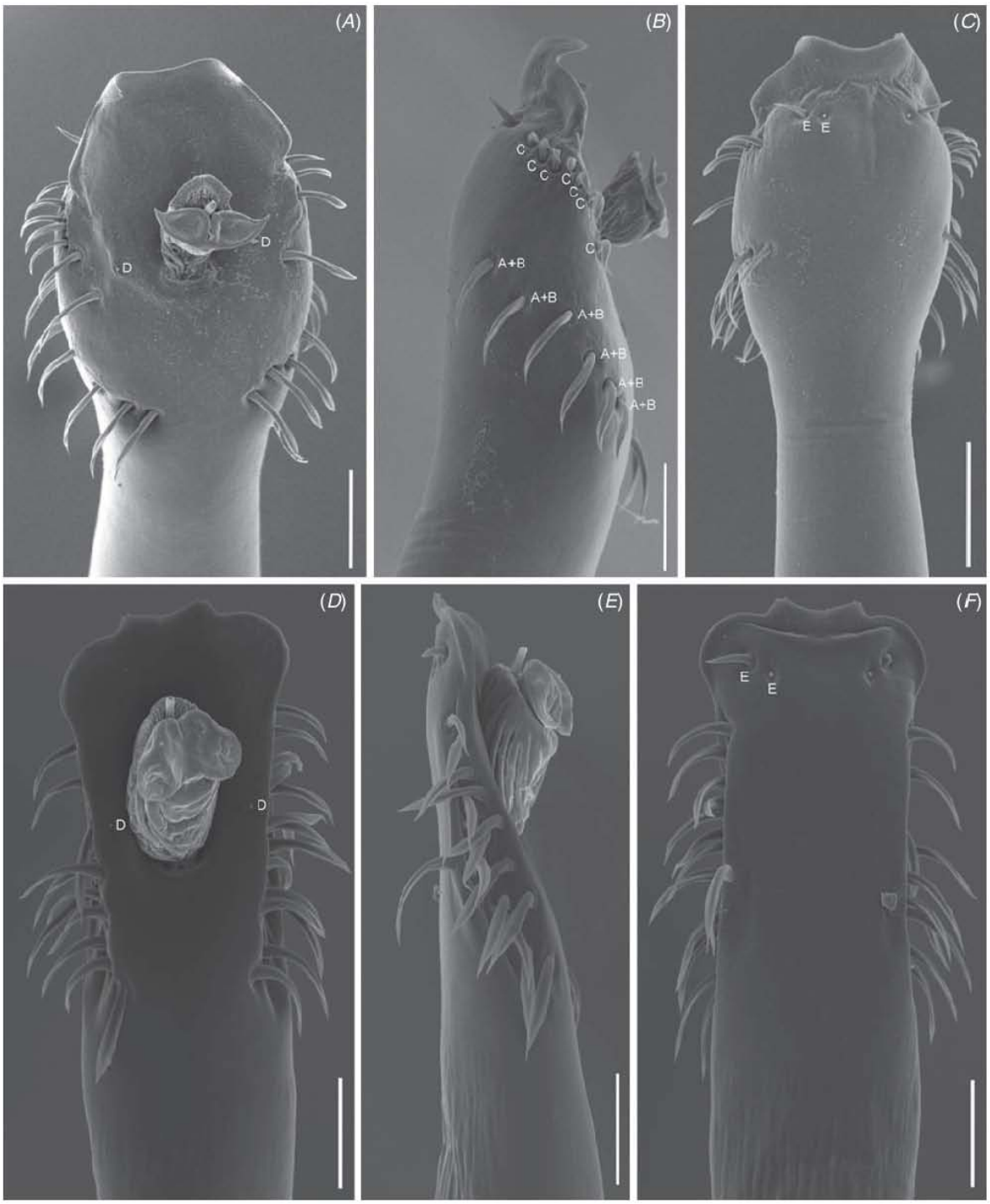

Fig. 40. Male genitalia of *Paramitraceras*-group members. (*A*) Dorsal view of *Paramitraceras* aff. *granulatum*. (*B*) Lateral view of *Paramitraceras* aff. *granulatum*. (*C*) Ventral view of *Paramitraceras* aff. *granulatum*. (*D*) Dorsal view of *Paramitraceras tzotzil*. (*E*) Lateral view of *Paramitraceras tzotzil*. (*F*) Ventral view of *Paramitraceras tzotzil*. Small letters C, D, E and A+B indicate setal groups. Scale bars: A, B, D, E, F = 100 µm, C = 200 µm.

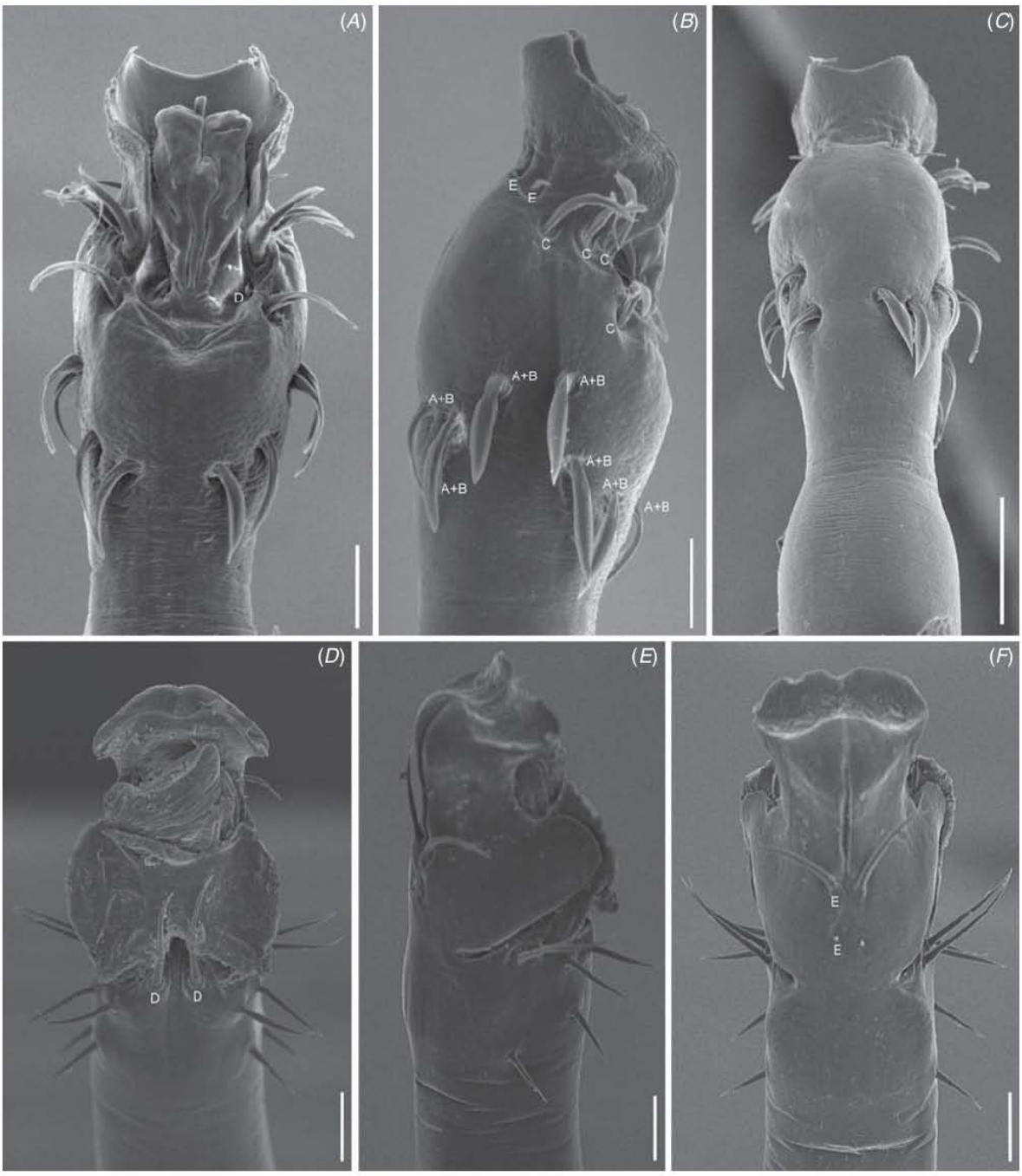

Fig. 41. Male genitalia of Paramitraceras-group members. (*A*) Dorsal view of *Paramitraceras* aff. *hispidulum*. (*B*) Lateral view of *Paramitraceras* aff. *hispidulum*. (*C*) Ventral view of *Paramitraceras* aff. *hispidulum*. (*D*) Dorsal view of *Sbordonia* aff. *parvula*. (*E*) Lateral view of *Sbordonia* aff. *parvula*. (*F*) Ventral view of *Sbordonia* aff. *parvula*. Small letters C, D, E and A+B indicate setal groups. Scale bars: A, B, D, E, F = 50 µm, C = 100 µm.

dimorphism (Fig. 46*D*), mesal armature on the pedipalpal femur and patella (Fig. 46*H*, *I*), and the male genitalia is similar to the *Karos*-pattern (Fig. 47). This combination of character states places *Mexotroglinus* in Karosinae. However, the ocularium located on the frontal margin of the prosoma (Fig. 46*A*, *B*), the straight mesotergal sulci (Fig. 46*A*, *B*, *E*), the lateral channels not projected laterally and the absence of associated pores (Fig. 46*A*, *B*, *E*, *F*) suggest its position within Stygnopsinae. The three analyses are consistent in the inclusion of *Mexotroglinus* in Stygnopsinae. In our results, both BI and ML analyses of total evidence showed a sister-group relationship between *Mexotroglinus* and *Chinquipellobunus*, with high support value in the BI analysis, but without significant support in ML. Based on the phylogenetic evidence,

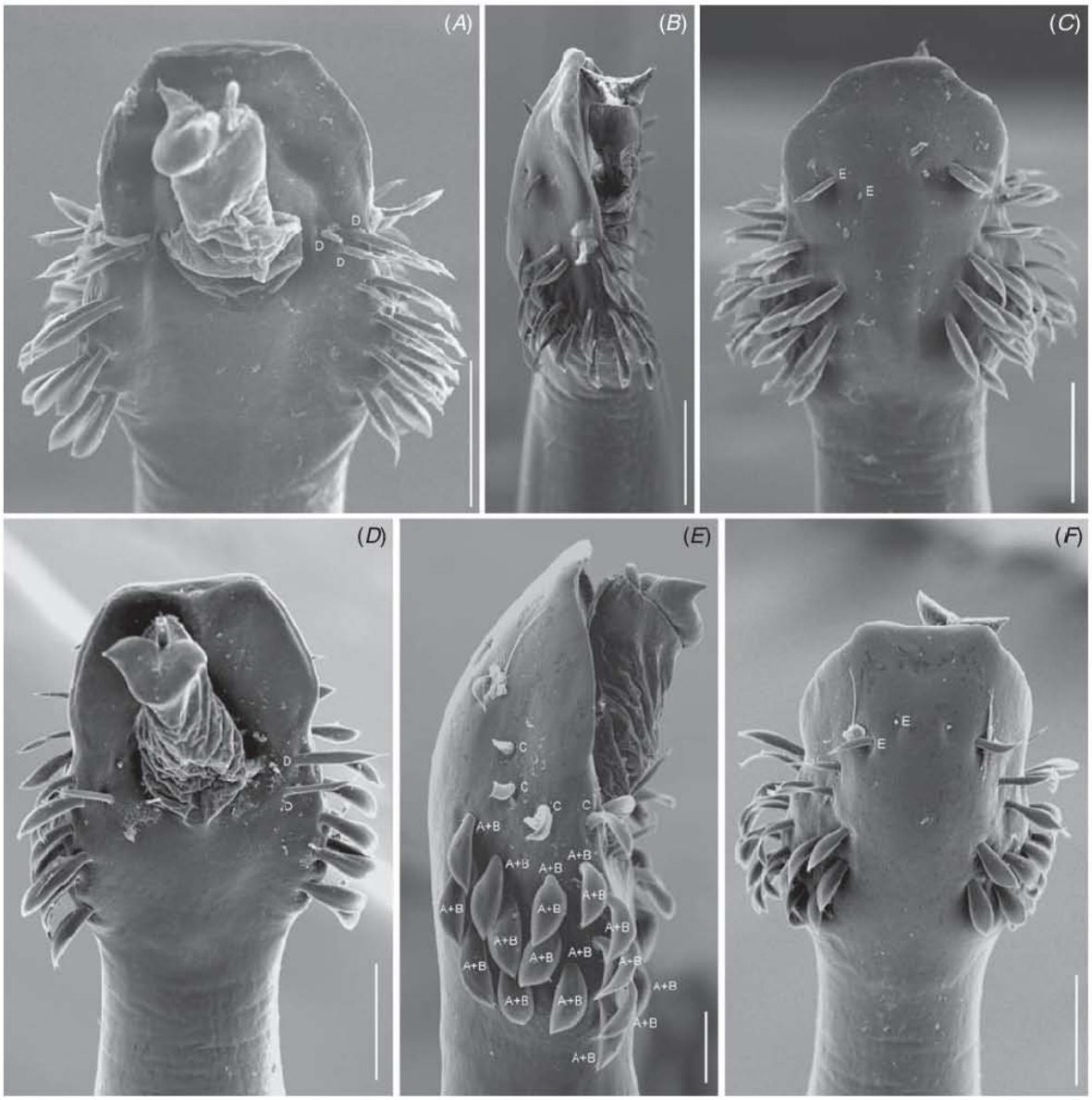

Fig. 42. Male genitalia of *Paramitraceras*-group members. (*A*) Dorsal view of *Sbordonia* sp. 0055. (*B*) Lateral view of *Sbordonia* sp. 0055. (*C*) Ventral view of *Sbordonia* sp. 0055. (*D*) Dorsal view of *Troglostygnopsis* sp. 0049. (*E*) Lateral view of *Troglostygnopsis* sp. 0049. (*F*) Ventral view of *Troglostygnopsis* sp. 0049. Small letters C, D, E and A+B indicate setal groups. Scale bars: A, B, C, D, F = 100 µm, E = 50 µm.

Mexotroglinus is the most extreme case of morphological convergence, allocated to Stygnopsinae, but also showing some important diagnostic morphological characters of Karosinae, as mentioned above.

Together with the description of Stygnopsidae, Sørensen (1932) described the monotypic genus *Isaeus* from Mexico. He considered that the ectal and mesal armature on the pedipalpal patella were significant characters to differentiate between *Stygnopsis* and *Isaeus*, respectively. Also, Sørensen (1932) considered *Isaeus* related to the monotypic Mexican genus *Metaconomma* Pickard-Cambridge, 1905, a taxon which currently is *incertae sedis* in Grassatores (Laniatores) (Kury 2003). Later, Goodnight and Goodnight (1953) considered *Isaeus* a junior synonym of *Hoplobunus*. We here

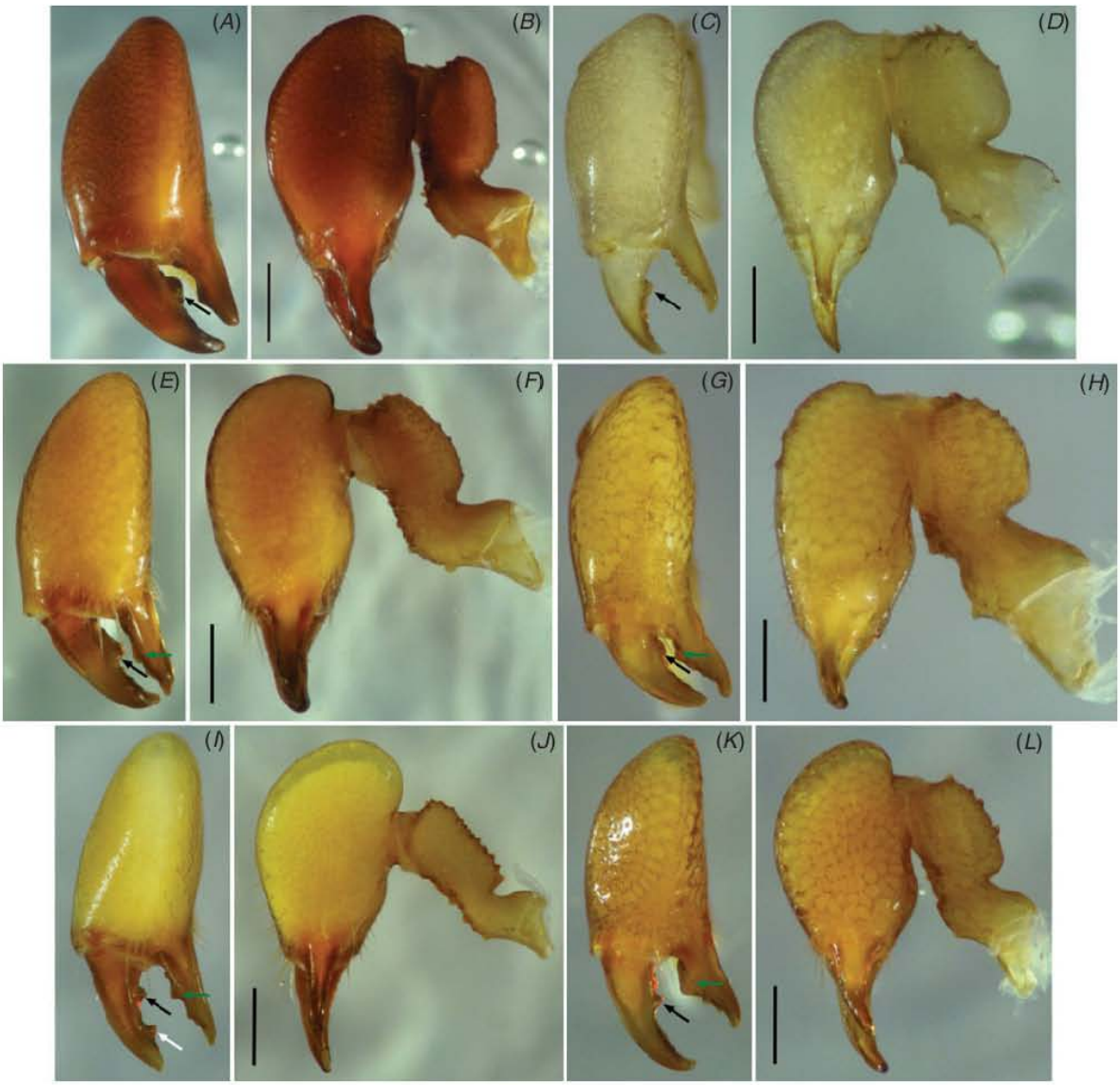

Fig. 43. Chelicera of *Paramitraceras*-group males. (*A*) Frontal view of *Paramitraceras* aff. *granulatum*. (*B*) Mesal view of *Paramitraceras* aff. *granulatum*. (*C*) Frontal view of *Paramitraceras* aff. *hispidulum*. (*D*) Mesal view of *Paramitraceras* aff. *hispidulum*. (*E*) Frontal view of *Paramitraceras tzotzil*. (*F*) Mesal view of *Paramitraceras tzotzil*. (*G*) Frontal view of *Paramitraceras veracruz*. (*H*) Mesal view of *Paramitraceras veracruz*. (*I*) Frontal view of *Sbordonia* sp. 0055. (*J*) Mesal view of *Sbordonia* sp. 0055. (*K*) Frontal view of *Sbordonia* aff. *parvula*. (*L*) Mesal view of *Sbordonia* aff. *parvula*. Black arrows indicate the basal blunt tooth on movable finger, green arrows indicate the basal tooth on fixed finger, and white row indicates the median tooth un movable finger. Scale bars: A, B = 1.6 mm, C, D = 0,4 mm, E, F = 1.0 mm, G, H = 0.5 mm, I, J = 0.8 mm, K, L = 0.7 mm.

demonstrate the polyphyly of *Hoplobunus*, revalidating all of the synonymised genera. In the case of *Isaeus*, we revalidate it below, hoping that in the future this genus can be studied properly, a nomenclatural act similar to those generic revalidations in Cosmetidae proposed by Kury (2003).

Genus ***Isaeus*** Sørensen, stat. rev.

Isaeus Sørensen, 1932: 276.
Hoplobunus (in part): Goodnight & Goodnight, 1953: 19.
Included taxa: *Isaeus mexicanus* Sørensen, 1932, by monotypy.

Remarks

We were unable to examine any specimens of *I. mexicanus*, and therefore cannot assign *Isaeus* to a subfamily.

Discussion

Genital evolution and homoplastic characters

The capsula externa forming a multifolded follis has been considered a plesiomorphic condition by some authors under different approaches (Kury 1997; Mendes and Kury 2007; Kury and Villarreal 2015). This multifolded follis has been considered a synapomorphy or a convergence among some Epedanoidea, Assamioidea and Stygnopsidae, depending on different authors (Kury 1997; Sharma *et al.* 2011). The detailed examination of penes in Assamiidae, Epedanidae, Pyramidopidae and Tithaeidae, corroborated that the genital capsula externa and glans are different structures (not homologous), and that they exhibit morpho-mechanical differences when the capsula externa is expanded using chemical sustances such as lactic acid (Martens 1986; Zhang and Zhang 2010; Lian *et al.* 2011; Sharma *et al.* 2011; Cruz-López *et al.* 2016).

Stygnopsidae exhibits a great diversity in genital morphology, especially in the shape of the pars distalis and in penial setation. However, within each genus, the general pattern of the genital morphology is stable. The only known genital convergence occurs between *Karos* and *Crettaros*, according to the morphological cladistics analysis presented by Cruz-López and Francke (2015). This convergence is corroborated here in the BI and ML analyses using combined data. In the present contribution, we observed another genital convergence between *Hoplobunus* and the *Tampiconus*-like clade (Figs 1, 14, 19), and, unlike *Karos* and *Crettaros*, these taxa are similar externally, as discussed previously.

All members of *Paramitraceras*, plus *Sbordonia parvula* and *S.* aff. *parvula* exhibit very uniform external morphology

Fig. 44. Pedipalps of members of *Paramitraceras*-group males. (*A*) Mesal view of *Paramitraceras* aff. *granulatum*. (*B*) Mesal view of *Paramitraceras* aff. *hispidulum*. (*C*) Mesal view of *Paramitraceras tzotzil*. (*D*) Mesal view of *Paramitraceras veracruz*. (*E*) Ectal view of *Sbordonia* sp. 0055. (*F*) Mesal view of *Sbordonia* aff. *parvula*. (*G*) Mesal view of *Sbordonia armigera*. Scale bars: A = 3.0 mm, B = 0.9 mm, C = 1.9 mm, D = 1.3 mm, E = 1.5 mm, F, G = 1.0 mm.

and unarmed pedipalps, ornate only with spiniform setae on longitudinal keels on tibia and tarsus, and sometimes with few spiniform setiferous tubercles (Figs 44, 45). Surprisingly, males of these taxa have glandular tubercles on the stigmatic area (Figs 38, 39), characters reported here for the first time in Laniatores. According to Cruz-López and Francke (2013*a*), the robust body, a dorsally convex opisthosoma and unarmed pedipalps are diagnostic characters for *Paramitraceras*. Subsequently, Cruz-López and Francke (2013*b*) described the male genitalia as *Paramitraceras*-pattern, which is present in

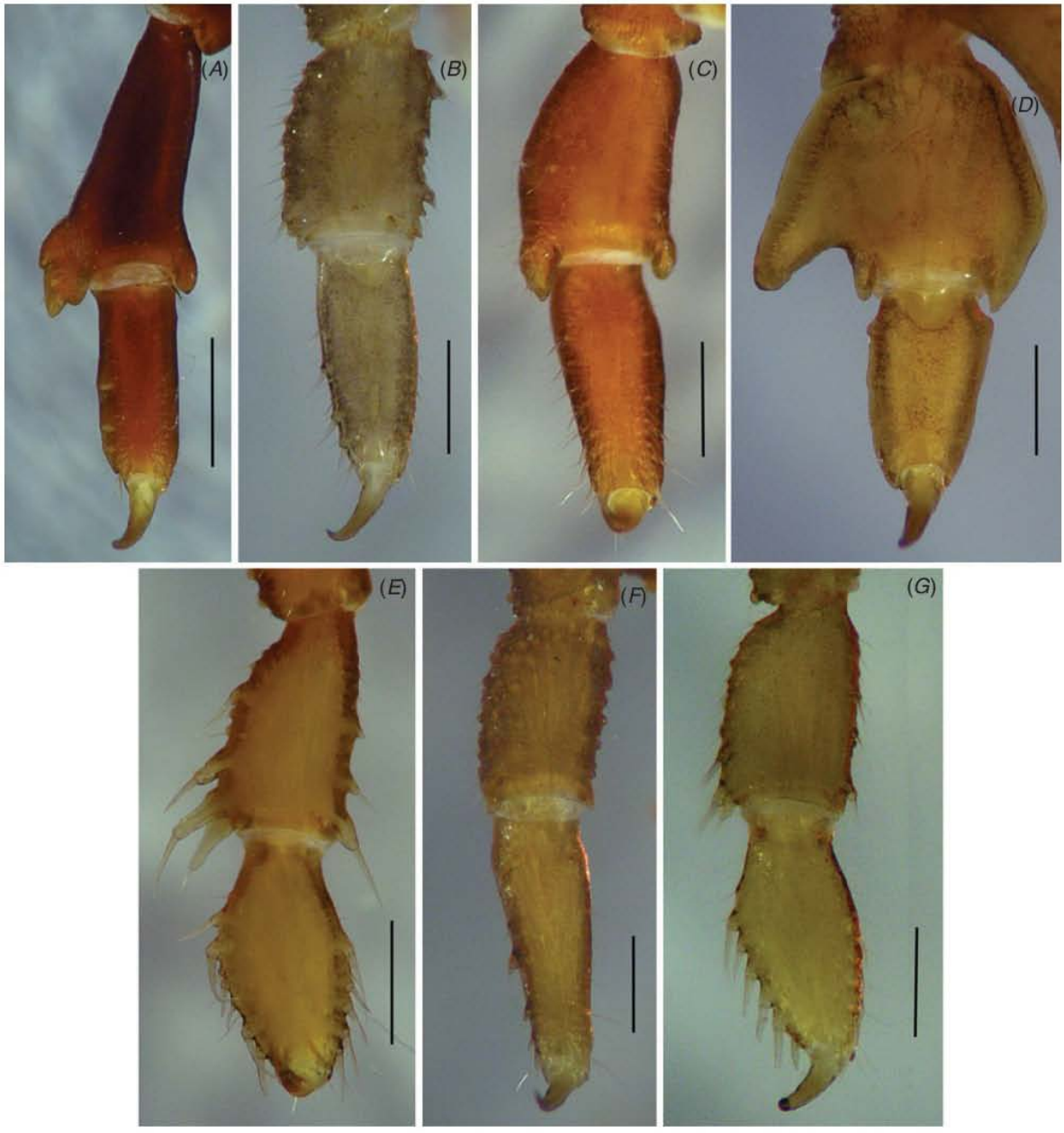

Fig. 45. Ventral views of pedipalp tibia and tarsus of *Paramitraceras*-group males. (*A*) *Paramitraceras* aff. *granulatum*. (*B*) *Paramitraceras* aff. *hispidulum*. (*C*) *Paramitraceras tzotzil*. (*D*) *Paramitraceras veracruz*. (*E*) *Sbordonia* sp. 0055. (*F*) *Sbordonia* aff. *parvula*. (*G*) *Sbordonia armigera*. Scale bars: A = 1.7 mm, B = 0.4 mm, C = 0.9 mm, D = 0.6 mm, E = 0.7 mm, F, G = 0.5 mm.

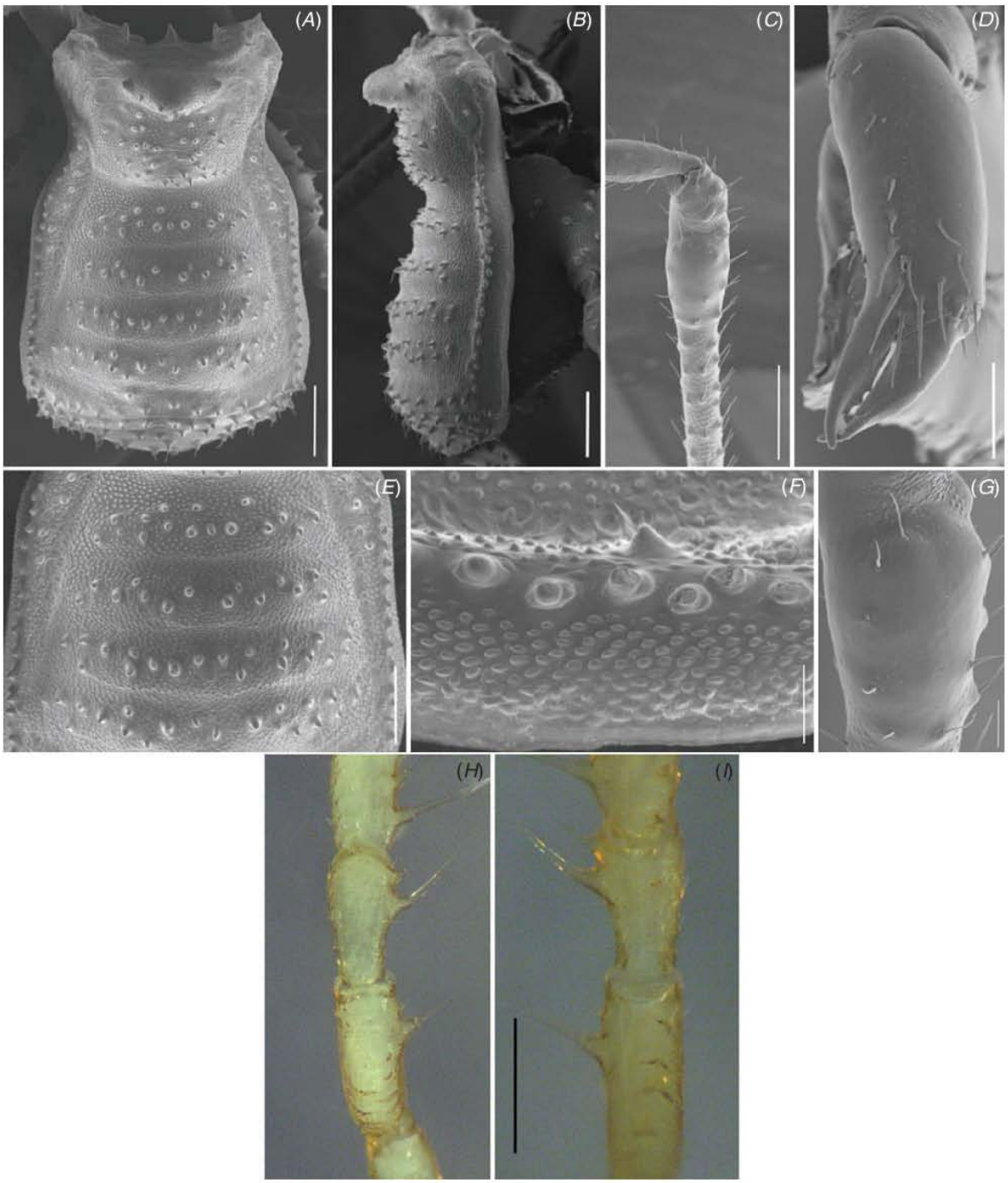

Fig. 46. External morphology of *Mexotroglinus* aff. *sbordonii* male. (*A*) Dorsal habitus. (*B*) Lateral habitus. (*C*) Mesal view of tibia II. (*D*) Frontal view of chelicera. (*E*) Detail of mesotergal sulci II–IV. (*F*) Lateral channels at level of mesotergal area I. (*G*) Ventro-mesal detail of apical swollen in tibia II. (*H*) Dorsal view of pedipalp femur and tibia. (*I*) Ventral view of pedipalp femur and tibia. Scale bars: A, B, C = 250 µm, D = 150 µm, E = 200 µm, F, G = 50 µm.

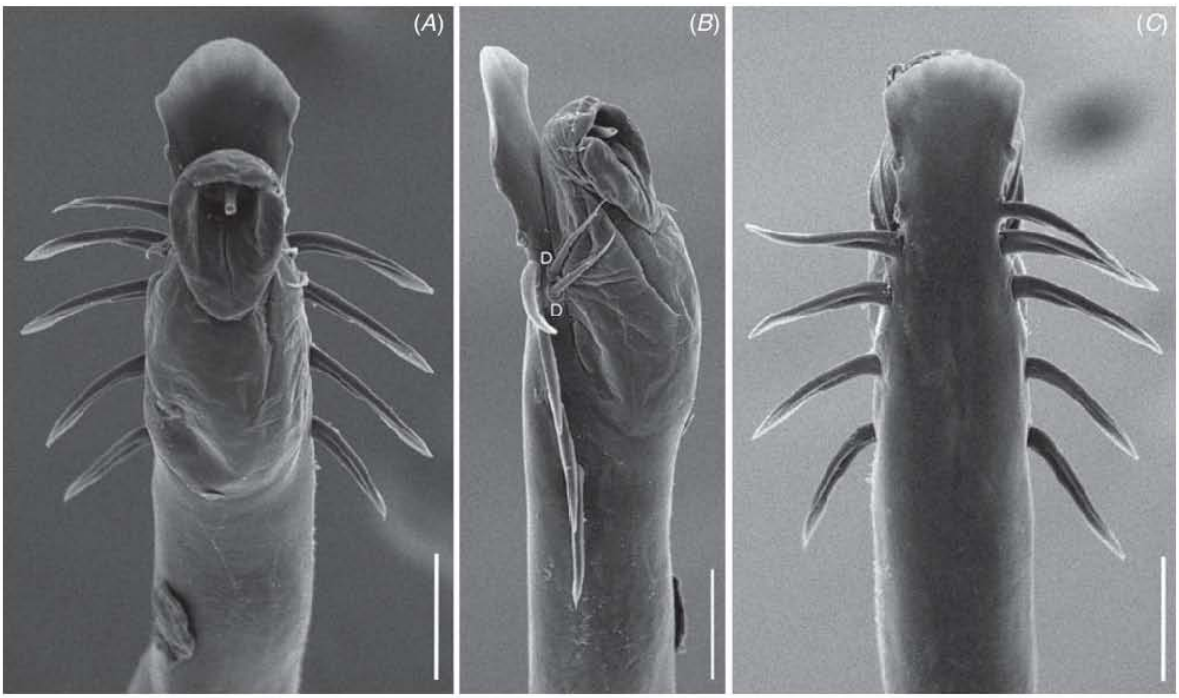

Fig. 47. Male genitalia of *Mexotroglinus* aff. *sbordonii*. (*A*) Dorsal view. (*B*) Lateral view. (*C*) Ventral view. Small letters D indicate setal groups. Scale bars: A, B, C = 50 µm.

Paramitraceras, *Philora* and *Troglostygnopsis*. Surprisingly, the male genitalia of *Paramitraceras tzotzil* Cruz-López & Francke, 2013, exhibits penial modifications, as dorso-ventral constriction of pars distalis and nonrecognition of setal groups A, B and C (Fig. 40*D–F*). The *Paramitraceras* genital pattern in the clade (*Serrobunus* (*Sbordonia* aff. *parvula* (*P. veracruz* ((*P.* aff. *granulatum* (*Troglostygnopsis* + *Sbordonia* sp. 0055)) (*Philora* + *P. tzotzil*)))), according to the BI analyses of combined data (Fig. 1), has apparently evolved as follows. In *Serrobunus*, the setae D are present, with similar lengths of the other macrosetae, whereas setae E are absent. In *S. parvula* and *S.* aff. *parvula*, the setal pattern is unrecognisable, and these taxa also have a dorsal expandable lobe, which is broken through by the one pair of long setae D (Fig. 41*D–F*). In the remaining taxa, the *Paramitraceras* genital pattern is expressed as Cruz-López and Francke (2013*b*) described, except in *P. tzotzil*, in which the pars distalis and the ventral lamina are contiguos, without apical depression, and the lateral macrosetae groups are unrecognisable. Also, this modified genital pattern is present in an undescribed *Paramitraceras* species similar to *P. tzotzil*.

According to the BI analysis of combined data, the unarmed pedipalps could be a homoplastic character, present in the *Paramitraceras*-group in one clade, and in *P. hispidulum* + *P.* aff. *hispidulum* in a totally different clade. In the *Paramitraceras*-group, the unarmed pedipalps could have appeared only once in the clade, with subsequent reversal in *Philora* and *Troglostygnopsis* + *Sbordonia* sp. 0055 (Figs 44, 45). However, spiniform setiferous tubercles in *Philora* and *Sbordonia* sp. 0055 are reduced in size compared with *Troglostygnopsis*. This may be due to the troglobitic habits in *Troglostygnopsis*, since the only other known cave-dwelling species in the clade, *Philora nympha* Cruz-López & Francke, 2016, also exhibits very long pedipalpal armature (Cruz-López and Francke 2016*b*). The glandular tubercles present ventrally on males of *Paramitraceras*, *S. parvula*, *S.* aff. *parvula* and *Philora* are another remarkable convergence, which may have evolved in a similar way as the unarmed pedipalps, as in the *Paramitraceras*-group clade, with subsequent loss in *Troglostygnopsis*, and *S. parvula* + *S.* aff. *parvula* group.

Pores associated with median projections on the lateral channels are convergently found in Karosinae and *Paramitraceras*, *Philora* and *Sbordonia* aff. *parvula* (Fig. 37*A–F*). Detailed examination of *Troglostygnopsis* did not reveal the presence of these pores, although this genus has median lateral projections similar to those on *Paramitraceras* (Fig. 37*F*, *G*). The function of these pores and their relationship to the lateral median projections are unclear.

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CONCLUSIONES GENERALES

Se reconoció un patrón genital llamado "Paramitraceras" dentro de la familia, el cual sólo se observa en los géneros *Paramitraceras*, *Philora* y *Troglostygnopsis*. Los géneros que comparten este patrón genital se recuperaron como un grupo monofilético utilizando información morfológica. Por otro lado, utilizando información molecular y evidencia total, al menos *Paramitraceras* se recuperó como un grupo polifilético, contradiciendo el origen único de este patrón en la familia.

Los análisis filogenéticos bajo los criterios de Máxima Verosimilitud e Inferencia Bayesiana empleando información molecular y evidencia total, consistentemente apoyan la monofilia de la familia Stygnopsidae con valores de soporte altos. A su vez, se detectaron dos grandes clados dentro de la familia, los cuáles fueron reconocidos como subfamilias: Stygnopsinae Sørensen, 1932 y Karosinae subfam. nov.

Dentro de Stygnopsinae, los géneros *Hoplobunus* y *Paramitraceras* se recuperaron como grupos polifiléticos, tomándose decisiones taxonómicas para el primero de ellos. Dentro de los cambios taxonómicos propuestos, se propusieron nuevas diagnosis para los géneros: *Hoplobunus*, *Stygnopsis* y *Serrobunus* stat. rev., este último había sido sinonimizado bajo *Hoplobunus*. Además, se erigieron los siguientes taxones: *Iztlina venefica* gen. nov. *et* sp. nov., y *Tonalteca* gen nov. Adicionalmente se propusieron nuevas combinaciones de taxones previamente descritos como *Hoplobunus*: *Serrobunus queretarius* (Šilhavý, 1974) comb. nov., *Stygnopsis apoalensis* (Goodnight y Goodnight, 1973) comb. nov., *Stygnopsis mexicana* (Roewer, 1915) comb. nov., *Stygnopsis oaxacensis* (Goodnight y Goodnight, 1973) comb. nov. y *Tonalteca spinooculorum* (Goodnight y Goodnight, 1973) comb. nov. Adicionalmente se revalidó al género *Isaeus* Sørensen, 1932 de su sinonímia bajo *Hoplobunus*.

Finalmente, *'Hoplobunus' planus* Goodnight y Goodnight, 1973 y *'Hoplobunus' zullinii* Šilhavý, 1977 se propusieron como *incertae sedis* dentro de Karosinae y Stygnopsinae respectivamente, debido a que por el momento no se conocen ejemplares masculinos de estas especies. *Mexotroglinus* resultó ser un taxón complejo, ya que comparte caracteres morfológicos de las dos subfamilias, pero de acuerdo con los análisis filogenéticos, éste se anida dentro de

Stygnopsinae, como grupo hermano de *Chinquipellobunus*, aunque esta relación no presentó soporte en el análisis de Máxima Verosimilitud.

Respecto a los genitales masculinos, utilizando técnicas de expansión de estructuras internas, se demostró que la cápsula externa en forma de un *follis* multi-lobado es la condición plesiomórfica del glande en los restantes miembros de Gonyleptoidea, con el *stylus* originándose dentro del *follis* en Stygnopsidae, y apical al glande en los restantes grupos. De igual manera, la morfología morfo-mecánica del *follis* en Stygnopsidae no es homóloga al movimiento del glande en Assamiidae, Epedanidae, Pyramidopidae y Tithaeidae, familias del sureste de Asia las cuáles presentan estructuras internas expandibles con sustancias químicas, a diferencia del *follis* rígido y expuesto en Stygnopsidae.

Mediante fotografías electrónicas de barrido, se identificaron tubérculos con aberturas glandulares en la región estigmática de los machos en los géneros *Paramitraceras*, *Philora* y *Sbordonia*, siendo la primera vez que se reportan aberturas glandulares de este tipo en Laniatores. A pesar de la exclusividad de presentar estas aberturas glandulares, estas estructuras resultaron ser convergentes dentro de Stygnopsinae, presentándose en diferentes linajes de acuerdo a los análisis filogenéticos. De igual manera, los pedipalpos desarmados (sin tubérculos setíferos espiniformes), que habían sido considerados previamente exclusivos para *Paramitraceras*, en realidad son convergentes, al igual que las aberturas glandulares dentro de éste género polifilético.

Respecto a la diversidad de Stygnopsidae, en diversos catálogos y listados se consideró que ésta estaba compuesta por nueve géneros y 36 especies. Con los datos generados en el presente proyecto de investigación, (ver Cruz-López y Francke 2012, 2013a, b, 2015, 2016a, b, 2017) la composición taxonómica de la familia consiste es de 21 géneros y 57 especies, en su mayoría endémicos para México.

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