



## Two new genera and one new species of freshwater crabs of the subfamily Pseudothelphusinae (Decapoda: Brachyura: Pseudothelphusidae) from southwestern Mexico

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### Abstract

Two new genera from the Chimalapas region in eastern Oaxaca, and from Zongolica, Veracruz, Mexico are presented. *Mokayathelphusa angelsotoi* n. gen., n. sp., which is described from Oaxaca, is placed in the subfamily Pseudothelphusinae due to the presence of a caudomarginal projection that ends apically in an ornamented plate. *Alvarezius* n. gen. is erected to accommodate *A. zongolicae* (Alvarez, Villalobos & Moreno, 2012) n. comb. This species was described in *Pseudothelphusa*, but a recent molecular phylogenetic analysis based on partial sequences of three genes (COI, 16S and H3) places this species outside the genus *Pseudothelphusa* and as a sister lineage to *Tehuana*. These results in combination with a morphological analysis support the establishment of the new genus.

**Key words:** freshwater crabs, taxonomy, *Mokayathelphusa*, *Alvarezius*, Neotropical region

### Introduction

The diversity of freshwater crabs in Mexico is noteworthy at a continental scale (Villalobos *et al.* 1993; Alvarez *et al.* 2014; Cumberlidge *et al.* 2014). In particular, the family Pseudothelphusidae is richly represented by 68 species, second only to Colombia, with 109 species (Alvarez *et al.* 2020; Campos & Campos, 2020; Moreno-Juárez *et al.*, 2022). The diversity of pseudothelphusids in Mexico is also significant at higher taxonomic levels, being represented by three subfamilies: Potamocarcininae (1 genus, 3 species), Raddausinae (10 genera, 23 species) and Pseudothelphusinae (6 genera, 42 species) (Villalobos-Hiriart *et al.* 2019; Alvarez *et al.* 2020). The distribution areas of these subfamilies overlap in southern Mexico in the region known as the Isthmus of Tehuantepec (Alvarez *et al.* 2020), creating one the most taxa rich areas in the whole distribution range of the family (Fig. 1).

In this paper we describe *Mokayathelphusa angelsotoi* n. gen., n. sp., from the Chimalapas region, Isthmus of Tehuantepec, in Oaxaca, a place with a complex geological history where three tectonic plates are in contact, and where Central American lineages intermingle with lineages from Central Mexico (González 1976; Ferrusquía-Villafranca 1999; Padilla & Sánchez 2007). Although zoogeographically important, this region remains poorly explored for freshwater crabs, a situation that is evident by the regular discovery of new genera and species in the region (Moreno-Juárez *et al.* 2022). In addition, we introduce *Alvarezius* n. gen. to accommodate *Pseudothelphusa zongolicae* Alvarez, Villalobos & Moreno, 2012 after a molecular analysis based on partial sequences of three genes (COI, 16S and H3) of several species in the subfamily Pseudothelphusinae which places it as a sister lineage to *Tehuana* Rodríguez and Smalley in Smalley, 1970.

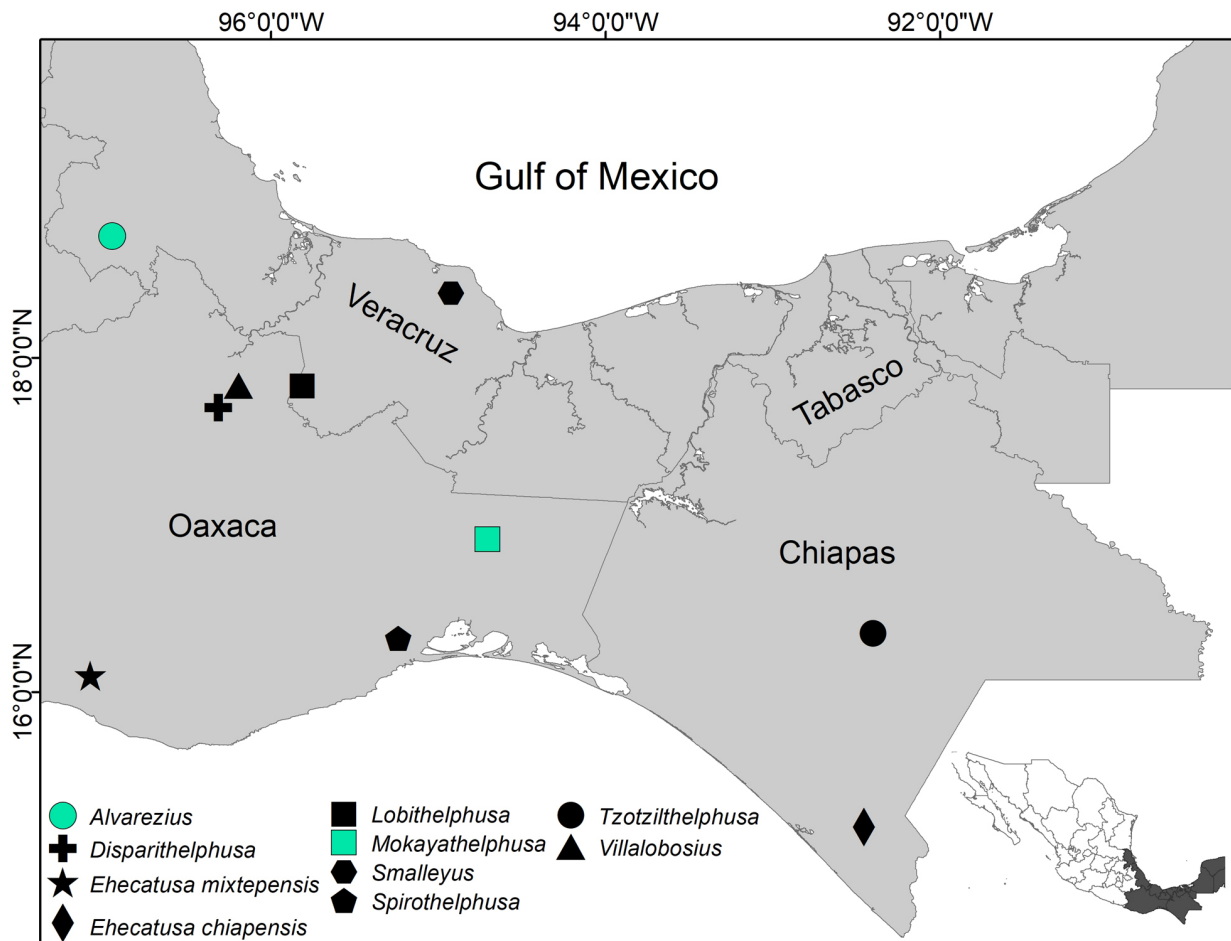


FIGURE 1. Distribution of monotypic genera in Mexico, subfamilies Pseudothelphusinae and Raddausinae.

## Material and methods

All specimens studied are deposited in the Colección Nacional de Crustáceos (CNCR), Instituto de Biología, Universidad Nacional Autónoma de México (IB-UNAM), in Mexico City. For each species, adult male specimens were selected for the taxonomic work. The left male G1 was dissected and photographed with a Leica DFC490 camera adapted to a Leica Z16 APOA microscope, at the Laboratorio de Microscopía y Fotografía de la Biodiversidad, IB-UNAM. The Leica Application Suite (LAS) software was used to finish the photographs. The male gonopod description follows the terminology proposed by Villalobos & Alvarez (2010). Some general abbreviations used here are: carapace length (CL), carapace width (CW), above sea level (asl).

**DNA extraction, amplification and sequencing.** Muscle tissue was dissected from the fifth pereopods and preserved in 70% ethanol. DNA purification was performed with the Animal and fungi DNA preparation kit<sup>®</sup> from Jena Bioscience<sup>®</sup>, following the manufacturer's protocol. DNA concentration was measured with a NanoDrop 2000<sup>®</sup> spectrophotometer. The polymerase chain reaction (PCR) was performed with the MyTaq Kit<sup>®</sup> from Bioline<sup>®</sup>, following the manufacturer's protocol. Three molecular markers were amplified: COI (dgLCO 5'-GGT CAA CAA ATC ATA AAG AYA TYG G-3'; dgHCO 5'-TAA ACT TCA GGG TGA CCAAAR AAY CA -3'; Meyer 2003); 16S (16Sa 5'-ACT TGA TAT ATA ATT AAA GGG CCG-3'; 16Sb 5'-CTG GCG CCG CTC TGA ACT CAA ATC-3'; Palumbi & Benzie 1991) and H3 (H3AF 5'-ATG GCT CGT ACC AAG CAG ACV GC-3, H3AR 5'-ATA TCC TTR GGC ATR ATR GTG AC-3'; Colgan *et al.* 1998). The PCR thermal profiles were as follows: COX 1 and H3, with an initial step of 5 min at 95°C; 35 cycles of 45 s at 94°C, 45 s at 50°C and 1 min at 72°C; with a final extension of 10 min at 72°C. For the 16S gene: an initial step of 5 min at 95°C; 35 cycles of 45 s of 94°C, 45 s at 48°C and 1 min at 72°C; with a final extension of 10 min at 72°C. The PCR products were processed with an ABI Prism 3100 Genetic Analyzer, Applied Biosystems automated sequencer.

Sequences were processed and cleaned with MEGA v.7.0 (Kumar *et al.* 2016) and Finch T.V. v.1.4 (Geospiza Inc. 2012). The presence of stop codons was corroborated in MESQUITE v.3.6.1 (Maddison & Maddison 2019) and finally deposited in GenBank (Table 1). The alignment was performed in MAFFT v.7 (Kato *et al.* 2019) with the default parameters. The analysis of best partition scheme through PartitionFinder v.2.1.1 (Lanfear *et al.* 2016) obtained six partitions. The models for each partition were obtained in jModelTest v.2.1.10 (Darriba *et al.* 2012) with the Akaike corrected information criterion (AICc) (Hurvich & Tsai 1989), they are as follows.

**TABLE 1.** Specimens considered to the phylogenetic analyzes of this work.

Species	Museum Voucher	Locality	COI	16S	H3
Subfamily Pseudothelphusinae					
<i>Tehuana poglayenorum</i> (Pretzman, 1980)	CNCR 33931	Río Basura, San Andrés Tuxtla, Veracruz. 18°31'55"N, 95°03'30"W	OK165442	OK256890	OK188918
<i>Tehuana lamellifrons</i> (Rathbun, 1893)	CNCR 33939	Nizanda, Ixtepec, Oaxaca. 16°39'30"N, 95°00'37"W	OK165446	OK256894	OK188922
<i>Tehuana chontalpaensis</i> Villalobos & Álvarez, 2003	CNCR 25445	Arroyo Frío, Cerro Cola de Sapo, Reserva de la Biósfera del Ocote, Ocozocoautla, Chiapas. 17°07'52"N, 93°46'58"W	MT852948	MT871970	MT860380
<i>Mokayathelphusa angelsotoi</i> <b>n. sp.</b>	CNCR 34843	Santa María Chimalapa, Oaxaca. 16°54'41.5"N, 94°42'21"W	ON407122	ON406438	ON409201
<i>Alvarezius zongolicae</i> (Álvarez, Villalobos & Moreno, 2012) <b>n. comb.</b>	CNCR 35458	Choapa, Sierra de Zongolica, Veracruz. 18°43'32"N, 96°57'07"W	ON407123	ON406437	ON409200
<i>Pseudothelphusa americana</i> De Saussure, 1857	CNCR 25527	Río Ajajalpa, Zacatlán, Puebla 19°52'19"N, 97°58'52"W	MT852944	MT871966	MT860376
<i>Pseudothelphusa doenitzi</i> Bott, 1968	CNCR 26190	La Lobera, Zaachila, Oaxaca 16° 56'55"N, 96°50'10"W	OK165451	OK256900	OK188928
<i>Pseudothelphusa belliana</i> Rathbun, 1898	CNCR 19228	Chautipan, Chilpancingo, Guerrero 17°30'28"N, 99°44'30"W	MT860377	MT871967	MT852945
<i>Ehecatusa mixtepecensis</i> (Rodríguez & Smalley, 1972)	CNCR 309	San Gabriel Mixtepec, Oaxaca 16°05'33"N, 97°04'53"W	MT852943	-	MT860375
<i>Smalleyus tricristatus</i> Álvarez, 1989	CNCR 7034	Sierra de Santa Marta, Los Tuxtlas, Veracruz 18°26'00"N, 94°57'00"W	MT852947	MT871969	MT860379
<i>Disparithelphusa pecki</i> Smalley & Adkison, 1984	CNCR 34625	Cerro Cangrejo, San Juan Bautista Valle Nacional, Oaxaca 17°48'04"N, 96°19'06"W	OK165450	OK256899	OK188927
Subfamilia Raddausinae					
<i>Raddaus bocourti</i> (A. Milne-Edwards, 1866)	CNCR 25488	Camino a San Isidro, Chiapas. 16°24'50"N, 92°19'53"W	MT852046	MT871953	MT860363

For the Maximum Likelihood analysis, each partition was analyzed under the GTR model (Tavaré 1986); assuming the following parameters: COI position 1 nucleotide frequencies: A = 0.3272, C = 0.1631, G = 0.2744, T = 0.2351; substitution model (A/C: 0.00; A/G: 2.93; A/T: 0.49; C/G: 0.00; C/T: 260.87; G/T: 1.00; alpha: 0.1409, invar: 0.4901). COI position 2 nucleotide frequencies: A = 0.1267, C = 0.2596, G = 0.1513, T = 0.4622; substitution model (A/C: 42746.76; A/G: 304.44; A/T: 0.00; C/G: 0.00; C/T: 90.32; G/T: 1.00; alpha: 1,000, invar: 0.9674). COI

position 3 nucleotide frequencies: A = 0.5000, C = 0.1127, G = 0.0122, T = 0.3750; substitution model (A/C: 0.03; A/G: 7.99; A/T: 0.02; C/G: 0.00; C/T: 0.82; G/T: 1.00; alpha: 1.2257, invar: 0.0001). 16S nucleotide frequencies: A = 0.3610, C = 0.0979, G = 0.1756, T = 0.3653; substitution model (A/C: 0.37; A/G: 177.56; A/T: 4.02; C/G: 0.00; C/T: 5.83; G/T: 1.0; alpha: 0.13303, invar: 0.4314). H3 positions 1 and 3 nucleotide frequencies: A = 0.2692, C = 0.2932, G = 0.2748, T = 0.1826; substitution model (A/C: 0.00; A/G: 0.00; A/T: 0.00; C/G: 0.00; C/T: 0.00; G/T: 1.0; alpha: 0.0200, invar: 1.0000). H3 position 2 nucleotide frequencies: A = 0.0817, C = 0.3597, G = 0.3293, T = 0.2291; substitution model (A/C: 1.08; A/G: 2.00; A/T: 0.00; C/G: 0.14; C/T: 1.21; G/T: 1.0; alpha: 0.1475, invar: 0.6195).

For the Bayesian analysis the following models were used: COI position 1 = GTR + G (Tavaré 1986); position 2 = F81 (Felsenstein 1981); position 3 = GTR + G. 16S) GTR + I. H3 position 1 and 3 = JC (Jukes & Cantor 1969), position 2 = F81.

The final concatenated matrix had a length of 1,362 bp that was analyzed in RAxML-HPC BlackBox v.8.2.12 (Stamatakis 2014) on CIPRES and the optimal number of bootstraps obtained (Miller *et al.* 2010) for the first tree; simultaneously the matrix was run in MrBayes v.3.2.7 (Ronquist & Huelsenbeck 2003) on CIPRES to obtain a second tree. Analytical parameters were as follows: two independent runs with four Monte Carlo Markov chains, three hot and one cold with a temperature of 0.1 with 10 million generations and sampling every 1,000 generations and a burn-in of 25%. The convergence of the chains and the optimal ESS values were corroborated in Tracer v.1.7.1 (Rambaut *et al.* 2018), and the optimal PSRF values were verified (Gelman & Rubin 1992). Both trees were visualized and edited in Figtree v.1.4.3 (Rambaut *et al.* 2018) and of the trees obtained, we only reported clades with a branch support greater than 50%.

## Results

### *Phylogenetic analysis*

The phylogenetic analysis recovered *Mokayathelphusa angelsotoi* n. gen., n. sp., within the subfamily Pseudothelphusinae and as the sister lineage of the genus *Disparithelphusa* Smalley & Adkison, 1984. Regarding *Pseudothelphusa zongolicae*, the analysis does not recognize it as part of *Pseudothelphusa*, but rather as a sister lineage of *Tehuana*. The morphological analysis corroborated the previous results since its characteristics are unique within the subfamily Pseudothelphusinae (Fig. 2).

## Taxonomy

### Family Pseudothelphusidae Ortmann, 1893

### Subfamily Pseudothelphusinae Ortmann, 1893

#### *Mokayathelphusa* Moreno, Villalobos & Álvarez n. gen.

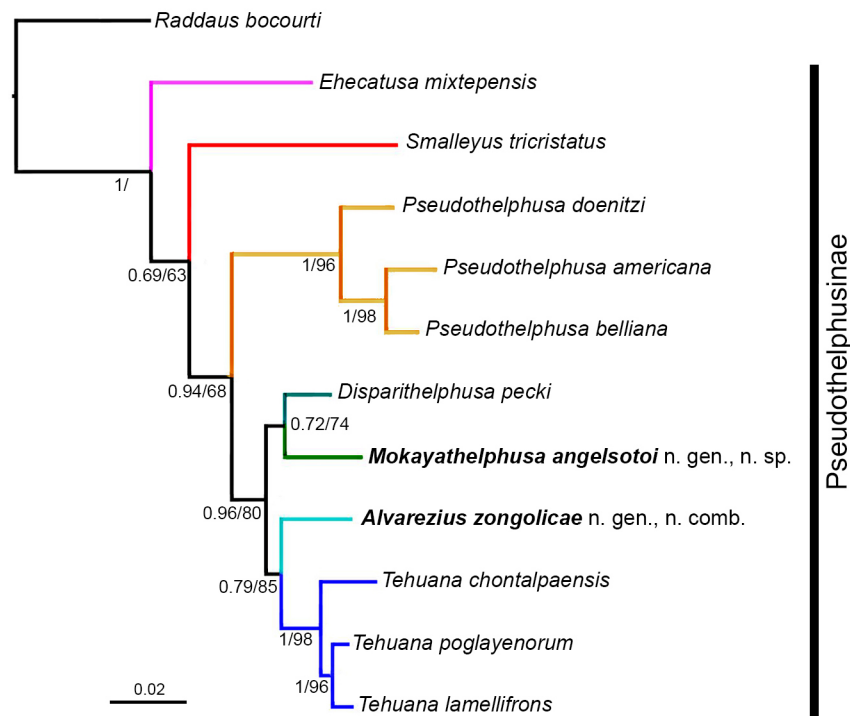
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**Diagnosis.** G1 with the distal portion of principal axis twisted counterclockwise. Apical cavity oriented mesocephalically, compressed and closed cephalically by the internal angle of mesial process. Caudo-marginal projection trilobed distally, middle and distal lobes spiniform of same length, proximal lobe as elongated sheet, curved, extending through distal third of main gonopod axis. Mesial process large, subrectangular, with lateral margin ornamented with several spiniform teeth.

**Type species.** *Mokayathelphusa angelsotoi* n. sp., by present designation.

**Etymology.** The name of the genus is taken from the ancient tribe “Mokaya” that inhabited the Chimalapas region about 3,600 ybp. The word “Mokaya” comes from the earliest Zoque language, that means “people of the corn”. The gender of this name is feminine.

**Distribution.** Currently known only from the municipality of Santa María Chimalapa, State of Oaxaca, Mexico.



**FIGURE 2.** Consensus tree resulting from ML and BI analyzes of the concatenated matrix (COX 1, 16S and H3) from the genus of the Pseudothelphusinae subfamily.

**Remarks.** The description of *Mokayathelphusa n. gen.* is justified by its unique male G1 morphology and clear genetic separation from related genera. The new genus can be related to other genera of the subfamily Pseudothelphusinae by the presence of the caudo-marginal projection, which ends distally in a trilobed distal plate. The phylogenetic analysis (Fig. 2) recovers it as the sister lineage to *Disparithelphusa* Smalley & Adkison, 1984. Morphologically the G1 of both genera present a torsion that modifies the shape and orientation of the apical cavity and have a trilobed distal plate in the caudo-marginal projection, where the distal lobes are smaller than the proximal one. They can also be differentiated by the size of the mesial process and the ornamentation of its lateral border, while in *Disparithelphusa* it is small, oval and without lateral ornamentation; in *Mokayathelphusa n. gen.*, it is evidently developed and ornamented laterally.

***Mokayathelphusa angelsotoi* Moreno, Villalobos & Álvarez n. sp.**

(Figs. 3, 4)

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**Type material. Holotype:** CNCR 34843, ♂, CL 14.9 mm, CW 23.1 mm; tributary of Río Negro, near the town of Santa María Chimalapa, 16°54'41"N, 94°42'21"W; 144 m asl, Municipality of Santa María Chimalapa, Oaxaca, Mexico, coll. A. Soto, 20 July 2018.

**Description.** Surface of carapace flat, smooth, except finely punctate branchial region. Cardiac, mesogastric, urogastric and branchial regions, discernible. Postfrontal area swollen, curved anteriorly to reach poorly defined superior frontal margin; postfrontal lobes low, separated by narrow, shallow median groove, ending anteriorly in median notch dividing superior frontal border. Cervical groove straight, narrow, well-marked, short, not reaching anterolateral margin. Lateral margin with 30 denticles and two shallow notches, anterior notch behind external angle of orbit, posterior notch at level of cervical groove (Fig. 4a). In frontal view, front, antennules, proepistome, epistome, and merus of third maxillipeds with minute dark spots; superior frontal margin marked by acute frontal bend of carapace, inclined towards median groove, with small granules, divided by V-shaped median notch; inferior frontal margin sinuous, with blunt granules, adjacent portion to antennular cavity higher than rest; interantennular septum concealed by inferior frontal margin. Antennules and antennular fossae visible, fossae wider in middle.

Antennal peduncle filling orbital hiatus. Orbital margin well defined, internal surfaces of ocular cavities with scattered dark spots and short setae; inner tooth slender, elongate, concave longitudinally, superior margin subtriangular. Opercular plate of antennal gland ovoid. Superior margin of proepistome sharp in middle, oval-shaped at lateral ends. Epistome setose, surrounding buccal cavity; laterally with rounded granules; epistomal tooth triangular, apex directed anteriorly at same level of interantennular septum, between palps of third maxillipeds when closing buccal cavity. Opening of efferent branchial channel subquadrate, superior margin curved, ratio width/length 1.25.

Third maxilliped with ischium trapezoidal, 1.33 times wider than long; merus narrower than ischium, anterior margin widely rounded with shallow, rounded notch next to insertion of palp; ratio exopod/ischium length 0.65 (Fig. 4b).

Chelipeds asymmetrical. Merus of larger cheliped with row of blunt tubercles along internal margin, carpus with strong triangular spine on internal margin. Chela with internal surface smooth, swollen; fingers gaping, curved inwards distally, cutting edges with triangular teeth (Fig. 4b). Dactylus narrow, dorsal surface with longitudinal rows of small pits, cutting edge with two proximal triangular teeth, remaining edge with alternate small and big teeth, ending in curved acute point. Propodus cutting edge with two small proximal teeth, six medial triangular and acute ones, seventh smallest, final point acute, incurved.

G1 slender, with torsion throughout its length, distal half curved mesially making apical cavity visible in meso-cephalic position. In mesial view (Fig. 3a), principal axis twisted counterclockwise, distal crest of caudal surface (Cdc) cephalically oriented, projected mesially; distal portion of caudo-marginal projection directed cephalad, with distal lobe (DI) as a strong spine with flat distal surface, delimited by well marked external crest (Ecdl); medial lobe (MI) not visible; proximal lobe (PI) partially evident in proximal half, as curved sheet, with subacute end; distal crest of apical cavity ornamented with acute, hooked spinules. In caudal view (Fig. 3b), principal axis with distal half twisted, mesially inclined; medial portion with curved, sharp caudal edge (Ce), lateral surface with sharp rib-like border (Le); mesial process (Mp) as laminate rectangular plate, lateral margin raised, produced into irregular crest (Lbmp), armed with acute teeth; distal crest of lateral surface (Ldc) widely rounded. In lateral view (Fig. 3c), distal half of gonopod straight, surface smooth, Ldc rounded; Lbmp thin, armed with nine irregular teeth, distally forming right angle with superior border; lobes of caudo-marginal projection partially visible, DI and MI conical, acute, PI triangular. In cephalic view (Fig. 3d), distal half inclined mesially; lobes of caudo-marginal projection evident, DI and MI conical, acute, latero-cephalically directed, distal one moderately stouter; PI as curved sheet, distal end slender, rounded; mesial process as thin plate with toothed lateral border (Lbmp); distal portion forming right angle with superior border (Dbmp); apical cavity U-shaped, mesial distal crest (Mdc) with row of acute, hooked spinules, field of apical spines adjacent to internal lateral surface with several chitinized setae, aperture of spermatic channel on caudal position, distal crest of lateral surface projecting distally. In distal view (Fig. 3e), apical portion evidently curved cephalad, apical cavity (Ac) barely visible; Ldc smooth laterally, mesially armed with short spinules; distal lobe of caudo-marginal projection conical, slender, acute; mesial process partially noticeable. Apical cavity only visible distally in meso-cephalic position (Fig. 3f), U-shaped, aperture on cephalic surface, closed by internal angle of mesial process (Imp); field of spines (Sf) adjacent to lateral surface, with 10 long, conical and slender corneous setae, and 20 shorter conical tubercles scattered on caudal portion of cavity; aperture of spermatic pore (Sp) in caudal position, with spinules on caudal internal surface; distal crest of mesial surface (Mdc) armed with slender spinules. DI and MI of caudo-marginal projection, almost totally visible, conical, subacute, fused at base, directed cephalad.

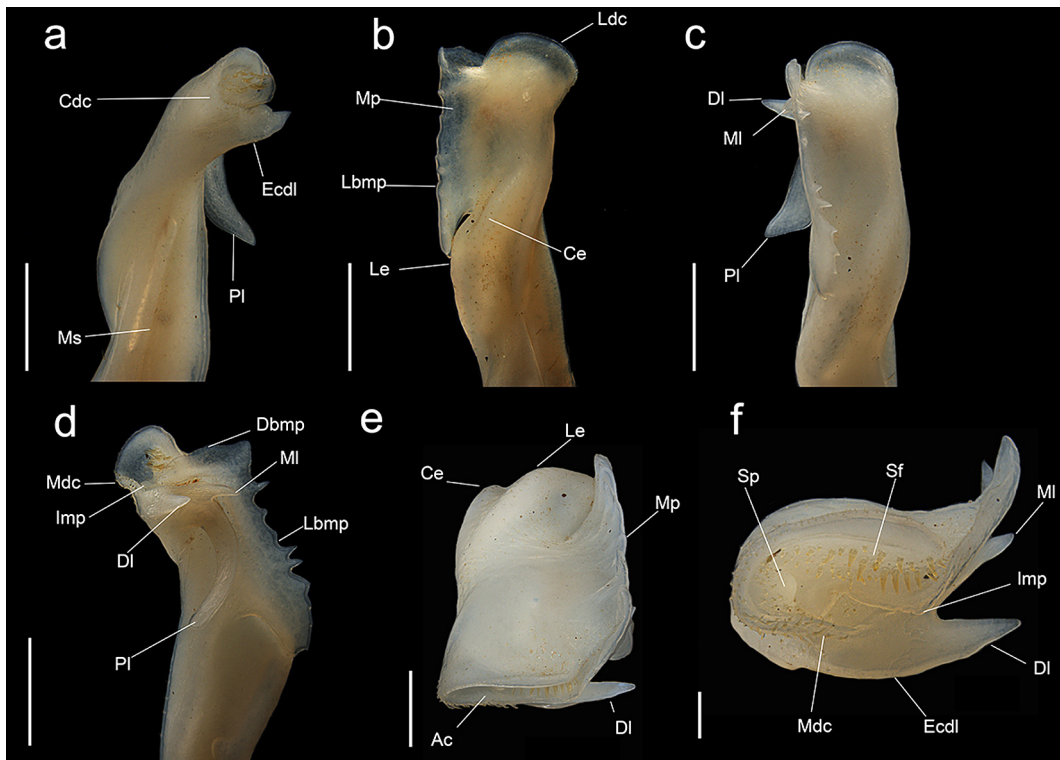
**Distribution.** Known only from the type locality.

**Type locality.** Stream tributary of Río Negro (16°54'41"N, 94°42'21"W; 144 m asl), Municipality of Santa María Chimalapa, Oaxaca, Mexico.

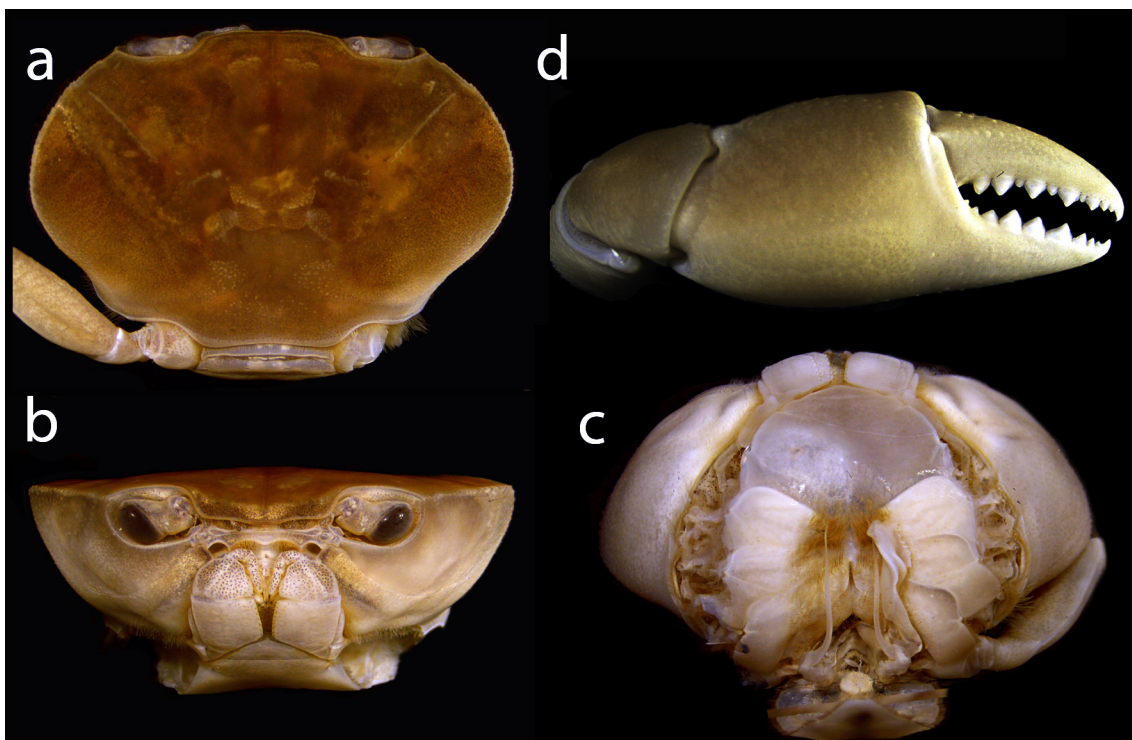
**Etymology.** This species is named after Ángel Fernando Soto Pozos, enthusiastic herpetologist interested in the biodiversity of the Chimalapas region, and collector of the type specimen.

**Remarks.** The G1 morphology of *Mokayathelphusa angelsotoi* sp. nov., is unique among the members of the subfamily Pseudothelphusinae. The new species is genetically related to *Disparithelphusa pecki* Smalley & Adkison, 1984. Both species present a trilobed caudo-marginal projection, the two short distal lobes and the elongated proximal one. However, the shape, arrangement and orientation of these lobes are completely different. Other apical elements such as the mesial process, and the form and ornamentation of apical cavity, also show differences.

Geographically, *Diparithelphusa pecki* occurs in northern Oaxaca, in the Sierra de Juárez near the town of Tuxtepec, whereas *Mokayathelphusa angelsotoi* n. sp. occurs in the Chimalapas region about 190 km to the southeast (Fig. 1). Genetically, both species are clearly different as seen in their phylogenetic placement (Fig. 2).



**FIGURE 3.** *Mokayathelphusa angelsotoi* sp. nov., holotype G1 views: a) mesial, b) caudal, c) lateral, d) cephalic, e) distal, f) apical cavity. Abbreviations: Ac) apical cavity; Cdc) caudal distal crest; Ce) caudal edge; DI) distal lobe of the caudo-marginal projection; Dbmp) distal border of the mesial process; Eccl) external crest of the distal lobe; Imp) internal angle of the mesial process; Lbmp) lateral border of the mesial process; Ldc) lateral distal border; Le) Lateral edge; Mdc) mesial distal crest; MI) mesial lobe of the caudo-marginal projection; Mp) mesial process; Ms) Marginal suture; Sf) spine field; Sp) spermatic pore. Scales as broad lines a-e: 1mm; f: 0.5 mm.



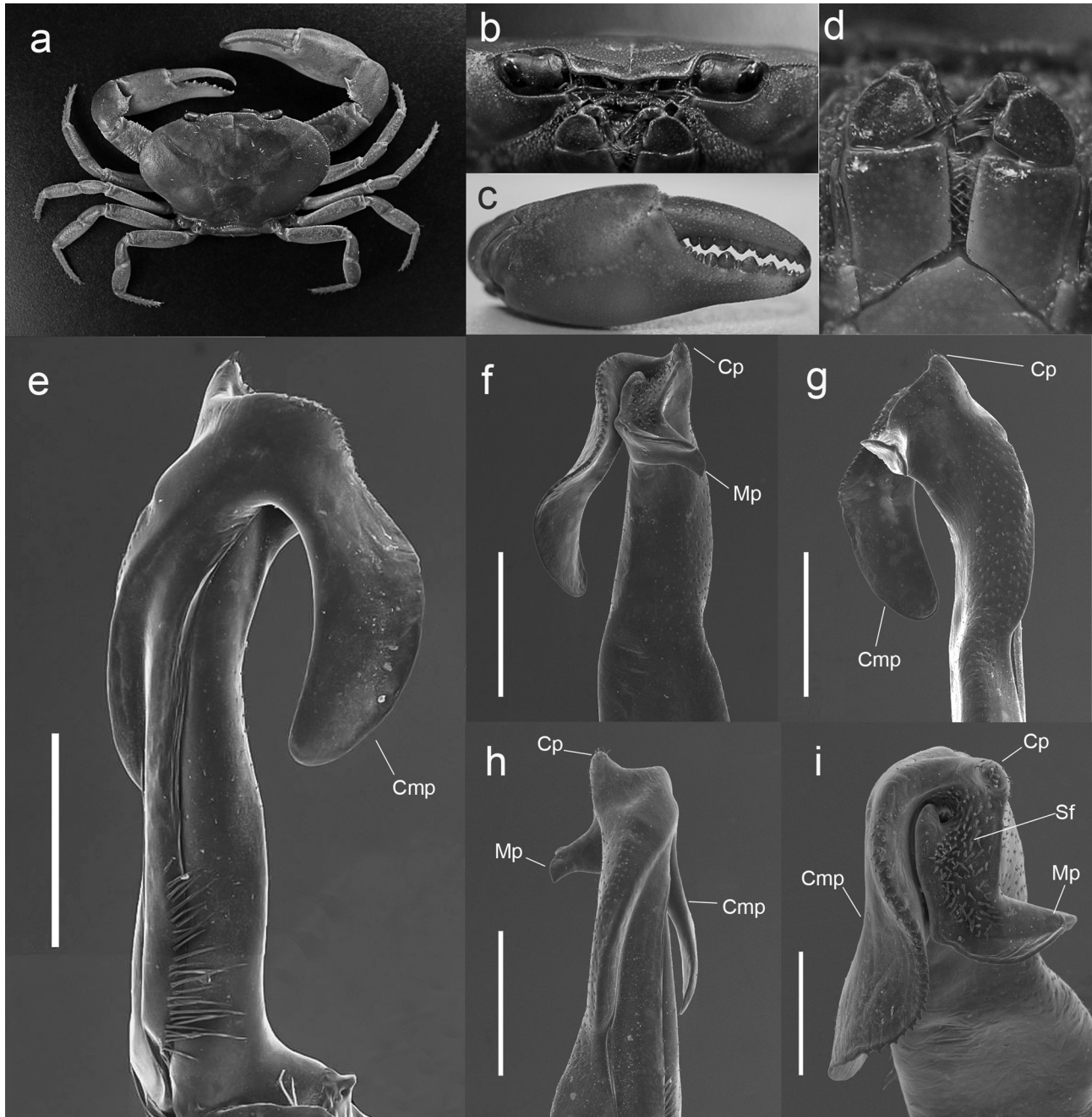
**FIGURE 4.** *Mokayathelphusa angelsotoi* sp. nov. a) carapace dorsal view, b) carapace frontal view, c) chela, d) carapace ventral view, abdomen removed.

*Alvarezius* Moreno & Villalobos n. gen.

(Fig. 5)

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**Diagnosis.** G1 with conical setiferous prominence on latero-caudal portion of distal border of apical cavity. Caudo-marginal projection unilobed, which extends proximally reaching proximal half of gonopod principal axis, disto-cephalic border serrate. Mesial process subrectangular, proximal inferior angle ending in acute triangle proximally oriented.



**FIGURE 5.** *Alvarezius zongolicae* n. comb. a) carapace dorsal view, b) carapace frontal view, c) chela, d) third maxilliped. G1 views: e) mesial, f) cephalic, g) lateral; h) caudal, i) distal. Abbreviations: Cmp) caudo-marginal projection; Csp) Conical setiferous prominence; Mp) Mesial process; Sf) spine field. Scales as broad lines e-h: 2 mm; i: 1 mm (taken and modified from Alvarez *et al.* 2012).

**Type species.** *Pseudothelpusa zongolicae* Alvarez, Villalobos & Moreno, 2012.

**Species included.** *Alvarezius zongolicae* (Alvarez, Villalobos & Moreno, 2012) n. comb.



**Etymology.** The genus name is dedicated to Dr. Fernando Álvarez, eminent Mexican carcinologist and curator of the CNCR. The gender of this name is masculine.

**Distribution.** Only known from Zongolica region, Veracruz, Mexico.

**Remarks.** When *Pseudothelphusa zongolicae* was first described, it was included in this genus because of the similarities in the G1 regarding the caudo-marginal projection and the mesial process as in other species of this genus, as explained by Alvarez *et al.* (2012). In the phylogenetic analysis presented in this paper *P. zongolicae* was recovered as the sister lineage to *Tehuana*, with mean genetic distance of 4.0% with respect to all the species of the genus, and 8.0–9.0% with respect to species of *Pseudothelphusa*. Combining the genetic evidence with a new morphological description, we place *P. zongolicae* in the new genus *Alvarezius* **n. gen.**

*Alvarezius zongolicae* (Alvarez, Villalobos & Moreno, 2012) **n. comb.**

*Pseudothelphusa zongolicae* Alvarez, Villalobos & Moreno, 2012, figs. 2, 3. — Villalobos *et al.*, 2019: 157 (Table 1). — Álvarez *et al.*, 2020: 10 (Supplementary material, Table 1).

**Type material.** *Holotype*: CNCR 26641; 1 ♂, CL 18.1 mm, CW 30.0 mm; spring at Choapa (18°43'32"N, 96°57'07"W, 1053 m asl), Municipality of Zongolica, Veracruz, Mexico; colls. E. Moreno, O. Trejo; 19 April 2011. *Paratype*: CNCR 26642; 1 ♂, CL 17.7 mm, CW 28.7 mm; same locality as holotype; 12 June 2011.

**Other material examined.** CNCR 26643, 4 ♂, 1 ♀, CL 15.8–22.8 mm, CW 25.5–37.5 mm, Macuilca (18°38'49"N, 96°56'58"W, 528 m asl), Municipality of Zongolica, Veracruz, Mexico, coll. E. Moreno & O. Trejo, 11 June 2011; CNCR 29494, 5 ♂, CL 8.9–19.9 mm CW 13.6–32.7 mm, spring of water, Tepeplampa (18°33'41"N, 96°56'51"W, 891 m asl), Municipality of Zongolica, Veracruz, Mexico, coll. E. Moreno & S. Rodríguez, 12 December 2012; CNCR 29495, 6 ♂, 1 ♀, CL 11.2–23.3 mm, CW 12.5–40.6 mm, stream near Tepetlampa (18°33'10"N, 96°56'30"W, 110 m asl), Municipality of Zongolica, Veracruz, Mexico; colls. E. Moreno & S. Rodríguez; 11 December 2012; CNCR 35458, 2 ♂, 2 ♀, CL 18.1–21 mm, CW 22.4–36.2 mm, same locality as holotype, coll. E. Moreno, A. Soto & R. Rodríguez, 10 October 2019; CNCR 36478, 4 ♂, 4 ♀, CL 7.8–9.8 mm, CW 10.6–15.6 mm, spring inside cave, Cintalapa (18°38'12"N, 96°54'0.4"W, 1050 m asl), Municipality of Zongolica, Veracruz, Mexico; colls. E. Moreno & L. Gómez; 3 April 2022. CNCR 36479; 2 ♂, spring in Acahualco, Cuahutilica (18°36'19.6"N, 96°56'26"W, 1169 m asl), Municipality of Zongolica, Veracruz, Mexico; colls. E. Moreno & L. Gómez, 3 April 2022; CNCR 36480, 1 ♂, CL 23.2 mm, CW 39.9 mm, waterfall on the road, Coapa-Pinopa (18°37'16.2"N, 96°56'21.5"W, 1063 m asl), Municipality of Zongolica, Veracruz, Mexico, coll. E. Moreno & L. Gómez, 3 April 2022; CNCR 36481, 3 ♂, CL 20.7–24.2 mm, CW 34.9–41.4 mm, Acahualco Cave, Cuahutilica (18°36'16"N, 96°56'09"W, 1,111 m asl), Municipality of Zongolica, Veracruz, Mexico, coll. E. Moreno & L. Gómez, 3 April 2022.

**Description.** Carapace transversely oval, dorsal surface slightly convex, smooth, finely punctate, regions faintly marked, except for moderately swollen mesobranchial region (Fig. 5a). Superior frontal border present, incomplete towards middle portion, formed by incomplete row of granules, in frontal view inclined towards median groove (Fig. 5b). Inferior frontal border complete, thick, slightly rounded in dorsal view, bilobed in frontal view, extending laterally to form superior margin of orbits. Median groove deep, narrow, arising above inferior frontal border, extending posteriorly beyond postfrontal lobes. Postfrontal lobes low, well defined. Cervical grooves wide, shallow, straight towards margin of carapace, ill-defined, slightly arching towards central portion of carapace, not reaching anterolateral margin. Walking legs typical of genus. Chelipeds asymmetrical. Major chela right, palm somewhat swollen, movable finger half-length of chela, fingers not gaping; both fingers with irregular arrangement of teeth of varying sizes, both fingers curved inwards (Fig. 5c). Third maxilliped with merus showing complete rounded external margin, ischium rectangular, ratio ischium/exopod 0.85 (Fig. 5d).

G1 moderately slender, distal half of principal axis showing mesial torsion of caudo-marginal projection. In mesial view (Fig. 5e), marginal suture evident, arching distally, disappearing under caudo-marginal projection; lobe of caudo-marginal projection (Cmp) axe-shaped, large, about half length of gonopod, cephalic border smooth; caudo-marginal distal crest straight, spinulated at cephalic curvature. In cephalic view (Fig. 5f), mesial process (Mp) oriented laterally, slightly inclined proximally, tapering laterally, ending in two acute tips, superior margin closing apex cavity, extending towards internal portion of apex cavity forming central crest; caudo-marginal projection with single large, axe-shaped lobe, extending proximally slightly beyond half-length of gonopod, cephalic margin armed with small, acute teeth; crest of caudo-marginal projection becoming less thick cephalically; conical prominence

(Cp) on caudal angle of lateral crest bearing apical setae. In lateral view (Fig. 5g), mesial process with two tips oriented laterally; caudo-marginal projection (Cmp) appearing as large tongue-shaped lobe; conical prominence (Cp) emerging from lateral crest. In caudal view (Fig. 5h), caudal surface showing torsion of gonopod; mesial process (Mp) subtriangular; conical prominence (Cp) of lateral crest evident; lobe of caudo-marginal projection (Cmp) elongate, slender, extending parallel to main axis of gonopod; marginal suture straight, visible along proximal two thirds of gonopod. In apical view (Fig. 5i), apex cavity approximately rectangular, field of spines (Sf) on lateral side of cavity, extending to conical prominence (Cp); central crest of apex cavity sharp, slightly undulated; distal crest of lateral surface straight; mesial process (Mp) subtriangular, distal margin rounded; lobe of caudo-marginal projection (Cmp) as undulated sheet, cephalic margin with minute spines; opening of sperm channel caudal.

**Distribution.** Mexico, Veracruz, in the surroundings of the Municipality of Zongolica.

**Type locality.** Spring at Choapa (18°43'32"N, 96°57'07"W; 1,053 m asl), Municipality of Zongolica, Veracruz, Mexico (CNCR 26641).

**Remarks.** The term “conical projection” of the latero-caudal portion of the distal border of the apical cavity from the original description by Álvarez *et al.* (2012) is now changed to “conical lobe”, since the former suggests the fusion of two plates in a single apical process (Hobbs 1942, 1945; Smalley 1964); however, in this case the structure develops directly from the lateral surface.

## Discussion

The continuous discovery of new taxa in Pseudothelphusidae is remarkable, especially if we consider that not only new species, but also new genera are being recognized (Pedraza *et al.* 2016; Magalhães 2017; Magalhães & Ng 2019). Several regions within the distributional range of the family are particularly diverse, such as the region in eastern Colombia and western Venezuela where three particularly speciose subfamilies co-occur (Hypolobocerinae, Strengerianinae, Kingsleyinae) and the Isthmus of Tehuantepec in southern Mexico where another three subfamilies co-occur (Pseudothelphusinae, Potamocarcininae, Raddausinae) (Alvarez *et al.* 2020). In the latter region is where the two new genera presented herein are distributed.

*Mokayathelphusa angelsotoi* **n. gen., n. sp.**, exhibits a unique G1 morphology. While it has the torsion that places it within the Pseudothelphusinae, it has a bent apex, strong teeth on the cephalic surface and a toothed mesial process. Owing to this complexity it is necessary to observe the natural position of the gonopod in the crab to correctly interpret the position and orientation of lobes and processes (Fig. 4c). Interestingly, the molecular phylogeny associates the new genus with *Disparithelphusa*, the other genus within the Pseudothelphusinae that has a G1 with a bent apex (Smalley & Adkison 1984). As noted above *Alvarezius zongolicae* **n. gen., n. comb.**, represents another case where a taxonomic reappraisal resulting from a molecular phylogenetic analysis has refined the classification.

## Acknowledgments

The first author gratefully acknowledges CONACYT for the PhD scholarship 2020-000013-01NACF-12928 and the Programa de Posgrado en Ciencias Biológicas (PCB)—UNAM for their support. This contribution is presented in partial fulfillment of the requirements for the PhD degree of EGMJ in the PCB-UNAM. We also thank the technical assistance in the molecular analysis of Andrea Jiménez, Laura Márquez and Nelly Ortiz from LaNaBio of the Institute of Biology, UNAM. The photographic record was possible thanks to the technical advice of Susana Guzmán from the Biodiversity Microscopy and Photography Laboratory of the Institute of Biology, UNAM. Finally, we want to thank to Célio Magalhães and Shane Ahyong for their valuable comments on this work.

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