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Xoconochcothelphusa, a new genus for *Ehecatusa chiapensis* (Rodríguez & Smalley, 1972), with notes on *Spirothelphusa* Pretzmann, 1965 (Crustacea: Decapoda: Pseudothelphusidae)

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Abstract

The species of the genus *Ehecatusa* Ng & Low, 2010, *E. chiapensis* (Rodríguez & Smalley, 1972) and *E. mixtepensis* (Rodríguez & Smalley, in Smalley, 1970), were referred to as *incertae sedis* in the classification system of the tribe Pseudothelphusini Ortmann, 1897, proposed by Villalobos-Hiriart (2005) and Villalobos & Alvarez(2010) and as members of the subfamily Pseudothelphusinae in the recent phylogenetic proposal by Álvarez *et al*. (2020), supported with morphology and molecular information. The recent discovery of a new specimen of *E. chiapensis*, from Chiapas, Mexico, comes to expose again the unresolved taxonomic situation of this species in the genus *Ehecatusa*. New morphologic evidence from the male first gonopod and a phylogenetic analysis based on partial DNA sequences of mitochondrial and nuclear genes (COI, 16S and H3), support the placement of the two species in different genera. Consequently, *Xoconochcothelphusa* **n. gen.** is erected to receive *X. chiapensis* **n. comb.** The phylogenetic relationships of *X. chiapensis* **n. gen.**, **n. comb.** and *E. mixtepensis* with other genera of the subfamily Pseudothelphusinae Ortmann, 1893 (*Ehecatusa, Smalleyus* Alvarez, 1989, and *Spirothelphusa* Pretzmann, 1965) distributed in Mexico, are examined and a key to the identification of the genera of this subfamily is provided.

Key words: Chiapas, freshwater crabs, Mexico, Neotropical region, phylogenetic analysis, taxonomy

Introduction

The freshwater crabs of the family Pseudothelphusidae Ortmann, 1893, distributed in southern Mexico, in the states of Oaxaca, Veracruz, Tabasco and Chiapas, represent different lineages of the subfamilies Potamocarcininae Ortmann, 1897, Raddausinae Álvarez, Ojeda, Souza-Carvalho, Villalobos, Magalhães, Wehrtmann & Mantelatto, 2020, and Pseudothelphusinae Ortmann, 1893 (Álvarez *et al*. 2020). The extraordinary variety of apical ornamentation patterns seen in the male first gonopod (G1), reflects the strong diversification that these lineages have undergone in the region. Within the Pseudothelphusinae, species of seven other genera (*Pseudothelphusa* de Saussure, 1857, *Tehuana* Rodríguez & Smalley, in Smalley, 1970, *Smalleyus* Alvarez, 1989, *Ehecatusa* Ng & Low, 2010, *Mokayathelphusa* Moreno, Villalobos & Álvarez, 2022b, *Disparithelphusa* Smalley & Adkison, 1984, *Alvarezius* Moreno & Villalobos, in Moreno, Villalobos & Álvarez, 2022b) occur in the region.

The original taxon *Epithelphusa* Rodríguez & Smalley, in Smalley, 1970, was established to receive *Ep. mixtepensis* Rodríguez & Smalley, in Smalley, 1970, from San Gabriel Mixtepec, state of Oaxaca, has a G1 that is considered morphologically intermediate between a complex shaped G1 like in *Spirothelphusa* Pretzmann, 1965, and a simpler one as in *Pseudothelphusa*, but with a marginal process (distal lobe of caudo-marginal projection in the nomenclature of Villalobos & Alvarez (2010)) anterior but not fused to the mesial lobe. The second species, *E. chiapensis* (Rodríguez & Smalley, 1972), was first described as *Spirothelphusa chiapensis* by Rodríguez & Smalley (1972). Rodriguez (1982) removed it from *Spirothelphusa* without any comment and placed it as the second species

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of *Epithelphusa*, disregarding the strong differences in the G1 morphology compared to *Eh. mixtepensis*, and considered the genus as a primitive form in the evolution of the Pseudothelphusidae. He placed this genus within the tribe Pseudothelphusini based on the presence of a well-developed distal lobe of the marginal process (distal lobe of caudo-marginal projection in the nomenclature of Villalobos & Alvarez (2010)), situated on top of the mesial process and mentioned that the position of this character separated it from the tribe Potamocarcinini Ortmann, 1987. Further, Rodríguez (1986) hypothesized that *Epithelphusa* could derive from *Elsalvadoria* Bott, 1967, considering some similarities such as the ax-shaped mesial lobe and the presence of a cephalic process and accessory lateral spines.

Villalobos-Hiriart (2005) and Villalobos & Alvarez (2010), in their phylogenetic analyses of the tribe Pseudothelphusini, based on morphological characters, found that the two species of *Epithelphusa* were excluded from the internal group (tribe Pseudothelphusini), and they were placed in different positions through the consensus tree, suggesting that they should be accommodated in two different genera. This result reflected important morphological differences in the G1 morphology related to the lateral process: in the case of *Eh. chiapensis*, it is fused to the mesial process and forming three large tooth-like distal projections on the distal portion of the principal axis (Fig. 6), whereas in *Eh. mixtepensis*, the lateral process is formed by two curved spines, like vertical horns, which are separated from the mesial process (Fig. 3).

With regard to nomenclature, Ng & Low (2010) proposed the replacement of the genus name *Epithelphusa* because it was found preoccupied and erected the new name *Ehecatusa* to receive the two species; they maintained *Eh. mixtepensis* as the type species of the genus. Also, Guinot & Hendrickx (2014), proposed that the correct year and authorship of *Epithelphusa* and *Eh. mixtepensis*, was Smalley (1970) due to the fact that Rodríguez & Smalley's article, despite being dated 1969, was actually published until 1972, leaving the correct citations as *Epithelphusa* Rodríguez & Smalley, in Smalley 1970, and *Eh. mixtepensis* (Rodríguez & Smalley, in Smalley, 1970).

Álvarez *et al*. (2020) reorganized the classification system of Pseudothelphusidae family through an integrative analysis with molecular and morphological data. They could obtain DNA sequences of *Eh. mixtepensis* and placed it in the Pseudothelphusinae subfamily; in contrast, *Eh. chiapensis* was not sequenced and provisionally placed in the same subfamily due the presence of a caudo-marginal projection on its gonopod, a diagnostic character for the subfamily. The authors opened the question about the monophyletic validity of *Ehecatusa* when they explained that *Eh. chiapensis* has a unique morphology that makes it difficult to relate it to other pseudothelphusinean species.

The recent finding of crabs belonging to *Ehecatusa chiapensis* near the town of Escuintla, Chiapas, brings up the unresolved taxonomic situation of this species in the genus *Ehecatusa*. In the present study, based on a morphological analysis and on a phylogenetic analysis using partial sequences of three genes (two mitochondrial 16S, CO1; one nuclear H3) from 26 species and 17 genera from the subfamilies Pseudothelphusinae, Potamocarcininae, Ptychophallinae, and Raddausinae (see Table 1 for details), we propose *Xoconochcothelphusa* **n. gen.** to receive *Eh. chiapensis* **n. comb.** and also, to move *Spirothelphusa*, formerly included in Raddausinae by Álvarez *et al*. (2020), into the subfamily Pseudothelphusinae.

TABLE 1. Specimens examined for this work (CNCR—Colección Nacional de Crustáceos; CCDB—Coleção de Crustáceos do Departamento de Biología, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo; INPA—Instituto Nacional de Pesquisas da Amazônia; UCR-MZ—Museo de Zoología, Escuela de Biología, Universidad de Costa Rica; ZSMA—Zoologische Staatssammlung München).

Species	Museum Voucher	Locality	COI	16S	H3
Subfamily Potamocarcininae					
Potamocarcinus chajulensis Alvarez & Villalobos, 1998	CNCR 27158	Río Tzendales, Chiapas, México (16°17'54. 56" N, 90°53'12.09" W)	MT852039	MT868931	MT849827

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TABLE 1. (Continued)

Species	Museum Voucher	Locality	COI	16S	H3
Potamocarcinus magnus (Rathbun, 1896)	CCDB 4554	Quebrada Ciccaba, Parque Veraguas, Limón, Costa Rica (09°55'27.06" N, 83° 11'28.55" W)	MT852040	MT868932	MT849828
Subfamily Pseudothelphusinae					
Alvarezius zongolicae (Álvarez, Villalobos & Moreno, 2012)	CNCR 35458	Choapa, Sierra de Zongolica, Veracruz, México (18°43'32" N, 96°57'07" W)	ON407123	ON406437	ON409200
Ehecatusa mixtepensis (Rodríguez & Smalley, in Smalley, 1970)	CNCR 309	San Gabriel Mixtepec, Oaxaca, México (16°05' 33" N, 97°04'53" W)	MT852943	-	MT860375
Disparithelphusa pecki Smalley & Adkison, 1984	CNCR 34625	Cerro Cangrejo, San Juan Bautista Valle Nacional, Oaxaca, México (17°48' 04" N, 96°19'06" W)	OK165450	OK256899	OK188927
Mokayathelphusa angelsotoi Moreno, Villalobos & Álvarez, 2022b	CNCR 34843	Santa María Chimalapa, Oaxaca, México (16°54' 41.05" N, 94°42'21.00" W)	ON407122	ON406438	ON409201
Pseudothelphusa americana de Saussure, 1857	CNCR 25527	Río Ajajalpa, Zacatlán, Puebla, México (19°52'19" N, 97°58'52" W)	MT852944	MT871966	MT860376
Pseudothelphusa belliana Rathbun, 1898	CNCR 19228	Chautipan, Chilpancingo, Guerrero, México (17°30' 28" N, 99°44'30" W)	MT860377	MT871967	MT852945
Pseudothelphusa doenitzi Bott, 1968	CNCR 26190	La Lobera, Zaachila, Oaxaca (16° 56'55" N, 96°50'10" W)	OK165451	OK256900	OK188928
Smalleyus tricristatus Alvarez, 1989	CNCR 7034	Sierra de Santa Marta, Los Tuxtlas, Veracruz, México (18°26'00" N, 94°57'00" W)	MT852947	MT871969	MT860379
Spirothelphusa verticalis (Rathbun, 1893)	CNCR 25444	Río La Venta, Chiapas, México (16°47'26" N, 93° 29'20" W)	MT852043	MT871950	MT860361
Tehuana chontalpaensis Villalobos & Alvarez, 2003	CNCR 25445	Arroyo Frío, Cerro Cola de Sapo, Reserva de la Biósfera del Ocote, Ocozocoautla, Chiapas, México (17°07'52.72" N, 93°46'58.36" W)	MT852948	MT871970	MT860380

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TABLE 1. (Continued)

Species	Museum Voucher	Locality	COI	16S	H3
Tehuana lamellifrons (Rathbun, 1893)	CNCR 33939	Nizanda, Asunción Ixtaltepec, Oaxaca, México (16°41'24"N, 95°22'53"W)	OK165446	OK256894	OK188922
Tehuana poglayenorum (Pretzmann, 1978)	CNCR 33931	Río Basura, San Andrés Tuxtla, Veracruz, México (18°31'55" N, 95°03'30" W)	OK165442	OK256890	OK188918
Xoconochcothelphusa chiapensis (Rodríguez & Smalley, 1972) **n. comb.**	CNCR 34841	Arroyo tributario del río Vado Ancho, aproximadamente 10 km NE del poblado de Escuintla, Chiapas, México (15°22' 58.78" N, 92°35' 05.20" W)	OP344942	OP341851	OP341881
Subfamily Ptychophallinae					
Achlidon agrestis (Rathbun, 1898**)**	UCR-MZ321401	La Flor, plantation near Torito, Costa Rica	MT852036	MT868918	MT849826
Ptychophallus montanus (Rathbun, 1898)	ZSMA 20160512	Quebrada Palmital, San Antonio, Costa Rica (09°47'24.49" N, 83°57' 31.03" W)	KU578923	KU578848	KU578986
Subfamily Raddausinae					
Odontothelphusa lacandona Alvarez & Villalobos, 1998	CNCR 11204	Arroyo pequeño 8 km S de Benemérito de las Américas, Municipio de Ocosingo, Chiapas, México (16°26'53.31" N, 90°36'46.90" W)	MT852048	MT871956	MT860366
Odontothelphusa toninae Alvarez & Villalobos, 1991	CNCR 5770	Arroyo en la entrada a las ruinas de Toniná, Chiapas, México (16°54'08.57" N, 92°00' 33.56" W)	MT852049	MT871957	MT860367
Phrygiopilus acanthophallus Smalley, 1970	UCR-MZ	Río Quilila, Salamá, Alta Verapaz, Guatemala (15°04' 40.04" N, 90°18' 52.09" W)	MT852056	MT871964	MT860373
Phrygiopilus montebelloensis Alvarez & Villalobos, 1998	CNCR 33789	Laguna de Tziscao, Chiapas, México (16°09' N, 91°40' W)	MT852055	MT871963	MT860372
Sylvathelphusa cavernicola Villalobos & Álvarez, 2013	CNCR 27210	Cueva de las Arañas, cerca del poblado de San Fernando, Chiapas, México (16° 51'26" N, 93°16'01.5" W)	MT852051	MT871959	MT860368

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TABLE 1. (Continued)

Species	Museum Voucher	Locality	COI	16S	H3
Sylvathelphusa kalebi Villalobos & Álvarez, 2013	CNCR 26180	Área de Reserva Natural "La Pera", 12 km al NE de Berriozábal, Chiapas, México (16° 49'53.42" N, 93°17'42.13" W)	MT852052	MT871960	MT860369
Raddaus bocourti (A. Milne-Edwards, 1866)	CNCR 25488	Camino a San Isidro, Chiapas, México (16°24' 50" N, 92°19'53" W)	MT852046	MT871953	MT860363
Raddaus mertensi (Bott, 1956)	INPA 1964	Río Cusuco, San Pedro Sula, Parque Nacional Cusuco, Cortés, Honduras (15°29'47" N, 88°12'42" W)	MT852047	MT871954	MT860364

Material and methods

The specimens examined in this study are deposited in the Colección Nacional de Crustáceos (CNCR), Instituto de Biología, Universidad Nacional Autónoma de México, in Mexico City; Coleção de Crustáceos do Departamento de Biología (CCDB), Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo; Instituto Nacional de Pesquisas da Amazônia (INPA); Museo de Zoología (UCR-MZ), Escuela de Biología, Universidad de Costa Rica; Zoologische Staatssammlung München (ZSMA). The abbreviations used in the text are: cl = carapace length; cw = carapace wide; coll. = collected by.

DNA sequences. DNA sequences of 26 species from 17 genera, representing five subfamilies were used; most of them came from Genbank and three were obtained from the present study (Table 1). Genomic DNA was extracted from the muscle of the fifth pair of pereopods with the Animal and fungi DNA Preparation Kit, Jena Bioscience, following the manufacturer's protocol. The quantity of the DNA was tested in a NanoDrop 2000 spectrophotometer, Thermo Fisher Scientific, and the integrity in an agarose gel at 1%. Three genes were obtained (Cytochrome Oxidase Subunit I—COI, 16 S ribosomal RNA—16S rRNA and histone 3—H3) with MyTaq Kit, Bioline; following the manufacturer's protocol. Primers and thermic profiles are in table 2. The amplicons were purified with Sephadex CentriSep spin columns, Princeton Separations. The sequencing reaction was made with BigDye Terminator v3.1 cycle sequencing kit, Thermo Fisher Scientific, following the manufacturer´s protocol. The final products were sequenced in an Applied Biosystems 3500XL genetic analyzer, Thermo Fisher Scientific.

Phylogenetic analysis. The sequences quality was visualized on Finch T.V. 1.4 (Geospiza Inc.) and the consensus sequences were obtained in MEGA v. 7 (Kumar *et al*. 2016). For the protein coding genes, the presence of stop codons and the framework were determined in MESQUITE v.3.61 (Maddison & Maddison 2019). The alignments were made in MAFFT v.7 with the predetermined parameters (Katoh *et al*. 2019). The best partition scheme was obtained with PartitionFinder v.2.1.1 (Lanfear *et al*. 2016). The nucleotide substitution models were obtained with JModeltest v. 2.1.10 (Darriba *et al*. 2012) and the corrected Akaike information criterion (AICc) (Hurvich & Tsai 1989) (Table 2). A final concatenated matrix with 1,477 nucleotides was analyzed using Maximun Likelihood (ML) and Bayesian Inference (BI). The ML analysis was run in RAxML-HPC BlackBox v. 8.2.12 (Stamatakis 2014) on CIPRES (Miller *et al*. 2010). The optimal number of bootstrap replications was calculated by the same software. The BI analysis was run in MrBayes v. 3.2.7 (Ronquist & Huelsenbeck 2003) on CIPRES, with the substitution models inferred previously. The parameters were the following: two independent runs with four Monte Carlo Markov Chains, 10 million generations and sampling every 1,000 generations and 25% of burn-in. The convergence of the chains and optimal scores of effective sample size (ESS) were corroborated in Tracer v.1.7.1 (Rambaut *et al*. 2018), and the optimal values of the potential scale reduction factor (PSRF), were verified (Gelman & Rubin 1992). From both analyses only, clades with confidence numbers up to 50% were reported.

TABLE 2. Primers for the PCR reaction and its thermal profile.

Gene	Primers	Author	Thermal profile
COI	F 5'-GGT CAA CAA ATC ATA AAG AYA TYG G-3' R 5'-TAA ACT TCA GGG TGA CCA AAR AAY CA-3'	Meyer 2003	5' at 95°C; 35 cycles of 45" of 94°C, 45" at 50°C and 1' at 72°C; 10' at 72°C.
16S	F 5'- ACT TGA TAT ATA ATT AAA GGG CCG-3' R 5'-CTG GCG CCG CTC TGA ACT CAA ATC-3'	Palumbi *et al.* 1991	5' at 95°C; 35 cycles of 45" of 94°C, 45" at 50°C and 1' at 72°C; 10' at 72°C.
H3	F 5'-ATG GCT CGT ACC AAG CAG ACV GC-3' R 5'-ATA TCC TTR GGC ATR ATR GTG AC-3'	Colgan *et al*. 1998	5' at 95°C; 35 cycles of 45" of 94°C, 45" at 48°C and 1' at 72°C; 10' at 72°C

Results

Phylogenetic analysis

The final concatenated matrix of 1,417 base pairs (bp) was analyzed under seven partitions. For the ML analysis, each partition was analyzed under the GTR model (Tavaré 1986), and the BI analysis was performed with the following substitution models: COI position 1 SYM+G (Zharkikh 1994), COI position 2 JC (Jukes & Cantor 1969), COI position 3 HKY+G (Hasegawa *et al*. 1985), 16S GTR+I+G, H3 position 1, 2 and 3 JC.

The resulting trees of both phylogenetic reconstructions were similar, with small differences in the internal organization of the Raddausinae clade, as well in the branches support values (Fig. 1). The genus *Ehecatusa* resulted paraphyletic with each one of its species representing a different genus. We propose to leave *Eh. mixtepensis* as the single representative and type species of the genus, and erect *Xoconochcothelphusa* **n. gen.** to place *X. chiapensis* **n. comb.** Both genera are included in the subfamily Pseudothelphusinae, as it was previously recognized (Álvarez *et al*. 2020). Further, in our analysis *Spirothelphusa verticalis* (Rathbun, 1893) is recovered as a member of the subfamily Pseudothelphusinae, consequently we present a modified diagnosis of the subfamily considering the new results.

Taxonomy

Family Pseudothelphusidae Ortmann 1893

Subfamily Pseudothelphusinae Ortmann 1893

Diagnosis (modified from Álvarez *et al*. 2020). Anterolateral margin often finely serrate or granulated to unarmed, lateral armature indistinct. Exopod of third maxilliped always more than half of ischium length, ratio exopod/ischium length ranging between 0.50 and 0.84. Branchial efferent channel without spine or tooth next to aperture; orifice of efferent channel open, gap between jugal and lateral angles. Gonopod slender to robust, with obvious torsion towards median axis of body. Marginal plate and caudal surface fused to end apically in caudo-marginal projection, directed cephalically with one to three lobes. Lateral lobes along main axis absent, except in *Ehecatusa*, *Xoconochcothelphusa* **n. gen**. and *Spirothelphusa* (see diagnosis of those genera), the latter one with a wide rounded lobe on distal half of principal axis and one accessory subapical spine on the caudolateral border (Figs. 3, 5, 7). Mesodistal lobe can be present (*Tehuana*). Mesial process as triangular, subrectangular or as irregular plate or ax-shaped laminar expansion, commonly in longitudinal position relative to principal axis of gonopod and closing the apical cavity, rarely reduced (some species of *Tehuana*). Apical cavity oblique or transversal to principal axis of gonopod, u-shaped (*Alvarezius*, *Mokayathelphusa*, *Pseudothelphusa*, *Smalleyus*, *Tehuana*), closed cephalically by internal angle of mesial process, or rounded (*Disparithelphusa*, *Ehecatusa*), or elongated and narrow (*Spirothelphusa*, *Xoconochcothelphusa* **n. gen.**); field of spines distally located, irregularly disposed, with variable number of terminal-pore setae; opening of spermatic channel in caudal position, median crest present or absent.

Type genus. *Pseudothelphusa* de Saussure, 1857.

Genera included. *Alvarezius* Moreno & Villalobos, in Moreno, Villalobos & Álvarez, 2022b; *Disparithelphusa* Smalley & Adkison, 1984; *Ehecatusa* Ng & Low, 2010; *Mokayathelphusa* Moreno, Villalobos & Álvarez, 2022b; *Pseudothelphusa* de Saussure, 1857; *Smalleyus* Alvarez, 1989; *Spirothelphusa* Pretzmann, 1965; *Tehuana* Rodríguez & Smalley, in Smalley, 1970, and *Xoconochcothelphusa* **n. gen.**

Remarks. The subfamily Pseudothelphusinae is distributed exclusively in Mexico. The genus *Pseudothelphusa*, occupies a large area in Mexico, along the Pacific slope from the southern of Sonora, which is the northernmost limit of the superfamily Pseudothelphusoidea, to the south reaching coastal rivers of Oaxaca; in the central portion of the country, it extends its presence through the Transmexican Volcanic Belt from the west in Nayarit to the east in Puebla, with one extra record of *P. parabelliana* Alvarez 1989, in Los Tuxtlas region in Veracruz. The other eight genera in the subfamily occur in southern Mexico, in the states of Veracruz, Oaxaca, Tabasco and Chiapas, in the latter one a new region is added that includes the Pacific slope from the town of Tonalá, to the border with Guatemala, known as the Soconusco region, which is the distribution area of *Xoconochcothelphusa chiapensis* **n. comb.**

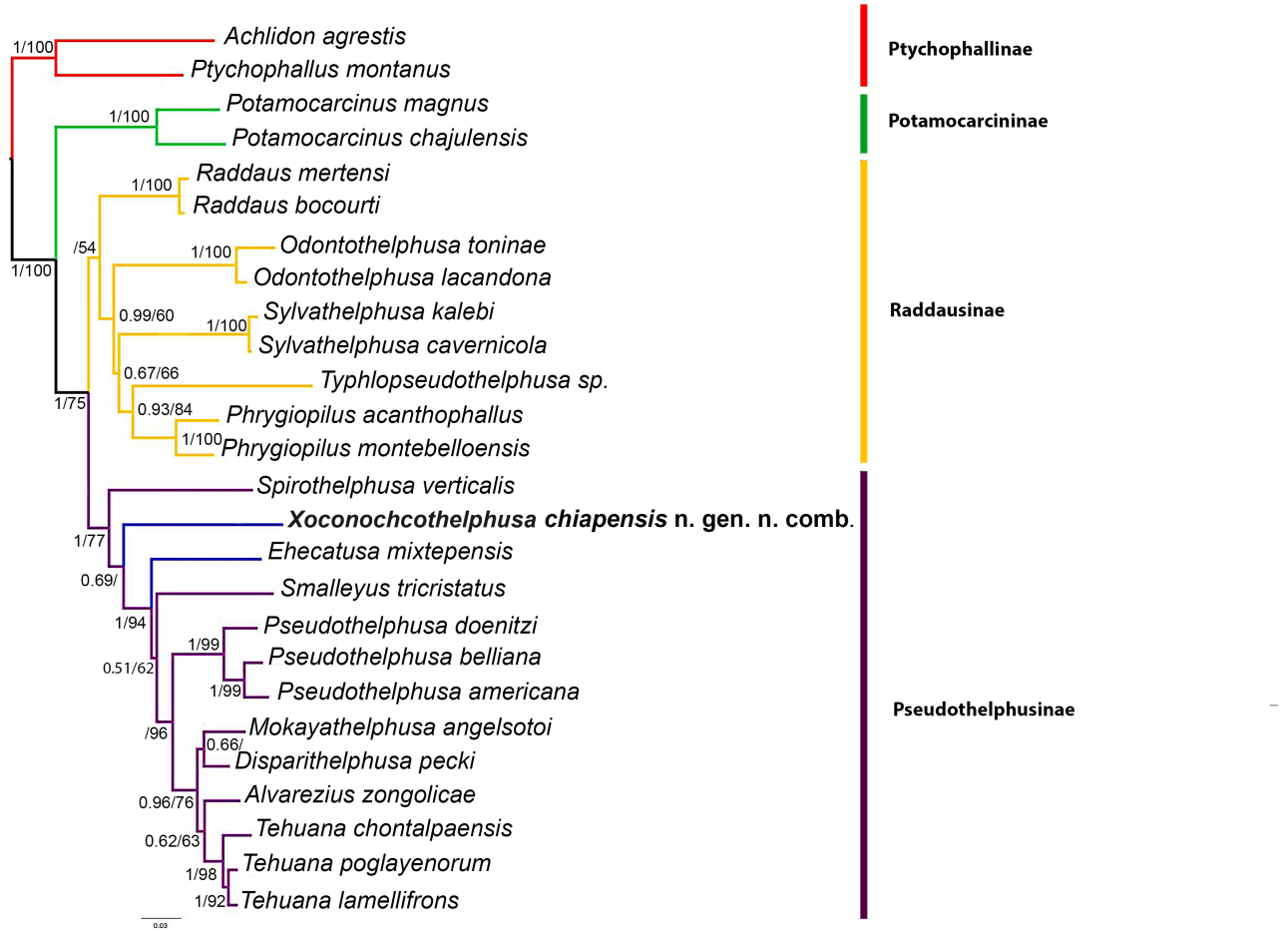

FIGURE 1. Tree obtained from the concatenated analysis of H3, 16S and COI through Maximum Likelihood and Inference Bayesian. Each color represents the subfamilies recognized by Álvarez *et al*. (2020): red—Ptychophallinae; green—Potamocarcininae; yellow—Raddausinae and purple—Pseudothelphusinae. The lineages of *Ehecatusa* and *Xoconochcothelphusa* genera were colored with blue. Values at nodes represent bootstrap values for the Maximum Likelihood analysis (above branches, scores 1–100) and posterior probabilities (below branches, scores 0-1).

Ehecatusa Ng & Low, 2010

Epithelphusa Rodríguez & Smalley, in Smalley, 1970: 103 (list), 105 (key).—Pretzmann 1972: 109.—Pretzmann 1974: 297.—Rodríguez & Smalley 1972: 75-76.—Rodriguez 1982: 126.—Villalobos-Hiriart *et al*. 1993: 287 (list).—Villalobos-Hiriart 2005: 2, 3 (tabla 1), 4, 7, 8, 10, 14-15, 17, 22, 51-53, 58, 59, 85, 87-89, 96, 105, 175, 181, 183.—Villalobos-Hiriart &

Álvarez 2008: 248 (tabla 1), 284, 299 (list).—Ng *et al*. 2008: 173 (list).—Villalobos & Alvarez 2010: 466, 471, 472.—Ojeda-Escoto 2017: 8, 10, 11.

Ehecatusa Ng & Low, 2010: 35 [nom. nov. for *Epithelphusa* Rodríguez & Smalley, in Smalley, 1970].—Guinot & Hendrickx 2014: 478 (table 1).—Alvarez & Villalobos 2016: 243.—Ojeda-Escoto 2017: 10, 11, 16, 26 (fig.), 27, 40 (fig.), 41 (tabla 2.2), 90–91 (apéndice 2).—Villalobos-Hiriart *et al*. 2019: 156 (table 1).—Álvarez *et al*. 2020: 12 (table 4), 20, supplementary material (table 1).—Moreno-Juárez *et al*. 2022a: 2.

Diagnosis. Carapace with dorsal surface slightly convex; posterior to cervical grooves with scattered short black bristles; cervical and mid frontal grooves wide, shallow, but marked; frontal portion regularly curved downward, to reach inferior frontal margin; superior frontal margin absent; lateral margin rounded and smooth. Orbits with internal inferior tooth, forming slender, grooved plate, slightly curved up, leaving orbital hiatus open, lodging antennal peduncle (Fig. 2). Exopod of third maxilliped shorter than ischium lateral border (0.72 × its length). G1 straight, somewhat slender, with distal third twisted towards median axis of sternal surface of body; caudolateral border with crenate crest on distal half of principal axis, and two subapical prominences, distal one forming part of apical cavity border. In mesial view, marginal plate and caudal surface fused on distal third to form caudo-marginal projection ending apically in slender rectangular lobe (3.2 × as wide as long) cephalad directed and lying over distal portion of mesial process, with its superior and inferior borders straight; cephalic end rounded (Fig. 3A). Mesial process in form of large, ax-shaped plate, cephalad directed, proximally elongated, with cephalic border straight through superior half and widely rounded along inferior one to reach caudal border; this border straight, slightly serrated and parallel regarding principal axis of G1. Marginal suture straight and evident along principal axis. Horns of lateral process slightly perceptible between principal axis and mesial process. In cephalic view, principal axis straight, lobe of caudo-marginal projection narrow, extending cephalically close to distal portion of mesial process and with final third curved mesially, separated from mesial plate (Fig. 3B). Mesial process as laminate plate, cephalic border entire and regularly curved in proximal third; superior border slightly concave. Lateral process formed by two conical spines, like vertical horns laterally directed; proximal spine larger than distal; space between them somewhat convex; distal spine forming part of border of apical cavity. Principal axis with crenate crest on distal half of caudolateral border evident and armed with 11 subtriangular teeth. In lateral view, distal half of principal axis slightly inclined laterally; mesial process as big ax-shaped plate, proximally elongated, with cephalic border widely and slightly curved, reaching caudal border; this border straight and parallel regarding principal axis of gonopod (Fig. 3C). Lateral process formed by two conical spines in vertical position; proximal spine conical, acute, and larger than distal; space between them with short and sharp medial border; distal spine forming part of border of apical cavity, with rounded and excavated apex. Caudolateral border of principal axis with crenate crest on distal half armed with 11 subtriangular teeth, and two accessory prominences, the distal one as elongate spoon, incurved, forming part of caudal portion of crest delimiting apical cavity; subdistal cylindrical, smooth, with acute apex. Apical cavity partially visible, with scattered setae on surface. In caudal view, distal half of principal axis straight, distal crest delimiting apical cavity concave, rising by distal prominence of caudolateral border (Fig. 3D). Cephalic portion of apical cavity and field of setae noticeable; central crest of apical cavity, straight and thin, delimiting field of setae. Caudolateral border with crenate crest on distal half with 11 subtriangular teeth; distal accessory prominence as elongate spoon, incurved, forming part of crest delimiting apical cavity; subdistal prominence cylindrical, smooth, with acute apex. Lateral process formed by two vertical horns, proximal spine larger, conical and acute; distal one shorter and triangular, continuing from apex cavity and laterally directed. In distal view, apical cavity subcircular, like shallow funnel, delimited by distal crests of apical lobe of caudo-marginal projection, caudal surface, distal prominences of caudolateral border and lateral process, mesial surface, and central crest; central crest as an internal extension of distal crest of mesial process (Fig. 3E). Setae field with short setae and conical granules, narrowly disseminated around opening of spermatic channel; spermatic channel in caudomesial position.

Type species. *Epithelphusa mixtepensis* Rodríguez & Smalley, in Smalley, 1970, by original designation.

Species included. *Ehecatusa mixtepensis* (Rodríguez & Smalley, in Smalley, 1970).

Distribution. This monotypic genus is known only from the type locality of *Eh. mixtepensis* at 36 km N of San Gabriel Mixtepec (approximately 16°20’42.19”N, 97°05’21.61”W; 858 m asl), municipality of San Gabriel Mixtepec, Oaxaca, Mexico.

Remarks. *Ehecatusa*, a replacement name for *Epithelphusa* Rodríguez & Smalley, in Smalley, 1970, belongs to a group of genera, each with one or two species, with a complex G1 morphology. Morphologically, *Ehecatusa* belongs to the subfamily Pseudothelphusinae because the G1 has a caudo-marginal projection that distally ends

in a slender lobe, extended cephalad. It can be distinguished from the other genera of Pseudothelphusinae by the presence of the lateral process, which is formed by two curved spines, like vertical horns; and by the unique form of the mesial process, which is a large, ax-shaped plate, cephalad directed, and proximally elongated. Also, the genetic analysis of the genus *Ehecatusa* shows that it is sister clade to all the genera of the former Pseudothelphusini tribe, after genus *Smalleyus* Alvarez, 1987 (Fig. 1).

Ehecatusa mixtepensis (Rodríguez & Smalley, in Smalley, 1970)

(Figs. 2, 3)

Epithelphusa mixtepensis Rodríguez & Smalley, in Smalley, 1970: 105 (key).—Pretzmann 1972: 109.—Pretzmann 1974: 297.—Rodríguez & Smalley 1972: 76.—Rodriguez 1982: 126 (key), 127.—Villalobos-Figueroa 1982: 220 (list).—Villalobos-Hiriart *et al*. 1993: 287 (list).—Villalobos-Hiriart 2005: 3 (tabla 1), 7, 8, 17, 51, 52, 58, 59, 87-89, 105, 181, 183.—Villalobos-Hiriart & Álvarez 2008: 248 (tabla 1), 285, 299 (list).—Ng *et al*. 2008: 173 (list).—Villalobos & Alvarez 2010: 466, 467 (table 2), 468 (fig.), 471 (fig.), 473 (fig.).

Ehecatusa mixtepensis Ng & Low, 2010: 35 [nom. nov. for *Epithelphusa* Rodríguez & Smalley, in Smalley, 1970].—Guinot & Hendrickx 2014: 478 (Table 1).—Alvarez & Villalobos 2016: 253 (table 8.1).—Ojeda-Escoto 2017: 16, 26 (fig.), 27, 38, 39 (fig.), 44, 50, 88 (apéndice 1), 90-91 (apéndice 3), 94 (apéndice 3).—Villalobos-Hiriart *et al*. 2019: 156 (table 1).—Álvarez *et al*. 2020: 6 (table 1), 10 (fig.), 13 (fig.), 20, 23 (key), supplementary material (table 1).—Moreno-Juárez *et al*. 2022a: 2.

Material examined. Holotype: male cl 16.8 mm, cw 26.9 mm (CNCR 309), 36 km N of San Gabriel Mixtepec (approximately 16°20’42.19”N, 97°05’21.61”W; 858 m asl), municipality of San Gabriel Mixtepec, Oaxaca, Mexico, coll. W. J. Schaldach, 10 December 1964.

Remarks. The only specimen existent of *E. mixtepensis* is the holotype, since its collection in 1964, there have been no new samplings in the type locality, although in some nearby streams, crabs of the species *Pseudothelphusa sulcifrons* Rathbun, 1898, have been captured.

Xoconochcothelphusa n. gen.

urn:lsid:zoobank.org:act:03B4A3CA-FD36-4CBC-82BD-A5CCA65E5BC3

Diagnosis. Carapace with dorsal surface flat, smooth; cervical and mid frontal grooves deep, well marked; frontal portion vertical, superior border present, ornamented with blunt granules; lateral margin slender, serrated with acute granules. Orbits with small, triangular, internal tooth, on inferior portion; orbital hiatus open (Fig. 4). Exopod of third maxilliped subequal in length to lateral border of ischium (0.9 × its length). G1 straight, stout, without lateral lobes or crenate border on mid length of principal axis, distal third twisted towards median axis of sternal surface of body. In mesial view, marginal plate and caudal surface fused distally to caudo-marginal projection, ending apically in broad subrectangular distal lobe (1.6 × as wide as long), cephalad directed, superior border straight, inferior one undulated ending in subterminal triangular tooth (Fig. 5A). Apical cavity concealed by distal lobe of caudo-marginal projection, narrowly opened, in transversal position. Apical portion of mesial surface with three prominent triangular teeth, similar in size, cephalad directed, proximal one being mesial process, two distal ones constituting lateral process, both extending beyond apical cavity of gonopod. In total view, principal gonopod axis straight, surface smooth; marginal suture well marked through proximal 2/3 of its length, with row of long setae on proximal portion (Fig. 6A). In cephalic view, apical portion with three prominent teeth, distal one somewhat rounded, medial and proximal ones triangular, similar in size, cephalad directed, ending in subacute tip (Fig. 5B). Apical cavity and setal field partially visible. Distal lobe of caudo-marginal projection broad, inferior border and subterminal triangular tooth discernible. Lateral shoulder evident, rounded. In total view, principal gonopod axis straight along mesial surface; lateral surface sinuous, with subdistal rounded prominence, constrained at middle length, straight proximally, slightly widening at base (Fig. 6B). In lateral view, lateral surface ending distally in well-marked lateral shoulder, forming 90º angle having vertex widely rounded. Distal crest of caudal surface forming part of apical cavity (Fig. 5C). Apical portion with three prominent triangular teeth fused at base, cephalad directed, distal one shorter, basal portion subrectangular, superior margin moderately rounded; median and proximal ones similar in size, triangular. In total view, principal gonopod axis with cephalic surface flat, almost straight; lateral surface ending in subdistal shoulder, caudal surface with subdistal widely rounded prominence, proximally constrained

at distal third and ending in small notch, extending slightly curved to base of G1 (Fig. 6C). In caudal view, distal crest sharp, mesocaudally projected forming caudal portion of apical cavity; distal lobe of lateral process flat, overreaching distal crest of caudal surface; median lobe triangular; lateral shoulder rounded (Fig. 5D). In total view, principal gonopod axis with marginal plate discernible, fringe of setae on proximal third of marginal suture, lateral surface ending in subdistal rounded prominence, continued proximally as wide concavity at base of G1 (Fig. 6D). In distal view, apical cavity slit like, slender, transversal relative to principal axis of gonopod, delimited by distal crest of caudal surface, distal border of lobe of caudo-marginal projection and lateral process; central crest as irregular plate in center of apical cavity; setae field subapical, with scarce apical setae, some extending to medial lobe of lateral process; opening of spermatic channel irregular shape, in caudal position (Fig. 5E). Prominences of lateral process evident, distal lobe rounded, margins curved, reaching well beyond apical cavity; median one as half circle, external border rounded, internal one straight, with sparse setae extending proximally. Lateral shoulder perceptible, margin rounded.

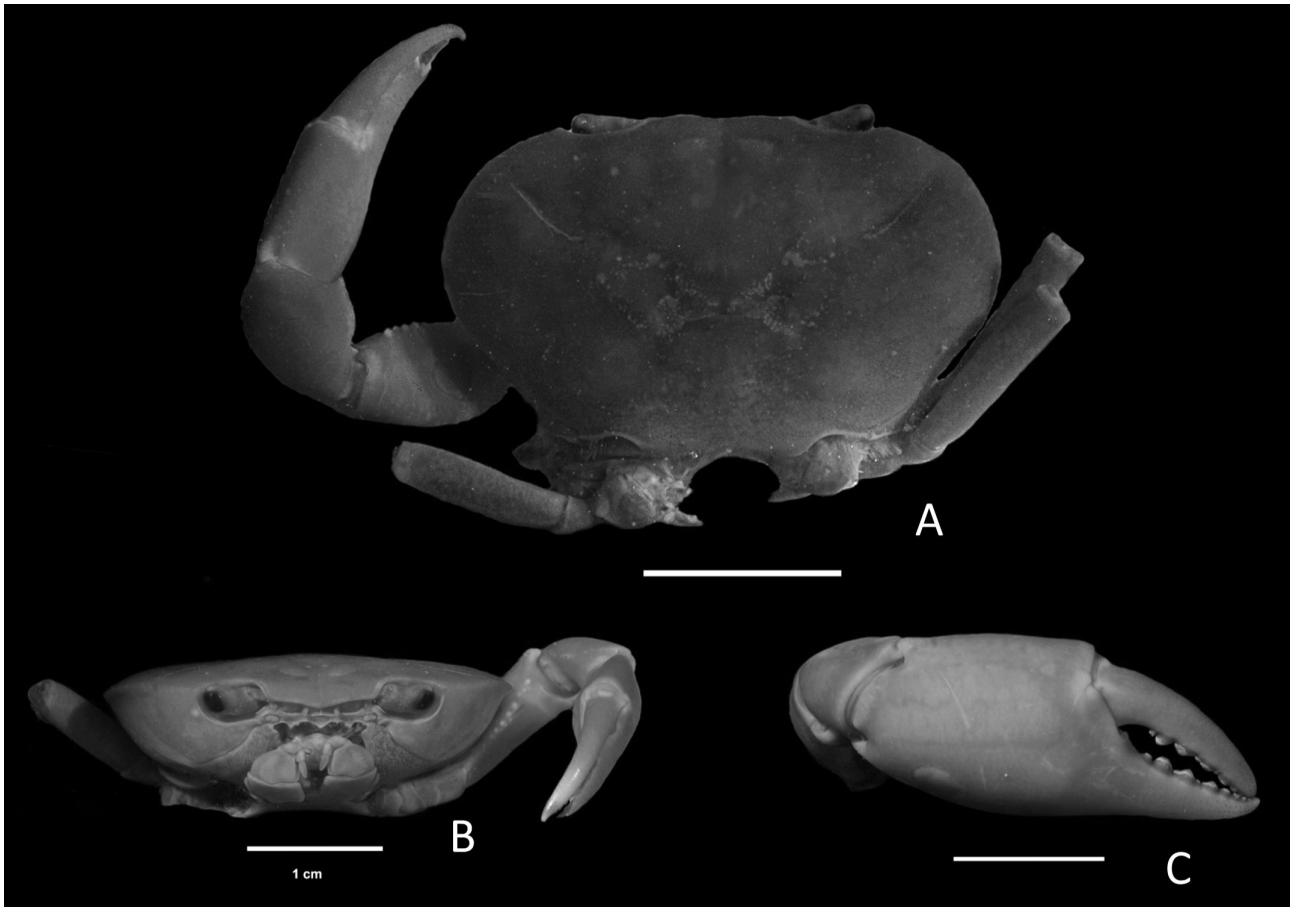

FIGURE 2. *Ehecatusa mixtepensis* (Rodríguez & Smalley, in Smalley, 1970), male holotype (cl 16.8 mm, cw 26.9 mm) (CNCR 309). A, carapace dorsal view; B, carapace frontal view; C, major chela.

Type species. *Xoconochcothelphusa chiapensis* **n. comb.**, designated herein.

Species included. *Xoconochcothelphusa chiapensis* (Rodríguez & Smalley, 1972), **n. comb.**

Etymology. The name of the new genus comes from the Nahuatl "Xoconochco" (= Soconusco), which is the regional designation for the Pacific slope of Chiapas state, the region of the Xoconochtli (nochtli—Prickly pear or pear cactus, xocotl—Fruit, xococ—Sour), that is the place where the sour fruit of the prickly pear grows.

Distribution. The genus is so far known to be endemic to the state of Chiapas, Mexico.

Remarks. The concatenated tree obtained from a multigene analysis based on partial DNA sequences of mitochondrial and nuclear genes (COI, 16S and H3) recovered *Xoconochcothelphusa chiapensis* **n. comb.** and *Ehecatusa mixtepensis* as independent branches within the subfamily Pseudothelphusinae. The new position of *X. chiapensis* is supported by the presence of the caudo-marginal projection, a diagnostic character of the subfamily

(Villalobos & Álvarez 2010; Álvarez *et al*. 2020). Morphological differences between *Ehecatusa* and the new genus *Xoconochcothelphusa* are described in the taxonomic section.

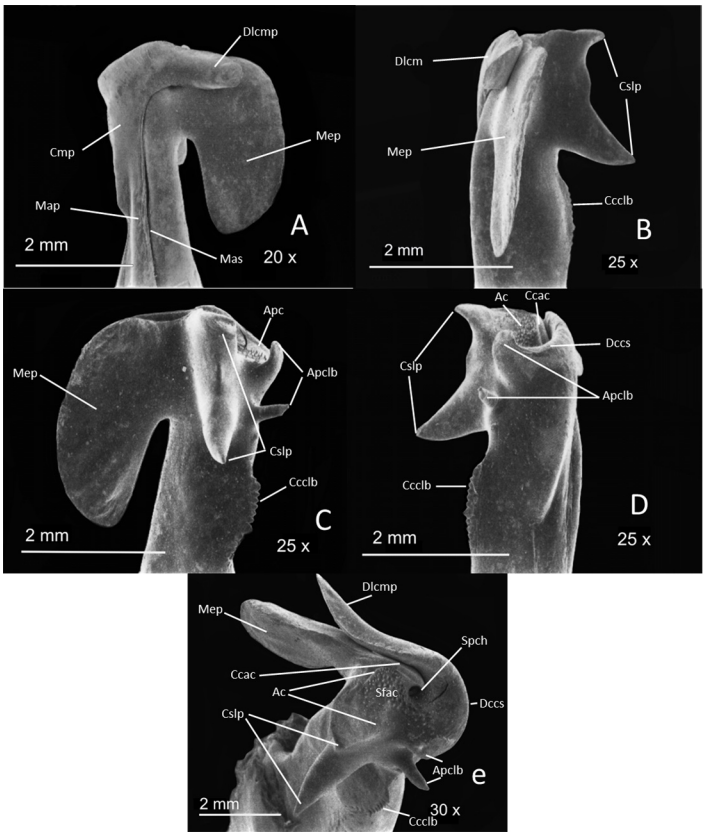

FIGURE 3. *Ehecatusa mixtepensis* (Rodríguez & Smalley, in Smalley, 1970), male holotype (cl 16.8 mm, cw 26.9 mm) (CNCR 309), distal portion of left G1. A, mesial view; B, cephalic view; C, lateral view; D, caudal view; E, distal view. Abbreviations: Ac = apical cavity; Apclb = accessory prominences of caudolateral border; Ccac = central crest apical cavity; Ccclb = crenate crest of caudo-lateral border; Cmp = caudo-marginal projection; Cslp = conical spines of lateral process; Dlcmp = distal lobe of caudo-marginal projection; Map = marginal plate; Mas = marginal suture; Mep = mesial process; Sfac = setae field of apical cavity; Spch = spermatic channel.

Based on the morphology of the G1, the relationships of the new genus with the rest of the known genera of Pseudothelphusinae are hard to establish. Nevertheless, it can be assigned to the subfamily by the distal fusion of the marginal plate with the caudal surface, to form a caudo-marginal projection that ends distally in a transversal broad, subrectangular plate, cephalad directed, with the superior border straight and the inferior one undulated. The characteristics that distinguish *Xoconochcothelphusa* **n. gen.**, from other genera in the subfamily Pseudothelphusinae are: 1) the shape of the caudo-marginal projection and 2) the fusion of the mesial and lateral processes forming an apical portion of the principal axis with three triangular teeth, like a trident, prominent, similar in size, cephalad directed, and distally surpassing the apical cavity.

Xoconochcothelphusa chiapensis (Rodríguez & Smalley, 1972), n. comb.

(Figs. 4, 5, 6)

Spirothelphusa chiapensis Rodríguez & Smalley, 1972: 75, fig 6, pl.3.

Epithelhusa chiapensis.—Rodriguez 1982: 128, 129, fig. 83.—Villalobos-Figueroa 1982: 220 (list).—Magalhães 1987: 57 (fig. 5), 58.—Villalobos-Hiriart *et al*. 1993: 287 (list).—Álvarez & Villalobos 1995: 90.—Villalobos-Hiriart 2005: 3 (table 1), 8, 17, 22 (table 2), 26 (table 3), 43, 51, 52, 58, 152.—Villalobos- Hiriart & Álvarez 2008: 248 (tabla 1), 284, 299 (list);—Ng *et al*. 2008: 173 (list).—Villalobos & Álvarez 2010: 461 (table 1), 466, 471, 472.—Ojeda-Escoto 2017: 44.

Ehecatusa chiapensis.—Ng & Low 2010: 35.—Guinot & Hendrickx 2014: 478 (table 1).—Alvarez & Villalobos 2016: 252 (table 8.1).—Ojeda-Escoto 2017: 16, 27, 50, 64, 95 (apéndice 3).—Villalobos-Hiriart *et al*. 2019: 156 (list).—Álvarez *et al*. 2020: 21, 23 (key)

Material examined. Holotype: male, cl 15.3 mm, cw 26.5 mm (CNCR 310) Finca Victoria (15°28'79.50"N, 92°42'14.89"W; 988 m asl), Municipality of Motozintla, Chiapas, Mexico, coll. Anonymous, 2 April 1962. Paratypes: male, cl 15.5 mm, cw 25.8 mm; same catalog number, locality, collector, and date as holotype; male, cl 20.0 mm, cw 32.5 mm (CNCR 34841), stream tributary of Vado Ancho River (15°22'58.78"N, 92°35'05.20"W; 365 m asl), approximately 10 km NE of Escuintla, Municipality of Escuintla, Chiapas, Mexico, coll. Angel Soto, July 2018.

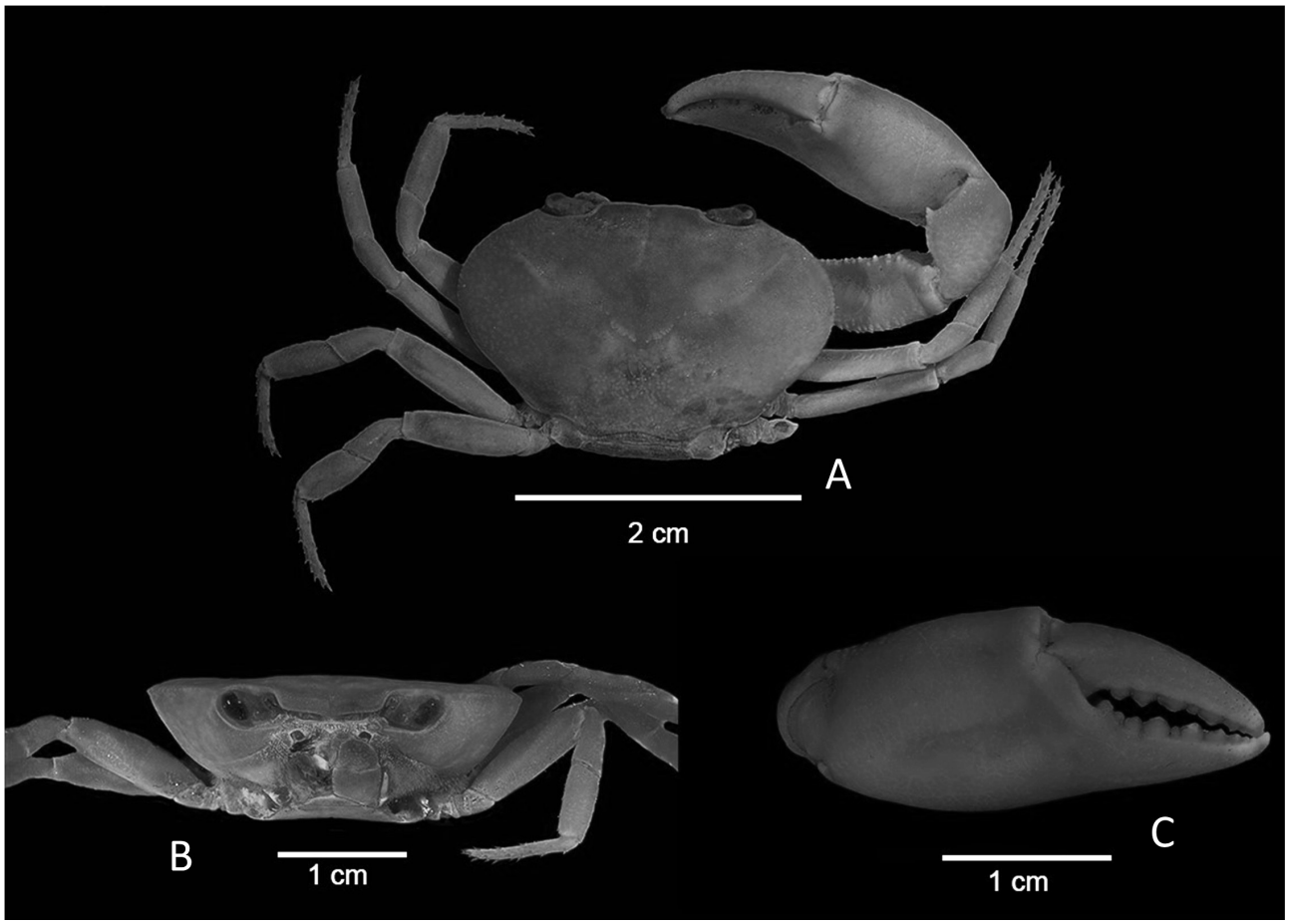

FIGURE 4. *Xoconochcothelpusa chiapensis* (Rodríguez & Smalley, 1972) **n. comb.**, male holotype (cl 15.3 mm, cw 26.5 mm) (CNCR 310). A, carapace, dorsal view; B carapace, frontal view; C, major chela.

Description. Moderate sized crab (cl 15.3–20.0 mm; cw 25.8–32.5 mm). In dorsal view, carapace transversally oval, widest anteriorly, dorsal surface flat, smooth, regions faintly indicated, gastric and branchial inflated, separated by wide, straight, shallow cervical groove, narrowing towards anterolateral margin of carapace, and disappearing well before reaching it (Fig. 4A). Frontal region punctate, depressed with respect to carapace surface. Postfrontal lobes low, slightly distinct, anteriorly marked by light depressions, separated by narrow, shallow median groove, anteriorly forming V-shaped notch dividing straight superior frontal margin, fading posteriorly. Pair of gastric furrows on metagastric region, approximately straight, divergent, forming wide V. Lateral margins of carapace sharp, finely serrated, posterior half smooth; portion between external orbital tooth and cervical groove straight, smooth. Posterior margin of carapace convex. In frontal view, front vertically deflexed, smooth, bilobed; inferior frontal border granulated, projected, slightly concave in middle; superior frontal border bilobed, lobes defined by low, rounded granules, irregularly disposed, separated by mesial notch (Fig. 4B). Superior margin of orbit granulated, continuous with inferior frontal border; lower orbital margin marked by row of granules; exorbital angle smooth;

internal inferior tooth, triangular, moderately high; orbital hiatus, occupied by basal segment of antennal peduncle. Medium septum dividing antennular fossae sharp, concealed by inferior frontal border. Epistomal space with setae, margin with median, triangular tooth; tip acutely rounded, separated of lateral ones by wide, rounded notches with granulated borders. Orifice of efferent branchial channel open, quadrangular, jugal and lateral angles gaping. Pterygostomial area hairy, faintly granulated. Ratio of exopod/ischium of third maxilliped 0.9.

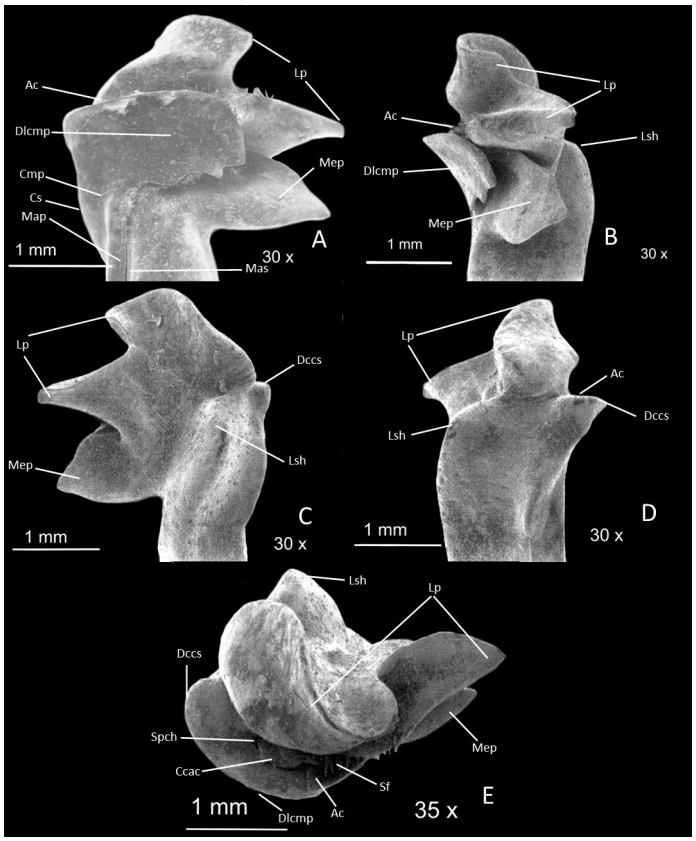

FIGURE 5. *Xoconochcothelphusa chiapensis* (Rodríguez & Smalley, 1972) **n. comb.**, male holotype (cl 15.3 mm, cw 26.5 mm) (CNCR 310), distal portion of left G1. A, mesial view; B, cephalic view; C, lateral view; D, caudal view; E, distal view. Abbreviations: Ac = apical cavity; Ccac = central crest apical cavity; Cmp = caudo-marginal projection; Cs = caudal surface; Dccs = distal crest of caudal surface; Dlcmp = distal lobe of caudo-marginal projection; Lp = lateral process; Lsh = lateral shoulder; Map = marginal plate; Mas = marginal suture; Mep = mesial process; Sf = spine field of apical cavity; Spch = spermatic channel.

First pereopods distinctly heterochelous, robust; major chela right. Larger cheliped with merus subtriangular in cross section; inner border sharp with conical granules, outer margin rounded, armed with low granules; inferior surface smooth. Carpus surface smooth, internal border armed with row of conical tubercles, ending anteriorly in small conical spine. Palm moderately swollen, smooth. Fingers with longitudinal rows of punctations, some of them black on distal half; slightly curved inwards, leaving narrow gap, tips crossing, bearing triangular sharp teeth on cutting edges. Dactyl slender, tip abruptly curved downwards, with longitudinal rows of low, rounded granules on dorsal surface; proximal half of cutting edge with three large teeth, rest decreasing in size distally. Propodus slightly more robust, punctate, cutting edge with alternate large-small triangular teeth, proximal tooth slender, large, followed by two smaller ones; remaining teeth triangular decreasing in size distally (Fig. 4C). Smaller cheliped moderately slender; merus internal surface smooth, superior border tuberculate, inferior one granulated; palm smooth, inferior surface delicately granulated; chela with fingers gently curved inwards, closing completely, cutting edges armed with triangular teeth, tips crossing; dactyl with dorsal surface punctated; cutting edge of propodus with alternate large and small sized teeth.

Ambulatory pereopods normal, decreasing in length posteriorly; ischia, meri, carpi and propodi smooth; dactyli slender, slightly longer than propodus, bearing 4-5 longitudinal rows of small, sharp, corneous spinules. Ventral

surface of carapace smooth, sternal sutures discernible; first sternite triangular, second to fourth fused, fifth to eight well marked. Abdomen triangular, all somites free, third somite broadest, sixth longest. Telson triangular, proximal margin slightly sinuous, lateral margins straight, apex subacutely rounded.

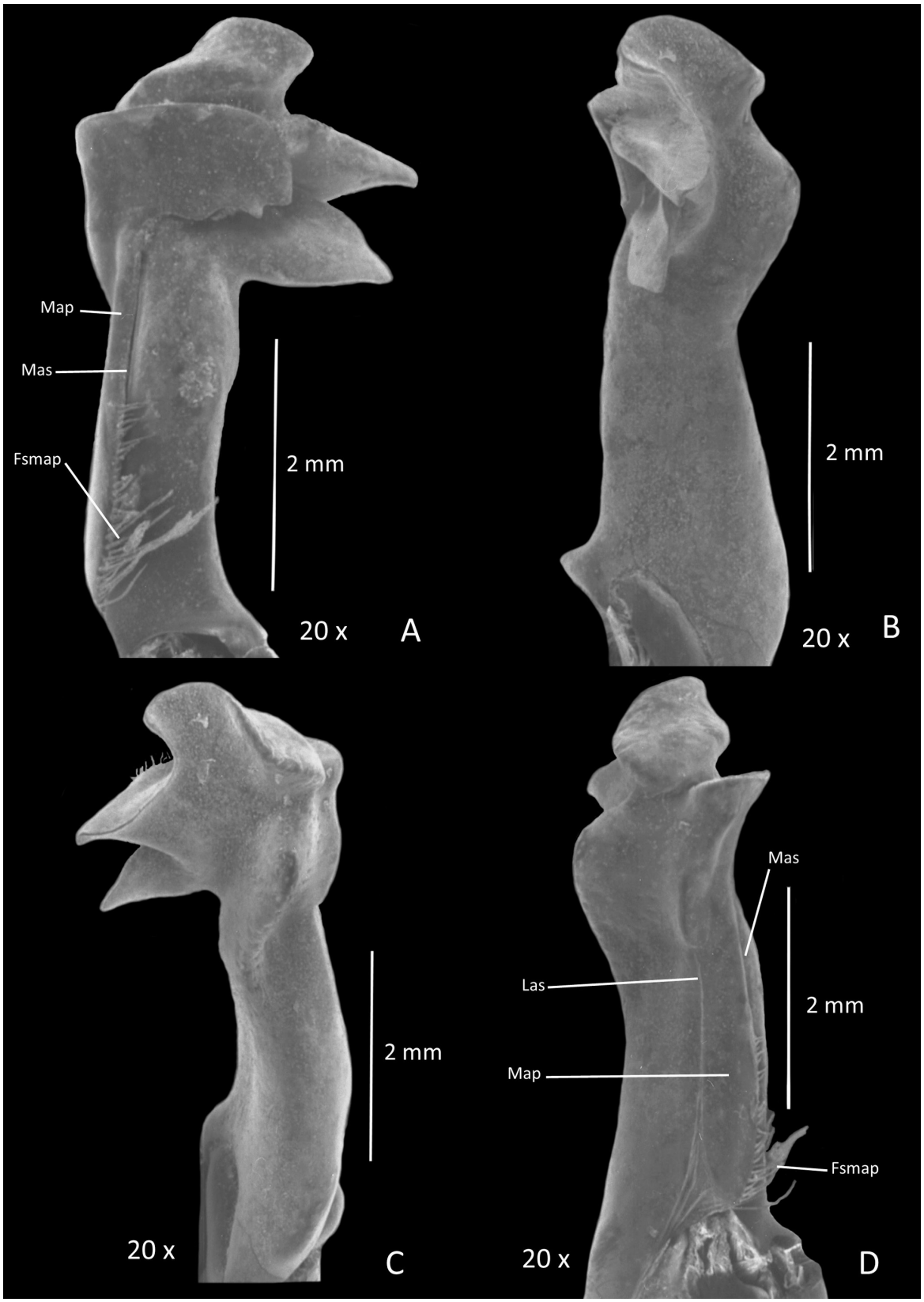

FIGURE 6. *Xoconochcothelphusa chiapensis* (Rodríguez & Smalley, 1972) **n. comb.**, male holotype (cl 15.3 mm, cw 26.5 mm) (CNCR 310), total view of left G1. A, mesial view; B, cephalic view; C, lateral view; D, caudal view. Abbreviations: Fsmap = fringe setae marginal plate; Las = lateral suture; Map = marginal plate; Mas = marginal suture.

G1 as in diagnosis of the genus.

Remarks. The specimen CNCR 34841, collected near the town of Escuintla, Chiapas, extends the distribution of *X. chiapensis* **n. comb.** approximately 20 km to the northwest, from Finca Victoria, near the Guatemalan border. This specimen is slightly bigger than the holotype and presents some differences in the G1 morphology, mainly in the size of the caudo-marginal plate, which is shorter, not as wide, and the inferior margin presents only one indentation. This rare species is known from only four males (one of them deposited in the Museu de Zoologia da Universidade de São Paulo, MZUSP 6380 (see Magalhães 1987)), therefore, it is difficult to assess the degree of variation in the G1 and other structures.

Spirothelphusa Pretzmann 1965

Strengeria (*Spirothelphusa*) Pretzmann, 1965: 8 [part].
Pseudothelphusa (*Ptychophallus*)—Bott 1968: 42 [part].
Spirothelphusa—Smalley 1970: 103 (list), 105 (key).—Rodríguez & Smalley 1972: 74.—Pretzmann 1972: 108.—Pretzmann 1974: 297.—Rodriguez 1982: 89.—Villalobos-Hiriart 2005: 17, 21, 22, 23 (tabla 2), 24, 39, 85, 88, 89, 183, 361 (Apéndice 1), 375 (anexo 1).—Villalobos-Hiriart *et al*. 1993: 286 (list).—Villalobos Hiriart & Álvarez 2008: 248 (tabla 1), 251, 297 (list).—Ng *et al*. 2008: 177 (list).—Villalobos & Alvarez 2010: 465, 471.—Alvarez & Villalobos 2016: 243.—Ojeda-Escoto 2017: 8, 11 (tabla 1.1), 13, 15, 16, 26 (fig. 1.12), 27, 38, 41 (tabla 2.2), 43, 90-91 (apéndice 2), 95 (apéndice 3).—Villalobos-Hiriart *et al*. 2019: 156 (table 1).—Álvarez *et al*. 2020: 12 (table 4), 19–21, 23–24 (key), supplementary material (table 1).—Moreno-Juárez *et al*. 2022b: 25 (fig. 1).—Moreno-Juárez *et al*. 2023: 2.
Pseudothelphusa (*Spirothelphusa*)—Pretzmann 1971: 22.

Diagnosis. Carapace with dorsal surface slightly convex, smooth; cervical and mid frontal grooves moderately deep, noticeable; frontal portion regularly curved downwards to form vertical front, superior border not well marked, smooth; lateral margin thin, serrated with small granules. Orbits with small, triangular, internal tooth, on inferior portion, triangular, low; orbital hiatus open. Exopod of third maxilliped subequal in length to lateral border of ischium (0.8 × length). G1 twisted, somewhat sturdy, distal third twisted towards median axis of sternal surface of the body; caudolateral border of principal axis with lateral lobe as wide subcircular laminar plate, with slightly irregular, sharp edge; caudo-marginal projection ending apically in prominent oval lobe, which wraps around gonopod cephalic surface. In mesial view, marginal plate and caudal surface fused on distal third to form caudo-marginal projection, twisted mesially, ending apically in prominent oval lobe that extend distally beyond apical cavity, borders serrated with small spinules (Fig. 7A). Lateral plate extending transversly along apical cavity, distal crest with spinules and setae, internal surface with scattered spinules. Mesial process hidden by distal lobe of caudo-marginal projection. Marginal plate and marginal suture straight, perceptible on proximal two thirds of principal axis, fusing with caudo-marginal projection on distal third. In cephalic view, principal axis straight with evident median notch below lateral lobe of caudolateral border; inner surface of caudo-marginal distal lobe, partially visible, cephalic and distal margins spinulated (Fig. 7B). Mesial process, as laminate triangular plate with smooth borders, acute apices, cephalad directed to overlap inner surface of caudo-marginal projection lobe, closing apical cavity, separated from the apical plate of lateral surface by a shallow notch. Lateral process with distal crest convex, spinulated. Accessory subapical spine slender, conical, acute. Lateral lobe on distal half of caudolateral border of principal axis entirely visible, surface with sparce granules, widely convex sharp edge. In lateral view, distal half of principal axis slightly inclined caudally; apical plate of lateral surface transversly ovoidal, cephalic end triangular, distal crest spinulated, caudal end rounded, surface with some granules and low protuberance (Fig. 7C). Mesial process just protruding from lower margin of apical lateral plate cephalic end. Accessory subapical spine slender, conical, acute. Lateral lobe on distal half of principal axis with surface granulated, margin slightly irregular, widely convex. In caudal view, principal axis distal half straight, median notch evident, caudal border broad, rounded (Fig. 7D). Caudo-marginal projection lobe oval shaped, overlying on distal portion of caudal border, marginally ornamented with spinules, surface smooth. Transversal lateral plate ovoid, marginally ornamented with spinules and short stout setae, internal surface with scattered spinules on central portion, cephalic end triangular, apices little projected, caudal portion rounded. Mesial process partially visible, hidden by lobe of caudo-marginal projection, triangular, superior margin with mid bulge, separated of cephalic end of transversal lateral plate by V-shaped notch. Lateral lobe of principal axis not completely visible, smooth caudal surface, moderately curved cephalically. In distal view, apical cavity narrow, widening towards cephalic portion; delimited by lobe of caudo-marginal projection,

distal crest of lateral process, and mesial process, which is partially fused to lateral plate. Internal surface of lateral plate with spinules (Fig. 7E). Setae field not perceptible. Spermatic channel opening slit-like, in caudal position, bordered by a short and vertical median crest.

Type species. *Pseudothelphusa verticalis* Rathbun, 1893, designated by Bott (1968).

Species included. *Spirothelphusa verticalis* (Rathbun, 1893).

Distribution. This monotypic genus is known from Tehuantepec region, Oaxaca, Mexico, with specimens collected by Dr. Spear, 4 males, 5 females, without a precise locality and date of collect, are deposited in the U. S. National Museum of Natural History (USNM 2537). It can be applied both to the entire isthmus of this name and only to the town of Santo Domingo Tehuantepec located near the Pacific coast of the state of Oaxaca (Rodríguez & Smalley 1972). New records extend the presence of *S. verticalis* to the northwest of the state of Chiapas in the municipalities of Ocozocoautla de Espinosa and Jiquipilas.

Spirothelphusa verticalis (Rathbun, 1893)

(Fig. 7)

Pseudothelphusa verticalis Rathbun, 1893: 652, plate LXXIV, figs. 8, 9.
Potamocarcinus verticalis Ortmann, 1897: 317.
Pseudothelphusa verticalis Rathbun, 1898: 510 (key), 513, 536–537 (list).—Young, 1900: 213.—Rathbun, 1905: 274 (key), 285, 286.—Coifmann, 1939: 109 (list).
Strengeria (*Spirothelphusa*) *verticalis* Pretzmann, 1965: 8 [part].
Pseudothelphusa (*Ptychophallus*) *verticalis*—Bott 1968: 42 [part].
Spirothelphusa verticalis—Smalley 1970: 103 (list), 105 (key).
Pseudothelphusa (*Spirothelphusa*) *verticalis*—Pretzmann 1971: 22.
Spirothelphusa verticalis—Rodríguez & Smalley 1972: 74, 75.—Pretzmann 1972: 108- 109.—Rodriguez 1982: 89–90.—Villalobos-Figueroa 1982: 220 (list).—Villalobos-Hiriart 2005: 22, 23 (tabla 2), 24, 27 (tabla 4), 40, 51, 59, 60, 86, 360 (apéndice 1).—Villalobos-Hiriart *et al*. 1993: 286 (list).—Villalobos Hiriart & Álvarez 2008: 248 (tabla 1), 251, 297 (list).—Ng *et al*. 2008: 177 (list).—Villalobos & Alvarez 2010: 461, 467 (table 2), 468 (fig. 5), 471 (fig. 8), 473 (fig. 9).—Alvarez & Villalobos 2016: 254 (table 8.1).—Ojeda-Escoto 2017: 27, 38, 43, 64, 88 (apéndice 1), 95 (apéndice 3).—Villalobos-Hiriart *et al*. 2019: 156 (table 1).—Álvarez *et al*. 2020: 5 (table 1), 10 (fig. 1), 13 (fig. 2), 23–24 (key), supplementary material (table 1).

Material examined. Male cl 20.7 mm, cw 33.2 mm (CNCR 25444), La Venta river, El Aguacero cascade (16°47’26.00”N, 93°29’ 20.00”W) (850 m asl), Biosphere Reserve Selva El Ocote, Municipality of Ocozocuautla de Espinoza, Chiapas, Mexico, coll. E. Moreno, K. Zárate & M. Casella, 20 August 2008; 2 males cl 18.1–21.3 mm, cw 30.0–33.5 mm, 2 females, cl 23.0–29.9 mm, cw 36.4–46.1 mm (CNCR 28900), Los Bordos Cave (16°49’38.08”N, 93°31’35.06”W) (643 m asl), near of the Biosphere Reserve Selva El Ocote, Municipality of Ocozocoautla de Espinosa, Chiapas, Mexico, coll. K. Zárate, 28 April 2013; 3 males cl 17.3–25.5 mm, cw 21.3–41.4 mm, 1 female, cl 23.6 mm, cw 37.7 mm (CNCR 31677), El Encanto Cave (16°47’26.00”N, 93°29’20.00”W) (748 m asl), Los Bordos Cave (16°49’38.08 N, 93°31’35.06” W) (643 m asl), near of the Biosphere Reserve Selva El Ocote, Municipality of Ocozocoautla de Espinosa, Chiapas, Mexico, coll. K. Zárate, O.R. Sánchez, 14–17 April 2014; 7 males cl 10.7–26.8 mm, cw 17.1–44.7 mm, 1 female, cl 23.3 mm, cw 37.2 mm (CNCR 35575), El Encanto Cave (16°47’26.00”N, 93°29’20.00”W) (748 m asl), Ecotourism Center El Aguacero Cascade, Municipality of Ocozocoautla de Espinoza, Chiapas, Mexico, coll. E. Moreno, K. Zárate & M. Casella, 16 March 2020; 4 males cl 16.1–26.1 mm, cw 23.7–41.2 mm (CNCR 36532), Los Bordos Cave (16°49’38.08 N, 93°31’35.06” W) (643 m asl), near of the Biosphere Reserve Selva El Ocote, Municipality of Ocozocoautla de Espinosa, Chiapas, Mexico, coll. J. Arroyave, M. Buenavad, D. Torres, J. López & K. Zárate, 20 March 2022; 1 male cl 22.4 mm, cw 37.9 mm, 2 females cl 19.7–25.7 mm, cw 31–41.9 mm (CNCR 37054), Colonia Tierra y Libertad, Municipality of Juquipilas (16°40’08.34 N, 93°38’52.47” W) (530 m asl), coll. C. Chávez, 2 November 1998.

Remarks. An important result derived from the present integrative molecular and multigene analysis is the new position of *Spirothelphusa verticalis*, previously included in the subfamily Raddausinae (Álvarez *et al*. 2020), and now recovered in the subfamily Pseudothelphusinae. The complex morphological pattern of the apical elements of the G1 thus far prevented a satisfactory classification of the species. A more detailed morphological revision showed the presence of a unique caudo-marginal projection. The fusion of the marginal plate and the caudal surface forming a twisted distal and laminate, oval apical lobe, which is bordered with small spines and turned around the

cephalic surface of the final third of principal axis. This result, based on molecular evidence, improve the current classification of the Pseudothelphusinae.

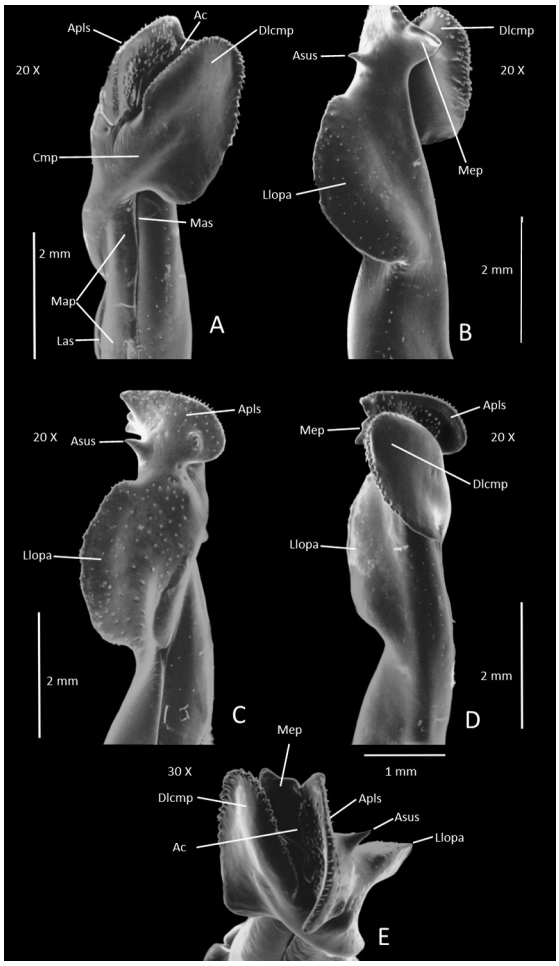

FIGURE 7. *Spirothelphusa verticalis* Rathbun, 1893, male (cl 20.7 mm, cw 33.2 mm) (CNCR 25444), distal portion of left G1. A, mesial view; B, cephalic view; C, lateral view; D, caudal view; E, distal view. Abbreviations: Ac = apical cavity; Apls = apical plate of lateral surface; Asus = accessory subapical spine; Cmp = caudo-marginal projection; Dlcmp = distal lobe of caudo-marginal projection; Las = lateral suture; Llopa = lateral lobe of principal axis; Map = marginal plate; Mas = marginal suture; Mep = mesial process.

Key to the genera of the subfamily Pseudothelphusinae Ortmann, 1897

1. Apex of the G1 with lateral process 2
- Apex of the G1 without lateral process 4
2. G1 with caudolateral border of principal axis bearing a wide subcircular laminar plate or reduced to a crenate crest on distal half 3
- G1 with caudolateral border of principal axis smooth, without any additional ornamentation; apex with the mesial and lateral processes fused, forming an apical plate with three triangular lobules, in transversal position and distally extended beyond the apical cavity . . . . . *Xoconochcothephusa* **n. gen.** (one species: *X. chiapensis* (Rodríguez & Smalley, 1972) **n. comb.**)
3. G1 principal axis ornamented on the distal half of caudolateral border with a crenate crest, divided in 11 subtriangular teeth; apical cavity subcircular, as a shallow funnel; caudo-marginal projection ending apically in a slender, rectangular distal lobe (3.2 × as wide as long), which is cephalad directed and extended in front of the distal portion of mesial process, with its superior and inferior borders straight, and the cephalic end rounded . . . . . .*Ehecatusa* (one species: *E. mixtepensis* (Rodríguez & Smalley, in Smalley, 1970))
- G1 principal axis ornamented on the distal half of caudolateral border with a wide subcircular laminar plate, with some irregular, sharp edge; apical cavity narrow, widening to cephalic portion; caudo-marginal projection ending apically in a prominent oval lobe, which is twisted around the gonopod cephalic surface, its margin is serrated with small spinules . . . . . *Spirothelphusa* (one species: *S. verticalis* (Rathbun, 1893))

4. G1 apex ornamented with spines; caudo-marginal projection single-lobed and finished cephalically in a border armed with spines or acute indentation . . . . . *Smalleyus* (one species: *Sm. tricristatus* Alvarez, 1987)
- G1 apex smooth without spines or ornamented with small spinules on the distal crests or on the inner faces of caudal, caudo-marginal and lateral surfaces of the apical cavity; caudo-marginal projection ending cephalad in 1-3 lobes, the distal one may be absent or appear as an acute, triangular, or rounded tooth 5
5. Distal conical prominence emerging from lateral crest, bearing apical setae; caudo-marginal projection single-lobed, lobe axe-shaped, large, about half of G1 length, cephalic border smooth, spinulated on the fusion with distal crest; mesial process as a subtriangular plate, tapering laterally, ending in two tips . . . . . *Alvarezius* (one species: *Alvarezius zongolicae* (Alvarez, Villalobos & Moreno, 2012))
- Distal conical prominence on lateral crest absent; caudo-marginal projection uni, bi or tri-lobed, proximal lobe when present frequently axe-shaped; mesial process as a rectangular, subtriangular, or irregular plate, lateral margin ending in 1–2 spines, or in a different number of triangular teeth 6
6. Mesodistal prominence present, conical or compressed caudo-cephalically; internal surface of proximal lobe of caudo-marginal projection with a high and well-marked carina; principal axis of G1 with the lateral constriction at mid-length. . . . . *Tehuana* (10 species)
- Mesodistal prominence absent; internal surface of proximal lobe of caudo-marginal projection with a softly or moderated marked carina; principal axis of the G1, with the lateral constriction on the distal third of his length 7
7. Caudo-marginal projection uni or bilobed, small triangular-shaped distal lobe, with an acute cephalic end (rarely rounded), or transformed into a row of denticles; may be separated from the proximal lobe by a V- or U-shaped notch, or may simply protrude from the superior angle of the proximal lobe; proximal lobe elongated or suboval (wider than long), and with the inner surface smooth or armed with a smooth to moderate straight carina; mesial process in the form of a triangular or subrectangular blade, terminating laterally in a long sharp spine or two or more teeth or denticles, and mesially usually with a small subtriangular expansion that closes the cavity of the gonopod apex . . . . . *Pseudothelphusa* (27 species)
- Caudo-marginal projection trilobed, distal and middle lobes triangular and rounded or spiniform of same length, without V- or U-shaped notch, and simply protrude from the superior angle of the proximal lobe; proximal lobe ax-shaped, elongated and straight, or as slender sheet, curved, extending through distal third of main gonopod axis; mesial process large, subrectangular with lateral margin ornamented with several spiniform teeth or moderately small and triangular 8
8. Caudo-marginal projection trilobed, distal and middle lobes triangular and rounded, respectively, proximal as elongated and straight lobe, ax-shaped; mesial process moderately small and triangular, lateral margin ended in an acute spine, internal angle projected above the inner surface of proximal lobe of caudo-marginal projection, as a triangular plate apically subacute; apical cavity with the central crest rounded, armed on the surface and internal faces of the apical cavity with numerous spinules and short setae . . . . . *Disparithelphusa* (one species: *D. pecki* Smalley & Adkison, 1987)
- Caudo-marginal projection trilobed, distal and middle lobes spiniform of same length, proximal as elongated and curved sheet extending through distal third of main gonopod axis; mesial process large, subrectangular, with lateral margin ornamented with several spiniform teeth; apical cavity with the central crest rounded in the portion adjacent to spermatic pore and straight towards the internal angle of mesial process, with his surface smooth; corneous setae present in the field of spines area and on the internal surface of the cavity caudal portion . . . . . *Mokayathelphusa* (one species: *M. angelsotoi* Moreno, Villalobos & Álvarez, 2022b)

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