

Taxonomy and systematics

Taxonomic revision of four terrestrial isopods (Crustacea: Oniscidea) from Mexico

Revisión taxonómica de cuatro isópodos terrestres (Crustacea: Oniscidea) de México

Ilse E. Segura-Zarzosa ^{a, b}, Hortencia Obregón-Barboza ^c, Gopal Murugan ^c,
Christopher B. Boyko ^{d, e}, Gabino A. Rodríguez-Almaraz ^a, Humberto García-Velazco ^f,
Alejandro M. Maeda-Martínez ^{c, *}

^a Universidad Autónoma de Nuevo León, Facultad de Ciencias Biológicas, Avenida Universidad s/n, Ciudad Universitaria, 66455 San Nicolás de los Garza, Nuevo León, Mexico

^b Universidad Juárez del Estado de Durango, Facultad de Ciencias Biológicas, Centro de Estudios Ecológicos, Avenida Universidad s/n, Fraccionamiento Filadelfia, 35010 Gómez Palacio, Durango, Mexico

^c Centro de Investigaciones Biológicas del Noroeste, S.C., Calle IPN 195, 23096 La Paz, Baja California Sur, Mexico

^d American Museum of Natural History, Division of Invertebrate Zoology, Central Park West @79th St., New York, NY 10024, USA

^e Hofstra University, Department of Biology, 114 Hofstra University, Hempstead, NY 11549, USA

^f Unidad de Educación Media Superior Tecnológica Agropecuaria y Ciencias del Mar, CBTA-198, kilómetro 25.5 carretera Ensenada - La Paz, 22790 Ensenada, Baja California, Mexico

*Corresponding author: almaeda04@cibnor.mx (A.M. Maeda-Martínez)

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Abstract

As part of a research project on the taxonomy of the woodlice (Oniscidea) of northern Mexico, isopod collections of Mexican academic institutions were examined. For the first time, the main diagnostic morphological traits of 4 native species are documented using SEM micrographs: *Alloniscus mirabilis* (Stuxberg, 1875) (Alloniscidae) and *Littorophiloscia richardsonae* (Holmes & Gay, 1909) (Halophilosciidae) from the northern Pacific coast of Baja California, *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) (Armadillidae) from northern central Durango, which is also the first record of this species in Mexico, and *Porcellio virgatus* (Budde-Lund, 1885) (Porcellionidae) from the northeastern states of Nuevo León and Tamaulipas. The first 2 COI haplotypes (mtDNA) for *P. virgatus* are reported. Bayesian phylogenetic analysis of COI haplotypes placed *P. virgatus* in a clade with a *Porcellio dilatatus* haplotype with high support, forming a group with *Porcellio scaber*.

Keywords: Alloniscidae; Armadillidae; Halophilosciidae; Porcellionidae; Systematics; Taxonomy

Resumen

Como parte de un proyecto de investigación sobre taxonomía de las cochinillas (Oniscidea) del norte de México se revisaron colecciones de isópodos en instituciones académicas mexicanas. En este trabajo presentamos una relación taxonómica de 4 especies nativas del norte de México y se documentan por primera vez sus características diagnósticas morfológicas principales con microfografías de MEB: *Alloniscus mirabilis* (Stuxberg, 1875) (Alloniscidae) y *Littorophiloscia richardsonae* (Holmes y Gay, 1909) (Halophilosciidae) de la costa norte del Pacífico de Baja California, *Venezillo apacheus* (Mulaik en Mulaik y Mulaik, 1942) (Armadillidae) de Durango, lo cual representa el primer registro de la especie en México, y *Porcellio virgatus* (Budde-Lund, 1885) (Porcellionidae) de los estados norteños de Nuevo León y Tamaulipas. Reportamos los primeros haplotipos de COI (ADNmt) para *P. virgatus*. El análisis filogenético Bayesiano de haplotipos COI colocó a *P. virgatus* en un clado con *Porcellio dilatatus* con alto soporte formando un grupo con *Porcellio scaber*.

Palabras clave: Alloniscidae; Armadillidae; Halophilosciidae; Porcellionidae; Sistemática; Taxonomía

Introduction

The Oniscidea (Crustacea: Isopoda) from Mexico have received little attention (Souza-Kury, 2000). The last taxonomic revision of terrestrial isopods from this country was published 64 years ago by Mulaik (1960). Jass and Klausmeier (2004) concluded that 86 oniscidean species belonging to 33 genera and 16 families have been recorded in Mexico; 10 of them are considered as exotic species (Garthwaite & Sassaman, 1985; Garthwaite et al., 1995; Mulaik, 1960; Rodríguez-Almaraz et al., 2014; Segura-Zarzosa et al., 2020; Souza-Kury, 2000; Treviño-Flores & Rodríguez-Almaraz, 2012). For the northern part of Mexico (including the states of Aguascalientes, Baja California, Baja California Sur, Chihuahua, Coahuila, Durango, Guanajuato, Jalisco, Nayarit, Nuevo León, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, and Zacatecas) 7 exotic species and only 28 native species have been recorded in this region (Jass & Klausmeier, 2004; Rodríguez-Almaraz et al., 2014; Segura-Zarzosa et al., 2020, 2022). Surprisingly, states with large geographic areas like Chihuahua, Durango, Guanajuato and Zacatecas do not have any native species registered (Jass & Klausmeier, 2004). As part of a research project on the taxonomy of the oniscideans of northern Mexico, we examined 258 isopod collection lots deposited in 4 academic institutions, from which 11 species, belonging to 8 genera and 5 families, were identified. Out of 1,820 specimens, 1,417 belong to 6 exotic species (see Segura-Zarzosa et al., 2020), and 160 specimens belong to 5 native species. The remaining 243 specimens are still under study. The first native species reported from this study, *Venezillo stuckchensis* (Mulaik, 1960), is endemic to the Baja California Peninsula, and was already redescribed (Segura-Zarzosa et al., 2022). In the present work we give a taxonomic account of 4 native species: *Alloniscus mirabilis* (Stuxberg, 1875) (Alloniscidae) and *Littorophiloscia richardsonae* (Holmes

& Gay, 1909) (Halophilosciidae) from the northern Pacific coast of Baja California, and *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) (Armadillidae) from Durango, which represents the first record of the species in Mexico. After examination and analysis of molecular data and morphological characteristics, we agree with Schultz's (1975, 1977, 1982) placement of *Porcellionides virgatus* (Budde-Lund, 1885) in the genus *Porcellio* Latreille, 1804. Thus, we report the fourth species, *Porcellio virgatus* (Budde-Lund, 1885) (Porcellionidae) from the northeastern states of Nuevo León and Tamaulipas with its first 2 identified COI haplotypes (mtDNA).

Materials and methods

The material examined is deposited in 2 scientific collections housed in the Facultad de Ciencias Biológicas, Universidad Juárez del Estado de Durango (UJED), Gómez Palacio, Durango, and Centro de Investigaciones Biológicas del Noroeste, S.C. (CIB), La Paz, Baja California Sur. Only adult specimens were examined and sorted by morphotypes according to the general shape of the cephalothorax, second antennae, pereon, pleon, uropods and pleotelson. Specimens of each morphotype were differentiated as males and females based on sexual dimorphism (Schmidt, 2002). Specimens were examined with a stereomicroscope and a digital caliper (Mitutoyo 700-113, Kawasaki, Japan) was used to record their total lengths (TL). The identity of the material examined was established following morphological descriptions published by Stuxberg (1875), Budde-Lund (1885), Holmes and Gay (1909), Van Name (1936, 1942), Mulaik and Mulaik (1942), Mulaik (1960), Schultz (1975, 1984), and Taiti and Ferrara (1986). The type material of *Venezillo apacheus* deposited in the Division of Invertebrates, American Museum of Natural History (AMNH) was also examined. Representative specimens of each species

were prepared for SEM examination. They were dissected and dehydrated individually in 100% ethanol baths for 24 h and critical-point dried (Samdri-PVT-3B, Tousimis, Rockville, MD, USA), sputter coated with gold (desk II, Denton Vacuum, Moorestown, NJ, USA), and analyzed with a scanning electron microscope (Hitachi S-300N), at CIB.

The classification and order of the families follow Ah Yong et al. (2011). The assignation of the species to their respective genera and families follows Schmalzfuss and Wolf-Schwenninger (2002), Schmalzfuss (2003) and Schmidt and Leistikow (2004). As we mentioned above, we agree with Schultz's (1975) placement of *Porcellionides virgatus* in the genus *Porcellio*. Citations of authorship for species described in Mulaik and Mulaik (1942) are given as "Mulaik in Mulaik and Mulaik, 1942", rather than "Mulaik and Mulaik, 1942" as is usually seen in publications (e.g., Schmalzfuss, 2003; Schultz, 1965). This is because all species in the 1942 paper are listed as being described by "Mulaik" alone, although with no indication of which Mulaik (Stanley or Dorothea) should be so credited.

The taxonomic account includes: name, author, and year of description of the family, genus, species, species synonymy (restricted to Mexican material, except for *V. apacheus* and *P. virgatus* where a complete synonymy is provided), diagnosis, and a taxonomic summary including the type locality, distribution in Mexico, general distribution, material examined, and remarks on the material examined. The diagnoses of the species are mainly based on the publications of several authors, which are indicated in each corresponding species account, and are updated according to morphological variations found in the material examined. Types of habitus are based on the eco-morphological categories proposed by Schmalzfuss (1984). For each species we present their main diagnostic morphological traits using SEM micrographs. The anatomical terminology used in this work is according to Schmidt (2002, 2003). The section of examined material is organized by state, site, geographical coordinates, collection date, collector's name, number of males and females examined (with TL range, mean \pm 1 sd, between brackets), and catalog code.

Attempts to obtain DNA from specimens of *A. mirabilis*, *L. richardsonae*, and *P. virgatus* were carried out, but useful genetic material was obtained only from specimens of the latter species, from 2 different localities. Genomic DNA was isolated from pereopods using the Genra Puregene kit (Qiagen). Fragments of COI were amplified with primers 22F (modified primer of LCO1490) (CAA CAA ATC ATA AAG ATA TTG GAA C) and HCO2198 by adopting the cycling conditions of Tizol-

Table 1

GenBank accession number and origin of COI sequences of Porcellionidae species used in the genetic distance and phylogenetic analyses.

Species	GenBank	Origin
<i>Porcellio virgatus</i> (Tamaulipas)	OK376217	Mexico
<i>P. virgatus</i> (Nuevo León)	OK376218	Mexico
<i>P. dilatatus</i>	KJ814238	Brazil
<i>P. scaber</i>	LC126629	Japan
<i>P. scaber</i>	MF748307	Canada
<i>P. scaber</i>	LC126628	Japan
<i>P. spinicornis</i>	MF748236	Canada
<i>P. laevis</i>	FN824121	Italy
<i>P. laevis</i>	MN689275	Mexico
<i>P. laevis</i>	KJ814239	Brazil
<i>Porcellionides pruinosus</i>	EU364627	Australia
<i>P. pruinosus</i>	MN689284	Mexico
<i>P. pruinosus</i>	MW449533	Egypt
<i>P. myrmecophilus</i>	FN824129	Italy
<i>P. myrmecophilus</i>	FN824131	Italy

Correa et al. (2009). The sequences were edited in DNA Baser 4.5 (www.dnabaser.com) and aligned in Clustal X (Thompson et al., 1997). Genetic distances (uncorrected *p*-distance) between the 2 *P. virgatus* sequences and also among the sequences of the porcellionids used in this study (Table 1) were determined in MEGA X (Kumar et al., 2018). The best nucleotide substitution model determined in jModeltest 2.1.10 (Darriba et al., 2012; Guindon & Gascuel, 2003) was used in the Bayesian phylogenetic analysis with MrBayes v3.2 (Ronquist et al., 2012). COI sequences of other species of Porcellionidae were obtained from GenBank (Table 1). The phylogenetic analysis was run for 10 million generations and a consensus tree was generated after eliminating 0.25 of the trees generated during the analysis. The consensus tree was viewed using the program FigTree v1.4.3.

Results

Descriptions

Order Isopoda Latreille, 1817

Suborder Oniscidea Latreille, 1802

Alloniscidae Schmidt, 2003

Alloniscus Dana, 1854

Alloniscus mirabilis (Stuxberg, 1875)

(Fig. 1A-N)

Rhinoryctes mirabilis Stuxberg, 1875, 51-55 (original description).

Alloniscus mirabilis (Stuxberg, 1875).- Schultz, 1984, 155-160; Schmalfuss, 2003, 10; Jass and Klausmeier, 2004, 4, 6, 18.

For a more comprehensive synonymy see Schultz (1984).

Diagnosis. Habitus type runner. Pleon not narrower than pereon. Dorsal surface covered by small tubercles with triangular setae or scales (Fig. 1A, B, M, N). Cephalothorax approximately 1.3 times as wide as long (Fig. 1A, B); frontal shield (lamina frontalis) with medial prominent quadrangular process (Fig. 1B, D); lateral lobes large and conical (Fig. 1B, D). Compound eyes on sides of cephalothorax, each with 17-20 ommatidia (Fig. 1B, C). First antennae 3-jointed, distal article with subapical and apical aesthetascs, basal article longest and broadest (Fig. 1E). Second antennae not reaching pereon-tergite 3 (Fig. 1A), first article short, second approximately 2 times as long as first (Fig. 1A, D), third and fourth subequal, each a little longer than second, fifth approximately 1.5 times longer than fourth (Fig. 1A, F); flagellum 3-jointed, first article little longer than second, third article lanceolate with apical cone, approximately 1.5 times longer than second; complete flagellum approximately 1.2 times longer than fifth article (Fig. 1F, G). Pereon with pereon-tergite 1 approximately 1.5 longer than rest, which are subequal in size (Fig. 1A), proximal-lateral angles produced forward to surround cephalothorax (Fig. 1A, D) up to anterior margin of compound eyes (Fig. 1A, C), pereon-tergites 1-3 with rounded posterolateral margins, pereon-tergites 4-7 produced posteriorly (Fig. 1A), pereopod 1 with transversal antennal brush composed of groove covered by fringed scales on anterior (frontal) side of carpus (Fig. 1H, I), pereopods 1-3 of male with brush of long setae on ventral side of carpus and merus (Fig. 1H), pereopod 7 with pattern of setae similar in males and females (Fig. 1J). Pleon with pleon-tergites 1 and 2 with lateral parts undeveloped, covered at sides by pereon-tergite 7, pleon-tergites 3-5 broadly expanded laterally, lateral margins forming continuous line with lateral margins of pereon-tergites (Fig. 1K, M), pleopod 1 endopodite (copulatory appendage) elongated with tip slightly divergent (Fig. 1K). Pleotelson (pleon-tergite 6) triangular, of same length or shorter than posterior margins of pleon-tergite 5 (Fig. 1M, N), uropod sympodites with wide lobed posterolateral margins, endopodites inserted in internal margin of sympodites bearing group of long setae on apex, exopodites lanceolate (Fig. 1L, N). Sources: Stuxberg (1875) and Schultz (1984).

Taxonomic summary

Type locality. San Pedro, Los Angeles, California, USA (Schultz, 1984; Stuxberg, 1875).

Distribution in Mexico. Only in northwestern Mexico on the Pacific coast of Baja California Sur in Bahía Magdalena, and in Baja California in Isla Cedros (Schultz, 1984), and Bahía San Quintín (this study).

General distribution. From Pacific Grove, Monterey, California, USA in the north, to Bahía Magdalena, Baja California Sur, Mexico in the south (Jass & Klausmeier, 2004; Schultz, 1984).

Material examined. Bahía Falsa, San Quintín, Baja California, Mexico (30°27'14.34" N, 116°00'06.50" W), on a sand beach, 02-12-2006, coll. A. Maeda, 1 male (8.8 mm), 5 females (8.1-9.7, \bar{x} 8.8 \pm 0.63 s.d. mm TL) (CIB-41B).

Remarks

As reported by Stuxberg (1875) for the *A. mirabilis* type specimens from California, the color of the dorsal side of alcohol-fixed specimens examined exhibited a light brown color with a dorsal medial dark line and lateral light and dark spots. Schultz (1984) reported *A. mirabilis* from Oxnard, California with 12-13 ommatidia, while our specimens have 17-20 ommatidia.

Armadillidae Brandt in Brandt and Ratzeburg, 1831

Venezillo Verhoeff, 1928

Venezillo apacheus (Mulaik, 1942 in Mulaik & Mulaik, 1942)

(Figs. 2-8)

Cubaris apacheus Mulaik, 1942 in Mulaik and Mulaik, 1942, 8-9 (original description).

Cubaris apachea Mulaik, 1942.- Van Name, 1942, 313.

Cubaris apacheus Mulaik, 1941 [sic].- Mulaik and Mulaik, 1943, 9.

Venezillo (Venezillo) apacheus (Mul.).- Arcangeli, 1957, 119.

Cubaris apacheus Mulaik and Mulaik, 1942.- Boyko, 1997, 7-8.

Venezillo apacheus (Mulaik, 1942).- Leistikow and Wägele, 1999, 46.

Venezillo apacheus (Mulaik & Mulaik, 1942).- Schmalfuss, 2003, 285.

Diagnosis. Habitus type endoantennal conglobator (Fig. 2A, B). Color pale yellowish (alcohol preserved specimens). Dorsal surface with scales and tricorn process inserted in diverse positions (Figs. 2E, F; 3E; 7E, F). Cephalothorax approximately 1/3 longer than

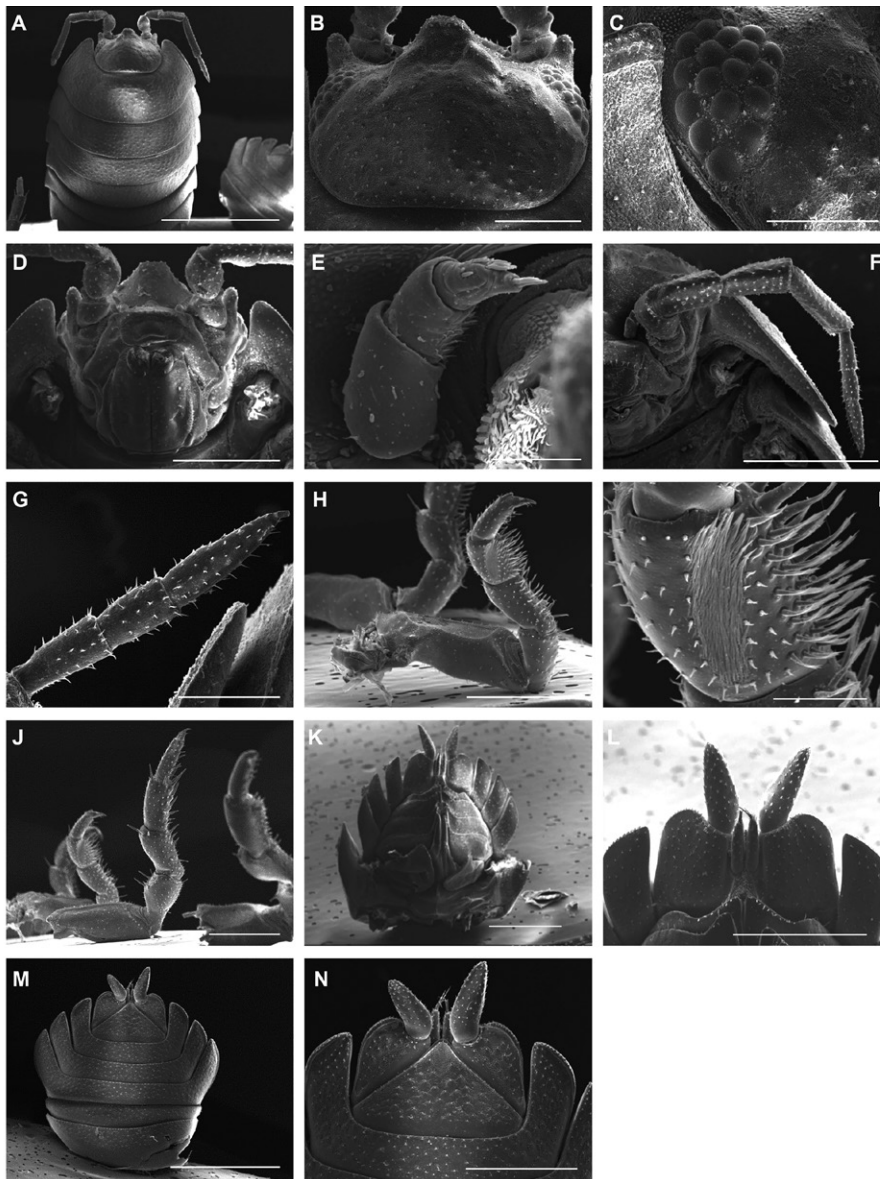


Figure 1. SEM micrographs of adult male *Alloniscus mirabilis* (Stuxberg, 1875) from Bahía Falsa, San Quintín, Baja California, Mexico. A, Cephalothorax, second antenna and pereon-tergites in dorsal view; B, cephalothorax in dorsal view; C, left compound eye with ommatidia in lateral view; D, cephalothorax in anteroventral view; E, left first antenna in lateral view; F, left second antenna in ventral view; G, flagellum of left second antenna in ventral view; H, left pereopod 1 in medial view; I, carpal brush of left pereopod 1 in medial view; J, left pereopod 7 in medial view (central appendage in the micrograph); K, pleopods 1-5, endopodites (copulatory appendages) of pleopods 1, uropod sympodites with endopodites and exopodites; L, uropod sympodites with endopodites and exopodites in ventral view; M, pleon-tergites 1-5, triangular pleotelson and uropod sympodites with exopodites in dorsal view; N, pleon-tergite 5, and triangular pleotelson with uropod sympodites and exopodites in dorsal view. Scale bars: A = 3 mm; B = 500 μ m; C, G = 300 μ m; D, F, H, J, K, L, N = 1 mm; E = 100 μ m; I = 200 μ m; M = 2 mm.

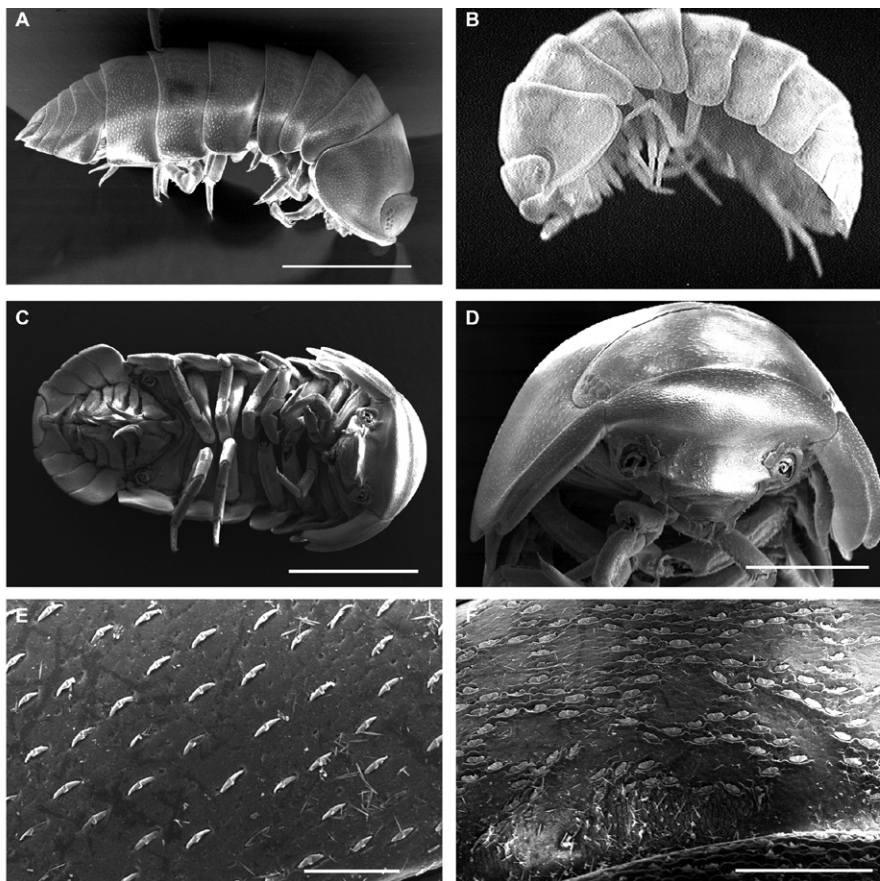


Figure 2. Adults of *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) from Gómez Palacio, Durango, Mexico. A, C-F are SEM micrographs; B is a stereo light microscope micrograph. A, Habitus of male in right lateral view; B, habitus of female in left lateral view; C, habitus of male in ventral view; D, cephalothorax and pereon-tergite 1 of male in right anterolateral view; E, external surface of frontal shield of male covered by semi-curved scales with scattered tricorn scales; F, external surface of vertex of cephalothorax of male covered by semi-curved scales with scattered tricorn scales. Scale bars: A-C = 2 mm; D = 1 mm; E = 100 μ m; F = 200 μ m.

wide (Fig. 2A-D); frontal shield (lamina frontalis) with proximal lateral antennal lobes for holding proximal portion of second antenna during conglobation (Fig. 2D), posterior margin expanded, remaining a groove behind frontal shield (Figs. 2B, D; 3A). Compound eyes on sides of cephalothorax, each with 8-9 ommatidia in 2 rows (Fig. 3A-D). First antenna 3-jointed with 13 aesthetascs on distal article (Figs. 2F; 4A), basal article wide and subequal in length as terminal one (Fig. 3A). Second antennae with first article short, second approximately 2 times as long as first, third subequal to second, fourth 1.5 times longer than third, fifth approximately 1.3-1.5 times longer than fourth (Fig. 4B); flagellum 2-jointed, distal article lanceolate, 3 times longer than first, complete flagellum approximately 2/3 of fifth antennal article

(Fig. 4B, C). Right and left mandibles with similar pars incisive, lacinia mobilis, and pars molaris (Fig. 5A-D); lateral side of mandibles covered by semi-curved scales with some acute scales (Fig. 5B), pars incisive with 3 round projections, central one largest (Fig. 5C), lacinia mobilis with basal setose lobe (Fig. 5D); second maxilla membranous, laminate, inner lobe smaller, covered by abundant short setae, outer lobe wide, rounded, covered by pubescence; maxilliped palp with 3 articles (Fig. 5E, F). Pereon with pereon-tergite 1 with notch (schisma) along epimeron (Fig. 6A) into which anterior corner of pereon-tergite 2 epimeron fits when animal conglobates; pereon-tergite 2 with large digitiform lobe on anterior ventral side (Fig. 6B); pereon-tergites 3-5 with rounded epimeron (Fig. 2A, B); pereopod 1 with antennal brush

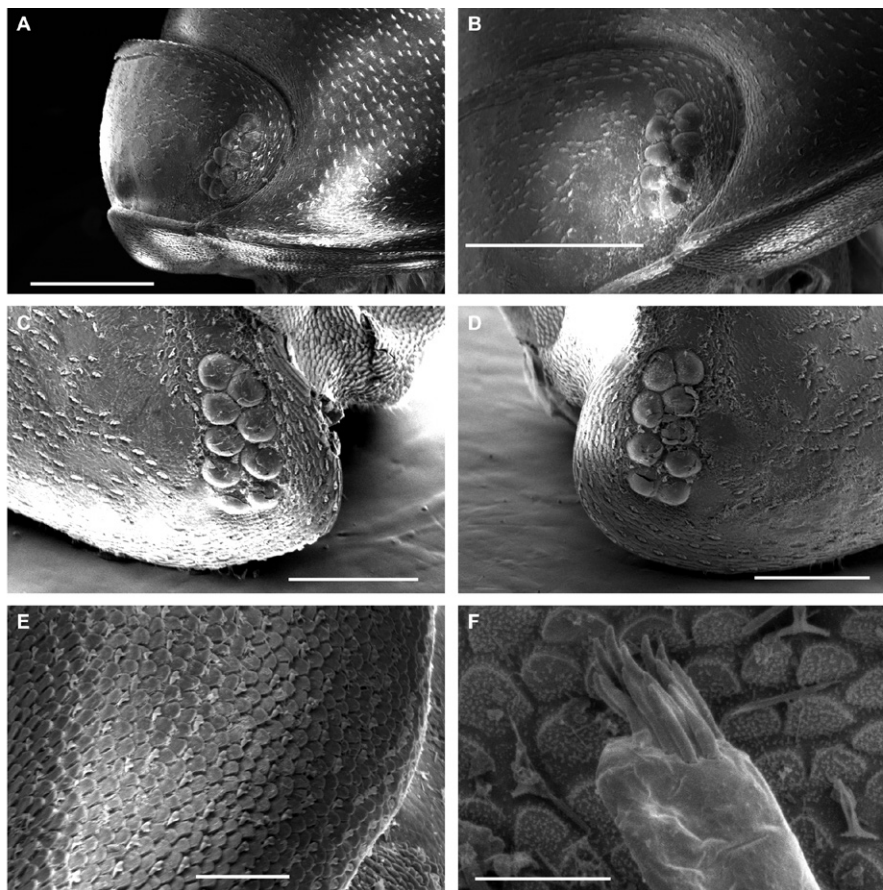


Figure 3. SEM micrographs of adult *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) from Gómez Palacio, Durango, Mexico. A, Cephalothorax and pereon-tergite 1 of male in lateral view showing ommatidia of the complex eye; B, left complex eye of male in anterolateral view showing ommatidia; C, right eye of female in lateral view showing ommatidia; D, left eye of female in lateral view; E, frontal shield of male in dorsal view covered with semicircular scales and tricorn scales; F, third article of right first antenna of male with aesthetascs. Scale bars: A, B = 500 μm ; C, D, F = 300 μm ; E = 100 μm .

composed of groove covered by transversal scales on anterior (frontal) side of carpus, inner side of merus, carpus and propodus with spines; sternite 7 with medial process apically bilobate, covering proximal portion of genital papilla (Fig. 6E, F). Pleon with pleon-tergites (pleon-segments) 1-2 with lateral parts undeveloped and covered at sides by pereon-tergite 7 (Fig. 2A, B); pleon-tergites 3-5 broadly expanded laterally, lateral margins forming continuous line with lateral margins of pereon-tergites (Fig. 2A, B); male genital papilla with lanceolate ventral shield (Fig. 6F); pleopod 1 endopodite (copulatory appendage) elongated with acute apex (Fig. 7A). Pleotelson wide at base, becoming constricted approximately at 3/4 of length, then expanding to truncate caudal margin, dorsomedial surface slightly raised, some specimens with line (somewhat keeled) (Fig. 7A-C); uropod sympodites

(uropod protopodites) enlarged and flattened (Fig. 7C), filling space between caudal side of pleon-tergites 5 and lateral side of pleotelson (Fig. 7C, D), exopodites conical and small, inserted on notch in medial margin of sympodites (Fig. 7C, D), endopodites oblong, flat, covered by scales and setae, base covered by basal plate of uropodal sympodite (Fig. 8A-D). Sources: Mulaik in Mulaik and Mulaik (1942) and Van Name (1942).

Taxonomic summary

Type locality. Alice, Brooks County, Texas, USA (Mulaik in Mulaik & Mulaik, 1942).

Type material examined. Holotype male (AMNH 17515) and allotype female (AMNH 17516) with the original label: “*Cubaris apacheus* M&M, Alice, Brooks Co., Texas, Dec 1939 S-D Mulaik.” Holotype (damaged),

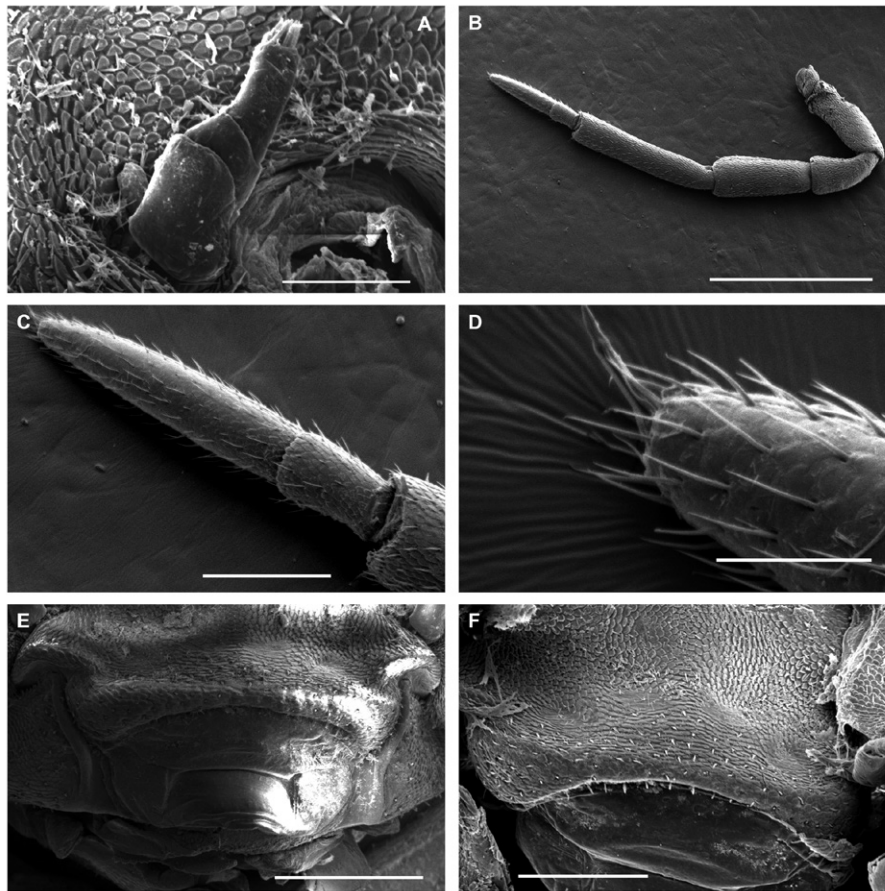


Figure 4. SEM micrographs of adult *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) from Gómez Palacio, Durango, Mexico. A, Left first antenna of male in lateral view; B, right second antenna of female in dorsal view; C, flagellum of right second antenna of female in dorsal view; D, apex of distal article of flagellum of right second antenna of female in dorsal view; E, labrum and clypeus of male in anteroventral view; F, clypeus and frontal shield of female in anterior view. Scale bars: A = 100 μm ; B = 500 μm ; C = 200 μm ; D = 50 μm ; E, F = 300 μm .

ca. 7 mm TL, allotype (partially conglobated), ca. 5 mm TL. Paratypes (AMNH 17517) with the original label: “*Cubaris apacheus* M&M, Alice, Brooks Co., Texas, Dec 1939 S-D Mulaik.” 12 specimens intact, partly conglobated, mixture of males and females (ca. 4.5-6.5 mm TL), and fragments of 5 specimens.

Mexican material examined. Gómez Palacio, Durango, Mexico, 23-06-1994, coll. A. Bedolla, 1 male (7.0 mm TL), 2 females (7.6-9.7 mm TL) from the garden of a house (UJED-09).

Distribution in Mexico. Known only from Gómez Palacio, Durango. This is the first record of the species in Mexico, and the first record of a native oniscidean species in the state of Durango.

General distribution. Known from Alice, Kerville, Laredo (Mulaik in Mulaik & Mulaik, 1942), and Jim Wells County (Mulaik & Mulaik, 1943), Texas, USA, and Durango, Mexico.

Remarks

The type material examined fits well the description published by Mulaik in Mulaik and Mulaik (1942). The only difference noted between the type material and the Mexican specimens is that the fifth article of the second antenna is approximately 1.3 times longer than the fourth article in the type specimens, while in the Mexican specimens it is approximately 1.5 times longer than the fourth article (Fig. 4B). According to Mulaik in Mulaik

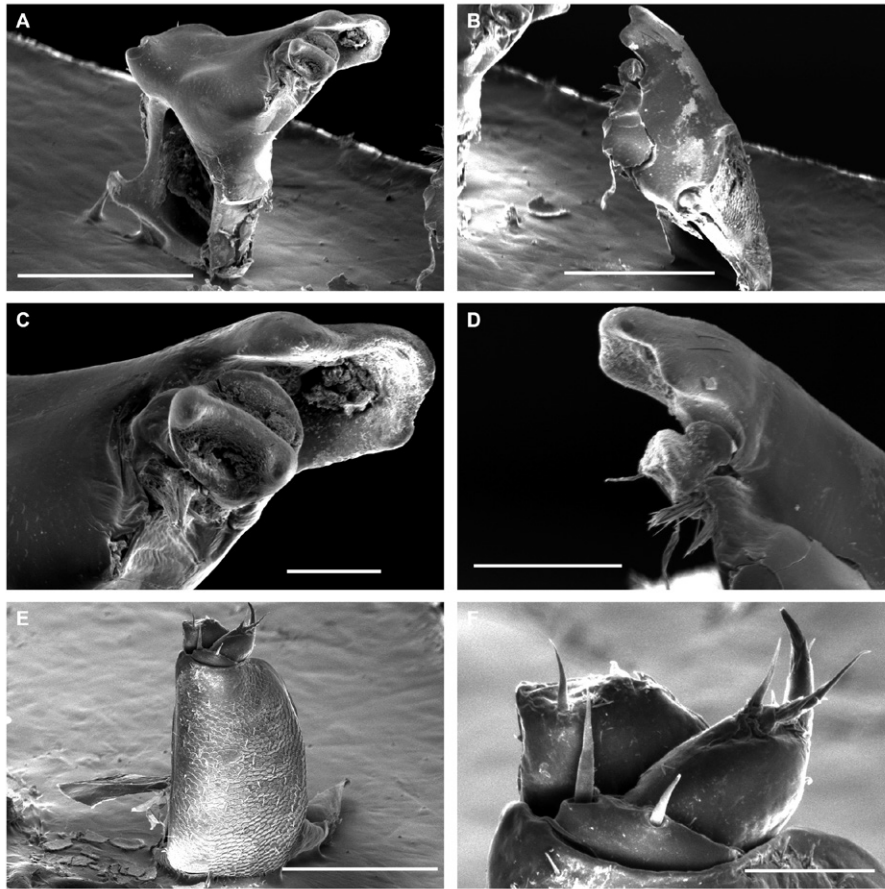


Figure 5. SEM micrographs of female *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) from Gómez Palacio, Durango, Mexico. A, Left mandible in posterior view; B, left mandible in anterior view; C, pars incisus and lacinia mobilis of left mandible, from A; D, pars incisus, lacinia mobilis, and pars molaris of left mandible, from B; E, left maxilliped in anteroventral view; F, left maxilliped palp with 3 articles in anteroventral view. Scale bars: A, B, E = 500 μ m; C, F = 100 μ m; D = 200 μ m.

and Mulaik (1942) the most similar species to *V. apacheus* is *V. chamberlini* (Mulaik in Mulaik & Mulaik, 1942), a oniscidean from Edinburg, Hidalgo County, Texas, USA, that can be differentiated by having 6 ommatidia, pleon-tergite 5 posterior margins visible in dorsal view, and the inner border of the epimeral schisma not visible in lateral view.

Halophilosciidae Verhoeff, 1908 (cf. Schmidt, 2003; Schmidt & Leistikow, 2004)

Littorophiloscia Hatch, 1947

Littorophiloscia richardsonae (Holmes & Gay, 1909)

(Fig. 9A-N)

Philoscia richardsonae Holmes and Gay, 1909, 378-379 (original description).

Philoscia richardsonae Holmes and Gay, 1909.- Mulaik, 1960, 158.

Littorophiloscia richardsonae (Holmes & Gay, 1909).- Leistikow and Wägele, 1999, 18; Souza-Kury, 2000, 245; Schmalzfuss, 2003, 133; Jass and Klausmeier, 2004, 3, 10; Taiti and Ferrara, 1986, 1350-1354.

For a more comprehensive synonymy see Taiti and Ferrara (1986).

Diagnosis. Habitus type runner (Fig. 9A). Pleon abruptly narrower than pereon. Color brownish with spots on dorsal and ventral sides of body, pereon-tergites with 3 longitudinal dark lines, 1 medial and 2 lateral. Dorsal surface with short minute scale-spines, margins with line of small spines (Fig. 9B). Cephalothorax 2 times as wide as long (Fig. 9B), vertex convex (Fig. 9D), frontal shield

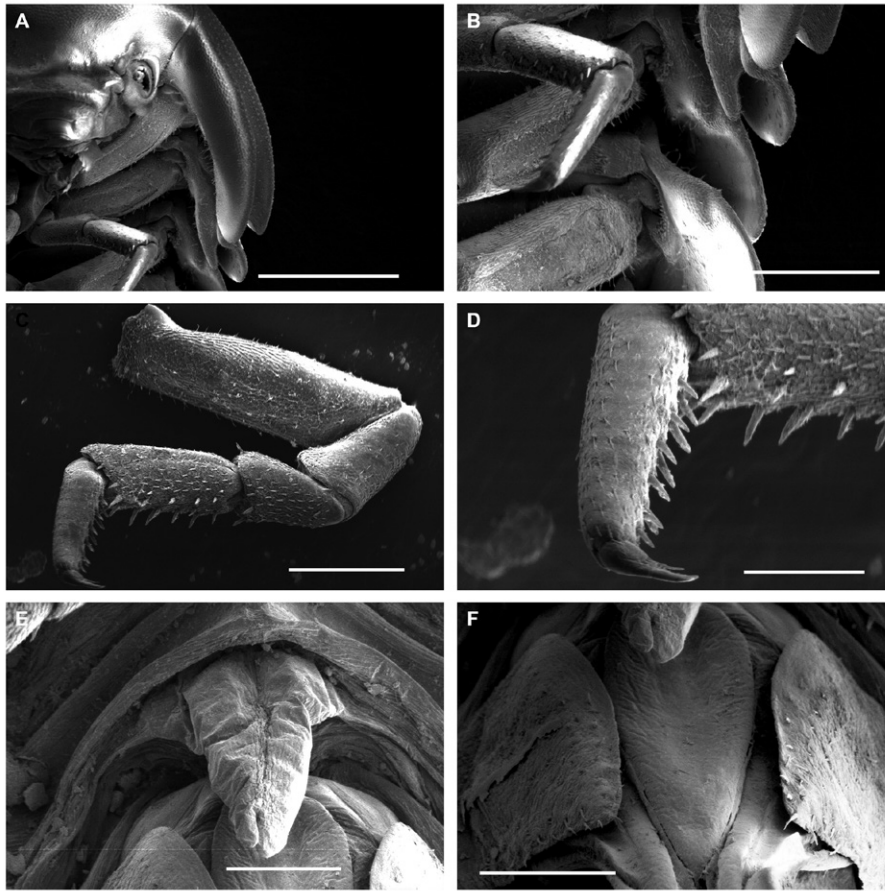


Figure 6. SEM micrographs of male *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) from Gómez Palacio, Durango, Mexico. A, Cephalothorax and pereon-tergite 1 with notch (schisma) along epimeron, pereon-tergite 2 with large digitiform lobe on anterior ventral side; B, lateral margins of pereon-tergites 1-4, and left pereopod 2 in ventral view; C, left pereopod 1 in anterior view; D, propodus and dactylus of left pereopod 1 in anterior view; E, sternite 7 with medial bilobate process covering proximal portion of genital papilla in posteroventral view; F, genital papilla with lanceolate ventral shield in posteroventral view. Scale bars: A = 1 mm; B, C = 500 μ m; D-F = 200 μ m.

prominent, rounded with posteromedial border concave (supra-antennal line) (Fig. 9D), lateral lobes small, subtriangular (Fig. 9B). Compound eyes at anterolateral sides of cephalothorax, each with 12-15 ommatidia (Fig. 9C). First antennae 3-jointed with aesthetascs on distal article, basal article longest, broadest (Fig. 9E). Second antennae long, approximately 1/2 of total length, first article short, second and third 2 times as long as first, fourth 2 times longer than third, fifth 1.5 times longer than fourth (Fig. 9F); flagellum 3-jointed, first and third articles subequal, slightly longer than second (Fig. 9G). Pereon with pereon-tergite 1 broadest (Fig. 9A), pereon-tergites 3-7 with rectangular lateral borders, pereopod 1 antennal brush with transversal scales on anterior (frontal)

side of carpus (Fig. 9H, I). Pleon with pleon-tergites 3-5 posterolateral margins strongly produced and curved backwards, margins with line of small scale-spines (Fig. 9J, M); male pleopod 1 endopodite (copulatory appendage) elongated with acute apex (Fig. 9J); pleopods 1-5 with triangular exopodites (Fig. 9J). Pleotelson triangular with rounded tip and concave lateral borders, margins with line of small scale-spines (Fig. 9M, N); uropod sympodites as long as wide, complete structure of endopodites approximately 2/3 as long as exopodites, in dorsal view endopodites approximately 1/3 as long as exopodites, with long apical setae, inserted in sympodites before exopodites, exopodites long, subconical, lateral margin nearly straight, medial margin somewhat convex

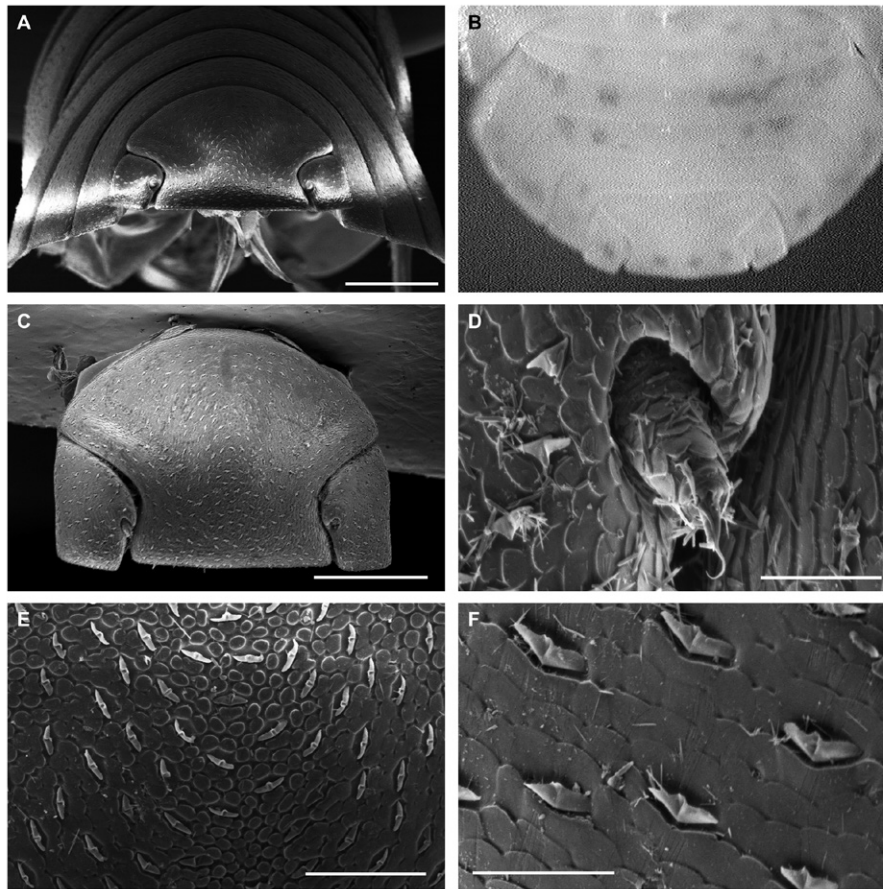


Figure 7. Adults of *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) from Gómez Palacio, Durango, Mexico. A, C, D-F are SEM micrographs; B, is a stereo light microscope micrograph. A, Pleon-tergites 3-5, pleotelson and uropod sympodites of male in posterior view; B, pleon-tergites 1-5, pleotelson and uropod sympodites of male in posterodorsal view; C, pleotelson and uropod sympodites with exopodites of female in posterior view; D, left uropod exopodite in sympodite from C; E, dorsal surface of female pleotelson; F, dorsal surface of pleotelson with semicircular scales and tricorn scales from E. Scale bars: A, C = 500 μ m; D = 300 μ m; E = 100 μ m; F = 50 μ m.

(Fig. 9J, L). Sources: Holmes and Gay (1909), Van Name (1936) and Taiti and Ferrara (1986).

Taxonomic summary

Type locality. San Diego, California, USA (Holmes & Gay, 1909).

Material examined. Bahía Falsa, San Quintín, Baja California (30°27'14.34" N, 116°00'06.50" W), on a sand beach, 02-12-2006, coll. A. Maeda, 8 males (4.8-8.3 mm, \bar{x} 6.9 \pm 1.02 s.d. mm TL), 10 females (4.7-8.0 mm, \bar{x} 6.6 \pm 0.94 s.d. mm TL) (CIB-42B).

Distribution in Mexico. Isla Cedros, Baja California (Mulaik, 1960; Taiti & Ferrara, 1986), and Bahía Falsa, San Quintín, Baja California, a new locality record for the species.

General distribution. From northwestern Mexico to Vancouver Island, Canada (Garthwaite et al., 1985; Schmalfuss, 2003; Taiti & Ferrara, 1986).

Remarks

Taiti and Ferrara (1986) reviewed *Littorophiloscia* and recognized 15 species, 2 of them recorded in Mexico: *L. richardsonae* from Baja California and *L. tropicalis* Taiti and Ferrara, 1986 from Yucatán. Taiti and Ferrara (1986) reported specimens of *L. richardsonae* up to 7 mm of length with 12 or 13 ommatidia and pereopod 1 with an antennal brush with transversal scales on the anterior (frontal) side of the carpus and propodus; our examined specimens have a mean TL of 6.9 mm for males, 6.6 mm for females, the number of ommatidia varied from

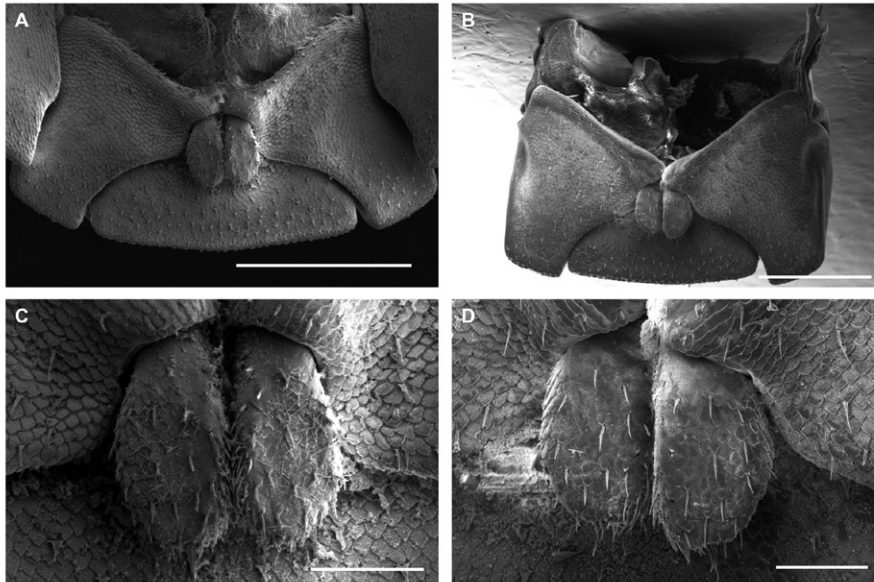


Figure 8. SEM micrographs of adults of *Venezillo apacheus* (Mulaik in Mulaik & Mulaik, 1942) from Gómez Palacio, Durango, Mexico. A, Pleotelson and uropod sympodites with endopodites of male in ventral view; B, pleotelson and uropod sympodites with endopodites of female in ventral view; C, uropod endopodites of male in ventral view; D, uropod endopodites of female in ventral view. Scale bars: A, B = 500 μm ; C, D = 100 μm .

13 to 15, and the antennal brush is only on the carpus (Fig. 9H, I).

Porcellionidae Brandt in Brandt and Ratzeburg, 1831

Porcellio Latreille, 1804

Porcellio virgatus (Budde-Lund, 1885)

(Fig. 10A-L)

Metoponorthus virgatus Budde-Lund, 1879, 4 (*nomen nudum*).

Metoponorthus virgatus Budde-Lund, 1885, 182 (original description).

Metoponorthus virgatus Budde-Lund, 1885.- Richardson, 1905, 630; Mulaik, 1960, 174.

Porcellionides virgatus (Budde-Lund, 1885).- Van Name, 1936, 241; 1940, 137; 1942, 327; Mulaik and Mulaik, 1942, 7; 1943, 7; Leistikow and Wägele, 1999, 36; Souza-Kury, 2000, 245; Jass and Klausmeier, 2004, 5.

Porcellionides mulaiki Van Name, 1936, 522.- Van Name, 1940, 137.

Porcellio virgatus (Budde-Lund, 1885).- Schultz, 1975, 185-193; 1977, 152; 1982, 2, 5, 6, 20-21.

“*Porcellionides*” *virgatus* (Budde-Lund, 1885).- Schmalfuss, 2003: 214.

Diagnosis. Habitus type runner. Color brown, mottled with light spots, 2 light lateral and 1 medial lines. Body surface with small tubercles and rounded tricorn scales

(Fig. 10A, B, D, L). Cephalothorax approximately 2 times as wide as long (Fig. 10B), vertex with convex medial part (Fig. 10B), frontal shield with small rounded lateral lobes (Fig. 10B), posterior frontal line forming slightly medial convex margin (Fig. 10B, D), supra antennal line V-shaped absent (Fig. 10D). Compound eyes each with 19-30 ommatidia (Fig. 10C). First antennae 3-jointed; basal article longest and broadest, second short, third with subapical and apical aesthetascs (Fig. 10F). Second antennae with first article short, second 2 times as long as first, third subequal to second, fourth 1.5 times longer than third, fifth approximately 1.5 times longer than fourth (Fig. 10G); flagellum 2-jointed, proximal article shorter or subequal to distal article, distal article lanceolate with apical cone (Fig. 10H). Maxilliped palp with 3 articles (Fig. 10E). Pereon-tergites 1-7 with a well marked dorsal transverse furrow (Fig. 10A); pereon tergite 1 with projected anterolateral sides not reaching cephalothorax anterior margin, 1.5 times longer than pereon-tergites 2-7 (Fig. 10A); sternite 7 without medial process (Fig. 10I). Pleon not abruptly narrower than pereon (Fig. 10K); pleon-tergites with acute lateral margins posteriorly directed (Fig. 10K); male pleopod 1 endopodites (copulatory appendages) lanceolate (Fig. 10I); pleopods 2-5 with exopodites semi-quadrangular (Fig. 10I). Pleotelson triangular with rounded tip (Fig. 10K, L); uropod

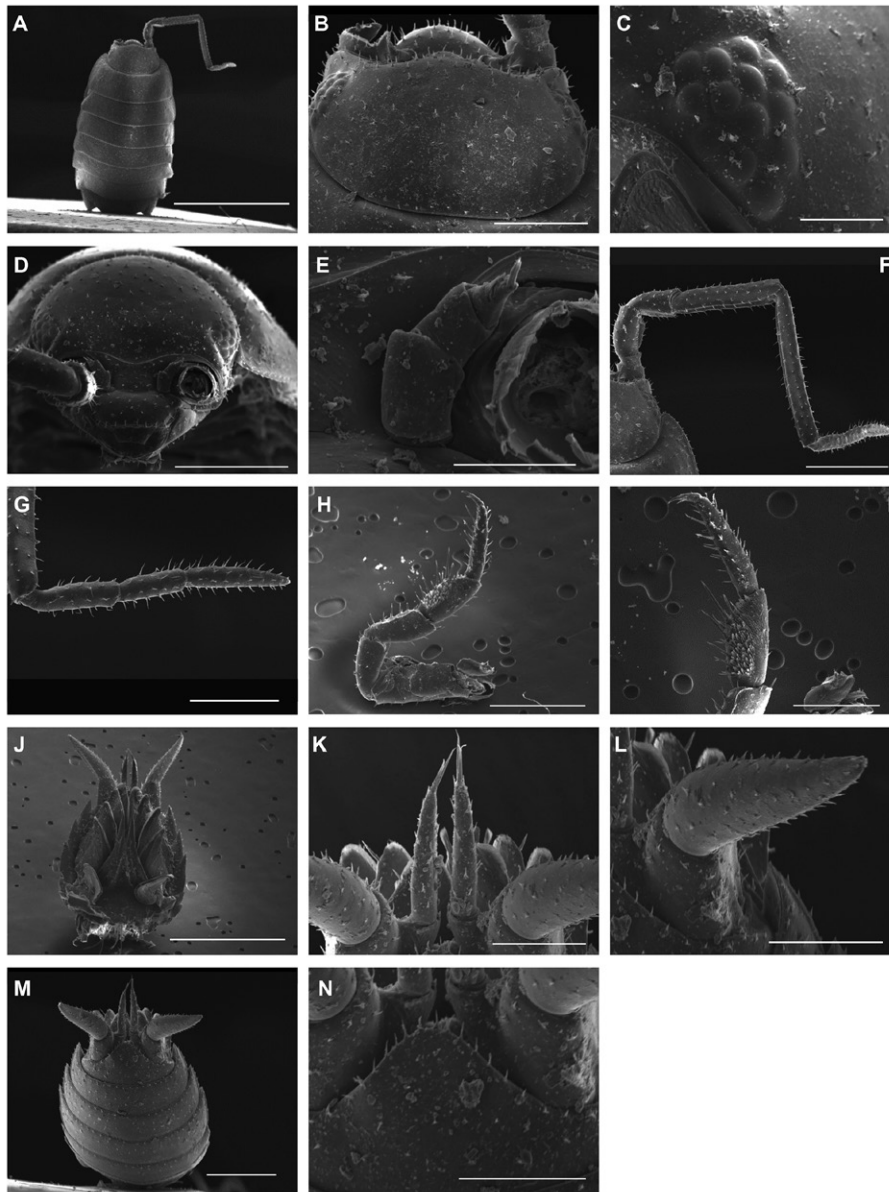


Figure 9. SEM micrographs of male *Littorophiloscia richardsonae* (Holmes & Gay, 1909) from Bahía Falsa, San Quintín, Baja California, Mexico. A, Cephalothorax with right antenna and pereon-tergites 1-6 in dorsal view; B, cephalothorax in dorsal view; C, left compound eye with ommatidia in anterolateral view; D, cephalothorax in anterior view (left second antenna removed); E, left first antenna in anterior view; F, right second antenna in dorsal view; G, flagellum of right second antenna in dorsal view; H, right pereopod 1 in medial view; I, carpus with brush, protopod and dactyl of pereopod 1 in medial view (from H); J, pleon-tergites 1-5 with pleopods, copulative appendages of pleopod endopodites, uropods sympodites with endopodites and exopodites in ventral view; K, endopodites of uropod sympodites in ventral view; L, right uropod sympodite with exopodite in posteroventral view; M, pleon-tergites 2-5, triangular pleotelson and uropod sympodites with endopodites and exopodites in posterdorsal view; N, triangular pleotelson in dorsal view. Scale bars: A = 2 mm; B, G, I = 300 μ m; C, E = 100 μ m; D, F, H, L, M = 500 μ m; J = 1 mm; K, N = 200 μ m.

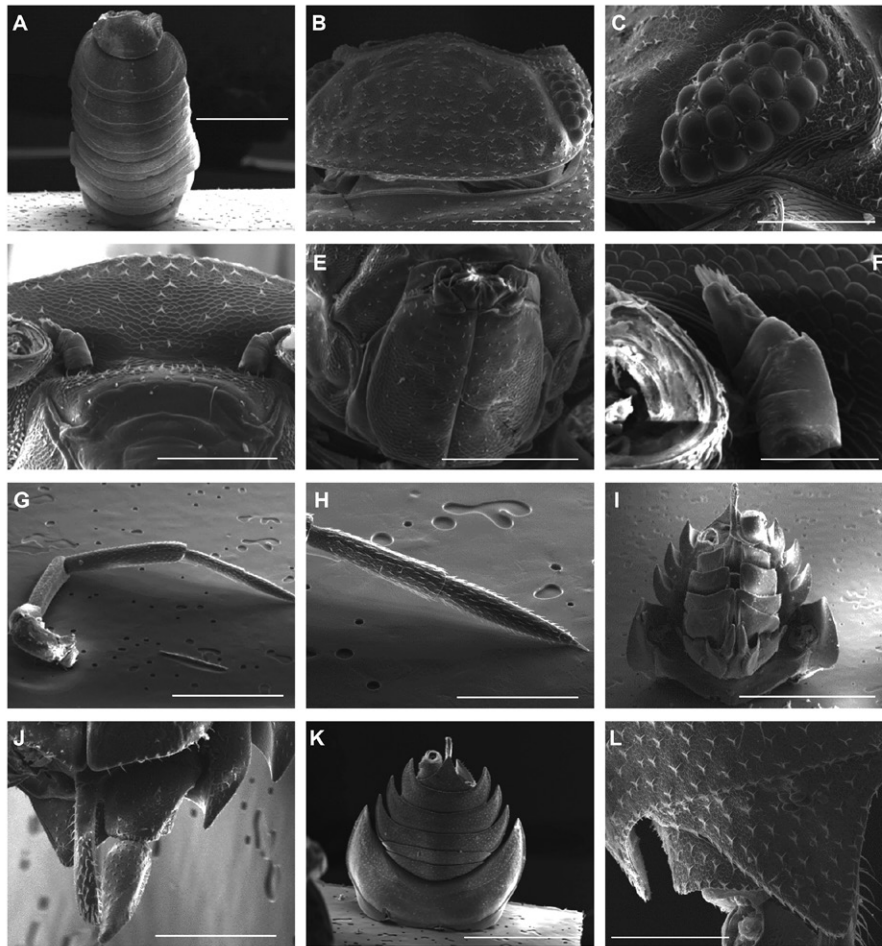


Figure 10. SEM micrographs of male *Porcellio virgatus* (Budde-Lund, 1885) from San José, Gómez Farías, Tamaulipas, Mexico. A, Cephalothorax and pereon-tergites 1-7 in dorsal view; B, cephalothorax in dorsal view; C, right compound eye in dorsal view; D, cephalothorax, first antennae, clypeus, and labrum in ventral view; E, maxillipeds in ventral view; F, left first antenna with aesthetascs in ventral view; G, second antenna in medial view; H, flagellum of second antenna in medial view; I, posterior part of body showing pereon-tergite 7, pleon-tergites 3-5, and pleopods 1-5 in ventral view; J, left uropod with sympodite, endopodite, and exopodite in ventral view; K, posterior part of body showing pereon-tergite 7, pleon-tergites 1-5, and pleotelson in dorsal view; L, pleon-tergite 5, and triangular pleotelson in dorsal view. Scale bars: A, I, K = 2 mm; B, E, H, J = 500 μ m; C = 200 μ m; D, L = 300 μ m; F = 100 μ m; G = 1 mm.

sympodites twice as long as wide, as long as exopodites, endopodites thin, lightly flattened, reaching tip of exopodites, exopodites subconical (Fig. 10J). Sources: Budde-Lund (1885), Richardson (1905), Van Name (1936), Mulaik (1960), and Schultz (1982).

Taxonomic summary

Type locality. New Orleans and Florida, USA (Budde-Lund, 1885).

Material examined. Nuevo León: Cola de Caballo, Santiago (25°26'12.18" N, 100°09'12.68" W), under stones,

06-05-2006, coll. A. Maeda, 2 females (5.4-6.8 mm) (CIB-49B); Parque Chipinque, Km 2, San Pedro Garza García (25°36'38.1" N, 100°21'20.8" W), under stones, 06-05-2006, coll. A. Maeda, 1 male (11.0 mm) (CIB-30B1). Tamaulipas: San José, Gómez Farías (23°05'23.1" N, 99°06'40.1" W), natural zone below stones, 30-07-2006, coll. A. Maeda, 3 males (6.8-9.6 mm, mean 7.9 ± 1.21 s.d. mm TL), 2 females (7.5-7.6 mm) (CIB-09B).

Haplotypic identity. COI haplotypes were obtained from a specimen from Chipinque, Nuevo León (GenBank accession number OK376218), and a specimen from San

José, Tamaulipas (GenBank accession number OK376217). The genetic distance between these haplotypes is 2.5% (Table 2). Prior to this study there was no record of DNA sequences for *Porcellionides virgatus*/*Porcellio virgatus* in GenBank. The Bayesian analysis placed these haplotypes in a well supported clade within the genus

Porcellio with high support rather than with species in the genus *Porcellionides* (Fig. 11).

Distribution in Mexico. Santiago and San Pedro Garza García, Nuevo León, and San José, Tamaulipas. Mulaik (1960) reported *Porcellio virgatus* (as *Porcellionides virgatus*) from Villagrán, Tamaulipas, and Tepic, Nayarit.

Table 2

Genetic *p*-distance (%) among COI sequences (623 bp) of Porcellionidae species used in the phylogenetic analysis.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 <i>Porcellio virgatus</i> Tamaulipas																	
2 <i>P. virgatus</i> Nuevo León	2.57																
3 <i>P. dilatatus</i> KJ814238	17.17	17.34															
4 <i>P. scaber</i> LC126629	15.57	15.57	16.69														
5 <i>P. scaber</i> MF748307	16.21	16.21	17.01	2.89													
6 <i>P. scaber</i> LC126628	16.53	16.53	16.85	2.57	1.93												
7 <i>P. spinicornis</i> MF748236	18.14	18.30	20.55	17.34	17.66	18.14											
8 <i>P. laevis</i> FN824121	17.66	17.82	18.78	18.62	18.62	19.10	15.25										
9 <i>P. laevis</i> MN689275	19.26	19.10	19.74	18.78	18.78	19.42	18.62	13.00									
10 <i>P. laevis</i> KJ814239	19.58	19.42	20.55	19.26	19.26	19.90	18.94	13.16	3.21								
11 <i>Porcellionides pruinus</i> EU364627	19.42	19.74	21.67	18.62	18.62	18.30	18.30	15.89	16.05	16.05							
12 <i>P. pruinus</i> MN689284	19.58	19.90	21.51	18.46	18.46	18.14	18.14	15.73	15.89	15.89	0.16						
13 <i>P. pruinus</i> MW449533	19.74	20.06	21.35	18.30	18.30	17.98	17.98	15.57	16.05	16.05	0.32	0.16					
14 <i>P. myrmecophilus</i> FN824129	21.03	20.87	21.35	19.10	18.30	18.78	18.62	18.30	18.78	18.62	17.50	17.34	17.17				
15 <i>P. myrmecophilus</i> FN824131	21.19	21.03	21.51	19.26	18.46	18.94	18.78	18.46	18.94	18.78	17.66	17.50	17.34	0.16			
16 <i>Periclimenes rathbunae</i> KX090114	23.49	24.14	23.82	23.33	23.33	23.65	21.21	22.02	19.90	21.86	22.02	22.19	22.35	21.04	21.21		
17 <i>P. imperator</i> GQ415636*	22.79	22.63	22.47	20.87	21.35	21.51	22.63	21.03	20.06	21.35	22.47	22.63	22.79	21.51	21.67	15.82	

* *Periclimenes imperator* = *Zenopontonia rex* (DecaNet eds., 2024).

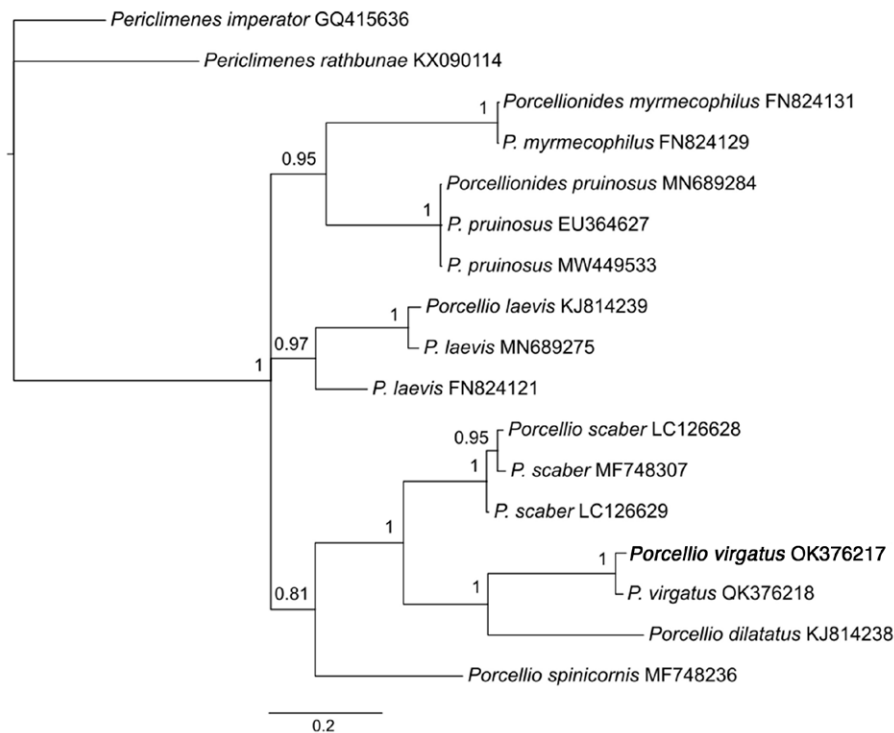


Figure 11. Bayesian consensus tree of phylogenetic relationships of *Porcellio virgatus* (Budde-Lund, 1885) COI haplotypes from Nuevo León and Tamaulipas, Mexico, with selected GenBank haplotypes of *Porcellionides* and *Porcellio* species. GenBank sequences of palaemonids *Periclimenes imperator* Bruce, 1967 (= *Zenopontonia rex* [Kemp, 1922]) (DecaNet eds., 2024), and *Periclimenes rathbunae* Schmitt, 1924 were used as outgroup.

General distribution. Budde-Lund (1885), Van Name (1936), Mulaik and Mulaik (1942, 1943), and Mulaik (1960) reported the species (as *Porcellionides virgatus*) from the USA in Florida, Louisiana, Mississippi and Texas. Schultz (1982) reported *Porcellio virgatus* from North Carolina and Georgia, USA.

Remarks

The species has been cited as belonging to *Metoponorthus* Budde-Lund, 1879 (Mulaik, 1960; Richardson, 1905), and to *Porcellionides* (the senior synonym, see Schmalzfuss & Ferrara, 1978) (Jass & Klausmeier, 2004; Leistikow & Wägele, 1999; Souza-Kury, 2000; Van Name, 1936, 1940, 1942). Schmalzfuss (2003) listed it as "*Porcellionides*" *virgatus*, indicating that the species does not belong to this genus. Schultz (1975, 1977, 1982) was the first carcinologist to recognize the species as *Porcellio virgatus* from Georgia and North Carolina, USA. The morphological similarity between *Porcellio* and *Porcellionides* has been, to date, an issue in recognizing them as separate genera (Dimitriou et al., 2018; Mattern, 2003; Mulaik, 1960; Schmalzfuss &

Ferrara, 1978; Van Name, 1936). Dimitriou et al. (2018) analysed 2 mitochondrial and 3 nuclear genes and found evidence against the monophyly of both *Porcellionidae* and *Porcellio*. The genetic distances they found were considerably high between *Porcellionidae* genera; e.g. for COI the variation was between 16.9-50.3% (Dimitriou et al., 2018). Mattern (2003) applied small subunit rRNA analyses to study the molecular phylogeny of Oniscidea and found that the genera *Porcellio* and *Porcellionides* are not monophyletic groups. He reported that *Porcellio scaber* Latreille, 1804 is more closely related to *Porcellionides sexfaciatus* Budde-Lund, 1885 than to *Porcellio spinicornis* Say, 1818, the latter branching as the sister group of *Porcellionides pruinus* (Brandt, 1833). However, considering Mattern's (2003: Fig. 2) molecular phylogenies, it can be concluded that *Porcellio scaber* and *Porcellionides pruinus* represent 2 different lineages. Herein, we report the first COI haplotypes of the species obtained from specimens from Tamaulipas and Nuevo León. Our molecular analysis is not intended as a revision of the phylogenetic systematics of the group but rather to provide the first information on the molecular identity

and the generic placement of these species. The results showed that the genetic distance of our haplotypes is larger when compared with haplotypes of *Porcellionides* (19.40 to 21.19%) than with haplotypes of *Porcellio* (15.57 to 19.58%) (Table 2). Besides, the Bayesian analysis placed our haplotypes in a clade with a specimen of *Porcellio dilatatus* Brandt in Brandt and Ratzeburg, 1831 haplotype with high nodal support, forming a group with *Porcellio scaber* (Fig. 11). Our specimens fit the diagnostic morphological features of the genus *Porcellio* proposed by Schmalzfuss and Ferrara (1978): 2 pairs of pseudotracheae, unable to conglobate, pereon tergite 1 with caudally concave epimera, eyes with more than 20 ommatidia. The typical supra antennal line V-shape showed by most species of *Porcellionides* (Schmalzfuss & Ferrara, 1978) is absent in our specimens (Fig. 10D) and in specimens examined by Van Name (1936, Fig. 135). Our specimens have the pereon-tergites 1-7 with a well marked dorsal transverse furrow (Fig. 10A), as figured for *Porcellionides virgatus* by Van Name (1936, Fig. 135). Mulaik (1960) recorded specimens of *P. virgatus* from Nayarit and Tamaulipas with 21 ommatidia and 10 mm TL. The specimens examined herein have 6.8-11.00 mm TL for males and 5.4-7.6 mm TL for females, with 19-30 ommatidia. The molecular data and morphological characteristics mentioned support Schultz's assignation of the species as *Porcellio virgatus*.

Discussion

According to Schultz (1984), 3 *Alloniscus* species are recognized in North America, *A. perconvexus* Dana, 1854, known from Laguna Beach, California, USA to Vancouver Island, British Columbia, Canada; *A. mirabilis* recorded from Magdalena Bay, Mexico to the Pacific Grove, California; and *A. thalassophilus* Rioja, 1963 known from Isla de Ixtapan, Zihuatanejo, Guerrero, Mexico. The presence of *Alloniscus* in Mexico was first recorded by Mulaik (1960) who reported *A. perconvexus* based on specimens from Bahía Magdalena, Baja California Sur, and Isla Cedros and Bahía San Quintín, Baja California. Schultz (1984) mentioned that *A. mirabilis* and *A. perconvexus* are similar species, but can be separated by the uropod sympodite which is larger in *A. mirabilis* resulting in a broadened, extended posterolateral margin (Schultz, 1984, Fig. 3B, H) (Fig. 1L-N), and by the cephalothorax anterolateral lobes, which are well developed and extending far beyond the eyes in *A. mirabilis* (Schultz, 1984, Fig. 3D, E) (Fig. 1B, D), but small and well defined in *A. perconvexus* (Schultz, 1984, Fig. 1D). Schultz (1984) argued that Mulaik's (1960) *A. perconvexus* illustrations actually represented

A. mirabilis. We disagree with Schultz's (1984) statement because the uropod sympodite illustrated by Mulaik (1960, Fig. 175) shows a straight posterolateral margin typical of *A. perconvexus* as also figured by Schultz (1984, Fig. 2B), while *A. mirabilis* has a wide-lobed posterolateral margin (Schultz, 1984, Fig. 3B, H) (Fig. 1L-N). Thus, we agree with Jass and Klausmeier (2004) that these 2 species are native to the northwest Mexican Pacific coast. As with all Mexican oniscideans, the populations of these similar species deserve more detailed morphological and genetic studies, including examination of material from their type localities.

The record of *V. apacheus*, formerly known only from Texas, USA, increases the number of species of *Venezillo* in Mexico from 18 (Jass & Klausmeier, 2004; Schmalzfuss, 2003) to 19. *Venezillo tanneri* (Mulaik in Mulaik & Mulaik, 1942) also has been recorded in both USA (Texas) and Mexico (Nuevo León) (Mulaik & Mulaik, 1942; Schultz, 1965). In the southern USA *Venezillo arizonicus* (Mulaik in Mulaik & Mulaik, 1942) has also been recorded from Robles, Nogales, Olberg and Rock Springs, Arizona, and *V. chamberlini* (Mulaik in Mulaik & Mulaik, 1942) from Edinburg, Texas; both species are likely also inhabiting northern Mexico (Mulaik, 1960).

The genus *Littorophiloscia* is not well known in Mexico. Taiti and Ferrara (1986) recognized the presence of *L. richardsonae* from Baja California and *L. tropicalis* Taiti and Ferrara, 1986 from the Yucatán. In this study, *L. richardsonae* was recorded as co-occurring with *A. mirabilis* on a sand beach of Bahía Falsa in San Quintín, Baja California, sharing a habitat under marine macroalgae.

In Mexico, the genus *Porcellio* is now represented by the exotic *P. laevis* and *P. scaber*, and the putative natives *P. scabriusculus* Mulaik, 1960 (Jass & Klausmeier, 2004; Schmalzfuss, 2003; Segura-Zarzosa et al., 2020), and *P. virgatus* (this study). Mulaik (1960) described and figured *P. scabriusculus* as very different from *P. virgatus*, with 9 ommatidia and spinous tubercles on the dorsal side of the cephalothorax, pereon tergites, and pleon tergites (except the pleotelson). Schmalzfuss (2003) suggested that *P. scabriusculus* is probably not a member of the genus *Porcellio*. Mulaik (1960) mentioned his decision to keep *Porcellionides saussurei* (Dollfus, 1896) (a species known from Córdoba, and San Luis Potosí, Mexico) in this genus until the *Porcellio-Porcellionides* complex is clarified. As mentioned above, these morphologically similar genera are not monophyletic groups (Dimitriou et al., 2018; Mattern, 2003) and delimiting them is an important unsolved problem that limits the understanding of the systematics of the species involved.

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References

- Ahyong, S. T., Lowry, J. K., Alonso, M., Bamber, R. N., Boxshall, G. A., Castro, P. et al. (2011). Subphylum Crustacea Brünnich, 1772. In Z. Q. Zhang (Ed.), *Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness*. *Zootaxa*, 3148, 165–191. <http://dx.doi.org/10.11646/zootaxa.3148.1.33>
- Arcangeli, A. (1957). I generi *Diploexochus*, *Venezillo*, *Paramardillo* [sic] (crostacei isopodi terrestri). *Bollettino dell'Istituto e Museo di Zoologia dell'Università di Torino (1955-56)*, 5, 101–142.
- Boyko, C. B. (1997). Catalog of recent type specimens in the Department of Invertebrates, American Museum of Natural History. IV. Crustacea: Isopoda. *American Museum Novitates*, 3217, 1–39.
- Brandt, J. F., & Ratzeburg, J. C. T. (1831). Isopoda. Gleichfüßler. In *Medizinische Zoologie oder getreue Darstellung und Beschreibung der Thiere die in der Arzneimittellehre in Betracht kommen, in systematischer Folge herausgegeben*, 2, 70–84.
- Brandt, J. F. (1833). Conspectus monographiae crustaceorum oniscidorum Latreillii. *Bulletin de la Société Impériale des naturalistes de Moscou*, 6, 171–193.
- Bruce, A. J. (1967). Notes on some Indo-Pacific Pontoniinae III–IX. Descriptions of some new genera and species from the western Indian Ocean and the South China Sea. *Zoologische Verhandelingen*, 87, 1–73.
- Budde-Lund, G. (1879). *Prospectus generum specierumque Crustaceorum Isopodum Terrestrium*. Copenhagen. 10 pp.
- Budde-Lund, G. (1885). *Crustacea Isopoda terrestria per familias et genera et species descripta*. Copenhagen: Nielsen & Lydiche. <https://doi.org/10.5962/bhl.title.109769>
- Dana, J. (1854). Catalogue and descriptions of Crustacea collected in California by Dr. John L. LeConte. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 7, 175–177.
- Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest2: more models, new heuristics and parallel computing. *Nature Methods*, 9, 772. <https://doi.org/10.1038/nmeth.2109>
- DecaNet eds. (2024). DecaNet. *Zenopontonia rex* (Kemp, 1922). Accessed through: World Register of Marine Species. <https://www.marinespecies.org/aphia.php?p=taxdetails&id=871470>
- Dimitriou, A. C., Taiti, S., Schmalzfuss, H., & Sfenthourakis, S. (2018). A molecular phylogeny of Porcellionidae (Isopoda, Oniscoidea) reveals inconsistencies with present taxonomy. In E. Hornung, S. Taiti, & K. Szlavecz (Eds.), *Isopods in a changing World*. *Zookeys*, 801, 163–176. <https://doi.org/10.3897/zookeys.801.23566>
- Dollfus, A. (1896). Sur les Crustacés Isopodes terrestres du Mexique. *Bulletin de la Société Zoologique de France*, 21, 46–49. <https://doi.org/10.5962/bhl.part.18717>
- Garthwaite, R. L., Hochberg, F. G., & Sassaman, C. (1985). The occurrence and distribution of terrestrial isopods (Oniscoidea) on Santa Cruz Island with preliminary data for the other California islands. *Bulletin of Southern California Academy of Sciences*, 84, 23–37.
- Garthwaite, R. L., Lawson, R., & Sassaman, C. (1995). Population genetics of *Armadillidium vulgare* in Europe and North America. *Crustacean Issues*, 9, 145–199.
- Garthwaite, R., & Sassaman, C. (1985). *Porcellionides floria*, new species, from North America: provinciality in the cosmopolitan isopod *Porcellionides pruinosus* (Brandt). *Journal of Crustacean Biology*, 5, 539–555. <https://doi.org/10.2307/1547923>
- Guindon, S., & Gascuel, O. (2003). A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, 52, 696–704. <https://doi.org/10.1080/10635150390235520>
- Hatch, M. (1947). The Chelifera and Isopoda of Washington and adjacent regions. *University of Washington Publications in Biology*, 10, 155–274.
- Holmes S. J., & Gay, M. E. (1909). Four new species of isopods from the coast of California. *United Proceedings of the United States National Museum*, 36, 375–379. <https://doi.org/10.5479/si.00963801.36-1670.375>
- Jass, J., & Klausmeier, B. (2004). Terrestrial isopod (Crustacea: Isopoda) atlas for Mexico. *Milwaukee Public Museum Contributions in Biology and Geology*, 100, 1–77.
- Kemp, S. (1922). Notes on Crustacea Decapoda in the Indian Museum, XV. Pontoniinae. *Records of the Indian Museum*, 24, 113–288.
- Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: Molecular evolutionary genetics across computing platforms. *Molecular Biology and Evolution*, 35, 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Latreille, P. A. (1802). *Histoire naturelle générale et particulière, des crustacés et des insectes*. Vol. 3. F. Dufart, Paris. <https://www.biodiversitylibrary.org/page/24884921>
- Latreille, P. A. (1804). *Histoire naturelle generale et particulière, des crustacés et des insectes*. Vol. 7. F. Dufart, Paris. <https://www.biodiversitylibrary.org/page/24882991>
- Latreille, P. A. (1817). *Les crustacés, les arachnides et les insectes*. Vol. 3. *Le règne animal distribué d'après son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie compare*. Deterville, Paris.

- Leistikow, A., & Wägele, J. W. (1999). Checklist of the terrestrial isopods of the new world (Crustacea, Isopoda, Oniscidea). *Revista Brasileira de Zoologia*, 16, 1–72. <https://doi.org/10.1590/s0101-81751999000100001>
- Mattern, D. (2003). New aspects in the phylogeny of the Oniscidea inferred from molecular data. In S. Sfenthourakis, P. B. De Auraujo, E. Hornung, H. Schmalfuss, S. Taiti, & K. Szlávecz (Eds.), *The biology of terrestrial isopods V, Crustaceana Monographs*, 2 (pp. 23–37). Koninklijke Brill NV, Leiden.
- Mulaik, S. (1960). Contribución al conocimiento de los isópodos terrestres de México (Isopoda, Oniscoidea). *Revista de la Sociedad Mexicana de Historia Natural*, 21, 79–292. <https://doi.org/10.18268/bsgm2009v61n2a15>
- Mulaik, S., & Mulaik, D. (1942). New species and records of American terrestrial isopods. *Bulletin of the University of Utah*, 32, 1–11.
- Mulaik, S., & Mulaik, D. (1943). New Texas terrestrial isopods with notes on other species. *Bulletin of the University of Utah*, 34, 1–15.
- Richardson, H. (1905). A monograph on the isopods of North America. *Bulletin of the United States National Museum*, 54, 1–727. <https://doi.org/10.5479/si.03629236.54.i>
- Rioja, E. (1963) [1964]. Estudios carcinológicos XXXVI. Descripción y algunos datos morfológicos de *Alloniscus thalassophilus* n. sp. (Isopoda, Oniscidae) del piso supralitoral de las costas mexicanas del Pacífico. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México*, 34, 285–306.
- Rodríguez-Almaraz, G. A., Ortega-Vidales, V., & Treviño-Flores, J. A. (2014). Macrocrustáceos del Parque Nacional Cumbres de Monterrey, México: distribución y estado de conservación. *Revista Mexicana de Biodiversidad*, 85, 276–293. <https://doi.org/10.7550/rmb.34967v>
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S. et al. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Say, T. (1818). An account of the Crustacea of the United States (concluded). *Journal of the Academy of Natural Sciences of Philadelphia*, 1, 423–441.
- Schmalfuss, H. (1984). Eco-morphological strategies in terrestrial isopods. *Symposia of the Zoological Society of London*, 53, 49–63.
- Schmalfuss, H. (2003). World catalog of terrestrial isopods (Isopoda: Oniscidea). *Stuttgarter Beiträge zur Naturkunde, Serie A*, 654, 1–341.
- Schmalfuss, H., & Ferrara, F. (1978). Terrestrial isopods from West Africa. Part 2: Families Tylidae, Ligiidae, Trichoniscidae, Stytoniscidae, Rhyscotidae, Halophilosciidae, Philosciidae, Platyarthridae, Trachelipidae, Porcellionidae, Armadillidiidae. *Monitore Zoologico Italiano. N. S. Supplemento*, XI, 15–97. <https://doi.org/10.1080/03749444.1978.10736575>
- Schmalfuss, H., & Wolf-Schwenninger, K. (2002). A bibliography of terrestrial isopods (Crustacea: Isopoda: Oniscidea). *Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie)*, 639, 1–120. <https://doi.org/10.18476/sbna.v9.a3>
- Schmidt, C. (2002). Contribution to the phylogenetic system of the Crinocheta (Crustacea, Isopoda). Part 1. (Olibrinidae to Scyphacidae s. str.). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe*, 78, 275–352. <https://doi.org/10.1002/mmnz.4850780207>
- Schmidt, C. (2003). Contribution to the phylogenetic system of the Crinocheta (Crustacea, Isopoda). Part 2. (Oniscoidea to Armadillidiidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe*, 79, 3–179. <https://doi.org/10.1002/mmnz.20030790102>
- Schmidt, C., & Leistikow, A. (2004). Catalogue of genera of the terrestrial Isopoda (Crustacea: Isopoda: Oniscidea). *Steenstrupia*, 28, 1–118.
- Schmitt, W. L. (1924). The macruran, anomuran and stomatopod Crustacea. Bijdragen tot de kennis der fauna van Curaçao. Resultaten eener reis van Dr. C.J. van der Horst in 1920. *Bijdragen tot de Dierkunde*, 23, 61–81.
- Schultz, G. A. (1965). Terrestrial isopods from caves and mines in Texas and northern Mexico with a description of *Venezillo tanneri* (Mulaik and Mulaik) allotype. *The Texas Journal of Science*, 17, 101–109.
- Schultz, G. A. (1975). Terrestrial isopod crustaceans from coastal sites in Georgia. *Bulletin of the Georgia Academy of Science*, 34, 185–194.
- Schultz, G. A. (1977). Terrestrial isopod crustaceans (Oniscoidea) from SI. Catherines Island, Georgia. *Georgia Journal of Science*, 35, 151–158.
- Schultz, G. A. (1982). Terrestrial isopods (Crustacea: Isopoda: Oniscoidea) from North Carolina. *Brimleyana*, 8, 1–26.
- Schultz, G. A. (1984). Four species of *Alloniscus* Dana, 1854, from the west coast of North America and Hawaii (Isopoda, Oniscoidea). *Crustaceana*, 47, 149–167.
- Segura-Zarzosa, I. E., Rodríguez-Almaraz, G. A., Obregón-Barboza, H., Murugan, G., Treviño-Flores, J. A., & Maeda-Martínez, A. M. (2020). New records of exotic species of Oniscidea (Crustacea: Isopoda) from northern Mexico. *Revista Mexicana de Biodiversidad*, 91, e913098. <https://doi.org/10.22201/ib.20078706e.2020.91.3098>
- Segura-Zarzosa, I. E., Maeda-Martínez, A. M., Murugan, G., & Obregón-Barboza, H. (2022). Redescription of *Venezillo stuckchensis* (Crustacea: Oniscidea: Armadillidae), a terrestrial isopod from the Baja California Peninsula, Mexico. *Revista Mexicana de Biodiversidad*, 93, e934028. <https://doi.org/10.22201/ib.20078706e.2022.93.4028>
- Souza-Kury, L. (2000). Oniscidea. In J. E. L. Bousequets, E. G. Soriano, & N. Papavero (Eds.), *Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento, Vol. II* (pp. 239–246). Ciudad de México: Universidad Nacional Autónoma de México.
- Stuxberg, A. (1875). Om Nord-Amerikas Oniscider. *Öfversigt af kongliga Vetenskaps Akademiens Förhandlingar (Stockholm)*, 2, 43–64.
- Taiti, S., & Ferrara, F. (1986). Taxonomic revision of the genus *Littorophiloscia* Hatch, 1947 (Crustacea,

- Isopoda, Oniscidea) with description of six new species. *Journal of Natural History*, 20, 1347–1380. <https://doi.org/10.1080/00222938600770911>
- Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F., & Higgins, D. G. (1997). The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, 25, 4876–4882. <https://doi.org/10.1093/nar/25.24.4876>
- Tizol-Correa, R., Maeda-Martínez A. M., Weekers, P. H. H., Torrentera, L., & Murugan, G. (2009). Biodiversity of the brine shrimp *Artemia* from tropical salterns in southern México and Cuba. *Current Science*, 96, 81–87. <https://doi.org/10.1651/s-2691.1>
- Treviño-Flores, J. A., & Rodríguez-Almaraz, G. (2012). Primeros registros de *Porcellio laevis* y *Porcellio scaber* (Crustacea: Oniscidea) del noreste de México. In M. López-Mejía, & L. M. Mejía-Ortiz (Eds.), *La carcinología en México: el legado del Dr. Alejandro Villalobos 30 años después* (pp. 13–21). Universidad de Quintana Roo. Cozumel, Quintana Roo, Mexico.
- Van Name, W. G. (1936). The American land and freshwater isopod Crustacea. *Bulletin of the American Museum of Natural History*, LXXI, 1–535.
- Van Name, W. G. (1940). A supplement to the American land and fresh-water isopod Crustacea. *Bulletin of the American Museum of Natural History*, LXXVII, 109–142.
- Van Name, W. G. (1942). A second supplement to the American land and fresh-water isopod Crustacea. *Bulletin of the American Museum of Natural History*, LVIII, 299–329.
- Verhoeff, K. W. (1908). Über Isopoden. 12. Aufsatz. Nene oniscoidea aus Mittel und Südeuropa und zur Klärung einiger bekannter Formen. *Archiv für Naturgeschichte*, 74, 163–198.
- Verhoeff, K. W. (1928). Über einige Isopoden der Zoologischen Staatssammlung in München. *Zoologischer Anzeiger*, 76, 25–36, 113–123.