zoosystema

2025 • 47 • 26

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art. 47 (26) — Published on 23 October 2025
www.zoosystema.com

PUBLICATIONS SCIENTIFIQUES

MUSÉUM NAL HIST NATURELLE

Couverture / *Cover* :
Phrygiopilus senticosus n. sp., holotype, UVGCR 31, habitus, dorsal view.

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Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / https://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9551/ ISSN (électronique / *electronic*) : 1638-9387

Taxonomic revision and distribution of the freshwater crabs of the family Pseudothelphusidae (Decapoda, Brachyura) from Guatemala, with the descriptions of two new species and keys to the species of all genera

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Submitted on 24 September 2024 | Accepted on 12 March 2025 | Published on 23 October 2025

urn:lsid:zoobank.org:pub:484420FE-9576-49AF-9049-0CAE5C6AC76E

Magalhães C. & Wehrtmann I. S. 2025. — Taxonomic revision and distribution of the freshwater crabs of the family Pseudothelphusidae (Decapoda, Brachyura) from Guatemala, with the descriptions of two new species and keys to the species of all genera. *Zoosystema* 47 (26): 581-615. https://doi.org/10.5252/zoosystema2025v47a26. http://zoosystema.com/47/26

ABSTRACT
The taxonomic status of several of the freshwater crab species from Guatemala is somewhat confused due to old and poor descriptions of some taxa, description of several species based on female specimens, synonymization and revalidation of species and subspecies, and new combinations made by different authors. Here, we revised the taxonomy and geographic distribution of the Pseudothelphusidae Ortmann, 1893 freshwater crabs from Guatemala, Central America. Historical material deposited in major collections of several institutions was examined, as well as previously unstudied material from the crustacean collection of the Universidad del Valle de Guatemala in Guatemala City. The pseudothelphusid crab fauna of Guatemala consists of 17 currently valid species assigned to six genera: *Elsalvadoria* Bott, 1967 (two species), *Phrygiopilus* Smalley, 1970 (five species), *Potamocarcinus* H. Milne Edwards, 1853 (two species), *Raddaus* Pretzmann, 1965 (three species), *Typhlopseudothelphusa* Rioja, 1953 (two species), and *Zilchia* Pretzmann, 1968 (three species). Five species described only from female specimens are treated as *incertae sedis*: they are too poorly defined to be classified reasonably. Two species, one from *Phygiopilus* and the other from *Zilchia*, are described as new. Illustrations of the first male gonopod and a keys to the species of all genera are provided, as well as a discussion of their geographic and altitudinal distribution accompanied by maps of the species occurrences.

KEY WORDS
Biodiversity, Central America, crustacean collections, faunal survey, Neotropical region, zoogeography, new species.

RÉSUMÉ

Révision taxonomique et distribution des crabes d'eau douce de la famille des Pseudothelphusidae (Decapoda, Brachyura) du Guatemala, avec la description de deux nouvelles espèces et une clé des espèces de tous les genres.
Le statut taxonomique de plusieurs espèces de crabes d'eau douce du Guatemala est quelque peu confus en raison de descriptions anciennes et médiocres de certains taxons, de plusieurs espèces basées sur des spécimens femelles, de la synonymisation et de la revalidation d'espèces et de sous-espèces, ainsi que de nouvelles combinaisons faites par différents auteurs. Nous avons ici révisé la taxonomie et la répartition géographique des crabes d'eau douce Pseudothelphusidae Ortmann, 1893 du Guatemala, en Amérique centrale. Nous avons examiné des spécimens historiques déposés dans les principales collections de plusieurs institutions, ainsi que du matériel non étudié auparavant provenant de la collection de crustacés de l'Universidad del Valle, à Guatemala City. La faune de crabes pseudothelphusidés du Guatemala comprend 17 espèces actuellement valides, réparties en six genres : *Elsalvadoria* Bott, 1967 (deux espèces), *Phrygiopilus* Smalley, 1970 (cinq espèces), *Potamocarcinus* H. Milne Edwards, 1853 (deux espèces), *Raddaus* Pretzmann, 1965 (trois espèces), *Typhlopseudothelphusa* Rioja, 1953 (deux espèces) et *Zilchia* Pretzmann, 1968 (trois espèces). Cinq espèces décrites uniquement à partir de spécimens femelles sont considérées comme *incertae sedis* : elles sont trop mal définies pour être classées de manière cohérente. Deux espèces, l'une de *Phygiopilus* et l'autre de *Zilchia*, sont décrites comme nouvelles. Des illustrations du premier gonopode mâle et une clé des espèces de tous les genres sont fournies, ainsi qu'une discussion sur leur distribution géographique et altitudinale agrémentée de cartes de répartition des espèces.

MOTS CLÉS
Amérique centrale,
biodiversité,
collections de crustacés,
inventaire faunique,
région néotropicale,
zoogéographie,
espèces nouvelles.

INTRODUCTION

Guatemala forms part of the Central American Isthmus, a land bridge that permitted the interchange of North and South American biota and which fostered the evolution of a highly diverse fauna in this region (Bacon *et al.* 2015; O'Dea *et al.* 2016). The Central American region harbors a rich fauna of freshwater crabs, which is comprised predominantly by representatives of Pseudothelphusidae Ortmann, 1893 (e.g., Smalley 1970; Pretzmann 1972, 1978, 1980; Rodríguez 1982; Rodríguez & Magalhães 2005; Lara *et al.* 2013; Magalhães *et al.* 2013, 2015; Wehrtmann *et al.* 2016; Magalhães & Ng 2019; Mantelatto *et al.* 2024) and just a few records of species belonging to Trichodactylidae H. Milne Edwards, 1853 (Rathbun 1893; Pretzmann 1968; Magalhães & Türkay 1996, 2008; Tejeda-Mazariegos *et al.* 2018; Magalhães & Ng 2019).

The primary freshwater crab fauna of Guatemala consists mostly of Pseudothelphusidae species (Cumberlidge *et al.* 2014). The taxonomic status of several of these species is somewhat confused due to old and poor description of some taxa, descriptions of several species based on female specimens, synonymization and revalidation of species and subspecies, and new combinations made by different authors that have dealt with this group (A. Milne-Edwards 1866; Rathbun 1897, 1905; Pretzmann 1965, 1971, 1972, 1975, 1978, 1980; Bott 1967, 1970; Smalley 1970; Bott 1967, 1970; Delamare Deboutteville 1976a, b; Delamare Deboutteville & Juberthie 1976; Rodríguez 1982; 2001; Rodríguez & Hobbs 1989). Cumberlidge *et al.* (2014) reviewed the conservation status of the Neotropical freshwater crabs and reported six genera and 12 species for Guatemala. In a more recent update of the diversity and conservation status of the country's fauna, however, Wehrtmann *et al.* (2016) listed 17 valid species, including two yet undescribed ones. The present study aimed to revise the taxonomy of the pseudothelphusid crabs from Guatemala, offers high-quality illustrations of their gonopods, describes the two new species mentioned in Wehrtmann *et al.* (2016), and provides keys for their identification.

MATERIAL AND METHODS

Taxonomy

The material examined herein is deposited in the crustacean collections of the following institutions: American Museum of Natural History, New York; Field Museum of Natural History, Chicago; Instituto Nacional de Pesquisas da Amazônia, Manaus; Muséum national d'Histoire naturelle, Paris; Museo de Zoología, Centro de Investigación en Biodiversidad y Ecología Tropical, Universidad de Costa Rica, San José; National Museum of Natural History, Smithsonian Institution, Washington, D.C.; The Natural History Museum of the United Kingdom, London; Naturhistorisches Museum Wien, Vienna; Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main; Tulane Museum of Natural History, New Orleans; and Universidad del Valle de Guatemala, Guatemala City. Specimens were also obtained from field surveys in Guatemala conducted in January and July 2014. Sampling and transportation were done according to the permit issued by CONAP # 177/2014. For the taxonomic identification we used the keys, descriptions, and illustrations available in Bott (1956, 1970), Smalley (1970), Pretzmann (1972, 1978, 1980), Rodríguez (1982, 2001), and Rodríguez & Hobbs (1989), and by comparison with the type material when available. The description of the gonopod morphology is based on the terminology proposed by Smalley (1964), Rodríguez (1982), and Villalobos & Alvarez (2010). In addition to the nominal names, the entries in the synonymic list cover explicitly or

implicitly records from Guatemala only. We followed the classificatory system of Álvarez *et al.* (2020), which also contains keys to the subfamilies. Genera can be identified using the keys in Rogers *et al.* (2020); keys to the species are offered before the taxonomic treatment of each genus.

The label data of some lots have been kept in the original language (Spanish) as much as possible. The meanings are: aldea, village; carretera, road; finca, farm; lago, lake; laguna, lagoon; quebrada, stream; río, river; sierra, mountain range.

Geographic distribution

The distribution maps were generated using the QGIS software, v. 3.16 (http://www.qgis.org/ptBR/site/); shape files for the hydrographic regions were obtained from the HidroBASINS website (https://www.hydrosheds.org/products/hydrobasins). The geographic coordinates and elevation data for each record were obtained either from a GPS apparatus during sampling or from data on the labels of the collection lots. When coordinates were unavailable, the localities were georeferenced using Google Earth® software, online gazetteers (GeoNames: http://www.geonames.org/), and selected charts of the Guatemala Topographic Maps 1:50,000 prepared by the Instituto Geográfico Nacional "Ingeniero Alfredo Obiols Gómez", Guatemala, and the U.S. National Imagery and Mapping Agency, Series E754 (available at https://maps.lib.utexas.edu/maps/topo/guatemala/, accessed in June 2024). Elevation data not available on labels were estimated by plotting geographic coordinates of the place of occurrence in Google Earth® and reading the corresponding elevation at the specific point. In this case, these data are indicated in square brackets.

Measurements

Measurements of the crab carapace are in millimeters when they are available; carapace width was measured across the carapace at its widest point, and carapace length was measured along the midline, from the frontal to the posterior margin. Both measurements follow the number and sex of the specimens examined and are given between parenthesis according to the following format: (carapace width:carapace length); in lots with more than three specimens, only the measurements of the smallest and the largest individuals are informed.

Abbreviations

Institutions

AMNH	American Museum of Natural History, New York;
FMNH	Field Museum of Natural History, Chicago;
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus;
NHMB	Naturhistorisches Museum Basel, Basel;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHM	The Natural History Museum of the United Kingdom, London;
NHMW	Naturhistorisches Museum Wien, Vienna;
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main;
TMNH	Tulane Museum of Natural History, New Orleans;
UCR-MZ	Museo de Zoología, Centro de Investigación en Biodiversidad y Ecología Tropical, Universidad de Costa Rica, San José;
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.;
UVGCR	Universidad del Valle de Guatemala, Guatemala City.

Other abbreviations used in the text

cw	carapace width;
cl	carapace length;
elev.	elevation;
juv	juvenile;
immat	immature;
G1, G2	male first and second gonopods, respectively;
ov	ovigerous;
P	pereiopod;
spec	specimen(s);
uncat	uncatalogued lot.

SYSTEMATICS

Family Pseudothelphusidae Ortmann, 1893
Subfamily Potamocarcininae Ortmann, 1897
Genus *Potamocarcinus* H. Milne Edwards, 1853

Potamocarcinus armatus
H. Milne Edwards, 1853
(Figs 1; 13)

Potamocarcinus armatus H. Milne Edwards, 1853: 208; 1854: 174, pl. 13, fig. 3. — Rathbun 1905: 308 (part). — Villalobos Hiriart & Álvarez 2008: 297 (part, in list). — Ng *et al.* 2008: 176 (part, in list). — Wehrtmann *et al.* 2016: 779 (in list). — Acevedo-Alonso & Cumberlidge 2022: 582 (Appendix 2, in list).

Potamocarcinus (*Potamocarcinus*) *armatus* – Bott 1967: 374. — Pretzmann 1971: 20 (in list). — Rodríguez 1982: 119, figs 69g, 70a, h, 71c.

Potamocarcinus (*Potamocarcinus*) *nicaraguensis aequispinosus* Pretzmann, 1971: 20; 1972: 69, figs 385, 386, 408, 409.

Potamocarcinus (*Potamocarcinus*) *armatus aequispinosus* – Pretzmann 1975: 617, pl. 2, pl. 6 figs 18, 19; 1980: 655, pl. 15 fig. 64.

Key to Guatemalan species of *Potamocarcinus* H. Milne Edwards, 1853

1. Carapace with anterolateral margin bearing large, acute teeth (Fig. 1A, C); G1 with marginal process and mesodistal lobe of apex erected, not folded over apex cavity (Fig. 1G-I); cephalic process vestigial, reduced to two low protuberances (Fig. 1I) ..... *Po. armatus* H. Milne Edwards, 1853
1'. Carapace with anterolateral margin bearing minute, blunt teeth (Fig. 2A); G1 with marginal process and mesodistal lobe of apex folded over apex cavity (Fig. 2E, F); cephalic process bifid, with two distinct spiniform teeth (Fig. 2F) ..... *Po. magnus* (Rathbun, 1896)

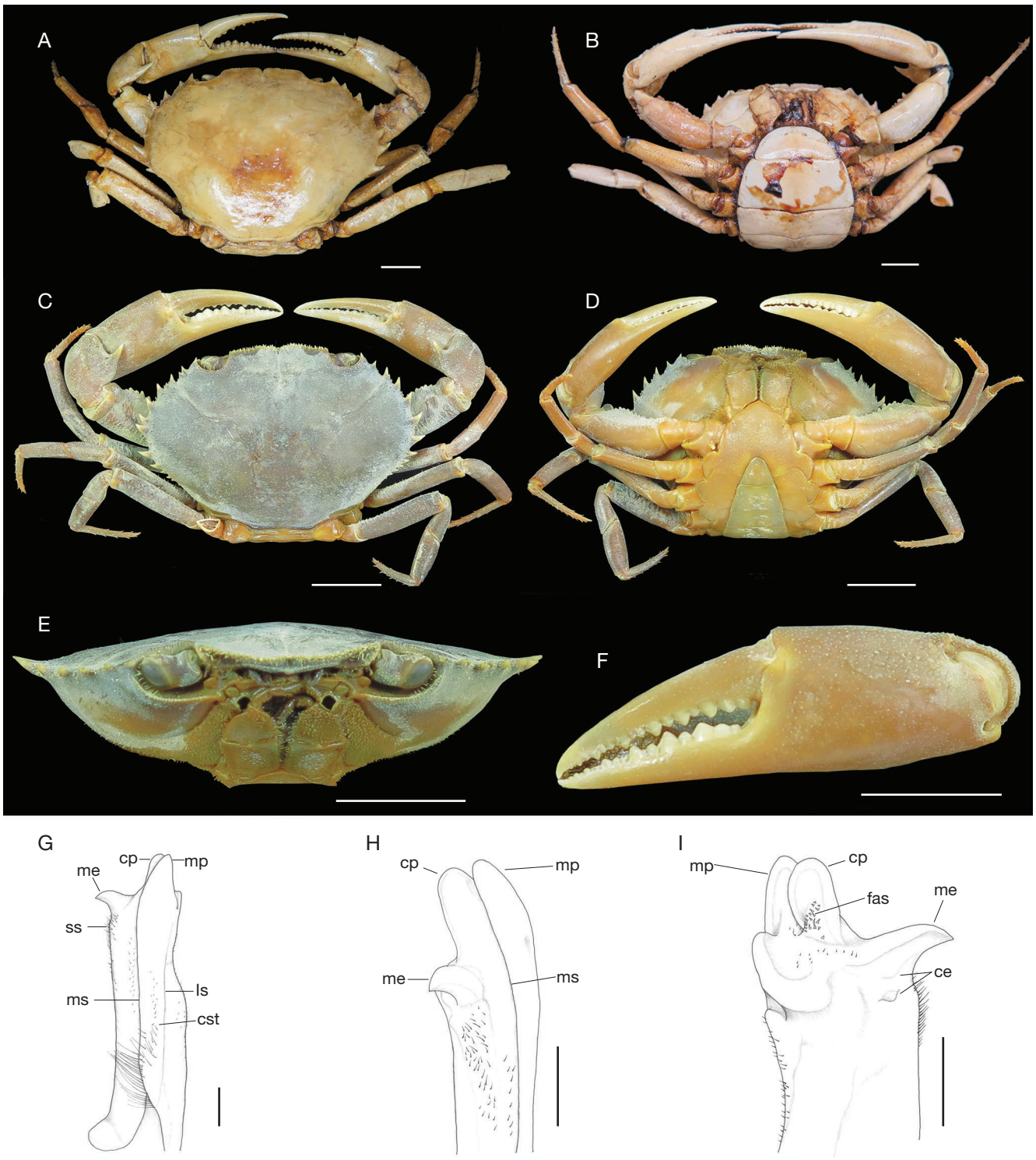

Fig. 1. — *Potamocarcinus armatus* H. Milne Edwards, 1853, **A**, **B**, female, holotype, dry specimen, MNHN-IU-2000-4025: **A**, habitus, dorsal view; **B**, habitus, ventral view; **C**-**I**, male, INPA 2123: **C**, habitus, dorsal view; **D**, ventral view; **E**, frontal view; **F**, left chelae (largest), lateral view; **G**, G1, left, mesocaudal view; **H**, left G1, distal portion, cephalic view; **I**, left G1, distal portion, laterocephalic view. Abbreviations: **ce**, cephalic process; **cp**, caudal process; **cst**, caudal patch of setae; **fas**, field of apical spines; **ls**, lateral suture; **me**, mesial process; **mp**, marginal process; **ms**, marginal suture; **ss**, mesocephalic subdistal patch of setae. Scale bars: A-F, 10 mm; G-I, 1 mm. Photos: C. Magalhães.

Type material examined. — **Holotype (by monotypy). Guatemala** • 1 ♀ (60.1:40.5), dry; collecting data unknown; MNHN-IU-2000-4025 (=MNHN-B4025).

Other material examined. — **Guatemala** • 1 ♂ 4 ♀; Petén, Laguna de Petén, outlet; [16°58'40.75"N, 89°42'04.80"W; 113 m elev.]; 20.II.1935; H. van der Schalie leg.; USNM 189301 • 1 juv. ♂ (17.3:11.8) 4 ♀ (20.3:14.4-32.6:22.0); Petén, Lago Petén-Itzá, northern portion; 16°59'48"N, 89°42'10"W; 122 m. elev.; 14.I.2014; I. S. Wehrtmann & M. Orozco leg.; UCR-MZ 3234 • 2 ♂, 2 ♀; Petén, Río Subín, Subín; 16°38'14"N, 90°10'59"W; 115 m. elev.; 15.I.2014; I. S. Wehrtmann & M. Orozco leg.; UCR-MZ 3235 •

2 ♂ (33.2:21.7; 41.5:25.9), 1 ♀ (36.3:24.0); Petén, Río Subín, Subín; 16°38'14"N, 90°10'59"W; 115 m. elev.; 15.I.2014; I. S. Wehrtmann & M. Orozco leg.; INPA 2123 • 1 ♂ (36.5:23.7) 2 ♀; Alta Verapaz, Río Chajmayic [= Chajmaic] [15°45'05"N, 89°56'45"W; 197 m elev.], about midway between Río San Simón and Celba; 14.IV.1935; C. L. Huffs *et al.* leg.; USNM 230095.

DISTRIBUTION. — Guatemala (Alta Verapaz, Petén) (Pretzmann 1980, Wehrtmann *et al.* 2016; this study) (Fig. 13).

OTHER RECORDS IN GUATEMALA. — Pretzmann (1980): Petén, Laguna Petén-Itzá, Flores [16°55'39"N, 89°54'10"W; 112 m elev.]; Petén, road to Belize, near Macanché [16°57'39"N, 89°38'02"W; 193 m elev.]; Petén, Mopan, at Río Melchor Mencos, border with Belize [17°03'27"N, 89°09'06"W; 92 m elev.].

DESCRIPTION OF G1 (Fig. 1G-I)

Stout, straight in both caudal, mesial views, moderately compressed mesolaterally; caudal margin nearly straight; lateral margin straight proximally, distinctly concave distally in mesial view; mesial surface with irregular rows of minute setae medially; caudal surface with elongated patch of caudal setae along proximal and median portions, setae longer proximally, decreasing in size medianly; mesocephalic surface with subdistal, elongated patch of setae slightly increasing in size distally. Spermatic channel distal opening on apex cavity, situated towards lateral end at base of caudal process. Marginal suture on mesial surface, straight along most of stem, regularly curved to lateral side distally in mesial view, proximal portion with row of large marginal setae. Marginal process subtriangular, erect, tip slightly rounded, as long as or slightly longer than caudal process in mesial and laterocephalic views, partially overlapping caudal process. Lateral suture incomplete, marked by somewhat deep sulcus on first 3/4 of caudal surface. Mesial process as strong subtriangular projection directed cephalad on distal portion of mesocephalic surface. Apex slightly distorted in cephalic direction; caudal process erect (not folded over apex cavity), largely projected distally, tip rounded in mesial, laterocephalic views. Apex cavity short; field of apical spines weakly developed, with few short, small spines slightly extended distally along half length of cephalic surface of caudal process. Cephalic process vestigial, reduced to two low protuberances subapically on cephalic surface at base of mesial process.

REMARKS

The type locality of this species is unknown (H. Milne Edwards 1853). The holotype of *Po.* (*Po.*) *nicaraguensis aequispinosus* Pretzmann, 1971, a junior synonym of *Po. armatus*, is a female (NHMB 550a – not examined) from an unknown locality in Guatemala. For the discussion of the taxonomic status and type locality issues regarding these taxa, see Rodríguez (1982: 120).

The presumptive occurrence of this species in Mexico was based on specimens from Río Macuspana (Monte Cristo, municipality of Macuspana, state of Tabasco) identified by Rathbun (1905) and Rodríguez & Smalley (1972) as *Po. armatus*. Pretzmann (1975) used these specimens to describe *Potamocarcinus* (*Po.*) *hartmanni* Pretzmann, 1975. The last species was later recorded from other localities in Tabasco (Villalobos Hiriart & Álvarez 2008). Therefore, it seems reasonable to assume that *Po. hartmanni* has a northwestern distribution in rivers of the Gulf of Mexico drainage in the Mexican state of Tabasco, whereas *Po. armatus* is restricted more in the Southeast in rivers of both the Gulf of Mexico and Caribbean drainages in Guatemala and probable Belize as well.

Potamocarcinus magnus (Rathbun, 1896)
(Figs 2; 13)

Pseudothelphusa magna Rathbun, 1896: 377, fig. 1, 2; pl. 29, 30, figs 7-10; 1906: 502 (in list).

Potamocarcinus guatemalensis Rathbun, 1904: 242 (*nomen nudum*).

Potamocarcinus guatemalensis Rathbun, 1905: 313, text-fig. 101, pl. 14 fig. 7; 1906: 503 (in list). — Coifmann 1939: 110 (in list).

Potamocarcinus (*Potamocarcinus*) *magnus guatemalensis* – Pretzmann 1965: 2 (in list); 1972: 70, figs 381-384, 396-398. — Smalley 1970: 102.

Potamocarcinus (*Megathelphusa*) *magnus guatemalensis* – Pretzmann 1971: 20 (in list); 1980: 654.

Potamocarcinus magnus – Rodríguez 1982: 111, fig. 72c, e. — Villalobos F. 1982: 220 (in list). — Ng *et al.* 2008: 176 (part, in list). — Wehrtmann *et al.* 2014: 123, fig. 1C, D; 2016: 781 (in list). — Acevedo-Alonso & Cumberlidge 2022: 582 (Appendix 2, in list). — Villalobos Hiriart & Álvarez 2008: 297 (form, México, Guatemala, El Salvador) (in list).

TYPE MATERIAL EXAMINED. — **Holotype**. **Guatemala** • 1 ♂, holotype by monotypy of *Potamocarcinus guatemalensis* Rathbun, 1905; precise location unknown; M. Bocourt leg.; MNHN Entry 453-1883; MNHN-IU-2017-8050 (= MNHN-B5170).

MATERIAL EXAMINED. — **Guatemala** • 1 ♂; collecting data unknown; UVGCR 506 • 1 ♂, collecting data unknown; UVGCR 508 • 1 ♂ (65.4:41.6) 1 ♀ (64.9:43.1); Guatemala, Amatitlán lake delta [14°28'34"N, 90°34'35"W; 1190 m elev.]; date and leg. unknown; FMNH 1830 • 3 ♂ (43.5:29.0-81.3:-) 1 ♀ (damaged); Guatemala, Amatitlán market; date and leg. unknown; FMNH 1825 • 1 ♂ (82.0:52.0); Guatemala, Lake Amatitlán [14°29'12"N, 90°36'38"W; 1190 m elev.]; 28.I-3.II.1906; S. E. Meek leg.; FMNH 1827, • 1 ♂ (74.5:47.9); Guatemala, Lake Amatitlán [14°29'12"N, 90°36'38"W; 1190 m elev.]; 28.I-03.II.1906; S. E. Meek leg.; FMNH 1831 • 1 ♂ (56.8:37.3); Guatemala, Lake Amatitlán; 26.VI.1906; S. E. Meek leg.; FMNH 1828 • 3 ♂ (45.3:30.0; 47.4:32.0; 1 damaged) 1 ♀ (45.0:30.4); Guatemala, Amatitlán [14°29'12"N, 90°36'40"W; 1190 m elev.], date and leg. unknown; FMNH 1832 • 1 immat. ♂; El Progreso, Río Morazán, near Morazán [14°55'54"N, 90°08'21"W; 349 m elev.], WNW of El Rancho, Motagua River basin; 8.V.1947; Miller leg.; USNM 1089243 • 1 juv. ♂; Izabal, Río Ciénaga [15°40'50"N, 88°57'58"W; 13 m elev.], below bridge from road to Sarstún; 18.III.1971; R. M. Boiley, R. C. & J. Lopez leg.; AMNH 8751 • 1 juv. ♂; Izabal, Río Ciénaga [15°40'50"N, 88°57'58"W; 13 m elev.], below bridge from road to Sarstún; 18.III.1971; R. M. Boiley, R. C. & J. Lopez leg.; AMNH 16670 • 2 ♂ (51.7:37.0; damaged) 1 ♀ (24.9:17.2); Zacapa, Río Palmilla, near Usumatlán; 14°58'30"N, 89°45'45"W; [245 m elev.]; 21.VII.2014; I. S. Wehrtmann & M. Orozco leg.; UCR-MZ uncat. • 1 ♂ (28.0:19.5) 2 immat. ♀ (31.7:21.7; 41.3:27.9); Zacapa, Río El Jutillo, near Usumatlán; 14°59'19"N, 89°49'25"W; [347 m elev.]; 21.VII.2014, I. S. Wehrtmann & M. Orozco leg.; UCR-MZ uncat. • 1 ♂; Suchitepéquez, Río Choyolate [= Coyolate] [14°22'39.31"N,

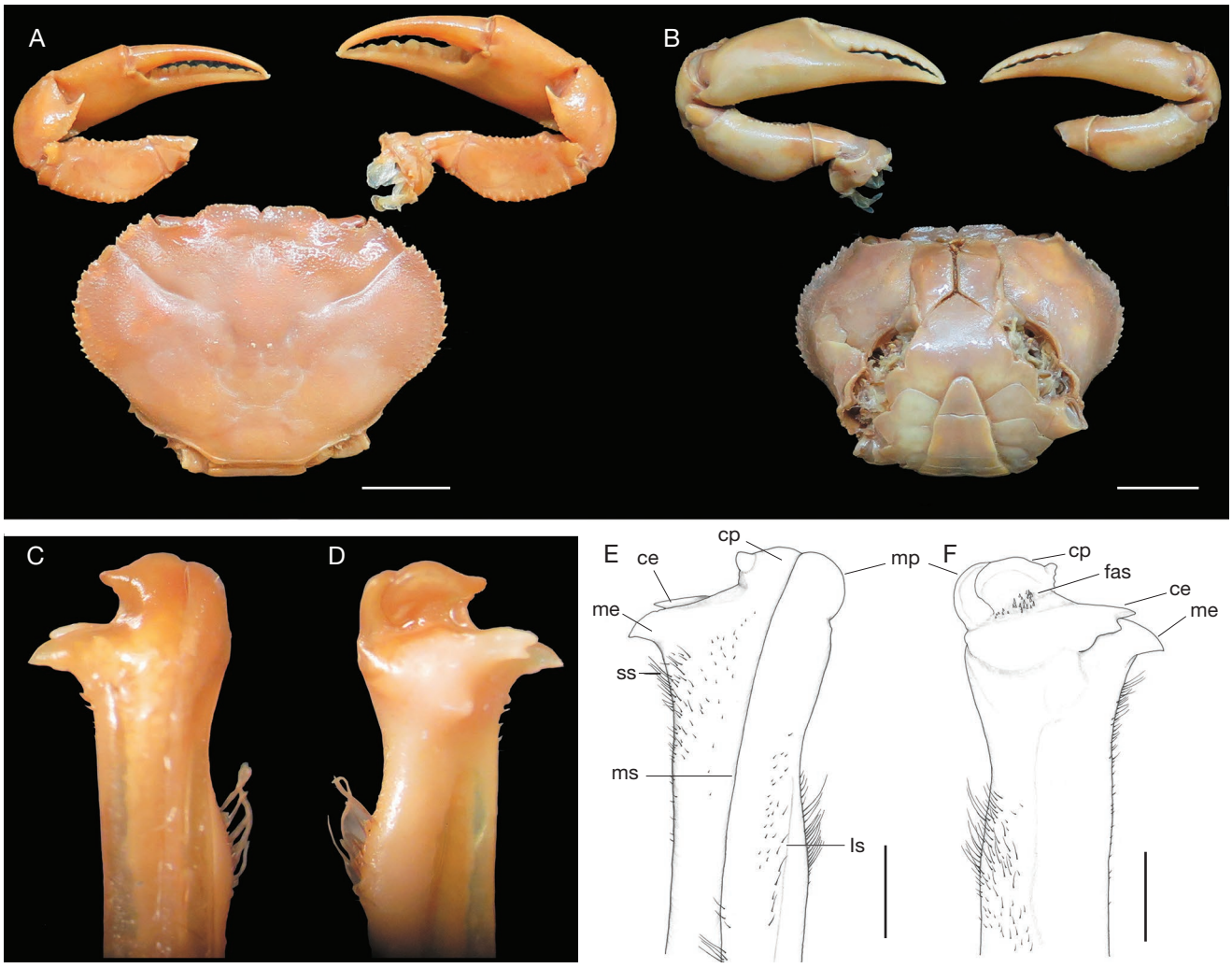

Fig. 2. — *Potamocarcinus magnus* (Rathbun, 1896): **A**-**D**, male, MNHN-IU-2017-8050 [holotype of *Potamocarcinus guatemalensis* Rathbun, 1905] (pereiopods 2-5 missing): **A**, habitus, dorsal view; **B**, habitus, ventral view; **C**, left G1, distal portion, mesial view; **D**, left G1, distal portion, lateralcephalic view; **E**, **F**, male, UCR-MZ 3114-02, left G1, distal portion: **E**, mesocaudal view; **F**, laterocephalic view. Abbreviations: **ce**, cephalic process; **cp**, caudal process; **fas**, field of apical spines; **ls**, lateral suture; **me**, mesial process; **mp**, marginal process; **ms**, marginal suture; **ss**, mesocephalic subdistal patch of setae. Scale bars: A, B, 10 mm; E, F, 2 mm. Photos: C. Magalhães.

91°08'13.14"W; 255 m elev.], Patulul; 21.V.1948; leg. unknown; USNM 189303 • 1 ♂; Solalá, Lago Atitlán [14°42'N, 91°12'W; 1558 m elev.]; 9.X.1993; J. Zunyge leg.; UVGCR 96 • 1 ♂; Solalá, Lago Atitlán; 28.XI.1993; leg. unknown; UVGCR 379 • 1 ♂; Solalá, Lago Atitlán; 6.XII.1984; J. Montúfar leg.; UVGCR 65 • 1 ♂; Solalá, Lago Atitlán; 28.X.1993; E. Pacay leg.; UVGCR 417 • 1 ♂ (70.0:45.0); Solalá, Panajachel (bought in the market, captured at Lago Atitlán); VII.2013; I. S. Wehrtmann leg.; UCR-MZ 3114-02 • 1 juv. ♂; Escuintla, carretera a Puerto Quetzal [13°56'N, 90°47'W; 8 m elev.]; 1.XI.1993; C. Cardona leg.; UVGCR 319.

Distribution. — Guatemala (El Progreso, Escuintla, Guatemala, Izabal, Solalá, Suchitepéquez, Zacapa) (Fig. 13), Mexico, Belize, Honduras, El Salvador, Costa Rica (Pretzmann 1980; Rodríguez 1982; Villalobos Hiriart & Álvarez 2008; Magalhães *et al.* 2015; Wehrtmann *et al.* 2016; this study).

Other records in Guatemala. — Rodríguez (1982): Escuintla, Aguna [? Río Aguná, 14°15'05"N, 91°07'26"W, 97 m elev.]. Pretzmann (1980): Solalá, Lake Atitlán; Zacapa, Rio Cayo, 7.3 miles W Estanzuela (128.8 km E Guatemala City) [15°00'N, 89°34'W, 190 m elev.]; Guatemala, 45 km E Guatemala City, Río Platanos [14°50'42.25"N, 90°24'12.67"W, 495 m elev.]; Izabal, 2 km S Mariscos [15°24'54.53"N, 89°04'43.86"W, 8 m elev.], Lake Izabal drainage; Izabal, Río Sena near Seno, 7 miles NW Livingston [15°51'12"N, 88°50'53"W, 7 m elev.]. The mention of the department of Jalapa in Wehrtmann *et al.* (2016) must be corrected to department of El Progreso since this is the correct location of the record referred to lot USNM 1089243.

Description of G1 (Fig. 2C-F)

Stout, straight in both caudal, mesial views, moderately compressed mesolaterally; caudal margin nearly straight in mesial view, with tuft of minute to short setae medially; lateral margin slightly concave distally in mesial view; caudal surface with sparce patch of caudal setae along median portion; mesocephalic surface with subdistal, elongated patch of setae increasing in size distally. Spermatic channel opening on apex cavity, situated towards lateral end at base of caudal process. Marginal suture on mesial surface, straight along most of stem, gently curved to lateral side distally in mesial

view, with row of large marginal setae proximally. Marginal process broadly rounded, as long as caudal process in mesial view, partially overlapping this lobe on its lateral side. Lateral suture incomplete, marked by somewhat deep sulcus on first 3/4 of caudal surface. Mesial process as strong subtriangular projection directed cephalad on distal portion of mesial border. Apex moderately distorted in cephalic direction; caudal process enlarged, subquadrate in mesocaudal view, bearing slight protuberance on cephalic end, folded over the apex cavity, partially covering field of apical spines. Apex cavity oblong; field of apical spines moderately developed, rather narrow, with short, small spines. Cephalic process (lateral process, *sensu* Rodríguez & Hobbs 1989) bifid, with two distinct spiniform teeth apically, both pointing cephalad.

Remarks

The current geographic distribution of *Po. magnus* ranges from Mexico to Costa Rica, but some authors (Rodríguez 1982; Villalobos Hiriart & Álvarez 2008) observed morphological differences in the populations of this species inhabiting southern Mexico, Guatemala, and El Salvador from those occurring in Costa Rica. However, at least concerning the G1 morphology, the specimen from Lake Atitlán (Fig. 2E, F) is very much similar to the holotype specimen from Costa Rica illustrated by Magalhães *et al.* (2015: 331, figs 71, 72), except for the cephalic end of the caudal process, which has a distinct protuberance in the Guatemalan specimen whereas it is angled in the holotype. A more detailed study, including molecular analyses, of this group along its distributional area is needed to clarify this issue.

The syntypes of *Po. magnus* are two males deposited at the USNM (USNM 19048 and 19049) from an unknown locality in Costa Rica. Magalhães *et al.* (2015) illustrated the G1 of the male USNM 19049 and erroneously considered it as the holotype in the caption of the figures 71 and 72. The holotype of *Potamocarcinus guatemalensis* Rathbun, 1905, a junior synonym of *Po. magnus*, is a male (MNHN-IU-2017-8050 [= MNHN-B5170] (Fig. 2A-D) from an unknown locality in Guatemala.

Subfamily Raddausinae Álvarez, Ojeda, Souza-Carvalho, Villalobos, Magalhães, Wehrtmann & Mantelatto, 2020
Genus *Elsalvadoria* Bott, 1967

Elsalvadoria tomhaasi Bott, 1970
(Figs 3A-C; 14)

Elsalvadoria tomhaasi Bott, 1970: 361, figs 5-8. — Pretzmann 1972: 97, figs 492-495, 578-580. — Rodríguez 1982: 95, figs 59b, c, e, 61a-d. — Villalobos F. 1982: 220 (in list). — Ng *et al.* 2008: 173 (in list). — Wehrtmann *et al.* 2016: 779 (in list). — Acevedo-Alonso & Cumberlidge 2022: 578 (Appendix 2, in list).

Elsalvadoria tomasi – Villalobos Hiriart & Álvarez 2008: 295 (in list) [error].

Type material examined. — **Holotype. Guatemala** • 1 ♂ (41.1:25.1); Sacatepéquez, river near Volcán de Aguas [14°27'54"N, 90°44'35"W]; 900 m elev.; date and leg. unknown; SMF 4354.

Other material examined. — **Guatemala** • 1 ♂ (25.8:16.5); Guatemala, Mixco [14°38'N, 90°36'W; 1637 m elev.]; Finca La Esmeralda; 17.VIII.1993; C. Cardona Gonzalez leg.; UVGCR 344.

Distribution. — Guatemala (Guatemala, Sacatepéquez) (Bott 1970; Wehrtmann *et al.* 2016; this study) (Fig. 14). The only two available records point to a distribution in the Pacific drainage of southern Guatemala.

Description of G1 (Fig. 3A-C)

Stem moderately sinuous, moderatley compressed in caudocephalic direction, distal portion distinctly curved in laterocephalic direction, slightly wider subdistally; caudal margin, in mesial view, with strong median constriction and enlarged subdistal hump-like lobe, followed by irregular row of variable-sized spines; cephalic margin regularly convex medially in mesial view. Marginal suture on mesial surface, sinuous, gently following curvature of stem, with row of long and short setae along its proximal portion. Marginal process simple, nearly straight in mesial view, not overreaching apex. Lateral suture incomplete, marked by sulcus extending slightly beyond level of median constriction of caudal surface. Mesial process absent. Cephalic surface with cephalic process greatly developed as subdistal unilobed or faintly bilobed enlargement, directed basally and partially twisted towards mesial side, with row of minute spines along its proximal margin. Lateral process enlarged, tongue-shaped; distal margin rounded, situated subdistally on laterocephalic surface, somewhat curved towards cephalic side. Distal portion of lateral surface with distinct rounded (in cephalic view) spiny distolateral lobe. Apex open, oblong, elongated mesolaterally, directed cephalad; mesocaudal margin smooth, produced into small angled lobe, slightly more elevated in relation to laterocephalic margin. Field of apical spines moderately developed, elongated mesolaterally, with small spines.

Remarks

When comparing the G1 of both examined specimens, we noticed a small variation in the morphology of the cephalic process: in the holotype it is clearly unilobed, with its distal margin broadly rounded (Fig. 3C), whereas in the male UVGCR 344 it seems to be faintly bilobed, with its distal margin bearing a slight median concavity.

Key to the species of *Elsalvadoria* Bott, 1967

1. G1 with cephalic process distally unilobed or faintly bilobed (Fig. 3A-C); lateral process enlarged, distal margin rounded (Fig. 3C) ..... *E. tomhaasi* Bott, 1970
— G1 with cephalic process distinctly bilobed (Fig. 3D-H); lateral process as three-dimensionally conical protuberance (Fig. 3E-H) ..... *E. zurstrasseni* (Bott, 1956)

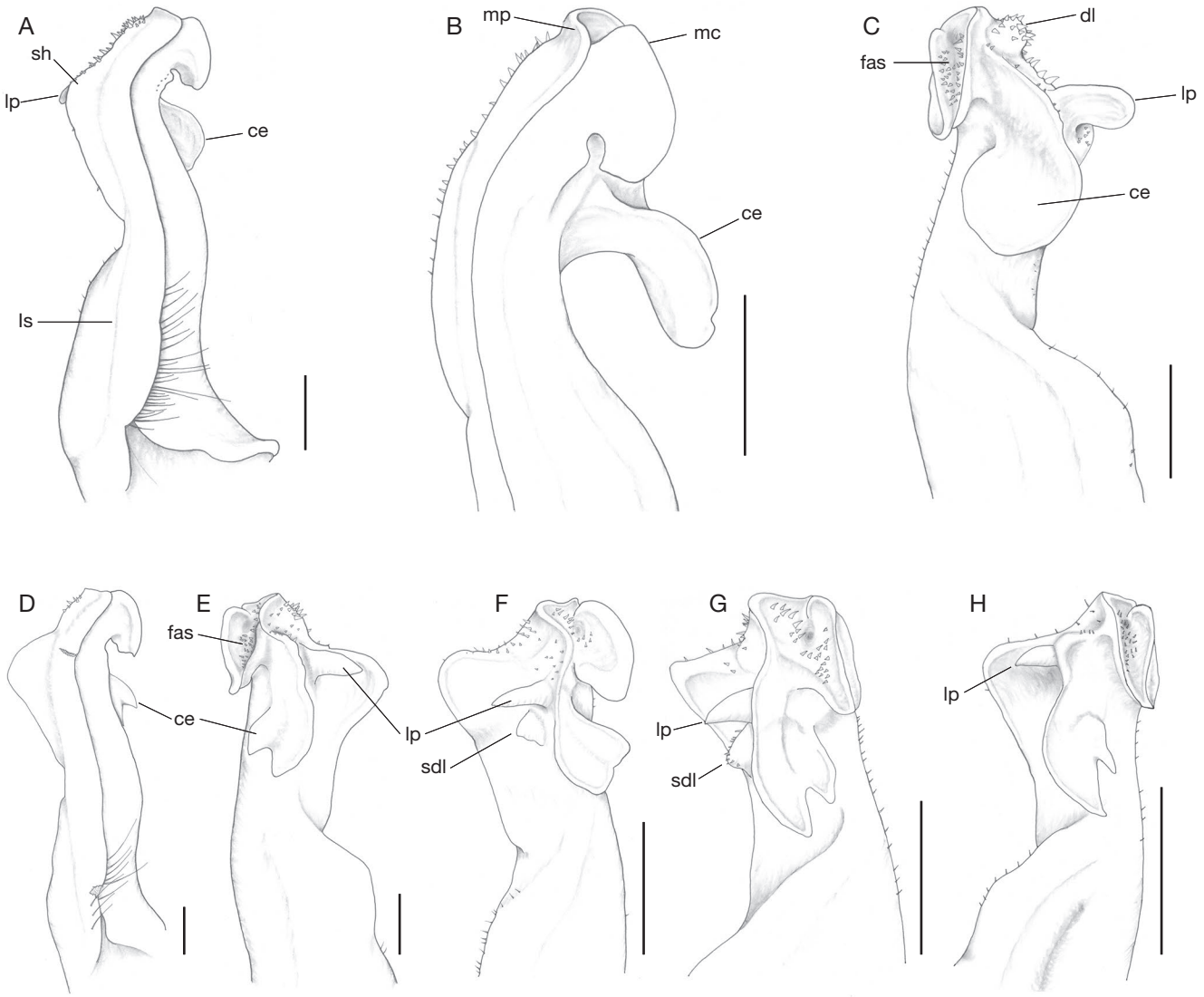

FIG. 3. — *Elsalvadoria* Bott, 1967 species, G1: **A**-**C**, *Elsalvadoria tomhaasi* Bott, 1970, holotype, SMF 4354, right G1: **A**, mesocaudal view; **B**, distal portion, mesocephalic view; **C**, distal portion, cephalic view; **D**-**H**, *Elsalvadoria zurstrasseni* (Bott, 1956), male, holotype, SMF 2449, right G1: **D**, mesocaudal view; **E**, distal portion, laterocephalic view; **F**, INPA 2124, left G1, distal portion, cephalic view; **G**, INPA 2474, left G1, distal portion, cephalic view; **H**, INPA 2137, left G1, distal portion, laterocephalic view. Abbreviations: **ce**, cephalic process; **dl**, distolateral lobe; **fas**, field of apical spines; **lp**, lateral process; **ls**, lateral suture; **mc**, mesocaudal margin of apex; **mp**, marginal process; **sdl**, subdistal lateral lobe; **sh**, subdistal hump-like lobe. Scale bars: 1 mm.

Elsalvadoria zurstrasseni (Bott, 1956)
(Figs 3D-H; 14)

Pseudothelphusa zurstrasseni zurstrasseni Bott, 1956: 229, 232, pl. 32, fig. 5; pl. 35, fig. 5a, b.

Elsalvadoria zurstrasseni – Smalley 1970: 100, fig. 15-17; 105 (in key). — Rodríguez 1982: 59: fig. 10f, g, j; 2001: 440 (in key). — Villalobos Hiriart & Álvarez 2008: 295 (in list). — Ng *et al.* 2008: 173 (in list). — Wehrtmann *et al.* 2016: 779 (in list). — Acevedo-Alonso & Cumberlidge 2022: 578 (Appendix 2, in list).

Elsalvadoria zurstrasseni zurstrasseni – Pretzmann 1971: 21 (in list); 1972: 96.

MATERIAL EXAMINED. — **Guatemala** • 1 ♂ (30.6:18.8); Escuintla, San José [13°55'37.5"N, 90°49'04.11"W; 6 m elev.]; 10.X.1993; A. Kepfer leg.; UVGCR 328 • 2 ♂ (17.2:11.6; 23.8:16.1) 3 ♀ (13.7:9.5; 13.8:9.5; 16.2:11.0); Suchitepéquez, Patutul, Finca Los Tarrales, stream inside the farm; 14°31'28"N, 91°08'07"W; 875 m elev.; 19.I.2014; I. S. Wehrtmann, M. Orozco, C. Magalhães & M. W. Dix leg.; UCR-MZ 3231-01 • 2 ♂ (23.4:15.5; 26.0:16.5); Suchitepéquez, Patutul, Finca Los Tarrales, stream inside the farm; 14°31'28"N, 91°08'07"W; 875 m elev.; 19.I.2014; I. S. Wehrtmann, M. Orozco, C. Magalhães & M. W. Dix leg.; INPA 2124 • 1 ♂ (19.6:13.0) 1 ♀ (21.1:13.6), dry; Guatemala, municipality of Fraijanes, aldea El Cerrito [14°26'N, 90°27'W; 1482 m elev.], quebrada La Escurana, tributary of Río Fraijanes; I.2000; leg. unknown; INPA 2137 • 1 ♂ (26.4:17.1), 1 ov. ♀ (26.6:16.3); Santa Rosa, Renacimiento [? Renacimiento, on the Panamerican highway to El Salvador; 14°15'24"N, 90°16'13"W; 733 m elev.]; date unknown; R. Chea leg.; INPA 2474.

COMPARATIVE MATERIAL EXAMINED. — *Elsalvadoria zurstrasseni zurstrasseni* (Bott, 1956): **El Salvador** • 1 ♂ (27.1:17.1), holotype; La Liberdad, La Joya, road to Ciudad Arce, Chilamatal; 18.VIII.1951;

A. Zilch leg.; SMF 2449 • 1 ♂ (24.8:16.6), paratype; El Salvador, Santa Ana, Laguna de Guija; 3.V.1951; A. Zilch leg.; INPA 2142 (ex-SMF 2452). — *Pseudothelphusa zurstrasseni arcuata* Bott, 1956: **El Salvador** • 1 ♂ (21.1:13.6), holotype, Morazán, Cacaguatique mountain near Osicala, Finca San Pedro; 13.IX.1951; A. Zilch leg.; SMF 2443. — *Pseudothelphusa zurstrasseni tridentata* Bott, 1956: **El Salvador** • 1 ♂ (25.7:15.7), holotype; Sonsonate, waterfall 2 km west from Juayua (Rio Santa Rita); 17.VII.1951; A. Zilch leg.; SMF 2441.

DISTRIBUTION. — Guatemala (Escuintla, Guatemala, Santa Rosa, Suchitepéquez) (Smalley 1970; Wehrtmann *et al.* 2016; this study) (Fig. 14) and El Salvador (Bott 1956; Rodríguez 1982).
The type locality is in El Salvador (La Liberdad, La Joya, road to Ciudad Arce, Chilamatal) (Bott 1956). Smalley (1970) mentioned the occurrence of this species in Guatemala but did not indicate any voucher specimen. Pretzmann (1972) probably just followed Smalley's citation, as he has not examined any specimen from the country. Wehrtmann *et al.* (2016) recorded the species from the departments of Escuintla, Guatemala, and Suchitepéquez based on material collected during their surveys, but they did not list the specimens and their specific localities; this information is now provided herein.

DESCRIPTION OF G1 (Fig. 3D-H)
Stem moderately sinuous, moderately compressed in caudocephalic direction, distal portion distinctly curved in laterocephalic direction, slightly wider subdistally; caudal margin, in mesial view, with strong median constriction and enlarged subdistal hump-like lobe, followed by irregular row of variable-sized spines; cephalic margin regularly convex medianly in mesial view. Marginal suture on mesial surface gently following the curvature of stem; row of long and short setae along proximal portion of marginal suture. Marginal process simple, slightly concave in mesial view, not overreaching apex. Lateral suture incomplete, marked by sulcus extending slightly beyond level of median constriction of caudal surface. Mesial process absent. Cephalic surface with cephalic process greatly developed as subdistal distinctly bilobed enlargment, directed basally and partially twisted towards mesial side, with irregular row of minute spines along its proximal margin. Lateral process as strong, three-dimensionally conical protuberance situated subdistally near base of cephalic process on laterocephalic surface, pointing towards lateral side. Distal portion of lateral surface without distinct distal spiny lobe; some specimens with subdistal small, rounded lateral lobe bearing minute spines situated obliquely slightly lower than subterminal spine. Apex open, oblong, elongated mesolaterally, directed cephalad; mesocaudal margin smooth, produced into rounded lobe, somewhat more elevated in relation to laterocephalic margin. Field of apical spines moderately developed, elongated mesolaterally, with small spines.

REMARKS
The specimens examined by us, which include the type material of the nominal and subspecific forms described by Bott (1956), showed a certain amount of variation in the morphology of G1, particularly in the shape of the cephalic process and in the presence or absence of the subdistal lobe of the lateral surface. At least in all Guatemalan specimens analyzed herein, the cephalic process is bilobed but can exhibit either: 1) nearly symmetrical rounded lobes separated by a slightly concave depression (e.g., INPA 2124 – Fig. 3F); 2) nearly symmetrical sharp lobes separated by deep cleft (e.g., INPA 2474 – Fig. 3G), which is similar to that of the holotype (SMF 2449 – Fig. 3E); or, 3) asymmetrical sharp lobes also separated by deep cleft (e.g., INPA 2137 – Fig. 3H). The morphology of the cephalic process is also variable in specimens from El Salvador, which led Bott (1956) to treat them as subspecies. Rodríguez (1982), in turn, considered it very possible that this is a normal variation for the species and treated them as synonyms.

As for the subdistal lobe of the lateral surface, some (e.g., INPA 2124 – Fig. 3F, 2137, 2474; UCR-MZ 3231-01) of the Guatemalan specimens show this lobe very clearly but it is absent in others (e.g., INPA 2137). However, it is not present in the holotype of the nominal species (Fig. 3E) nor in the subspecies described by Bott (1956), although it is present in one of the paratypes of the nominal species (INPA 2142) from El Salvador (Santa Ana, Laguna de Guija).

Such variability might suggest that we are dealing with a species complex and additional studies are required to resolve this question. For now, we prefer to maintain the concept adopted by Rodríguez (1982) and consider only one valid species until a more comprehensive study, including molecular analyses, can be conducted based on a more abundant series of specimens from the region.

Genus *Phrygiopilus* Smalley, 1970

Phrygiopilus acanthophallus Smalley, 1970
(Figs 4A-C; 15)

Phrygiopilus acanthophallus Smalley, 1970: 98, figs 18, 19. — Rodríguez 1982: 88, figs 53, 54. — Villalobos F. 1982: 220 (in list). — Hobbs 1994: 101 (in list). — Guinot 1988: 14. — Rodríguez 2001: 440 (in key). — Villalobos Hiriart & Álvarez 2008: 297 (in list). — Ng *et al.* 2008: 176 (in list). — Cumberlidge *et al.* 2014: 144 and 147 (in table). — Wehrtmann *et al.* 2016: 779 (in list). — Acevedo-Alonso & Cumberlidge 2022: 581 (Appendix 2, in list).

Isabellagordonia (*Phrygiopilus*) *acanthophallus* – Pretzmann 1971: 21 (in list); 1972: 93. — Hobbs *et al.* 1977: 149 (in list). — Reddell 1981: 111, fig. 16 (in map), 113. — Holthuis 1986: 594 (in list).

Isabellagordonia acanthophallus – Guinot 1994: 172.

TYPE MATERIAL EXAMINED. — **Holotype**. **Guatemala** • 1 ♂ (21.4:12.3); USNM 126110, Alta Verapaz, Seamay Cave [15°24'14"N, 89°48'27"W; 929 m elev.], 1 km S of Senahú, about 200 km NE of Guatemala City; 10.II.1968; G. Nicholas leg.

OTHER MATERIAL EXAMINED. — **Guatemala** • 1 ♂ (25.6:15.5); Zacapa, Santa Clara [? Finca Santa Clara: 15°07'N, 89°49'W; 1346 m elev.]; 7.VIII.1948; R. D. Michell leg.; FMNH 12210 • 1 ♂; Alta Verapaz, Seamay Cave, near Senahú; 3.I.1973; M. Frania leg.; USNM 189299 • 2 ♂, 2 ♀; Alta Verapaz, Senahú, Finca Seamay, Cueva Seamay [15°24'14"N, 89°48'27"W; 929 m elev.]; 24-26.VIII.1969; S. & J. Peck leg.; USNM 128408 • 1 ♂ (19.0:11.0), 1 ♀ (23.2:13.8); Alta Verapaz, Senahú, Finca Seamay, Cueva Seamay [15°24'14"N, 89°48'27"W; 929 m elev.]; 24-26.VIII.1969; S. & J. Peck leg.; INPA 2182 • 1 ♂ (21.8:13.1); Alta Verapaz, in the

KEY TO GUATEMALAN SPECIES OF *PHRYGIOPILUS* SMALLEY, 1970 (ADAPTED FROM RODRÍGUEZ 2001)

1. G1 with mesial process present 2
— G1 with mesial process absent (Fig. 4J) ..... *Ph. strengerae* (Pretzmann, 1965)

2. G1 with mesial process conical, unilobed 3
— G1 with mesial process subtriangular, bilobed (Fig. 4F, H, I) ..... *Ph. ibarrai* (Pretzmann, 1978)

3. G1 with lateral lobe absent 4
— G1 with lateral lobe present (Fig. 5F) ..... *Ph. senticosus* n. sp.

4 G1 with supra-apical process rounded (Fig. 4A-C) ..... *Ph. acanthophallus* Smalley, 1970
— G1 with supra-apical process subtriangular (Fig. 4D, E) ..... *Ph. chuacusensis* Smalley, 1970

surroundings of San Juan Chamelco [15°26'09"N, 90°20'17"W; 1375 m elev.], Río Chilax; 1975; Büttger leg.; SMF 8867 • 1 ♂ (22.9:13.4) 2 ♀ (23.7:13.8; 25.4:14.3); Baja Verapaz, ruta 5 (antigua carretera a Salamá), Río Quilila (tributary to Río Negro or Chixoy); 15°12'53"N, 90°17'39"W; 1305 m elev.; 21.I.2014; I. S. Wehrtmann, M. Orozco, C. Magalhães & M. W. Dix leg.; UCR-MZ 3766-01 • 1 ♂ (13.7:8.5) 1 ♀ (16.9:10.5); Baja Verapaz, ruta 5 (antigua carretera a Salamá), Río Quililá (tributary to Río Negro or Chixoy); 15°12'53"N, 90°17'39"W; 1305 m elev.; 20.VII.2014; I. S. Wehrtmann & M. Orozco leg.; INPA 2473 • 1 ♂ (28.8:16.5); Baja Verapaz, tributary of Río Negro, approximately 18 miles north of Salamá, on road to Cobán [15°11'24"N, 90°17'40"W, 1382 m elev.], 22.IV.1947, Miller & Holoway leg.; INPA 2181 • 2 ♂; Baja Verapaz, tributary of Río Negro, approximately 18 miles north of Salamá, on road to Cobán [15°11'24"N, 90°17'40"W, 1382 m elev.], 22.IV.1947, Miller & Holoway leg.; USNM uncat.

DISTRIBUTION. — Guatemala (Alta Verapaz, Baja Verapaz, Zacapa) (Smalley 1970; Rodríguez 1982; Wehrtmann *et al.* 2016; this study) (Fig. 15) and Mexico (Magalhães & Wehrtmann 2025).

DESCRIPTION OF G1 (Fig. 4A-C)

Stem moderately sinuous, distal portion slightly curved in laterocephalic direction, compressed in caudocephalic direction, approximately the same width along the entire stem in mesocaudal view; caudal margin, in mesocaudal view, concave, sometimes with slight median discontinuity due to barely noticiable angled or rounded smooth lateral lobe; cephalic margin regularly convex in mesocaudal view. Marginal suture on mesial surface gently following the curvature of the stem, distinctly curved towards lateral side distally in mesial view; row of long and short setae along proximal portion of marginal suture. Marginal process wide, broadly rounded in mesocaudal view, not overreaching mesocaudal margin of apex. Lateral suture incomplete, marked by sulcus along first 3/4 of caudal surface, shallower distally. Mesial process as subtriangular conical spine at base of supra-apical process, directed cephalad. Cephalic process absent. Mesial surface produced into variable-length, rounded supra-apical process densely covered with short spines along its regularly widened margins; patch of spines denser distally. Supra-apical process with cephalic surface distinctly folded proximally, concave medianly; mesocaudal surface smooth, slightly concave. Supra-apical process with variable length ranging approximately from 0.2 to 0.5 times G1's length in mesocaudal view, also ranging from slightly wider than long (ratio width/length roughly 1.2) to longer than wide (ratio width/length roughly 0.6); tip rounded. Apex oblong, elongated mesolaterally, directed cephalad; lower margin smooth (finely crenulated in some paratypes), upper margin (basal portion of supra-apical process) smooth. Field of apical spines poorly developed, narrow, elongated mesolaterally, with minute spines.

REMARKS

The number of male specimens assigned to *Ph. acanthophallus* available in the collections revised by us is somewhat low (see above). Nevertheless, one can notice some degree of variability in their G1s, particularly in the size of the supra-apical process. This process can be relatively short (roughly 1/5 the G1's length) and wider than long (ratio width/length roughly 1.2) as in the male INPA 2181 from Baja Verapaz, 18 miles north of Salamá (Fig. 4B), moderately long (roughly 1/3 the G1's length) and nearly as wide as long (ratio width/length roughly 0.9) as in the male USNM 1180974 from Chiapas, Mexico (cw 24.3 mm; see fig. 1A in Magalhães & Wehrtmann 2025), or longer than wide (ratio width/length roughly 0.6) and quite long (nearly half of the G1's length) as in male SMF 8867 (Fig. 4A) from Alta Verapaz, río Chilax. In the holotype, the supra-apical process is slightly longer than wide (ratio width/length roughly 0.8) and about 1/3 the G1's length (see Smalley, 1970: 100, fig. 18). Interestingly, the G1 with the shorter supra-apical process belongs to the largest specimen examined (cw 28.8: male, INPA 2181) whereas the G1 with the longest supra-apical process belongs to a smaller specimen (cw 21.8: male, SMF 8867); this latter specimen, however, is similar in size to the holotype (cw 21.4), which has a supra-apical process of intermediate size. It remains to be seen, pending the availability of a larger sample, whether this variability in terms of a negative allometry is related to age.

Despite the variability of the supra-apical process, the G1 of all specimens examined herein share a unilobed mesial process in the form of a distinctly conical and acute spine (Fig. 4A, B) and were, therefore, considered to be co-specific. However, the observed variability of the G1 might be indicative of the existence of a species complex (see also Remarks for *Pseudothelphusa proxima* Rathbun, 1905, below). A better understanding of this situation should wait until a more abundant series of specimens from the species' distributional range becomes available.

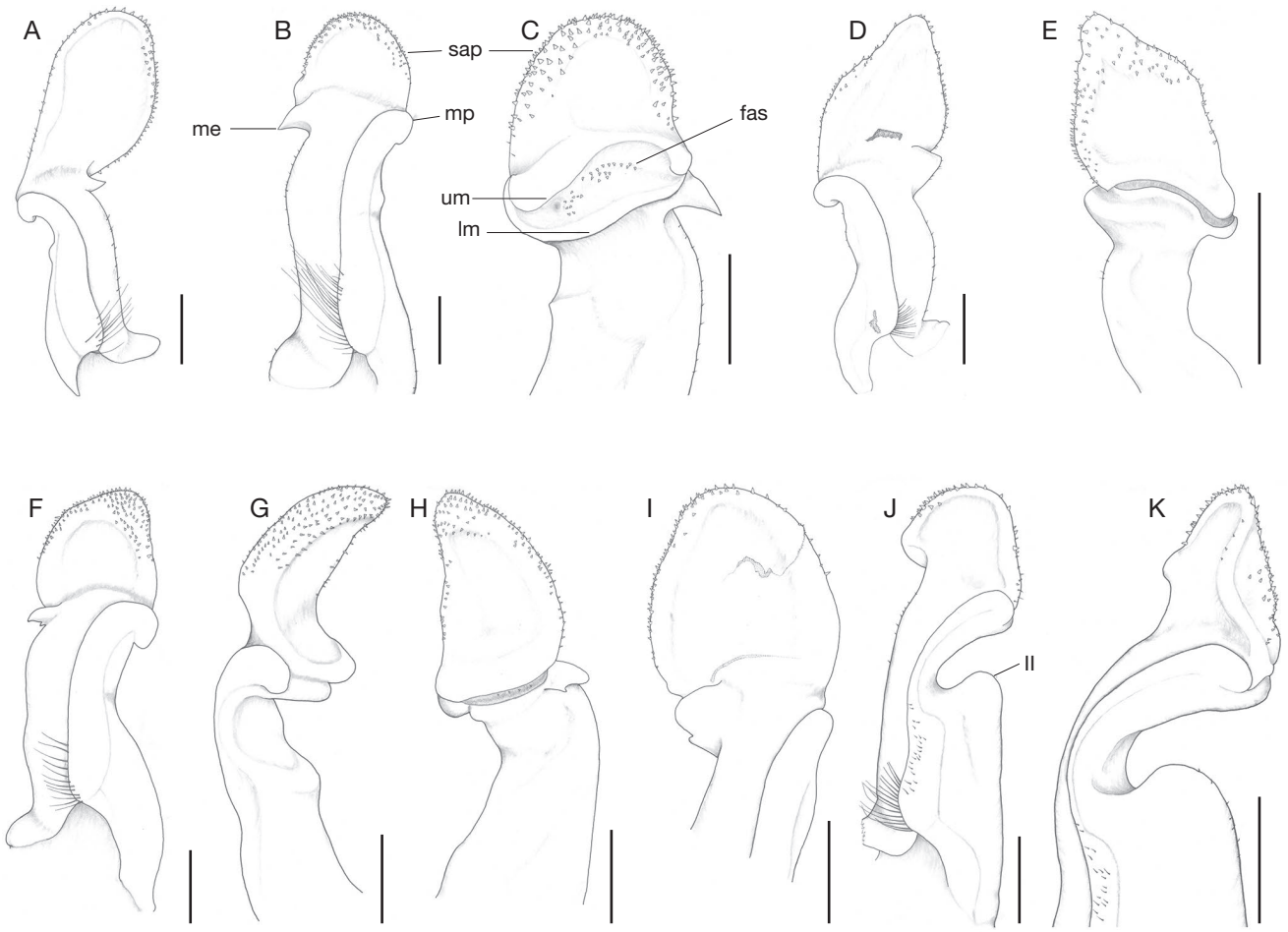

Fig. 4. — *Phrygiopilus* Smalley, 1970 species, G1: **A**-**C**, *Phrygiopilus acanthophallus* Smalley, 1970: **A**, SMF 8867, right G1, mesocaudal view; **B**, INPA 2181, left G1, mesocaudal view; **C**, INPA 2181, left G1, laterocephalic view; **D**, **E**, *Phrygiopilus chuacusensis* Smalley, 1970, holotype, USNM 12613, right G1: **D**, mesocaudal view; **E**, laterocephalic view; **F**-**I**, *Phrygiopilus ibarrai* (Pretzmann, 1978), holotype, NHMW 4065, left G1: **F**, mesocaudal view; **G**, lateral view; **H**, cephalic view; **I**, UVGCR 348, left G1, distal portion, mesocaudal view (partially damaged); **J**, **K**, *Phrygiopilus strengerae* (Pretzmann, 1965), holotype, USNM 79372, left G1: **J**, mesocaudal view; **K**, distal portion, caudal view. Abbreviations: **fas**, field of apical spines; **ll**, lateral lobe; **lm**, lower margin of apex; **me**, mesial process; **mp**, marginal process; **ms**, marginal suture; **sap**, supra-apical process; **um**, upper margin of apex. Scale bars: 1 mm.

Phrygiopilus chuacusensis Smalley, 1970
(Figs 4D, E; 15)

Phrygiopilus chuacusensis Smalley, 1970: 97, figs 20-23. — Rodríguez 1982: 88; 2001: 440 (in key). — Villalobos F. 1982: 220 (in list). — Villalobos Hiriart & Álvarez 2008: 297 (in list). — Ng *et al.* 2008: 176 (in list). — Wehrtmann *et al.* 2016: 779 (in list). — Acevedo-Alonso & Cumberlidge 2022: 578 (Appendix 2, in list).

Isabellagordonia (*Phrygiopilus*) *chuacusensis* – Pretzmann 1971: 21 (in list); 1972: 93.

Type material examined. — **Holotype. Guatemala** • 1 ♂ (19.9:12.2); Baja Verapaz, stream near summit of Sierra de Chuacús, 96 km by highway north of Guatemala City; 15°00'N, 90°26'W; [2029 m elev.] (see Remarks); 19.VIII.1967; A. E. & I. C. Smalley leg.; USNM 126113.
Paratypes. Guatemala • 4 ♂ 6 ♀; data as in holotype; USNM 126114 • 1 ♂; data as in holotype; TMNH 6090,

Distribution. — Guatemala (Baja Verapaz) (Smalley 1970) (Fig. 15).

Description of G1 (Fig. 4D, E)
Stem moderately sinuous; distal portion markedly curved in laterocephalic direction, compressed in caudocephalic direction, approximately the same width along entire stem in mesocaudal view; caudal margin medianly concave in mesocaudal view, lateral lobe indistinct; cephalic margin slightly convex medianly in mesocaudal view. Marginal plate fused subdistally to caudal surface. Marginal suture on mesial surface, gently following the curvature of the stem, distinctly curved towards lateral side distally in mesial view; row of long and short setae along proximal portion of marginal suture. Marginal process wide, broadly rounded in mesocaudal view, not overreaching mesocaudal margin of apex. Lateral suture incomplete, marked by sulcus along first 3/4 of caudal surface, shallower distally. Mesial process unilobed, broadly subtriangular, directed cephalad. Cephalic process absent. Mesial surface produced into large roughly subtriangular supra-apical process covered with short spines along cephalic, caudal margins and distal portion of laterocephalic surface; patch of spines denser along median

portion of cephalic and caudal margins. Supra-apical process with caudal margin moderately widened proximally; cephalic surface barely folded proximally, concave medianly; mesocaudal surface smooth, slightly concave. Supra-apical process slightly longer than wide (ratio width/length roughly 0.8), approximately 0.4 times length of entire stem in mesocaudal view; tip subtriangular, distinctly narrower than median portion. Apex narrow, slit-like and elongated mesolaterally, directed cephalad; lower margin smooth (finely crenulated in some paratypes), upper margin (basal portion of supra-apical process) smooth. Field of apical spines poorly developed, narrow, elongated mesolaterally, directed cephalad, with minute spines nearly concealed by basal portion of supra-apical process and distal margin of cephalic surface of G1.

Remarks

This species is only known from its type locality in the Sierra de Chuacús, department of Baja Verapaz, Guatemala. The types and only specimens available were collected by A. E. Smalley himself and he stated that the type locality ("stream near summit of Sierra de Chuacús") would be "96 km by highway north of Guatemala City" at 15°00'N, 90°26'W. These coordinates, however, must be a mistake because, when plotted in a map (Google Earth®, for instance) they do not match the textual information regarding the distance by road from Guatemala City, since these coordinates are placed both far from any road coming from Guatemala City and approximatelly 30 km SE from Sierra de Chuacús. In an attempt to obtain a roughly approximate location based on Smalley's (1970) textual information by plotting the road distance (96 km) along the highway from Guatemala City towards the Sierra de Chuacús in Google Earth®, the site could be located around the coordinates 15°10'03.45"N, 90°36'27.46"W, 828 m elev., which is more or less in line with information reported by the author.

Following a preliminary study of the material deposited at the UVGCR, Wehrtmann *et al.* (2016) listed the species as also occurring in the department of Zacapa. A more detailed examination of the male of lot UVGCR 348 for this study, however, showed that it actually belongs to *Ph. ibarrai* (Pretzmann, 1978) because of the subtriangular and bifid mesial lobe of the G1.

Phrygiopilus ibarrai (Pretzmann, 1978) (Figs 4F-I; 15)

Isabellagordonia (*Phrygiopilus*) *acanthophalla ibarrai* Pretzmann, 1978: 3; 1980: 659, pl. 9 figs 37-41, pl. 18 fig. 80 [see Remarks].

Phrygiopilus ibarrai – Rodríguez 2001: 437, fig. 2. — Ng *et al.* 2008: 176 (in list). — Wehrtmann *et al.* 2016: 779 (in list). — Acevedo-Alonso & Cumberlidge 2022: 581 (Appendix 2, in list).

Phrygiopilus acanthophalla ibarrai – Villalobos Hiriart & Álvarez 2008: 297 (in list).

Phrygiopilus chuacusensis – Wehrtmann *et al.* 2016: 779 (in list) (part, spec. from Zacapa).

Type material examined. — **Holotype. Guatemala** • 1 ♂ (25.7:16.5); Guatemala, 14 km south of Guatemala City, north of San José Pinula; [14°33'N, 90°25'W]; 1800 m elev.; 20.IV.1975; Dr I. Poglayen-Neuwall leg. through Germán Ibarra; NHMW 4065.

Other material examined. — **Guatemala** • 1 ♂; collecting data unknown; UVGCR 441 • 1 ♂ (31.4:18.7) 2 ♀ (18.1:9.9; 38.1:20.0); Baja Verapaz, ruta 5 (antigua carretera a Salamá), Río Quililá (tributary to Río Negro or Chixoy); 15°12'53"N, 90°17'39"W; 1305 m elev.; 20.VII.2014; I. S. Wehrtmann & M. Orozco leg.; UCR-MZ uncat. • 1 ♂; Zacapa, Río Hondo, Aldea San Lorenzo [15°07'N, 89°38'W], municipality Río Hondo, Sierra de Las Minas; 1800 m elev.; 7.XI.1986; leg. unknown; UVGCR 348.

Distribution. — Guatemala (Alta Verapaz, Guatemala, Zacapa) (Pretzmann 1978; Rodríguez 2001; Wehrtmann *et al.* 2016; this study) (Fig. 15).

Other records in Guatemala. — Rodríguez (2001): department of Guatemala, km 30 on road from San José Pinula [14°32'00.66"N, 90°23'09.32"W; 1735 m elev.] to Mataquesquintla.

Description of G1 (Fig. 4F-I)

Stem moderately sinuous, distal portion markedly curved in laterocephalic direction, compressed in caudocephalic direction, approximately the same width along the entire stem in mesocaudal view; caudal margin, in mesocaudal view, concave, lateral lobe indistinct; cephalic margin convex in mesocaudal view. Marginal plate fused subdistally to caudal surface. Marginal suture on mesial surface gently following the curvature of the stem, distinctly curved towards lateral side distally in mesial view; row of long setae along proximal portion of marginal suture. Marginal process wide, broadly rounded in mesocaudal view, not overreaching mesocaudal margin of apex. Lateral suture incomplete, marked by sulcus along first 3/4 of caudal surface, shallower distally. Mesial process asymmetrically bilobed, larger lobe rounded, at base of supra-apical process, directed cephalad. Cephalic process absent. Mesial surface produced into a rounded supra-apical process densely covered with short spines along its widened margins, patch of spines denser distally. Supra-apical process with cephalic surface distinctly folded proximally, concave medianly; mesocaudal surface smooth, slightly concave. Supra-apical process relatively short, length ranging approximately from 0.2 to 0.3 times G1's length in mesocaudal view, nearly as long as wide (ratio width/length roughly 1.0 to 1.3); tip rounded. Apex oblong, elongated mesolaterally, directed cephalad. Field of apical spines poorly developed, narrow, elongated mesolaterally, with minute spines.

Remarks

Phrygiopilus ibarrai is morphologically very similar to *Ph. acanthophallus* and their currently known distributions partially overlap in the departments of Baja Verapaz and Zacapa. They are mainly distinguished by the morphology of the G1's mesial process, which is bilobed and sometimes rounded in *Ph. ibarrai* (Fig. 4F, H, I) vs unilobed and acute in *Ph. acanthophallus* (Fig. 4A-C). In *Ph. ibarrai*, the length of the supra-apical process tends to be shorter than in *Ph. acanthophallus*, but this process was also relatively short in a few specimens of *Ph. acanthophallus* examined by us (e.g.,

male INPA 2181 – Fig. 4C). Whether these taxa represent a species complex remains to be better evaluated when a larger series of specimens is available from their distributional area.

The difference in the mesial process (bilobed, rounded in *Ph. ibarrai* vs unilobed, acute in *Ph. acanthophallus*) seems to be consistent but, curiously, specimens of both species were collected by one of us (ISW) in the same location and date (Río Quilila, a tributary to Río Negro or Chixoy, department of Baja Verapaz, near the bridge of the "ruta 5", the old road to Salamá, 15°12'53"N, 90°17'39"W, 20.VII.2014): whereas the male from INPA 2473 was determined as *Ph. acanthophallus*, that of the lot UCR-MZ uncat., is determined as *Ph. ibarrai*. The species could perhaps be part of the species complex that includes *Ph. acanthophallus*.

It is important to note that Pretzmann (1980: 659) mixed up the captions of the illustration for this species with those for *Potamocarcinus* (*Zilchia*) *zilchi germani* (see Pretzmann 1980: 658). The correct information for *Isabellagordonia* (*Phrygiopilus*) *acanthophalla ibarrai* in Pretzmann (1980: 659) should be: "plate 9 figs 37-41, plate 18 fig. 80" (CM, pers. observation).

Phrygiopilus strengerae (Pretzmann, 1965)
(Figs 4J, K; 15)

Strengeria (*Spirothelphusa*) *strengerae* Pretzmann, 1965: 8; 1971: 21; 1972: 94, figs 573-575, 581-583.

Phrygiopilus strengerae – Rodríguez 1982: 87; 2001: 440 (in key). — Villalobos F. 1982: 220 (in list). — Rodríguez Villalobos Hiriart & Álvarez 2008: 297 (in list). — Ng *et al.* 2008: 176 (in list). — Wehrtmann *et al.* 2016: 779 (in list). — Acevedo-Alonso & Cumberlidge 2022: 581 (Appendix 2, in list).

TYPE MATERIAL EXAMINED. — **Holotype. Guatemala** • 1 ♂ (23.4:14.1); Alta Verapaz, Cacao, Trace [= Trece] Aguas [probably Finca Trece Aguas, Hidroelectrica Secacao, at 15°24'35.27"N, 89°46'45.63"W; 805 m elev. – see Remarks]; VI.1907; G. P. Goll leg.; USNM 79372.

DISTRIBUTION. — Guatemala (Alta Verapaz) (Pretzmann 1965) (Fig. 15).

DESCRIPTION OF G1 (Fig. 4J, K)

Stem markedly sinuous, distal portion noticeable curved in laterocephalic direction, compressed in caudocephalic direction, wider proximally in mesocaudal view; caudal margin, in mesocaudal view, with clear median discontinuity due to distinct rounded lateral lobe bearing minute setae better seen in caudal view; cephalic margin slightly convex medianly in mesocaudal view. Marginal plate fused subdistally to the caudal surface; irregular row of short setae longitudinally along proximal half of marginal plate. Marginal suture on mesial surface gently following the curvature of the stem, distinctly curved towards lateral side distally in mesial view; row of long and short setae along proximal portion of marginal suture. Marginal process wide, broadly rounded in mesocaudal view, not overreaching mesocaudal margin of apex. Lateral suture incomplete, marked by sulcus along first 3/4 of caudal surface, shallower distally. Mesial process absent. Cephalic surface weakly crenulate distally, cephalic process absent; mesial surface produced into large, rounded supra-apical process. Supra-apical process with laterocephalic surface bearing spines larger and more compacted towards cephalic side and along caudodistal margin, lateral margin nearly smooth; cephalic surface not folded proximally, slightly convex in caudocephalic direction medianly; mesocaudal surface smooth, distinctly concave. Supra-apical process slightly wider than long (ratio width/length roughly 1.2), approximately 0.2 times length of entire stem in mesocaudal view; tip rounded. Apex narrow, elongated mesolaterally, directed cephalad, lower margin finely crenulated, upper margin (basal portion of supra-apical process) wringled. Field of apical spines poorly developed, narrow, elongated mesolaterally, with minute spines.

REMARKS

This species is only known from the type locality. Reddell (1981: 317) supposed that "Cacao, Trece Aguas" was probably in the Seamay-Sejul karstik system, department of Alta Verapaz, but Caudell (1908) explained that "Cacao is situated in the Province of Alta Vera Paz, between Panzos and Senahú, at an altitude of about 900 feet, near the foot of the waterfalls, above which the coffee plantation of Trece Aguas is situated". According to Google Earth®, "Cacao, Trece Aguas" most likely refers to the Trece Aguas farm, Secacao hydroelectric dam, Senahú, department of Alta Verapaz.

Phrygiopilus senticosus n. sp.
(Figs 5; 15)

urn:lsid:zoobank.org:act:4885342C-FE1E-463A-AC6E-0021767D0726

TYPE MATERIAL. — **Holotype. Guatemala** • ♂ (27.0:15.8), Escuintla, specific locality unknown; 3.XI.2000; R. Hernández leg.; UVGCR 31.

DIAGNOSIS. — G1 markedly sinuous, distal portion strongly curved in laterocephalic direction; caudal margin, in mesocaudal view, with clear median discontinuity due to distinct angled lateral lobe bearing minute setae. Mesial process as subtriangular conical spine at base of supra-apical process, directed cephalically. Supra-apical process with its margins and all over laterocephalic surface regularly and densely covered with spines (smaller proximally); mesial surface smooth, somewhat concave; supra-apical process slightly wider than long (ratio width/length roughly 1.2), approximately 0.2 times length of entire stem in mesocaudal view.

ETYMOLOGY. — The specific epithet "*senticosus*", from Latin, means thorny, an adjective that refers to the densely spined supra-apical process of the male first gonopod.

DISTRIBUTION. — Guatemala (Escuintla - the distribution record in the Fig. 15 is arbitrarily represented in the center of the department: approximately 14°10'N, 91°00'W).

DESCRIPTION OF THE HOLOTYPE

Carapace (Fig. 5A) outline ellipsoid, widest at the middle (cw/cl 1.70), dorsal surface smooth, nearly flat, regions ill-defined. Two distinct gastric pits, close to each other, on metagastric region. Cervical grooves somewhat deep, wide, slightly arched, distal end failing to reach anterolateral margin. Postfrontal

lobules small, almost indistinct; median groove shallow. Surface of carapace between front and postfrontal lobules smooth, distinctly deflected anteroventrally. Front (Fig. 5C, D) with upper border smooth, rounded, median notch absent; lower border carinate, slightly sinuous in dorsal and frontal views, slightly more projected anteriorly than upper one. Upper orbital margin (Fig. 5D) lined with faint papillae; lower orbital margin crenulate, lined with faint papillae; exorbital angle very low, obtuse. Anterolateral margin of carapace with set of faint, minute, rounded teeth increasing in size from anterior to posterior portion; posterolateral margin smooth, marked by faint suture. Epistome (Fig. 5C, D) narrow longitudinally; epistomial tooth low, slightly deflected anteroventraly, with carinate, smooth borders. Suborbital and subhepatic regions of carapace sidewall (Fig. 5C, D) smooth; pterygostomial regions (Fig. 5C) weakly pilose.

Endopod of Mxp3 (Fig. 5C) with ischium subquadrate, its outer and inner margins nearly straight; merus with outer margin broadly rounded, inner surface of palp bearing short and long setae; exopod of third maxiliped long, narrow, 0.73 times length of outer margin of ischium. Aperture of efferent branchial channel (Fig. 5D) wide, subretangular, upper margin slightly rounded, smooth.

Chelipeds (Fig. 5A, B) strongly heterochelous, similarly armed, right P1 larger. Larger cheliped (Fig. 5E) with merus subtriangular in cross section; dorsal margin rounded, with irregular row of low tubercles, fainter distally; ventromesial margin lined by longitudinal row of conical tubercles increasing in size distally; ventrolateral margin with single row of faint tubercles; distal upper margin arched, smooth; lower margin with subdistal row of faint tubercles. Carpus with inner margin bearing row of faint tubercles, a prominent median spine, and smooth distally; outer surface rounded, smooth. Palm (Fig. 5E) swollen (length/width 1.78), smooth on both mesial and lateral surfaces, ventral margin with irregular row of very faint tubercles. Fingers of larger chela (Fig. 5A, B, E) slightly gaping, those of smaller chela not gaping, tips not crossing; pollex with three subtriangular, large teeth interspaced with smaller ones. Dactylus of larger chela moderately arched, approximately as long as palm (dactylus/palm 1.054, measured dorsally); dorsal, mesial and lateral surfaces of dactylus and pollex with longitudinal rows of faint papillae. Ambulatory legs (Fig. 5A, B) mostly disarticulated or broken; P5 still attached to body, slender, ratios dactylus/propodus and dactylus/merus 1.40 and 0.79, respectively; P5 with dactylus bearing five longitudinal rows of sharp, corneous spines, increasing in size distally.

Thoracic sternum approximately as longer as broad (Fig. 5B). Thoracic sternites of 3rd maxillipeds and chelipeds completely fused, except for small notches at lateral edges of sternum. Male sternopleonal cavity densely pilose. Episternites 4-6 triangluar posteriorly, episternite 7 posteriorly truncate. Penis somewhat long and slender, hook-shaped, emerging from nearby coxo-sternal condyle articulation of P5 coxa, located proximally on sternite 8.

All pleonal somites free (Fig. 5B); lateral margins of somites fringed by line of short setae; male pleon with somite VI trapezoidal, longest, slightly shorter than telson (ration length of telson/length somite VI = 0.92), lateral margins slightly concave. Male telson (Fig. 5B) subtriangular, as long as wide, approximately as long as pleonal somite VI, lateral margins nearly straight, fringed by line of short seate, tip rounded.

G1 (Fig. 5F-H) markedly sinuous, distal portion noticeable curved in laterocephalic direction, compressed in caudocephalic direction, wider proximally in mesocaudal view; caudal margin, in mesocaudal view, with clear median discontinuity due to distinct angled lateral lobe bearing minute setae; cephalic margin broadly convex medianly in mesocaudal view; mesial surface with irregular row of short setae longitudinally along proximal half. Marginal suture on mesial surface, gently following the curvature of the stem, distinctly curved towards lateral side distally in mesial view; row of long and short setae along proximal portion of marginal suture. Marginal process wide, broadly rounded in mesocaudal view, not overreaching mesocaudal margin of apex. Lateral suture incomplete, marked by sulcus along first 2/3 of caudal surface, shallower distally. Mesial process as subtriangular conical spine at base of supra-apical process, directed cephalad. Cephalic surface distally and subdistally crenulate, cephalic process absent; mesial surface produced into large, suboval supra-apical process. Supra-apical process with its margins, and all over laterocephalic surface, regularly and densely covered with spines (smaller proximally); cephalic surface distinctly folded proximally, slightly convex in caudocephalic direction medianly; mesocaudal surface smooth, distinctly concave. Supra-apical process slightly wider than long (ratio width/length roughly 1.2), approximately 0.2 length of entire stem in mesocaudal view; tip rounded. Apex narrow, slit-like, elongated mesolaterally, directed cephalad, upper and lower margins finely crenulated. Field of apical spines poorly developed, narrow, elongated mesolaterally, with minute spines nearly concealed by basal portion of supra-apical process and distal margin of cephalic surface of G1.

G2 slightly shorter than G1, flagellum very slender, regularly tapering, tip flattened.

Remarks

In terms of the G1 morphology, *Ph. senticosus* n. sp. is most similar to *Ph. strengerae*, since their gonopods are strongly recurved cephalically and bear a strong median lobe due to a remarkable discontinuity on the median portion of the caudal margin (better seen in mesocaudal view). However, the following characters can readily distinguish both species: (a) the lateral lobe is less pronounced in *Ph. senticosus* n. sp., being shorter than the marginal process in mesocaudal view (Fig. 5F), whereas this lobe is distinctly more pronounced in *Ph. strengerae*, being nearly as wide as the marginal process in mesocaudal view (Fig. 4J); (b) the width of the stem median constriction is wider in *Ph. senticosus* n. sp. (ratio width at constriction/width at lateral lobe roughly 0.7 – measured in mesocaudal view) (Fig. 5F) than in *Ph. strengerae* (ratio width at constriction /width at lateral lobe roughly 0.4 – measured in mesocaudal view) (Fig. 4J); (c) the mesial process is present in *Ph. senticosus* n. sp. (Fig. 5F) as a conical spine whereas it is absent in *Ph. strengerae* (Fig. 4J); (d) the supra-apical process, particularly towards the mesocaudal surface, is more densely thorny in *Ph. senticosus* n. sp. (Fig. 5F-

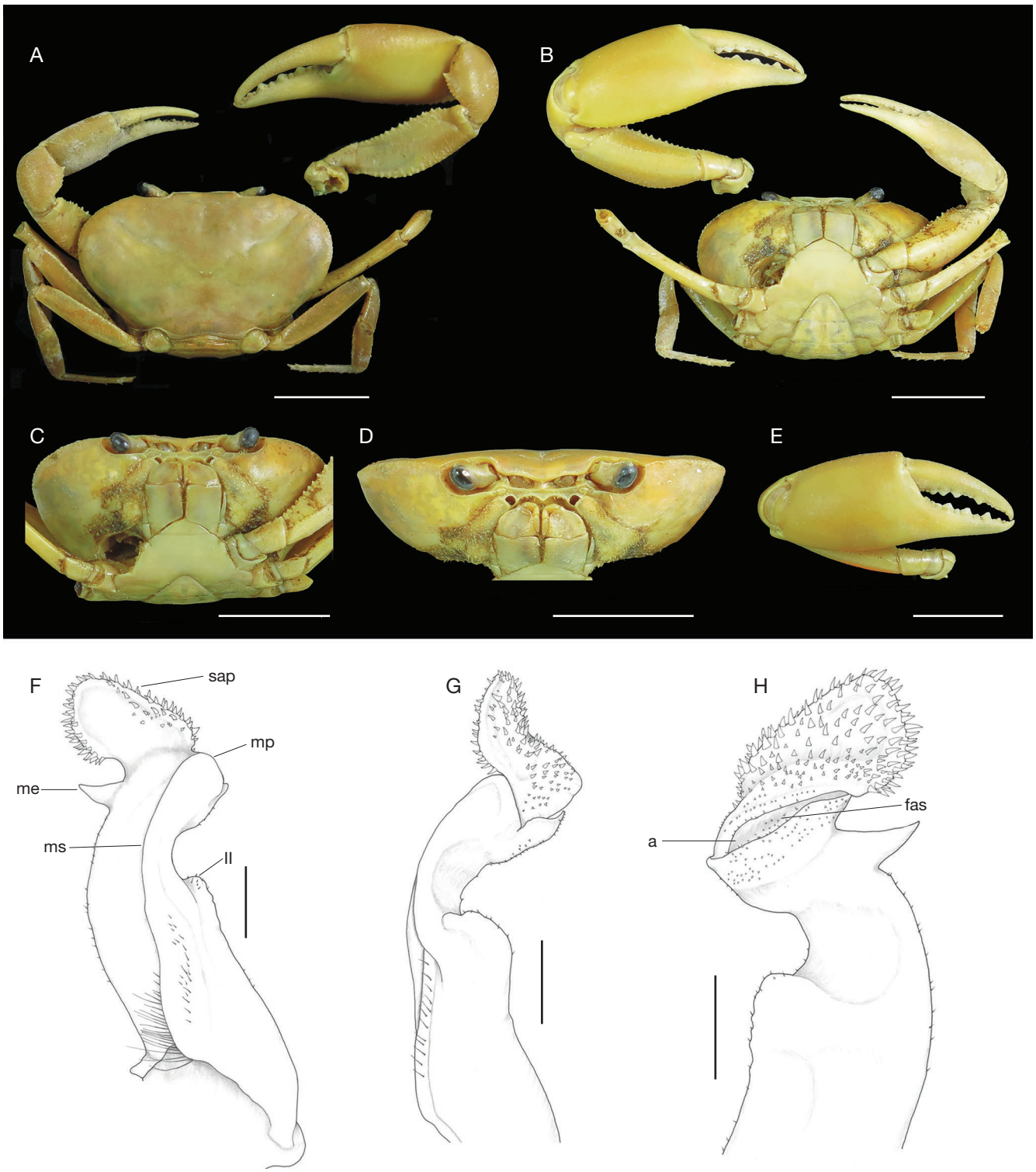

Fig. 5. — *Phrygiopilus senticosus* n. sp., holotype, UVGCR 31: **A**, habitus, dorsal view; **B**, habitus, ventral view; **C**, pterygostomial view; **D**, frontal view; **E**, right chelae (largest), lateral view; **F**, left G1, mesocaudal view; **G**, left G1, caudolateral view; **H**, left G1, cephalic view. Abbreviations: **a**, apex; **fas**, field of apical spines; **ll**, lateral lobe; **me**, mesial process; **mp**, marginal process; **ms**, marginal suture; **sap**, supra-apical process. Scale bars: A-E, 10 mm; F-H, 1 mm. Photos: C. Magalhães.

H) than in *Ph. strengerae* (Fig. 4J, K). Additionally, *Ph. senticosus* n. sp. is distributed in southern Guatemala (department of Escuintla), while *Ph. strengerae* occurs in the department of Alta Verapaz, in central-northern Guatemala.

The new species can be easily differentiated from the other Guatemalan species of *Phrygiopilus* by the strong lateral lobe and by the cephalic surface of the supra-apical process densely thorny.

Genus *Raddaus* Pretzmann, 1965

Raddaus bocourti (A. Milne-Edwards, 1866) (Figs 6A-C; 7; 16)

Boscia bocourti A. Milne-Edwards, 1866: 203. — Smith 1870: 146 (in list).

Potamocarcinus bocourti – Ortmann 1897: 317 (in list).

Pseudothelphusa bocourti – Pocock 1889: 10 (in list). — Rathbun 1898: 513, 533, 537 (in list); 1904: 242 (in list); 1905: 294, pl. 15 fig. 1; 1906: 502 (in list). — Young 1900: 220. — Coifmann 1939: 106 (in list).

Pseudothelphusa similis Rathbun, 1904: 242 (*nomen nudum*).

Pseudothelphusa similis Rathbun, 1905: 295, text-fig. 87, pl. 15, fig. 4; 1906: 502 (in list). — Coifmann 1939: 109 (in list).

Pseudothelphusa cobanensis Rathbun, 1904: 242 (*nomen nudum*).

Pseudothelphusa cobanensis Rathbun, 1905: 296, text-fig. 88, pl. 15, fig. 5; 1906: 502 (in list). — Coifmann 1939: 107 (in list). — Pretzmann 1965: 3 (in list). — Smalley 1964: 28, 29, fig. 1A, C, E.

Pseudothelphusa grallator Rathbun, 1904: 242 (*nomen nudum*).

Pseudothelphusa grallator Rathbun, 1905: 297, text-fig. 89, pl. 15, fig. 6; 1906: 502 (in list). — Coifmann 1939: 108 (in list). — Pretzmann 1965: 3 (in list).

Pseudothelphusa magna – Rathbun 1904: 242 (in list); 1905: 299 (part, ? ♀ from Pansos Palochie, Haute Vera Paz); 1906: 502 (in list).

Pseudothelphusa cobanensis cobanensis – Bott 1956: 230 (part, typus).

Pseudothelphusa (*Anaphyrmus*) *bocourti* – Smalley 1965: 651 (in list).

Pseudothelphusa (*Anaphyrmus*) *similis* – Smalley 1965: 651 (in list).

Pseudothelphusa (*Anaphyrmus*) *cobanensis* – Smalley 1965: 651 (in list).

Potamocarcinus (*Raddaus*) *similis* – Pretzmann 1965: 3 (in list).

Potamocarcinus (*Raddaus*) *grallator* – Pretzmann 1965: 3 (in list).

Potamocarcinus (*Raddaus*) *cobanensis* – Pretzmann 1965: 3 (in list). — Smalley 1970: 102, fig. 14.

Potamocarcinus (*Raddaus*) *boccourti* [sic] – Pretzmann 1965: 3 (in list).

Potamocarcinus (*Raddaus*) *bocourti bocourti* – Pretzmann 1971: 20 (in list); 1972: 76, text-figs 16, 17, figs 442, 443, 453, 698, 699; 1980: 656.

Potamocarcinus (*Raddaus*) *bocourti cobanensis* – Pretzmann 1971: 20 (in list).

Potamocarcinus (*Raddaus*) *bocourti similis* – Pretzmann 1971: 20 (in list); 1972: 76, figs 447-449, 453-456; 1980: 656.

Potamocarcinus (*Raddaus*) *bocourti grallator* – Pretzmann 1971: 20 (in list); 1972: 76, figs 444-446, 472-474.

Raddaus bocourti – Rodríguez 1982: 98, figs 64b, e, j, k, 65a-g; 2001: 442. — Villalobos F. 1982: 220 (in list). — Rodríguez & Magalhães 2005: 360 (in table). — Villalobos Hiriart & Álvarez 2008: 297 (in list). — Ng *et al.* 2008: 177 (in list). — Wehrtmann *et al.* 2014: 123, fig. 1A, B; 2016: 781 (in list). — Acevedo-Alonso & Cumberlidge 2022: 583 (Appendix 2, in list).

TYPE MATERIAL EXAMINED. — **Lectotype** (by inference of "type" by Rathbun 1905: 294, 295). **Guatemala** • 1 ♀ (damaged, 76.5:48.5 according to Rodríguez 1982), dry; Alta Verapaz, environs de Cobán [15°27'55.74"N, 90°22'20.10"W; 1303 m elev.]; M. Bocourt leg.; Expédition du Mexique, 1864-1866; MNHN Entry 190-1866; MNHN-IU-2000-4052 (= MNHN-B22814).
Paralectotype (by inference of "cotype" by Rathbun 1905: 295). **Guatemala** • 1 ♀ (cw 74.3 mm × cl 48.4 mm, according to Rodríguez 1982), dry; Alta Verapaz, environs de Cobán [15°27'55.74"N, 90°22'20.10"W; 1303 m elev.]; M. Bocourt leg.; Expédition du Mexique, 1864-1866; MNHN-IU-2000-4626 (= MNHN-B22814).
Holotype of *Pseudothelphusa cobanensis* Rathbun, 1905 (by original designation). Guatemala • 1 ♀ (62.5:40.5), dry, ; Alta Verapaz, environs de Cobán; M. Bocourt leg.; Expédition du Mexique, 1864-1866; MNHN Entry 190-1866; MNHN-IU-2000-4625 (= MNHN-B4625, ex B4053).
Paratype of *Pseudothelphusa cobanensis* Rathbun, 1905. Guatemala • 1 ♂ (carapace damaged), dry, ; Alta Verapaz, environs de Cobán; date unknown; M. Bocourt leg.; Expédition du Mexique, 1864-1866; MNHN-IU-2000-4628 (= MNHN-B4628, ex B4053).
Holotype of *Pseudothelphusa similis* Rathbun, 1905. Guatemala • 1 ♂ (70.2:42.5), dry; Alta Verapaz, rivière de Pansos-Palochie [= Polochic river, municipality of Panzós; 15°23'20.74"N, 89°37'30.23"W; 10 m elev.]; XII.1865; M. Bocourt leg.; Expédition du Mexique, 1864-1866; MNHN Entry 190-1866; MNHN-IU-2000-4624 (= MNHN-B4624, ex-B4058).
Holotype of *Pseudothelphusa grallator* Rathbun, 1905 (by original designation. Guatemala • 1 ♀ (61.3:38.9), dry, Totonicapán, montagnes des Altos, environs de Totonecapan [? San Francisco El Alto; 14°55'53.07"N, 91°26'42.10"W; 2351 m elev.], surrondings of Totonicapán]; M. Bocourt leg.; Expédition du Mexique, 1864-1866; MNHN-IU-2000-4627 (=MNHN-B4627, ex B4055).
Paratypes of *Pseudothelphusa grallator* Rathbun, 1905. Guatemala • 1 ♀, dry, 1 ♂ (remnants), dry; same data as in type; MNHN-IU-2000-4055 (= MNHN-B4627).

OTHER MATERIAL EXAMINED. — **Guatemala** • 1 ♂; collecting data unknown; UVGCR 46 • 1 ♂; collecting data unknown; UVGCR 209 • 1 ♂, UVGCR 510, collecting data unknown; 1 ♂; Costa

KEY TO GUATEMALAN SPECIES OF *RADDAUS* PRETZMANN, 1965

1. G1 with cephalic surface of distal portion bearing one subdistal spine (Fig. 6B, E); mesial process bilobed, enlarged, as wide as or wider than width of main stem in mesial view (Fig. 6A, D) 2
— G1 with cephalic surface of distal portion bearing two subdistal spines (Fig. 6G, H); mesial process unilobed, slightly narrower than width of main stem in mesial view (Fig. 6F) ..... *R. tuberculatus* (Rathbun, 1897)

2. G1 with mesial process trapezoidal, roughly as wide as main stem in mesial view; mesial process with proximal and distal lobes rounded, distal one narrowest (Fig. 6A) ..... *R. bocourti* (A. Milne-Edwards, 1866)
— G1 with mesial process subretangular, wider than main stem in mesial view; mesial process with proximal and distal lobes as subtriangular tooth, distal one smallest (Fig. 6D) ..... *R. mertensi* (Bott, 1956)

Sur; 28.X.1993; K. Ness M. leg.; UVGCR 97 • 1 ♂, Costa Sur; XI.1993; C. Cardona leg.; UVGCR 367 • 1 juv. ♂ (24.5:16.6); Petén, Poptún, Finca Ixobel, cerca a riachuelo; 16°18'14"N, 89°25'13"W; [537 m elev.]; 11.I.2014; I. S. Wehrtmann & M. Orozco leg.; UCR-MZ 3236-01 • 2 juv. ♂ (12.4:8.6; 19.8:13.3); Petén, Dolores, Río Sanicté; 16°36'55"N, 89°32'37"W; 270 m elev.; 12.01.2014; I. S. Wehrtmann & M. Orozco leg. UCR-MZ 3233 • 1 juv. ♂ (21.8:14.5) 1 juv. ♀; Quiché, Sacapulas, quebrada El Tesoro, Pacan, 15°18'11"N, 91°04'49"W; 1954 m elev.; 20.I.2014; I. S. Wehrtmann, M. Orozco, C. Magalhães & M. W. Dix leg.; UCR-MZ 3232-01 • 2 ♂ spec., Alta Verapaz, Río Chilax, in the surroundings of San Juan Chamelco; [15°26'15.30"N, 90°20'00.89"W; 1368 m elev.]; 1975; Böttger leg.; SMF 8866 • 2 ♂ (31.3:20.4; 48.3:30.4) 2 ♀ (22.7:14.7; 42.6:27.1); Izabal, Puerto Barrios, Río Las Escobas; [15°41'09.92"N, 88°38'40.91"W; 93 m elev.]; 18.X.1986; leg. unknown; UVGCR 430 • 1 ♂; Izabal, Río Dulce [15°39'26"N, 88°59'58"W; 4 m elev.]; 20.X.1997; F. Bolañoz leg.; UVGCR 173 • 1 juv. ♂; Izabal, Puerto Santo Tomás [15°41'37"N, 88°37'32"W; 22 m elev.], Playa Ramonastes; 29.V.1994; M. L. Priaz & W. Dio leg.; UVGCR 243 • 1 immat. ♂; Izabal, Cerro San Gil, Río Las Escobas [15°39'56.40"N, 88°46'54.72"W; 1113 m elev.]; 21.X.2001; Ecología Avanzada – grupo 2 leg.; UVGCR 454 • 2 ♂ (32.8:21.1; 38.8:24.0) 1 ♀ (58.1:35.2); Baja Verapaz, Salamá [15°06'01.88"N, 90°18'51.60"W; 940 m elev.]; 20.IV.1934; E. R. Blake leg.; FMNH 1829 • 1 ♂ (33.5:21.4) 3 ♀ (18.8:12.8-27.7:17.5); Zacapa, Villa Rocosa, Río El Jutillo, near Usumatlán; 15°00'45"N, 89°49'58"W; [717 m elev.]; 21.VII.2014; I. S. Wehrtmann & M. Orozco leg.; UCR-MZ uncat. • 1 ♂; Chimaltenango, Yepocapa [14°30'N, 90°57'W]; 1400 m elev.; 6.VI.1949; leg. unknown; USNM 230092 • 1 ♂ 2 ♀ 1 juv., Chimaltenango, Yepocapa; 1460 m elev.; XI.1949; leg. unknown; USNM 230093 • 1 ♂; Chimaltenango, Yepocapa, 13-14. VII.1949, H. T. Dalmat leg.; USNM 90364 • 1 ♂ (77.4:48.3) 1 ♀ (80.9:49.6), Chimaltenango, stream in area San Pedro Yepocapa; XII.1948; H. T. Dalmat leg.; USNM 88721, • 1 ♂; Guatemala, Lago de Amatitlán, Tacatón; [14°26'27.35"N, 90°33'33.02"W; 1195 m elev.]; 31.X.1993; C. MacVean leg.; UVGCR 135 • 1 ♂; Guatemala, Amatitlán; [14°28'29.74"N, 90°34'38.94"W; 1190 m elev.]; 6.IV.1991; J. Ruiz R. leg.; UVGCR 148 • 1 ♂; Guatemala, Ciudad de Guatemala, mercado La Plazita [probably captured in Lago Amatitlán]; 14.XI.2000; F. Peloéz leg.; UVGCR 58 • 1 ♂ (74.8:46.6); Guatemala, Santa Catarina Pinula, Puerta Parada [14°33'21.21"N, 90°27'09.28"W; 1837 m elev.], Río Acatán; 2.III.1987; W. Dix leg.; UVGCR 523 • 1 ♂; Guatemala, Santa Catarina Pinula, Puerta Parada; 1978; M. Dix leg.; UVGCR 438 • 1 ♂ (83.2:52.3); Guatemala, carretera to El Salvador, km 16; [14°32'47.82"N, 90°27'06.33"W; 1877 m elev.]; date unknown; S. Rodas leg.; UVGCR 499 • 1 ♂ (33.4:21.7) 1 ♀ (45.5:29.1); Solalá, boca del río Panajachel [14°44'04.96"N, 91°09'26.20"W; 1565 m elev.]; 13.ii.1970; W. Bussing leg.; UCR-MZ 2671-01 • 1 ♂ (70.7:45.8) 1 ♀ (61.1:42.3); Solalá, Lake Atitlán [14°42'N, 91°12'W; 1558 m elev.]; date unknown; G. A. Artamonoff leg.; FMNH 12288 • 1 ♂; Solalá, Lago Atitlán; V.1977; G. Martínez leg.; UVGCR 111 • 1 ♂, Solalá, Panajachel [14°44'29"N, 91°09'48"W]; 6.X.1997; J. Cruz leg.; UVGCR 172 • 1 ♂, Solalá, Panajachel, cerca del muelle; [14°44'29.25"N, 91°09'48.20"W; 1563 m elev.]; data unknown; J. Cruz leg.; UVGCR 146 • 1 ♂ (65.0:40.0); Solalá, Panajachel (bought in the market, captured at Lago Atitlán); 21.VII.2013; I. S. Wehrtmann leg.; UCR-MZ 3114-03 • 1 ovig. ♀, Solalá, Panajachel (bought in the market, captured at Lago Atitlán); 21.VII.2013; I. S. Wehrtmann leg.; UCR-MZ 3114-01 • 4 ♂ (53.4:33.9-59.0:36.6) 1 ♀ (61.8:38.8); Solalá, Panajachel (bought in the market, captured at lake Atitlán); I.2014; C. Magalhães leg.; INPA 2020 • 1 ♂, Sacatepéquez, Municipalidad Mixco, Finca La Esmeralda [? Finca La Esmeralda, in San Lucas Sacatepéquez, Department Sacatepéquez: 14°34'53.88"N, 90°37'03.71"W; 1637 m elev.]; 17.VIII.1999; C. Cardona leg.; UVGCR 16 • 1 ♂ (23.8:16.1); Suchitepéquez, Patutul, Finca Los Tarrales, stream inside the farm; 14°31'28"N, 91°08'07"W; 875 m elev.; 19.I.2014; I. S. Wehrtmann, M. Orozco, C. Magalhães & M. W. Dix leg.; UCR-MZ 3231-02 • 15 spec.; Santa Rosa, laguna de Ayarza; [14°25'07"N, 90°07'33"W; 1412 m elev.]; 10-11.V.1947; R. R. Miller leg.; USNM 1089230 • 1 ♂; Santa Rosa, Barbarena; [14°18'34"N, 90°21'40"W; 1225 m elev]; 9.XI.2000; J. Castillo leg.; UVGCR 171 • 1 ♂; Santa Rosa, Taxisco; [14°04'02"N, 90°28'04"W; 179 m elev.]; V.1994; J. R. Valdéz leg.; UVGCR 112 • 2 juv. ♂, Santa Rosa, Taxisco-Monterrico; [13°59'38.63"N, 90°27'52.75"W; 30 elev.]; 20.X.2000; leg. unknown.; UVGCR 456 • 1 ♂; Escuintla, Puerto San José; [13°55'45"N, 90°49'13"W; 5 m elev.]; 7.XI.2000; D. Maza leg.; UVGCR 390 • 1 ♂; Escuintla, Puerto San José; 21.IX.1997; A. Turcois leg.; UVGCR 159 • 1 ♂; Escuintla, aeropuerto Las Lisas [13°55'43"N, 90°49'53"W; 12 m elev.], municipalidad San José; 7.X.1976; M. W. Dix leg.; UVGCR 435.

Distribution. — Guatemala (Alta Verapaz, Baja Verapaz, Chimaltenango, Chiquimula, Escuintla, Guatemala, Izabal, Petén, Quiché, Santa Rosa, Solalá, Suchitepéquez, Totonicapán, Zacapa) (Fig. 16), Mexico, Belize, Honduras, and El Salvador (Pretzmann 1980; Rodríguez 1982, 2001; Villalobos Hiriart & Álvarez 2008; Wehrtmann *et al.* 2016; this study).

Other records in Guatemala. — Pretzmann (1980): Petén, Mopán, at Río Melchor Mencos, border with Belize [17°03'27"N, 89°09'06"W; 92 m elev.]; Petén, near Poptún [16°21'N, 89°26'W; 544 m elev]; Alta Verapaz, tributary of Río Colochie [= Polochic], NE Tucura [= Tucurú, 15°17'51.32"N, 90°06'58.78"W; 434 m elev.]; Chiquimula, Río Apantes [? Aldea Apantes, 14°32'45.73"N, 89°24'28.64"W; 984 m elev., municipality of Concepción Las Minas], Melen, NW Esquipulas; Guatemala, 14 km S Guatemala City, N San José Pinula [14°32'46"N, 90°24'41"W; 1748 m elev.]. Rodríguez (2001): Solalá, Lago de Atitlán, 4 miles E of Panajachel [14°41'50.43"N, 91°07'05.52"W; 1604 m elev.]; Guatemala, Río Piscaya [= Pixcaya, Department Chimaltenango, 14°51'24.85"N, 90°39'44.99"W; 759 m elev.], 2 km N junction National RT5-RT4, small tributary of Río Piscaya, at 40 km N from Guatemala; Guatemala, km 56 from Guatemala City on route 5 to Salamá, small tributary of Río Grande [El Quiché, 14°53'48.53"N, 90°40'20.42"W; 733 m elev.]; Guatemala, km 71 from Guatemala City on route 5 to Salamá, small tributary of Río Grande [Baja Verapaz, 14°54'48.73"N, 90°31'24.78"W; 967 m elev.].

Description of G1 (Fig. 6A-C)

Straight in mesial view, narrow in the proximal 2/3, wide in the distal third, moderately compressed mesolaterally; caudal margin moderately convex subdistally in mesial view; cephalic margin somewhat irregular, with few short setae more widely spaced medianly, close together subdistally at base of widened mesial process. Marginal suture on mesial surface, straight up to apex, with row of large marginal setae along proximal portion partially extending to marginal plate as row of short setae. Marginal process somewhat narrow, slightly rounded, extended as long as mesial margin of apex. Lateral suture incomplete, marked by shallow sulcus on caudal surface. Mesial process widened, nearly as wide as main stem, roughly trapezoidal, directed cephalad, bilobed, with proximal lobe larger, broadly rounded; distal lobe narrow, rounded, situated obliquely in relation to proximal lobe, slightly longer in mesial view; cephalic surface of mesial process distinctly concave in lateral view, convex in mesial view. Apex oblong, situated apically, open, mesial and lateral margins of same height; field of apical spines well developed, with short, small spines; spermatic channel opening on apex cavity, situated towards caudal end. Cephalic surface with strong triangular, subdistal cephalic spine, pointing cephalad.

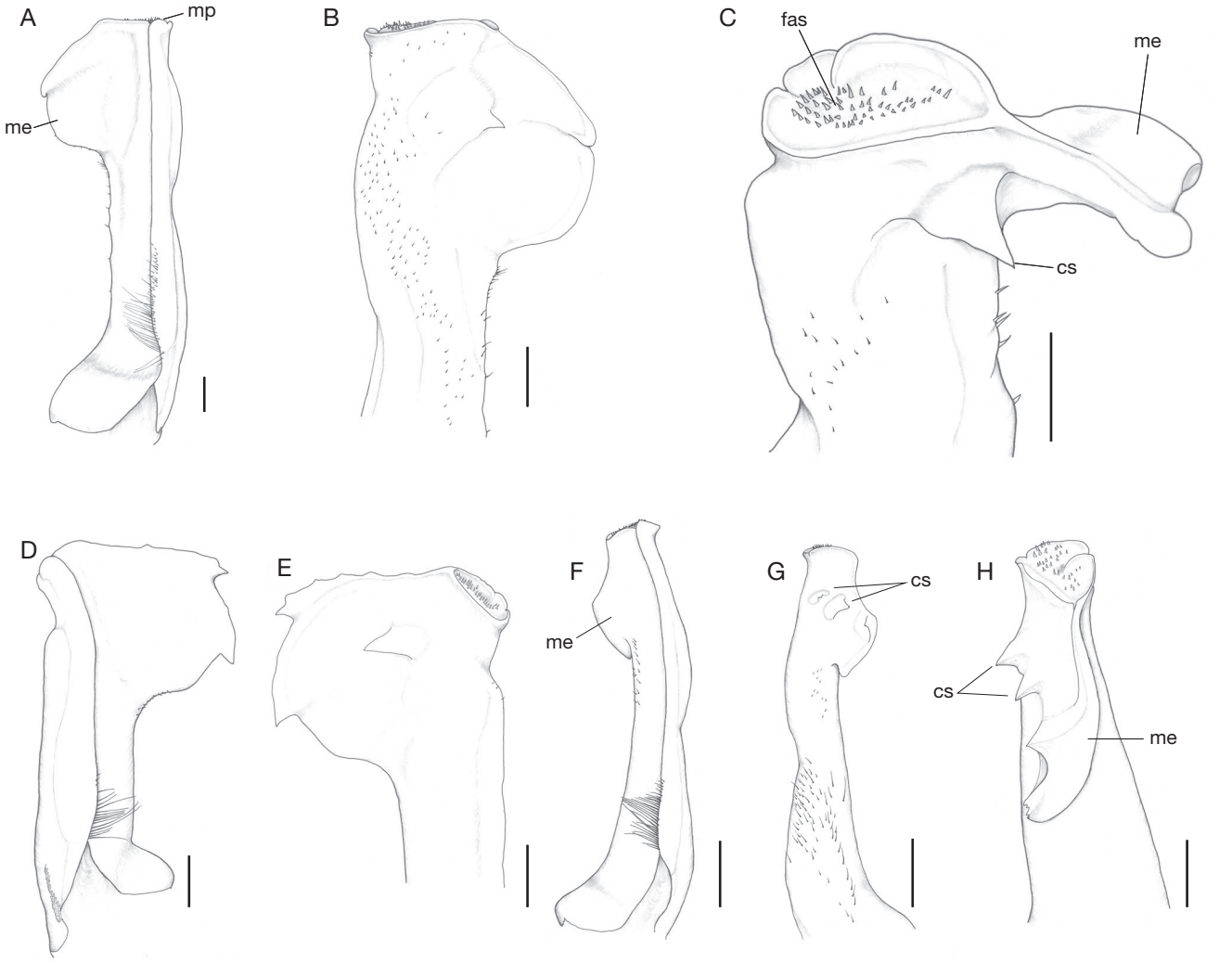

Fig. 6. — *Raddaus* Pretzmann, 1965 species, G1: **A**-**C**, *Raddaus bocourti* (A. Milne-Edwards, 1866), INPA 2020, left G1: **A**, mesocaudal view; **B**, lateral view; **C**, apical-cephalic view; **D**, **E**, *Raddaus mertensi* (Bott, 1956), holotype, SMF 1822, right G1: **D**, mesocaudal view; **E**, laterocephalic view; **F**-**H**, *Raddaus tuberculatus* (Rathbun, 1897), USNM 1089233, left G1: **F**, mesocaudal view; **G**, lateral view; **H**, apical-cephalic view. Abbreviations: **cs**, subdistal cephalic spine; **fas**, field of apical spines; **me**, mesial process; **mp**, marginal process. Scale bars: 1 mm.

Remarks

The correct status of the type material of this species and three other synonymous taxa is somewhat unclear. Alphonse Milne-Edwards (1866) offered a very brief description of apparently a single specimen from a river of Coban (Alta Verapaz) for which he provided measurement (cw 75 mm × cl 47 mm) but did not inform the sex. However, it is not explicitly mentioned in the text that the specimen would be the type (in the sense of the name-bearing specimen). Although it may seem that A. Milne-Edwards (1866) used a single specimen, this cannot be unequivocally assumed because Rathbun (1905) mentioned a slightly smaller female with the same characters in the MNHN collection that she treated as "cotype". Furthermore, when visiting the MNHN in September 2015 for examining the Guatemalan material, the senior author found a box containing two dry females of *R. bocourti* (MNHN entry 190-1866 in Bocourt's "Expédition du Mexique" [catalogued as MNHN-B22814]) with indications of "type" and "co-type", one of which partially disarticulated and with the carapace badly damaged (Fig. 7A). Rathbun (1905) mentioned that "Le type du *P. Bocourti*, c'est-à-dire l'individu que M. A. Milne-Edwards a mesuré, est une grande femelle" [The type of *P. Bocourti*, that is to say the individual that Mr. A. Milne-Edwards measured, is a large female] and that "Le femelle cotype est un peu plus petite que le type" [The female cotype is slightly smaller than the type]. By this action, Rathbun (1905) was the first author before the year 2000 to have "unambiguously selected a particular syntype to act as the unique name-bearing type of the taxon" as stated in the Article 74.5 (ICZN 1999), which can be taken as a valid lectotype designation. Later, Rodríguez (1982) measured the larger female with cw 76.5 mm × cl 48.5 mm, the smaller female with cw 74.3 mm × cl 48.4 mm, and remarked that the carapace of the former was broken; he treated them as "type" and "paratype", respectively. Thus, the larger, partially damaged female of MNHN-B22814

FIG. 7. — Type specimens of *Raddaus bocourti* (A. Milne-Edwards, 1866) and synonymus species: **A**, *Raddaus bocourti*, MNHN-B22814, habitus, dorsal view, female, dry (upper side) and female (damaged), holotype, dry (lower side); **B**, *Pseudothelphusa similis* Rathbun, 1905 [synonym of *Raddaus bocourti*], holotype, male, dry, MNHN-B4624:habitus, dorsal view; **C**, **D**, *Pseudothelphusa cobanensis* Rathbun, 1905 [synonym of *Raddaus bocourti*], syntypes, habitus, dorsal view: **C**, female, MNHN-B4625; **D**, male (damaged), MNHN-B4628; **E**-**G**, *Pseudothelphusa grallator* Rathbun, 1905 [synonym of *Raddaus bocourti*]: **E**, female, dry, holotype, MNHN-B4627, habitus, dorsal view; **F**, male (remnants) (upper side) and female (damaged) (lower side), MNHN-B4627, habitus, dorsal view; **G**, male (remnants) (lower side) and female (damaged) (upper side), MNHN-B4627, habitus, ventral view. Photos: C. Magalhães.

(Fig. 7A) must be considered a valid lectotype designation by Rathbun (1905) and, assuming that A. Milne-Edwards (1866) may have had another specimen at his disposal, the smaller female treated as "cotype" by Rathbun (1905) and kept under the same catalogue number should be treated as paralectotype.

Three *Pseudothelphusa* species from Guatemara were described by Rathbun (1905) based on female specimens: *Pseudothelphusa similis*, *Ps. cobanensis*, and *Ps. grallator*, which have been considered to be junior synomyms of *R. bocourti* (see Rodríguez 1982; Ng *et al.* 2008). Rathbun (1905) founded *Ps. similis* on a single male specimen but also mentioned 17 juvenile specimens from the same locality and attributed a slight morphological difference between them to age. As the male, to which she provided measurements, is unequivocally termed "type", this is the holotype fixed by original designation (ICZN 1999, Art. 73.1.1). The holotype of *Ps. similis* (MNHN-B4624) is a dry male with a longitudinal cleft along the middle and on the right side of the dorsal region of the carapace (Fig. 7B).

The type specimens of *Ps. cobanensis*, a well-preserved female (Fig. 7C) and a male in very bad condition (Fig. 7D), are also dry. Rathbun's (1905: 296, 297) action, by clearly treating only the female as "type", can be interpreted as she has set it as the unique name-bearing type of this taxon (Art. 73.1.1, ICZN 1999), therefore fixing the holotype by original designation. The male was designated as "co-type" (Rathbun, 1905: 297, text-fig. 88), which can then be considered as a reference to paratype. This was also Rodríguez's (1982: 101) interpretation when treated the female as the holotype and the male as paratype.

Rathbun (1905: 297) based the description of *Pseudothelphusa grallator* on at least two specimens: a female (cw 61.3 mm × cl 38.9 mm) and a male (cw 59.2 mm × cl 37.8 mm) and, in "Dimensions", provided a table with their measurements. In this table, she indicated the female as "Type". In the section "Distribution", she listed eight specimens from the same locality: three females (including the "type", numbered 623d in the Bocourt's material from the "Expédition du Mexique"), one male (no. 624d in Bocourt's catalogue), and additionally one female and three young specimens. Since the female with the number 623d (MNHN-B4627) is clearly marked as "Type" by Rathbun (1905), this specimen is the holotype fixed by original designation (Art. 73.1.1, ICZN 1999). Rodríguez (1982) remarked that the situation of these specimens in the Paris Museum is somewhat confusing but, even taking into account the poor condition of the material, he concluded that the reasonably well-preserved female measuring cw 60.5 mm × cl 39 mm should be the one Rathbun considered as the "Type". During a visit to the MNHN in September 2015, the senior author found that the condition of some of these specimens had worsened but this dry female was still in reasonably good condition and preserved in a box with the catalogue number 4627 and with a label stating "Bocourt (Expédition du Mexique) (no. 623^{d} de son catalogue)"; this box also had the indicative sign of holotype (the red circle label) attached to it (Fig. 7E). This specimen should be the one considered by Rodríguez (1982) as the holotype. Another box, bearing a handwritten label and stating "*Pseudothelphusa grallator* Type 4627", contained one dry female with the dorsal region of the carapace severely damaged and almost entirely disarticulated as well as the remnants of a male specimen with the abdomen partially broken and the sternopleonal cavity glued to the box (this male has the number "624d" written on the anterior portion of the sternum) (Fig. 7F, G). Although these lots bear a label with the word "TYPE" written in red, these specimens should be considered as paratypes; Rodríguez (1982) considered the male as being an allotype.

Raddaus mertensi (Bott, 1956)
(Figs 6D, E; 16)

Pseudothelphusa cobanensis mertensi Bott, 1956: 231, pl. 30, fig. 3a-c, pl. 35, fig. 3a, b.

Raddaus mertensi – Cumberlidge *et al.* 2014: 147 (in table). — Wehrtmann *et al.* 2016: 781 (in list). — Acevedo-Alonso & Cumberlidge 2022: 583 (Appendix 2, in list).

TYPE MATERIAL EXAMINED. — **Holotype. El Salvador** • 1 ♂ (37.3:24.4); Santa Ana, Los Planes Farm [northeast of Metapán, Montecristo National Park; 14°24'N, 89°22'W]; 1830 m elev.; 30.X.1950; R. Mertens leg.; SMF 1822.

OTHER MATERIAL EXAMINED. — **Guatemala** • 1 ♂ (soft carapace) 3 juv. ♀; Chiquimula, Río Atulapa, 3 miles east of Esquipulas, on road CA 10; [14°33'45"N, 89°18'37"W; 916 m elev.]; 5.IV.1971; R. M. Bailey leg.; USNM 1089229.

DISTRIBUTION. — Guatemala (Chiquimula) (Fig. 16), Honduras (Ocotepeque) and El Salvador (Santa Ana) (Bott 1956; Wehrtmann *et al.* 2016; Acevedo-Alonso & Cumberlidge 2022; Magalhães & Wehrtmann 2025; this study).

DESCRIPTION OF G1 (Fig. 6D, E)

Stout, straight in mesial view, narrow in proximal 2/3, very wide in distal third, moderately compressed mesolaterally; caudal and cephalic margins straight in mesial view. Marginal suture on mesial surface straight up to apex along most of stem, slightly curved in caudal direction in distal quarter, with short row of large marginal setae along proximal portion. Marginal process somewhat narrow, rounded, not extending beyond mesial margin of apex. Lateral suture incomplete, marked by shallow sulcus on caudal surface. Mesial process greatly widened, slightly wider (roughly 1.2 times) than main stem, subretangular, directed cephalad, bilobed, with proximal lobe bearing broadly subtriangular teeth pointing basally; distal lobe as narrow subtriangular teeth slightly shorter than proximal lobe in mesial view; mesial lobe with proximal margin bearing short row of minute setae; distal margin slightly crenulate, cephalic surface slightly concave in lateral view, bearing strong triangular, subdistal spine pointing cephalad, and small, rounded protuberance located just below subdistal spine. Apex oblong, short, situated obliquely, open, mesial slightly higher than lateral one; field of apical spines moderately developed, with short small spines; spermatic channel opening on apex cavity, situated towards caudal end.

REMARKS

This species was known only from its type locality, in the department of Santa Ana, in northwestern El Salvador. Later, Acevedo-Alonso & Cumberlidge (2022) listed the occurrence of this species in Guatemala and Honduras without specify-

FIG. 8. — *Raddaus tuberculatus* (Rathbun, 1897), male, lectotype, USNM 20047: **A**, habitus, dorsal view; **B**, habitus, ventral view; **C**, habitus, detail of the damaged posterior portion of the thoracic sternum. Photos: C. Magalhães.

ing voucher material or distributional data. Thus, our report herein represents the first published record of this species for Guatemala.

Raddaus tuberculatus (Rathbun, 1897)
(Figs 6F-H; 8; 16)

Pseudothelphusa tuberculata Rathbun, 1897: 61; 1898: 511 (in key), 513, 535, and 537 (in list); 1904: 242 (in list); 1905: 299, pl. 13, fig. 9; 1906: 502 (in list). — Young 1900: 217 — Coifmann 1939: 109 (in list).

Pseudothelphusa (*Anaphyrmus*) *tuberculata* – Smalley 1965: 651 (in list).

Potamocarcinus (*Raddaus*) *tuberculata* – Pretzmann 1965: 3 (in list).

Pseudothelphusa (*Raddaus*) *tuberculatus* – Pretzmann 1971: 20 (in list); 1972: 80, figs 461-464, 519-521.

Raddaus tuberculatus – Rodríguez 1982: 103, figs 64i, 66a-e. — Villalobos F. 1982: 220 (in list). — Villalobos Hiriart & Álvarez 2008: 297 (in list). — Ng *et al.* 2008: 177 (in list). — Wehrtmann *et al.* 2016: 781 (in list). — Acevedo-Alonso & Cumberlidge 2022: 583 (Appendix 2, in list).

TYPE MATERIAL EXAMINED. — **Lectotype** (designated by Smalley 1965). **Guatemala** • 1 ♂ (50.0:30.9, in bad condition); Suchitepéquez, stream of Saint Augustín, near Atitlán [? Finca San Agustím; 14°28'23.93"N, 91°12'53.26"W, 609 m elev.], Pacific drainage; date unknown, M. Bocourt; USNM 20047.
Paralectotype. Guatemala • 1 ♀, Suchitepéquez, stream of Saint Augustín, near Atitlán [? Finca San Agustin; 14°28'23.93"N, 91°12'53.26"W, 609 m elev.], Pacific drainage; M. Bocourt leg.; MNHN Entry 844-1866; MNHN-IU-2017-8048 (= MNHN-B5322).

OTHER MATERIAL EXAMINED. — **Guatemala** • 1 ♂ (69.5:41.4); San Marcos, Finca El Porvenir; [14°57'43"N, 91°56'26"W]; 1370 m elev.; 22.III.1952; W. Reeder leg.; USNM 1089233 • 2 ♂ (18.9:13.5-35.1:22.5) 3 ♀ (22.6:14.9-35.7:22.9), San Marcos, sítio San Rafael, San Marcos; 14°56'21"N, 91°54'38"W; 991 m elev.; 7.VIII.2015, I. S. Wehrtmann & M. Orozco leg. UCR-MZ uncat. • 1 ♂ (23.5:17.7); Suchitepéquez, carretera a Chicacao; 14°27'50"N, 91°09'01"W; [471 m elev.]; 19.I.2014, I. S. Wehrtmann, M. Orozco, C. Magalhães & M. W. Dix leg. UCR-MZ uncat.

DISTRIBUTION. — Guatemala (San Marcos, Suchitepéquez) (Fig. 16) and Mexico (Rathbun 1897, 1905; Pretzmann 1972; this study).

DESCRIPTION OF G1 (Fig. 6F-H)
Somewhat slender, slightly arched in cephalic direction in mesial view, moderately compressed mesolaterally; caudal margin with median constriction in mesial view; cephalic margin gently concave in proximal 2/3, with few short setae subdistally; lateral surface with irregular rows of short to large setae in first half and few minute setae subdistally. Marginal plate fused subdistally to caudal surface. Marginal suture on mesial surface straight up to apex, with row of large to short marginal setae along proximal portion. Marginal process subrectangular, nearly as long as mesial margin of apex. Lateral suture incomplete, marked by distinct sulcus on caudal surface. Mesial process broad, unilobed in mesial view, subtriangular, narrower than width of main stem in mesial view, directed cephalad; proximal corner rounded, distal corner with small sharp spine pointing lateralad in lateral and apical-cephalic views; cephalic surface of mesial process distinctly concave in lateral and apical views. Apex oblong, situated apically, open, mesial and lateral margins about same height; field of apical spines moderately developed, with short small spines; spermatic channel opening on apex cavity, situated medianly. Cephalic surface with two strong, triangular, subdistal spines, pointing cephalad.

REMARKS
Rathbun (1897) described the species based on a male and a female at this time deposited in the holdings of the MNHN (Paris); the male specimen was later sent to the USNM collection (Washington, D.C.). When Smalley (1965) introduced the subgenus *Pseudothelphusa* (*Anaphyrmos*), he designated *Raddaus tuberculatus* as the type species because it was the first species he

included in the subgenus to have been described from a male and, to consolidate his decision, he designated the specimen deposited in the USNM (20047) as lectotype. This specimen is in poor condition, completely disarticulated, the posterior ventral portion severely damaged, the posterior portion of the sternopleonal cavity broken, with both gonopods missing (they were not found in a small vial kept within the jar as usual) (Fig. 8).

Genus *Typhlopseudothelphusa* Rioja, 1953

Typhlopseudothelphusa juberthiei Delamare Debouteville, 1976a (Fig. 14)

Typhlopseudothelphusa juberthiei Delamare Debouteville, 1976a: 839, figs G-J.; 1976b: 125, figs 6, 7, 14, 15. — Delamare Debouteville & Juberthie 1976: 23. — Reddell 1981: 14, 17 (in list), 111, fig. 16 (map), 113, 321 (in list). — Rodríguez 1982: 123. — Villalobos F. 1982: 220 (in list). — Guinot 1988: 21, fig. 13, pl. 3 figs 3, 4; 1990: 894, fig. 6C; 1994: 170. — Ng *et al.* 2008: 177 (in list). — Villalobos Hiriart & Álvarez 2008: 297 (in list). — Cumberlidge *et al.* 2014: 144 (in table). — Wehrtmann *et al.* 2016: 782 (in list). — Acevedo-Alonso & Cumberlidge 2022: 584 (Appendix 2, in list).

Typhlopseudotelphusa juberthiei – Cottarelli & Argano 1977: 212 [error].

Typhlopseudothelphusa iuberthiei – Hobbs 1994: 101 (in list) [error].

Type material (not examined). — **Syntypes. Guatemala** • 1 ♂; MNHN-IU-2014-23193 (= MNHN-B18869) • 2 ♂; MNHN-IU-2014-23194 (= MNHN-B18870) • 1 ♀; MNHN-IU-2014-23192 (= MNHN-B19855) • 1 ♀; MNHN-IU-2014-23196 (= MNHN-B18873).

Type locality. — Guatemala, Alta Verapaz, Chamá mountains, municipality of San Pedro Carchá, Chiacam cave [15°32'49.46"N, 90°06'35.82"W; 858 m elev.].

Distribution. — Guatemala (Alta Verapaz) (Delamare Debouteville 1976a, 1976b) (Fig. 14).

Description of G1
See Delamare Debouteville (1976b).

Remarks
According to Delamare Debouteville (1976b), the syntypes were originally deposited at the Laboratoire d'Ecologie Generale of the MNHN. However, these specimens could not be located in the crustacean collection during the visit of the senior author to the MNHN in September 2015 but were subsequently incorporated into this collection (see at https://science.mnhn.fr/institution/mnhn/collection/iu/item/list?fulltext=juberthiei)

Typhlopseudothelphusa mitchelli Delamare Debouteville, 1976a (Fig. 14)

Typhlopseudothelphusa mitchelli Delamare Debouteville, 1976a: 839, figs D-F; 1976b: 125, figs 5, 9-13. — Delamare Debouteville & Juberthie 1976: 23. — Reddell 1981: 14, 17 (in list), 111, fig. 16 (map), 113, 321 (in list). — Rodríguez 1982: 123. — Villalobos F. 1982: 220 (in list). — Guinot 1988: 21, fig. 14, pl. 3 figs 5, 6; 1994: 170, fig. 2D, pl. 1 fig. 8, 9. — Hobbs 1994: 101 (in list). — Ng *et al.* 2008: 177 (in list). — Villalobos Hiriart & Álvarez 2008: 297 (in list). — Wehrtmann *et al.* 2016: 782 (in list). — Acevedo-Alonso & Cumberlidge 2022: 584 (Appendix 2, in list).

Typhlopseudotelphusa mitchelli – Cottarelli & Argano 1977: 212 [error].

Description of G1. — See Delamare Debouteville (1976b).

Type material (not examined). — **Syntypes. Guatemala** • 1 ♂; MNHN-IU-2017-8057 (= MNHN-B18874) • 2 ♀; MNHN-IU-2017-8058 (= MNHN-B19856) • 1 ♀; MNHN-IU-2014-23216 (= MNHN-B18868).

Type locality. — Guatemala, Alta Verapaz, caves C3 and G3 at Pampur mountains [15°27'38.93"N, 90°35'49.33"W; 906 m elev.]

Distribution. — Guatemala (Alta Verapaz) (Delamare Debouteville 1976a, 1976b) (Fig. 14).

Remarks
These syntypes were originally deposited at the Laboratoire d'Écologie generale of the MNHN (see Delamare Debouteville 1976b) but could not be located in the crustacean collection during the visit of the senior author to the MNHN in September 2015. However, they were subsequently incorporated into the crustacean collection (see at http://coldb.mnhn.fr/catalognumber/mnhn/iu/2017-8057 and http://coldb.mnhn.fr/catalognumber/mnhn/iu/2017-8058).

Genus *Zilchia* Pretzmann, 1968

Zilchia falcata Rodríguez & Hobbs, 1989 (Figs 9; 14)

Zilchia falcata Rodríguez & Hobbs, 1989: 184, figs 1, 2, 3G. — Rodríguez 1992: 184 (in list). — Guinot 1994: 171, pl. 1 fig. 7. — Hobbs 1994: 101 (in list). —Villalobos Hiriart & Álvarez 2008: 298 (in list). — Cumberlidge *et al.* 2014: 144 (in table). — Wehrtmann *et al.* 2016: 782 (in list). — Acevedo-Alonso & Cumberlidge 2022: 584 (Appendix 2, in list).

Potamocarcinus falcatus – Ng *et al.* 2008: 176 (in list).

Type material examined. — **Holotype. Guatemala** • 1 ♂; Alta Verapaz, exact locality unknown; 1975; collected by the Dreux

Key to Guatemalan species of *Typhlopseudothelphusa* Rioja, 1953 (adapted from Rodríguez 1982)

1. G1 with mesial process bearing three spines; apex with mesocaudal margin smooth (see fig. 5G, H, in Delamare Debouteville 1976b: 121) ..... *T. mitchelli* Delamare Debouteville, 1976
— G1 with mesial process bearing two spines; apex with mesocaudal margin crenulate (see fig. 6G, I, in Delamare Debouteville 1976b: 122) ..... *T. juberthiei* Delamare Debouteville, 1976

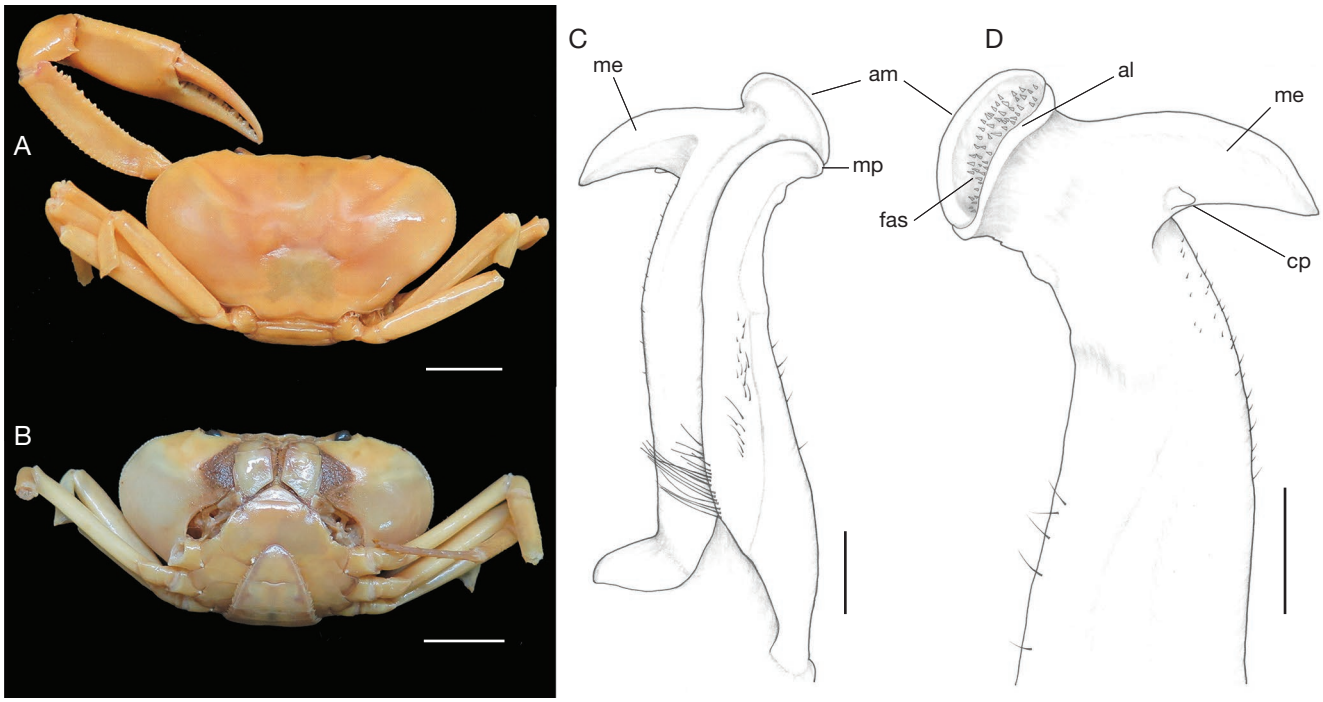

Fig. 9. — *Zilchia falcata* Rodríguez & Hobbs, 1989, male, holotype, MNHN-IU-2008-11065: **A**, habitus, dorsal view; **B**, habitus, ventral view; **C**, left G1, mesocaudal view; **D**, left G1, laterocephalic view. Abbreviations: **al**, mesocaudal margin of apex; **am**, laterocephalic margin of apex; **cp**, cephalic process; **fas**, field of apical spines; **me**, mesial process; **mp**, marginal process. Scale bars: A, B, 10 mm; C, D, 1 mm. Photos: C. Magalhães.

Expedition; MNHN-IU-2008-11065 (=MNHN-B20118) as in Rodríguez & Hobbs (1989).
Paratype. Guatemala • 1 ♂; MNHN-IU-2014-11972 (=MNHN-B20352), as in Rodríguez & Hobbs (1989).

Other material examined. — **Guatemala** • 1 ♂; Alta Verapaz, exact locality unknown; 1975; collected by the Dreux Expedition; MNHN-IU-2014-10311 (=B27918).

Distribution. — Guatemala (Alta Verapaz) (Rodríguez & Hobbs 1989) (Fig. 14).

Description of G1 (Fig. 9C, D)
Stem moderately compressed mesolaterally, falciform in overall appearance, distal portion distinctly arched cephalad in laterocephalic view; lateral margin convex, caudal margin concave in mesocaudal view; some short seta present along both margins. Caudal surface with small protuberance on median portion of caudal margin; mesial surface with irregular row of few long and short setae longitudinally along proximal half. Marginal suture on mesial surface distinctly curved caudally on distal end, with row of long setae along its proximal portion. Marginal process large, lamelliform in mesocaudal view, not overreaching mesocaudal margin of apex. Lateral suture incomplete, marked by sulcus along first 4/5 of mesocaudal surface, shallower distally. Mesial process ("cephalic process" *sensu* Rodríguez & Hobbs 1989) greatly developed, strong, subtriangular, long (approximately 1.2 longer than width of apex, measured in mesocaudal view), recurved. Cephalic surface strongly concave distally, with cephalic process as short conical spine ("basal spine" or "lateral process" *sensu* Rodríguez & Hobbs 1989) situated near base of mesial process; smooth otherwise. Apex oblong, elongated caudocephalicaly; its margins asymmetric, mesocaudal mar-

Key to Guatemalan species of *Zilchia* Pretzmann, 1968

1. G1 with apex oblong; field of apical spines well developed, open (not concealed by apical margins); cephalic surface distinctly curved towards cephalic side distally, cephalic lobe absent 2
— G1 with apex narrow, slit-like; field of apical spines poorly developed, nearly concealed by apical margins; cephalic surface of distal portion nearly straight distally, with well-developed spiny cephalic lobe (Fig. 10A, B... ..... *Z. germani* Pretzmann, 1978

2. G1 with mesial process bearing upper margin serrate; cephalic process as conical spine approximately as large as the mesial process; apex with mesocaudal margin entirely bordered by row of teeth (Fig. 11F-I) .... *Z. coronata* n. sp.
— G1 with mesial process bearing upper margin smooth; cephalic process as short conical spine distinctly smaller than mesial process; apex with mesocaudal margin unarmed (Fig. 10C, D)..... ..... *Z. falcata* Rodríguez & Hobbs, 1989

gin higher than laterocephalic one, both unarmed, outline of mesocaudal margin rounded. Field of apical spines well developed, open (not concealed by apical margins), obliquely directed towards cephalic side, narrow, with short spines distributed in caudocephalic direction.

Remarks

The exact locality in the department of Alta Verapaz where the types of *Z. falcata* were collected is unknown (the distribution record in the Figure 14 is arbitrarily represented in the center of the department: approximately 15°39'36"N, 90°05'10"W). Rodríguez & Hobbs (1989), based on Delamare Deboutteville (1976b) and Delamare Deboutteville & Juberthie (1976), only indicated that they were collected by the Dreux Expedition in 1975. This expedition explored more than 400 caves in that department in the years 1974-1975 (Courbon & Dreux 1976; Courbon *et al.* 1976).

Zilchia germani Pretzmann, 1978
(Figs 10A, B; 14)

Potamocarcinus (*Zilchia*) *zilchi germani* Pretzmann, 1978: 3; 1980: 658, pl. 8 figs 32-36, pl. 16 fig. 72 [see Remarks].

Potamocarcinus zilchi germani – Ng *et al.* 2008: 176 (in list).

Zilchia zilchi germani – Villalobos Hiriart & Álvarez 2008: 298 (in list). — Wehrtmann *et al.* 2016: 782 (in list).

Type material examined. — **Holotype. Guatemala** • 1 ♂ (26.4:16.5); Guatemala, 14 km south of Guatemala City, near San José Pinula; [14°33'01.34"N, 90°26'54.00"W; 1880 m elev.]; date unknown; I. Poglayen-Neuwall leg.; NHMW 4063.

Other material examined. — **Guatemala** • 1 ♂ (23.5:14.5); Guatemala, Santa Catarina Pinula [14°34'N, 90°30'W], km 14 en la carretera a El Salvador; 1850 m elev.; VIII.1993; R. Dix; UVGCR 309 • 1 ♂ (27.3:17.5); Guatemala, Santa Catarina Pinula, Puerta Parada [14°34'N, 90°27'W], Río Acatán; 1880 m elev.; X.1990; R. Dix leg. UVGCR 224.

Comparative material examined. — **El Salvador** • 1 ♂ (23.6:13.9), holotype of *Zilchi zilchi* (Bott, 1956); Department Santa Ana, hacienda Los Planes; date and leg. unknown; SMF 2445.

Distribution. — Guatemala (Guatemala) (Pretzmann 1978; this study) (Fig. 14).

Description of G1 (Fig. 10A, B)

Stem moderately compressed mesolaterally, nearly straight in mesocaudal view, distal portion slightly bend cephalad in laterocephalic view; cephalic margin slightly convex, caudal margin slightly concave in mesocaudal view. Mesial surface with irregular row of few long setae longitudinally on median portion. Marginal suture nearly straight on mesial surface, with row of long setae along its proximal portion. Marginal process large, lamelliform, not overreaching mesocaudal margin of apex. Lateral suture incomplete, marked by sulcus along first 4/5 of the caudal surface, shallower distally. Mesial process moderately developed, strong, subtriangular, its length subequal to width of apex, slightly recurved, both margins unarmed. Cephalic surface nearly straight distally, with cephalic process as short conical spine, and well-developed spiny cephalic lobe. Terminal portion of mesial surface with distinct rounded, spined subapical lobe nearly coalescent with also spined, enlarged portion of mesocephalic margin of apex. Apex narrow, slit-like, elongated in caudocephalical direction; its margins asymmetric, mesocaudal margin low and unarmed towards caudal side, with enlarged and spined lobe towards cephalic side and slightly projected in cephalic direction; laterocephalic margin unarmed. Field of apical spines poorly developed, directed towards cephalic side, narrow, with short spines distributed along the caudocephalic length, nearly concealed by margins.

Remarks

So far, this taxon has been treated as a subspecies of *Zilchia zilchi* (see Pretzmann 1978; Ng *et al.* 2008; Villalobos Hiriart & Álvarez 2008; Wehrtmann *et al.* 2016). A comparison with the G1 of the holotype of the nominal subspecies showed that *Z. germani* has a subapical, rounded, spined lobe on the distal portion of mesial surface ("sal" in Fig. 10A, B), whereas in *Z. zilchi* this lobe is reduced to a vestigial spine ("sal" in Fig. 10C). Furthermore, the cephalic lobe on the distal portion of the cephalic side is more developed and slightly larger and narrower than the cephalic spine in *Z. germani* ("cp" and "cl" in Fig. 10B), whereas it is less developed and slightly lower and wider than the cephalic spine in *Z. zilchi* (Fig. 10D). The mesocaudal margin of apex is somewhat more enlarged and slightly higher in *Z. germani* ("am" in Fig. 10A, B) than in *Z. zilchi* ("am" in Fig. 10C, D). These differences justify treating them as separated species.

Pretzmann (1980: 658) mixed up the captions of the illustration for this species with those for *Isabellagordonia* (*Phrygiopilus*) *acanthophalla ibarrai* (see Pretzmann 1980: 659); the actual information for *Potamocarcinus* (*Zilchia*) *zilchi germani* in Pretzmann (1980: 658) should be: "plate 8 figs 32-36, plate 16 fig. 72" (C. Magalhães, pers. observation). The information of the type locality was also mixed up in that publication: the correct type locality is "Guatemala, Department of Guatemala, 14 km south of Guatemala City, near San José Pinula", and not "Río Guyamas, NE El Progreso, Honduras" (Wehrtmann *et al.* 2016).

Zilchia coronata n. sp.
(Figs 11; 14)

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Type material. — **Holotype. Guatemala** • ♂ (32.7:20.6), Zacapa, San Lorenzo, Sierra de Las Minas [15°08'09"N, 89°37'22"W], Cerro de Los Monos, 2200 m elev., date and leg. unknown. UVGCR 518. **Paratypes. Guatemala** • 1 ♂ (28.4:17.7) 2 ♀ (23.7:15.6; 24.2:15.9); collecting data unknown; UVGCR 519.

Diagnosis. — G1 with mesial process strong subtriangular, large (approximately 1.1 wider than width of apex in mesocaudal view), obliquely pointing downwards, lower margin unarmed, upper margin

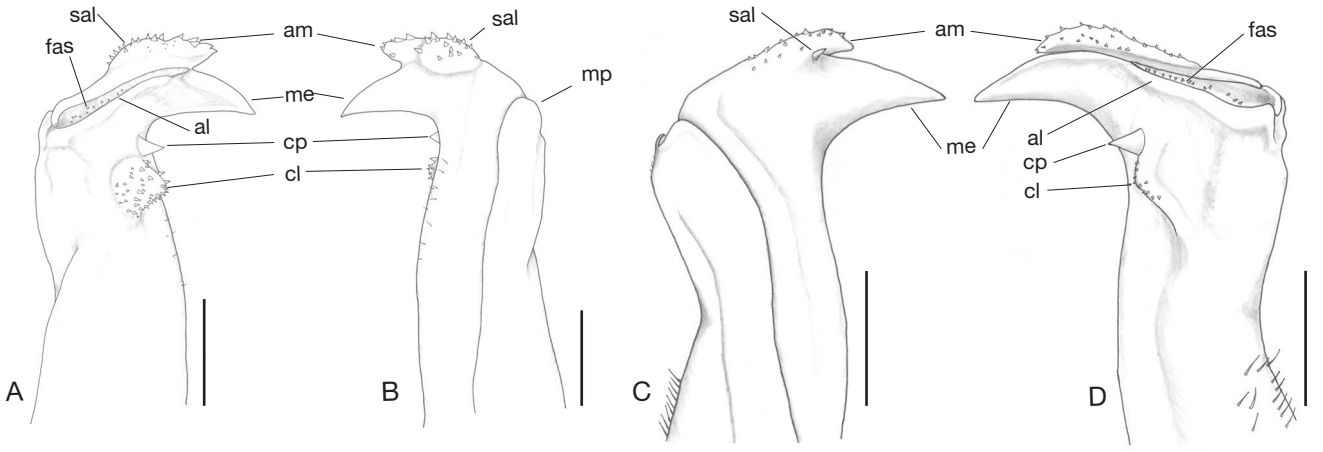

FIG. 10. — *Zilchia* Pretzmann, 1968 species, G1: **A**, **B**, *Zilchia germani* Pretzmann, 1978, holotype, left G1, NHMW 4063: **A**, cephalic view; **B**, mesocaudal view; **C**, **D**, *Zilchi zilchi* (Bott, 1956), holotype, SMF 2445: **C**, mesocaudal view; **D**, cephalic view. Abbreviations: **al**, mesocaudal margin of apex; **am**, laterocephalic margin of apex; **cl**, cephalic lobe; **cp**, cephalic process; **fas**, field of apical spines; **me**, mesial process; **mp**, marginal process; **sal**, subapical lobe. Scale bars: 1 mm.

irregularly serrate; cephalic process as conical spine approximately as large as mesial process; apex with asymmetric margins, mesocaudal margin higher than laterocephalic one, entirely bordered by row of teeth and not overhanging apical field of spines, laterocephalic margin unarmed.

ETYMOLOGY. — The specific epithet refers to the Latin word "*corona*" due to the crown-like appearance of the G1 apex in mesocaudal view.

DISTRIBUTION. — Guatemala (Zacapa); only known from the type locality (Fig. 14).

DESCRIPTION OF THE HOLOTYPE

Carapace (Fig. 11A, B) outline ellipsoid, widest at the middle (cw/cl 1.64), dorsal surface smooth, moderately convex longitudially, nearly flat transversally, regions ill defined, epi- and mesobranchial regions slightly more elevated. Pair of distinct gastric pits close to each other, on metagastric region. Cervical grooves nearly straight, deeper proximally, shallower distally, distal end failing to reach anterolateral margin. Postfrontal lobules small, almost indistinct; median groove distinct, shallow. Surface of carapace between front and postfrontal lobules smooth, distinctly deflected anteroventrally. Upper border of front smooth, strongly angulate, nearly straight in dorsal and frontal views, median notch indistinct; lower border carinate, nearly straight in dorsal and frontal views, slightly more projected anteriorly than superior one. Upper orbital margin carinate, lined with faint papillae to external side, smooth towards internal side; lower orbital margin crenulate, lined with faint papillae; exorbital angle very low, obtuse. Anterolateral margin of carapace with set of faint, minute, rounded teeth, increasing in size from anterior to posterior portion; posterolateral margin smooth, marked by faint suture. Epistome (Fig. 11C, D) narrow longitudinally; epistomial tooth low, slightly deflected anteroventraly, with carinate, smooth borders. Suborbital and subhepatic regions of carapace sidewall smooth (Fig. 11C, D); pterygostomial regions with narrow, mostly smooth, weakly pilose patches only along outer borders of bucal frame (Fig. 11C, D).

Endopod of Mxp3 (Fig. 11C) with outer margin of ischium slightly convex, inner margin straight; merus with outer margin broadly rounded, inner surface of palp bearing tuft of short setae; exopod of 3rd maxiliped long, narrow, 0.74 length of outer margin of ischium (Fig. 11C). Aperture of efferent branchial channel wide, subretangular, upper margin smooth (Fig. 11D).

Chelipeds (Fig. 11A, B) strongly heterochelous, similarly armed, right P1 larger. Larger cheliped (Fig. 11A, B, E) with merus subtriangular in cross section; dorsal margin rounded, with irregular row of low tubercles, fainter distally; ventromesial margin lined by longitudinal row of conical tubercles increasing in size distally; ventrolateral margin rounded, marked by single row of faint tubercles; distal upper margin arched, smooth. Carpus with inner margin with four faint low tubercles, prominent median spine, and smooth distally; outer margin rounded, smooth. Palm (Fig. 11E) swollen (length/breadth 1.43), lateral surface smooth, dorsal border and mesial surface with very faint scattered tubercles, ventral border with irregular row of faint tubercles. Fingers of larger chela (Fig. 11E) moderately gaping, those of smaller chela slightly gaping, tips not crossing; pollex with three subtriangular large teeth interspaced with smaller ones. Dactylus distinctly arched, slightly longer than palm (dactylus/palm 1.14, measured dorsally), proximal half of dorsal surface of dactylus with longitudinal, irregular rows of faint tubercles; pollex with lower surface bearing row of very faint tubercles. Ambulatory legs mostly disarticulated or broken; P4 and P5 still attached to body; slender, ratios dactylus/propodus and dactylus/merus as follows: P4 (right) = 1.42 and 0.82; P5 (left) = 1.50 and 0.92, respectively. P4 and P5 with dactyli bearing five longitudinal rows of sharp, corneous spines, increasing in size distally.

Thoracic sternum approximately as long as broad (Fig. 11B). Thoracic sternites of Mxp3 and chelipeds completely fused, except for small notches at lateral edges of sternum. Male sternopleonal cavity densely pilose. Epis-

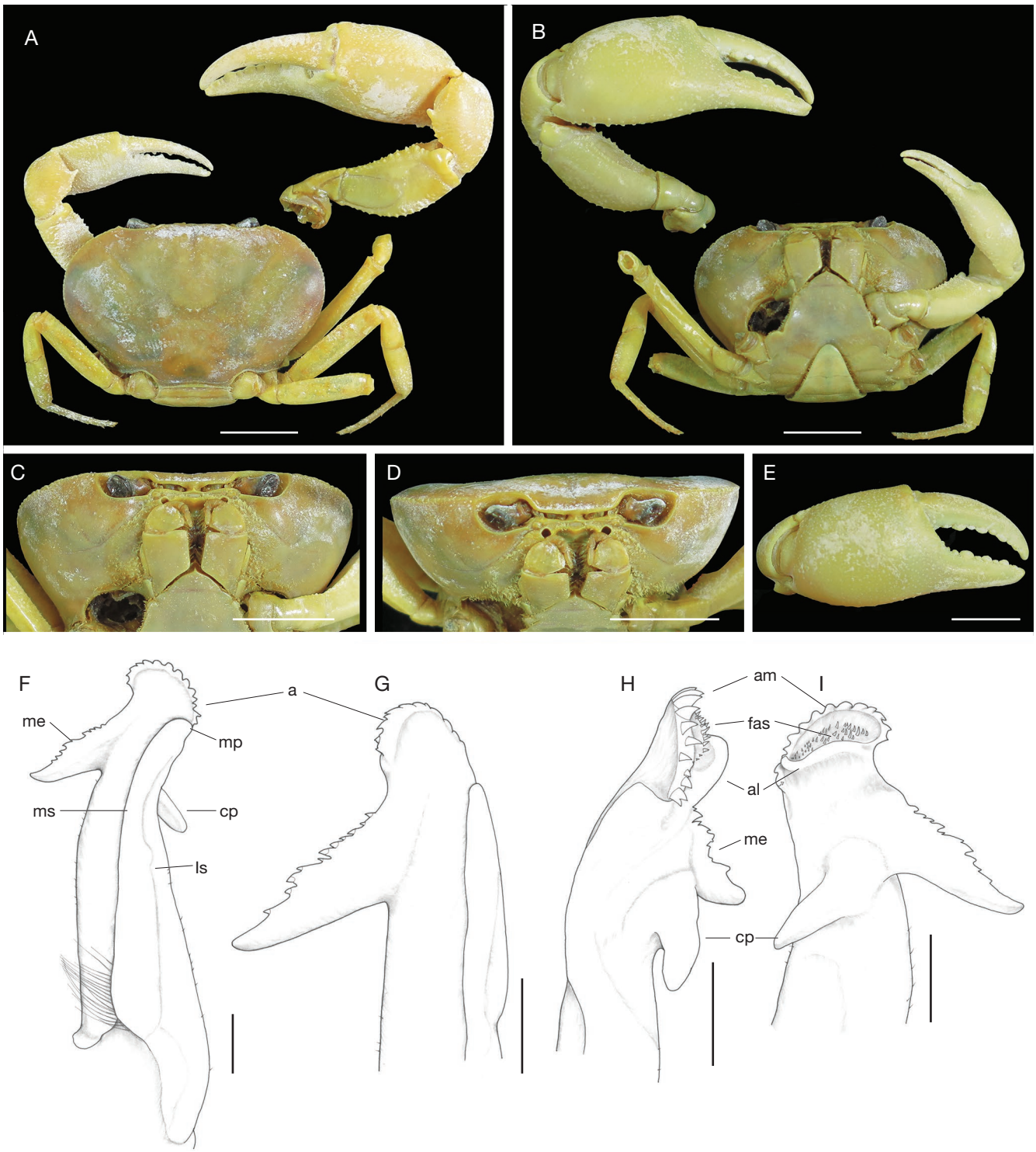

FIG. 11. — *Zilchia coronata* n. sp., male, holotype, UVGCR 518: **A**, habitus, dorsal view; **B**, habitus, ventral view; **C**, pterygostomial view; **D**, frontal view; **E**, right chelae (largest); **F**, left G1, mesocaudal view; **G**, left G1, distal portion, mesial view; **H**, left G1, distal portion, lateral view; **I**, left G1, distal portion, laterocephalic view. Abbreviations: **a**, apex; **al**, mesocaudal margin of apex; **am**, laterocephalic margin of apex; **cp**, cephalic process; **fas**, field of apical spines; **ls**, lateral suture; **me**, mesial process; **mp**, marginal process; **ms**, maginal suture. Scale bars: A-E, 10 mm; F-I, 1 mm. Photos: C. Magalhães.

ternites 4-6 triangluar posteriorly, episternite 7 posteriorly truncate. Penis short, thick, hook-shaped, emerging from nearby coxo-sternal condyle articulation, located proximally on sternite 8.

All pleonal somites free (Fig. 11B); lateral margins of somites fringed by line of short setae; male pleon with somite VI distinctly longer than preceding ones, slightly shorter than telson (ration telson/somite VI = 0.92), lateral margins slightly

concave. Male telson (Fig. 11B) subtriangular, as long as wide, lateral margins nearly straight, fringed by line of short seate, tip rounded.

G1 (Fig. 11F-I) somewhat compressed mesolaterally, distal portion moderately arched laterocephalically in mesocaudal view; cephalic margin convex, with irregular rows of minute setae longitudinally on proximal half in mesocaudal view; caudal margin concave in mesocaudal view. Marginal suture along mesial surface, gently curved caudally on distal end; row of long setae along proximal portion of marginal suture. Marginal process large, lamelliform in mesocaudal view, not overreaching mesocaudal margin of apex. Lateral suture incomplete, marked by sulcus along the first 4/5 of caudal surface, shallower distally. Mesial process strongly developed, subtriangular, large (approximately 1.1 wider than width of apex in mesocaudal view), obliquely pointing downwards, lower margin unarmed, upper margin irregularly serrate. Cephalic surface slightly concave distally, with strong cephalic process as conical spine approximately as large as mesial process, situated transversally and contiguously to mesial process, obliquely pointing downwards. Apex oblong, elongated caudocephalically; its margins asymmetric, with mesocaudal margin higher than latercephalic one, entirely bordered by row of rounded teeth directed cephalad, not overhanging apical field of spines; lateroapical margin unarmed. Field of apical spines well developed, distally open (not concealed by apical margins), obliquely directed towards cephalic side, narrow, with short spines distributed along caudocephalic length.

G2 approximately as long as G1, flagellum very slender, regularly tapering.

Remarks

The new species exhibits a quite peculiar G1, which appears to be similar to that of *Z. falcata* due to the strong, large mesial process. However, *Z. coronata* n. sp. can be easily distinguished from the other Guatemalan species of the genus by the following features of the G1: (1) upper margin of the mesial process serrate vs unarmed in *Z. falcata* (Fig. 9C, D), *Z. germani* (Fig. 10A, B), and *Z. zilchi* (Fig. 10C, D); (2) cephalic process strong, long, and pointing in lateral direction vs reduced to a short spine pointing in mesial direction in *Z. falcata* (Fig. 9D), *Z. germani* (Fig. 10B), and *Z. zilchi* (Fig. 10D); and (3) apex with mesocaudal margin entirely bordered by a row of teeth vs unarmed in *Z. falcata* (Fig. 9C, D) and partially spined and strongly elevated in *Z. germani* (Fig. 10B) or slightly elevated in *Z. zilchi* (Fig. 10D).

Incertae sedis

Pseudothelphusa bisuturalis Rathbun, 1897
(Figs 12A; 17)

Pseudothelphusa bisuturalis Rathbun, 1897: 60; 1898: 511 (in key), 513, 533, and 537 (in list); 1904: 242 (in list); 1905: 292, text-fig. 84; 1906: 502 (in list). — Young 1900: 216. — Coifmann 1939: 106 (in list).

Potamocarcinus (*Raddaus*) *bisuturalis* – Pretzmann 1965: 3 (in list); 1971: 20 (in list); 1972: 78, figs 475, 476, 553-555.

Potamocarcinus (*Raddaus*) *bisunturalis* – Wehrtmann *et al.* 2016: 782 (in list) [error].

Type material examined. — **Syntypes. Guatemala** • 3 ♀, in alcohol, syntypes; Suchitepéquez, stream Saint-Augustin, near Atitlán, Pacific slope; XI.1866; M. Bocourt leg.; n°571D, MNHN Entry 844-1866; MNHN-IU-2017-8063 (= MNHN-B5058).

Other material examined. — **Guatemala** • 2 ♀, in alcohol; Suchitepéquez, stream Saint-Augustin, near Atitlán, Pacific slope; XI.1866; M. Bocourt leg.; MNHN-IU-2017-8063 (= MNHN-B5058).

Remarks

Rathbun (1897) described this species based on a female with cw 31.4 mm × cl 19.2 mm but mentioned that the species was represented by three females numbered 571 in Bocourt's catalogue. Curiously, the single jar contaning the syntypes seen by one of us (CM) at the MNHN contains five (http://coldb.mnhn.fr/catalognumber/mnhn/iu/2017-8063) females and three labels with the species identity and similar curatorial and location data but in one of the labels is written "5 ♀" (Fig. 12A). Rathbun (1897) gave no indication whatsoever of a type specimen but reported measurements for only one of the females. She subsequently illustrated the Mxp3 and the front of one of the specimens which she called the "type" (Rathbun 1905: 292, text-fig. 84), however, without giving any indication of which specimen she was referring to. In the section "Habitat", Rathbun (1905) mentioned material from the same collecting site deposited both in the MNHN and the USNM (which would be USNM 20045, not examined, marked as "type" in the catalogue: see at http://n2t.net/ark:/65665/3102a85db-b40f-4390-8038-8802256fc16b). We could not find any information about these three additional female specimens not mentioned in Rathbun's (1897) original publication. Pretzmann (1972: 79) designed a male (USNM 85557) as allotype but mentioned it as holotype in the caption of the figures 475, 476, 553-555. This specimen, however, does not belong to the type series.

Rodríguez (1982) conjectured that *Ps. bisuturalis* could be synonymous with *R. bocourti* but the fact that the type material of *Ps. bisuturalis* and that of *R. tuberculatus* come from the very same locality ("stream Saint-Augustin, near Atitlán, Pacific slope"), in addition to exhibiting high similarity in their somatic characters, could be an indication that *Ps. bisuturalis* and *R. tuberculatus* could be synonymous.

Boscia gracilipes A. Milne-Edwards, 1866
(Figs 12B; 17)

Boscia gracilipes A. Milne-Edwards, 1866: 204. — Smith 1870: 146 (in list). — Guinot 1988: 14.

Potamocarcinus gracilipes – Ortmann 1897: 318 (in list).

Pseudothelphusa gracilipes – Pocock 1889: 10 (in list). — Rathbun 1898: 510 (in key), 513, 534, and 537 (in list); 1904: 242 (in list);

1905: 280, text-fig. 79, pl. 13 fig. 2; 1906: 501 (in list). — Young 1900: 212. — Coifmann 1939: 108 (in list).

TYPE MATERIAL EXAMINED. — **Holotype. Guatemala** • ♀, dry; Alta Verapaz, exact location and date unknown; M. Bocourt leg.; Expédition du Mexique, 1864-1866; MNHN Entry 191-1866; MNHN-IU-2000-4040 (= MNHN-B4040).

REMARKS

Rodríguez (1982) found the holotype of this species to be very similar to *Ph. acanthophallus*, except for a slight difference in the length/width ratio of the cheliped merus. As the type locality of both species is in the department of Alta Verapaz, the possibility that they are synonymous is quite reasonable. However, the validity of *B. gracilipes* cannot be ruled out since the exact collecting place of the holotype is unknown (the distribution record in the Fig. 17 is roughly represented in the center of the department: approximately 15°39'20"N, 90°06'22"W).

Isabellagordonia longipes Pretzmann, 1965
(Fig. 17)

Gordonia longipes Pretzmann, 1965: 9. — Rodríguez 1982: 191. — Wehrtmann *et al.* 2016: 782.

Isabellagordonia longipes – Smalley 1970: 102. — Guinot 1988: 14; 1994: 172. — Hobbs 1994: 101 (in list).

Isabellagordonia (*Isabellagordonia*) *longipes* – Pretzmann 1971: 21; 1972: 91, figs 567-570. — Hobbs *et al.* 1977: 149 (in list). — Holthuis 1986: 594 (in list).

Isabellagordonia (*Phrygiopilus*) *longipes* – Reddell 1981: 111, fig. 16 (in map); 113.

? *Phrygiopilus longipes* – Ng *et al.* 2008: 176.

Phrygiopilus longipes – Acevedo-Alonso & Cumberlidge 2022: 581 (Appendix 2, in list).

TYPE MATERIAL (NOT EXAMINED). — **Holotype. Guatemala** • ♀; Alta Verapaz, cave at Lanquín; [15°34'32"N, 89°58'50"W; 346 m elev.]; Champion leg.; NHM 1907.5.15.4.

REMARKS

The taxonomic history of *Isabellagordonia (Isabellagordonia)* Pretzmann, 1967 is somewhat complicated. Pretzmann (1965) introduced the genus *Gordonia* to describe *Gordonia longipes*, but soon after Pretzmann (1967) replaced it by *Isabellagordonia* since that name was preoccupied. Later, Pretzmann (1971) separated this genus into three subgenera: (a) *Isabellagordonia* (*Isabelagordonia*) Pretzmann, 1967, including *I.* (*I.*) *longipes* Pretzmann, 1965; (b) *Isabellagordonia* (*Pseudospirothelphusa*) Pretzmann, 1965, to accomodate *I.* (*Pp.*) *strengerae* (Pretzmann, 1965) [*Phrygiopilus strengerae*, chosen as type species], *I.* (*Pp.*) *propinqua* (Rathbun, 1905), and *I.* (*Pp.*) *proxima* (Rathbun, 1905); and (c) *Isabellagordonia* (*Phrygiopilus*) Smalley, 1970, comprising *I.* (*Ph.*) *acanthophallus* (Smalley, 1970) and *I.* (*Ph.*) *chuacusensis* (Smalley, 1970). In a subsequent publication (Pretzmann 1972), he also added *I.* (*I.*) *gracilipes* (A. Milne-Edwards, 1866) to the specific composition of the nominal subgenus.

In his seminal work on the Pseudothelphusidae, Rodríguez (1982) discussed this confusing situation. Since the description of four of these species were based on females and, hence, their specific identity and generic allocation were uncertain, he opted to recognize *Phrygiopilus* Smalley, 1970 as the valid genus since it is the oldest generic name available for this group whose type species (*Ph. chuacusensis* Smalley, 1970) is based on a male holotype. As pointed out by Ng *et al.* (2008), if *Isabellagordonia* (*Isabellagordonia*) Pretzmann, 1967 prove to be senior synonym of *Phrygiopilus* Smalley, 1970, then the latter name must be replaced by the former one.

The somatic features given by Pretzmann (1965) are not sufficiently diagnostic to clearly distinguish this species from others that occur in the region, especially those of the genus *Phrygiopilus*. Pretzmann (1971, 1972) provided a brief description of the G1 for this species but mentioned that it was after a drawing by Smalley concerning a specimen from the type locality ("nach einer Zeichnung von Smalley, ein Exemplar aus der Terra typica betreffend" – Pretzmann 1972: 93). The only species figured by Smalley (1970) from Alta Verapaz, where the type locality of *I.* (*I.*) *longipes* is situated, is *Ph. acanthophallus* from Seamay Cave, about 27 km SE from Lanquín but Smalley (1970) mentioned that these species differ in the shape of the carapace and the armature of the chelae. The collection site in a cave and some of the morphological features described (Pretzmann 1965, 1971, 1972) and illustrated (Pretzmann 1972: 169, figs 567-570), particularly the retracted frontal margin, the broad carapace as well as the slend and long legs suggest that this might be a valid troglobitic species and probably related to the species currently allocated in *Phrygiopilus*. Its real identity, however, can only be determined by obtaining adult males from the type locality region, as already pointed out by Smalley (1970) and Rodríguez (1982).

Pseudothelphusa propinqua Rathbun, 1905
(Figs 12C; 17)

Pseudothelphusa propinqua Rathbun, 1904: 242 (*nomen nudum*).

Pseudothelphusa propinqua Rathbun, 1905: 280, tex-fig. 78, pl. 13 fig. 11; 1906: 501 (in list). — Coifmann 1939: 109 (in list). — Rodríguez 1982: 192. — Rodríguez & Magalhães 2005: 360 (in table).

Isabellagordonia (*Pseudospirothelphusa*) *propinqua* – Pretzmann 1972: 95, fig. 572, text-fig. 23.

TYPE MATERIAL EXAMINED. — **Holotype. Guatemala** • ♀, dry; Alta Verapaz, Cobán [15°28'02"N, 90°22'52"W]; Expedition du Mexique; M. Bocourt leg.; MNHN Entry 189-1866; MNHN-IU-2000-3853 (= MNHN-B3853).

REMARKS

According to Rodríguez' (1982) comments, this species, as well as *Pseudothelphusa proxima* Rathbun, 1905, would be very close to *Ph. acanthophallus*. The holotype has the dorsal region of the carapace partially damaged (Fig. 12C).

Fig. 12. — *Incertae sedis* species recorded from Guatemala: **A**, *Pseudothelphusa bisuturalis* Rathbun, 1897, 5 females, syntypes, MNHN-IU-2017-8063, habitus, ventral view; **B**, *Boscia gracilipes* A. Milne-Edwards, 1866, female, holotype, dry, MNHN-B4040, habitus, dorsal view; **C**, *Pseudothelphusa propinqua* Rathbun, 1905, female (partially damaged), holotype, dry, MNHN-B3853, habitus, dorsal view; **D**, *Pseudothelphusa proxima* Rathbun, 1905, female, holotype, dry, MNHN-B3854. Scale bars: A, B, 10 mm. Photos: C. Magalhães.

Pseudothelphusa proxima Rathbun, 1905
(Figs 12D; 17)

Pseudothelphusa proxima Rathbun, 1904: 242 (*nomen nudum*).

Pseudothelphusa proxima Rathbun, 1905: 281, pl. 13 fig. 10; 1906: 501 (in list). — Coifmann 1939: 109 (in list). — Rodríguez 1982: 192.

Isabellagordonia (*Pseudospirothelphusa*) *proxima* – Pretzmann 1972: 94, fig. 571.

Type material examined. — **Holotype. Guatemala** • ♀, dry; Alta Verapaz, from the environs of Cobán; [15°28'40"N, 90°24'08"W]; M. Bocourt leg.; Expédition du Mexique, 1864-1866; MNHN Entry 192-1866; MNHN-IU-2000-3854 (=MNHN-B3854).

Remarks
Rodríguez (1982) conjectured that this species could be a junior synonym of *Ps. propinqua* and both are very closely related to *Ph. acanthophallus*. The somatic characters that describe these species do not allow a clear distinction between them and, as commented above (see Remarks on *Ph. acanthophallus*), even with the relatively little material available for this study, a certain degree of morphological variation in G1 of *Ph. acanthophallus* was noticed, which could indicate that a complex of species could occur in this region. The resolution of this issue can only be achieved through a study that carries out a much more comprehensive inventory of the crab fauna in the department of Alta Verapaz and the surrounding region.

DISCUSSION

Taxonomy
As long as adult male specimens are available, the pseudothelphusid crab fauna from Guatemala comprises six valid genera and 17 recognized species. Since the taxonomy of pseudothelphusid crabs depends on the morphological features of the adult male first gonopod (Smalley 1964, 1965; Rodríguez 1982), the generic and specific statuses of five species from

Guatemala described solely on female specimens remain uncertain. Smalley (1965) did not include *Pseudothelphusa gracilipes* A. Milne-Edwards, 1866, *Ps. propinqua* Rathbun, 1905, and *Ps. proxima* Rathbun, 1905 in his newly erected subgenus *Pseudothelphusa* (*Anaphyrmos*) because of this uncertainty. In addition to these, Rodríguez (1982) also included *Ps. bisuturalis* Rathbun, 1897 and *Gordonia longipes* Pretzmann, 1965 among the species he listed as *incertae sedis*. He argued that, despite being valid names and perhaps even valid species, the impossibility of determining their generic status made their respective taxonomic classification uncertain. Unfortunately, with the material available for this study, we were unable to improve the situation described by Smalley (1965) and Rodríguez (1982). A better understanding of the taxonomic status of these species will only be achieved when a series of additional specimens including adult males from their regions of occurrence to allow a more comprehensive morphological and molecular study.

Zoogeography

Wehrtmann *et al.* (2016) counted 11 pseudothelphusid species endemic to Guatemala and this number is kept here. Although *Ph. acanthophallus* was recently found also in Mexico (Magalhães & Wehrtmann 2025), the current records of *Po. armatus* show that it is restricted to hydrographic basins of the Caribbean Sea versant of Guatemala. *Phrygiopilus acanthophallus* does not occur in Nicaragua (see Cumberlidge *et al.* 2014), but it should occur in Belize as it was found in the Guatemalan side of the Mopan River, which flows in both countries.

Guatemala is crossed from west to east by two mountainous ranges that divide the country into the Pacific and the Atlantic hydrographic regions, with the latter further subdivided into river basins flowing north-northwest to the Gulf of Mexico and northeast to the Caribbean Sea (USAID 2002/2003; Suarez 2011). An almost equivalent number of species occur in each of these three hydrographic regions (Fig. 18): nine species have been recorded in the Pacific region, eight in the Gulf of Mexico region, and seven in the Caribbean region (Fig. 18; Table 1). Six species (*E. tomhaasi*, *E. zurstrasseni*, *Ph. senticosus* n. sp., *R. mertensi*, *R. tuberculatus*, and *Z. germani*) are found exclusively in Pacific river basins, whereas the other two regions have three exclusive species each: *Ph. chuacusensis*, *T. mitchelli*, and *Z. falcata* in the Gulf of Mexico basins, and *Ph. strengerae*, *T. juberthei*, and *Z. coronata* n. sp. in the Caribbean basins. Pseudothelphusids are characteristically a montane fauna (Rodríguez 1981, 1982) and the higher diversity and endemicity found in the Pacific region reflects this, as most occurrences are recorded in mountainous areas where the headwaters of rivers that drain into the Pacific are located (Figs 14-16). Even in the Gulf of Mexico and Caribbean basins, occurrences are mainly concentrated in the highlands of the country. Species with transbasinal distribution are *Ph. acanthophallus* and *Po. armatus*, both occurring in rivers of the Caribbean and Gulf of Mexico hydrographic basins; *Ph. ibarrai* that is found in the Caribbean and Pacific watersheds; and *Po. magnus* and *R. bocourti* are distributed

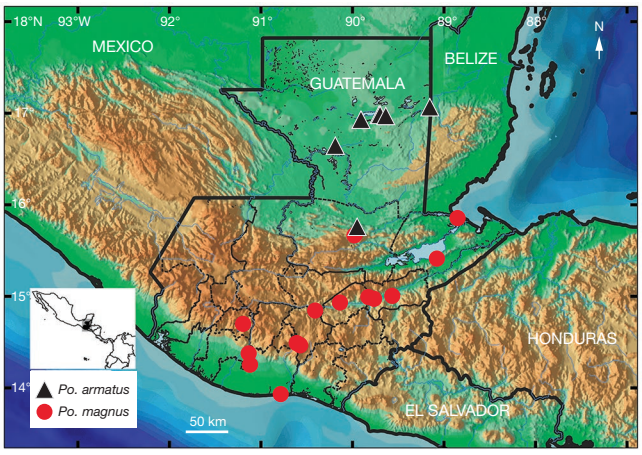

Fig. 13. — Geographic distribution of *Potamocarcinus armatus* H. Milne Edwards, 1853 (**black triangle**) and *Po. magnus* (Rathbun, 1896) (**red circle**) in Guatemala (some symbols may represent more than one record).

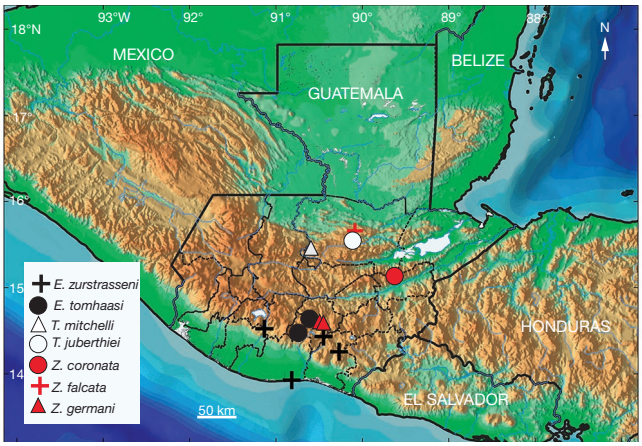

Fig. 14. — Geographic distribution of *Elsalvadoria zurstrasseni* (Bott, 1956) (**black cross**), *E. tomhaasi* Bott, 1970 (**black circle**), *Typhlopseudothelphusa juberthiei* Delamare Debouteville, 1976 (**white triangle**), *T. juberthiei* Delamare Debouteville, 1976 (**white circle**), *Zilchia coronata* n. sp. (**red circle**), *Z. falcata* Rodríguez & Hobbs, 1989 (**red cross**), and *Z. germani* Pretzmann, 1978 (**red triangle**) in Guatemala.

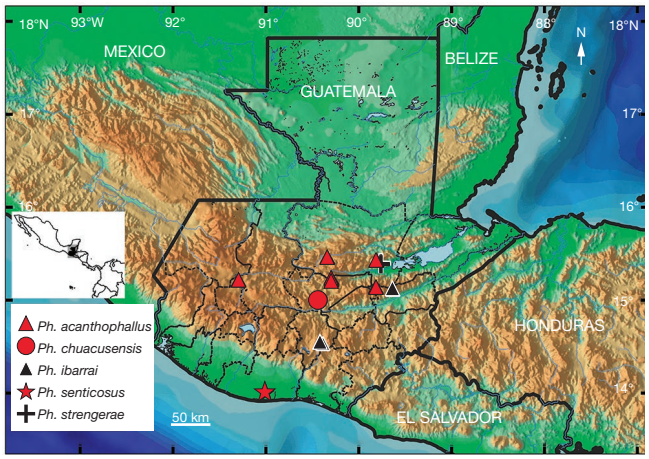

Fig. 15. — Geographic distribution of *Phrygiopilus acanthophallus* Smalley, 1970 (**red triangle**), *P. chuacusensis* Smalley, 1970 (**red circle**), *P. ibarrai* (Pretzmann, 1978) (**black triangle**), *Ph. senticosus* n. sp. (**red star**), and *P. strengerae* (Pretzmann, 1965) (**black cross**) in Guatemala (some symbols may represent more than one record).

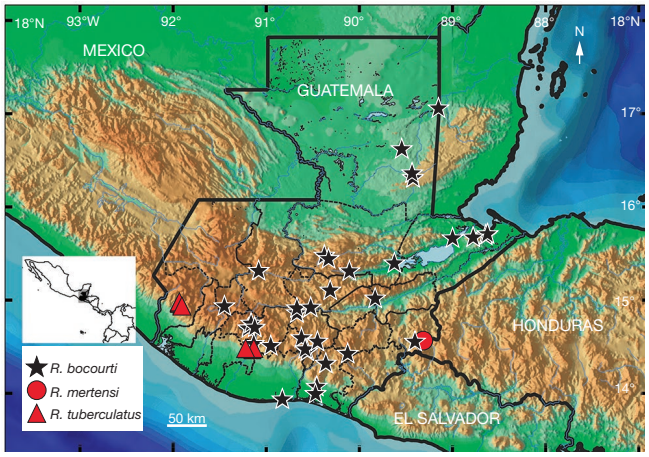

Fig. 16. — Geographic distribution of *Raddaus bocourti* (A.Milne-Edwards, 1866) (**black star**), *R. mertensi* (Bott, 1956) (**red circle**), and *R. tuberculatus* (Rathbun, 1897) (**red triangle**) in Guatemala (some symbols may represent more than one record).

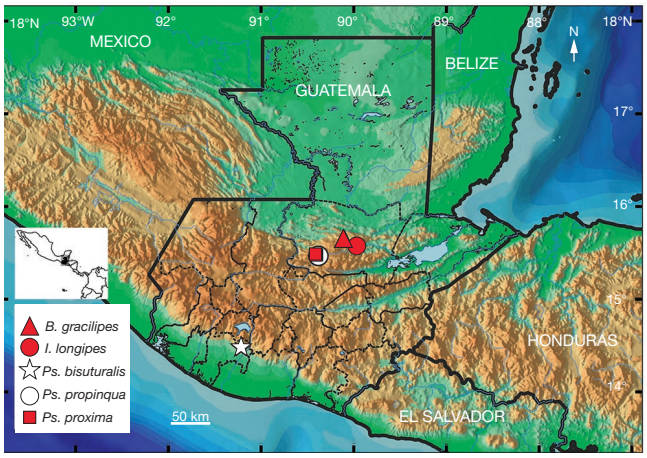

Fig. 17. — Presence of the incertae sedis species in Guatemala: *Boscia gracilipes* A. Milne-Edwards, 1866 (**red triangle**), *Isabelagordonia longipes* Pretzmann, 1965 (**red circle**), *Pseudothelphusa bisuturalis* Rathbun, 1897 (**white star**), *Pseudothelphusa propinqua* Rathbun, 1905 (**white circle**), and *Pseudothelphusa proxima* Rathbun, 1905 (**red square**).

across basins of the three versants (Fig. 18; Table 1). These last two species have very widespread distributions that encompass Mexico, Belize, El Salvador, Honduras and, in the case of *Po. magnus*, Costa Rica as well.

The mountainous physiography of much of the Guatemalan territory certainly favors a high taxonomic diversification of the pseudothelphusid crabs, which are more diverse and widespread throughout the country than the Trichodactylidae. Trichodactylid crabs, on the other hand, are very little known in the country. There is only one record of an unidentified species of the family in Guatemala, from El Boquerón, near El Estor, department of Izabal (Tejeda-Mazariegos *et al.* 2018). This family is a group distributed in lowland rivers mainly within the Atlantic drainage (Rodríguez 1981; 1992) and its occurrence in the Lake Izabal region, at 9 m elevation, is not surprising.

Table 1. — Presence of the pseudothelphusid species of freshwater crabs from Guatemala in the country's three major hydrographic regions (*, endemic to Guatemala).

Species	Caribbean Basin	Gulf of Mexico Basin	Pacific Basin
E. zurstrasseni			■
*E. tomhaasi**			■
Ph. acanthophallus	■	■	
*Ph. chuacusensis**		■	
*Ph. ibarrai**		■	■
Ph. senticosus n. sp.*			■
*Ph. strengerae**	■		
*Po. armatus**	■	■	
Po. magnus	■	■	■
R. bocourti	■	■	■
R. mertensi			■
R. tuberculatus			■
*T. juberthiei**	■		
*T. mitchelli**		■	
Z. coronata n. sp.*	■		
*Z. falcata**		■	
*Z. germani**			■
Incertae sedis:			
B. gracilipes		■	
I. longipes	■		
Ps. proxima	■		
Ps. propinqua	■		
Ps. bisuturalis			■

Table 2. — Elevation range of the pseudothelphusid species occurring in Guatemala according to data obtained from the labels of the studied material or inferred from Google Earth® based on the elevation of the estimated location of the occurrence (see Material and Methods).

Species	Elevation range (m asl)	Nr of records
Elsalvadoria tomhaasi	900-1637	2
Elsalvadoria zurstrasseni	6-1482	4
Phrygiopilus acanthophallus	929-1382	6
Phrygiopilus chuacusensis	828	1
Phrygiopilus ibarrai	1305-1800	4
Phrygiopilus senticosus n. sp.	–	No data
Phrygiopilus strengerae	805	1
Potamocarcinus armatus	92-197	7
Potamocarcinus magnus	7-1558	15
Raddaus bocourti	4-2351	37
Raddaus mertensi	916	1
Raddaus tuberculatus	471-1370	4
Thyphlopseudothelphusa juberthiei	858	1
Thyphlopseudothelphusa mitchelli	906	1
Zilchia coronata n. sp.	2200	1
Zilchia falcata	–	No data
Zilchia germani	1850-1880	3

The altitudinal distribution of the Guatemalan pseudothelphusids, obtained from recorded data or inferred from cartographic evidence based on georeferenced data, is presented in Table 2. The results indicate that the majority of the pseudothelphusid species occur at elevations above 450 m. The various records for *Po. magnus* and *R. bocourti* confirm their eurytopic condition also regarding their vertical distribution since they range from nearly sea level to 1558 and 2351 m elevation, respectively, in both the Pacific and Caribbean

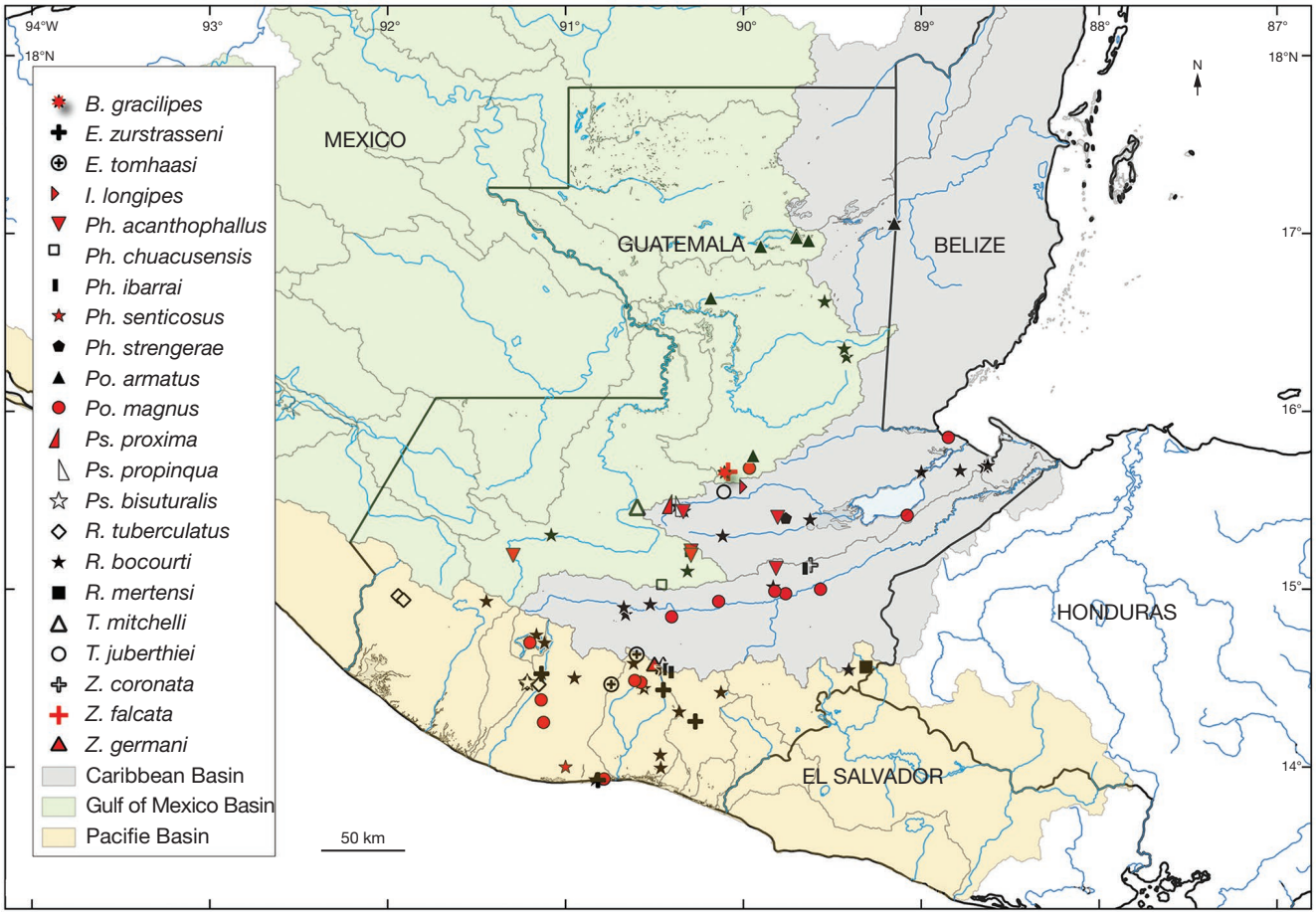

FIG. 18. — Geographic distribution of the valid and *incertae sedis* pseudothelphusid species from Guatemala in the country three major hydrographic regions (Carribean, Gulf of Mexico, and Pacific basins).

basins (Figs 13; 16). *Elsalvadoria zurstrasseni* also exhibts a wide vertical distribution, ranging from 6 up to 1482 m elevation, although most records point to an occurrence in mountainous habitats (Fig. 14). The only species not found in elevations higher than 300 m is *Po. armatus*, whose distribution seems to be restricted to the northern lowlands of Guatemala in watersheds of both the Gulf of Mexico and Caribbean hydrographic regions.

The revision presented herein contributes to a better understanding of the freshwater crab fauna in Guatemala, but a more realistic picture of the taxonomy as well as horizontal and vertical distributions of the country pseudothelphusid crabs will require a more comprehensive inventory of this group.

Acknowledgements

We thank the Consejo Nacional de Ciencia y Tecnología, Costa Rica (CONICIT; project IQ-0001-11) and the Conselho Nacional de Desenvolvimento Científico e Tecnologico (CNPq; Brazil, projects 490314/2011-2) for their financial support to ISW and CM. Additional support for ISW was received from Universidad de Costa Rica (projects B2718, B3504, B5655, B6773, and C2721). We are especially grateful to Octavio Cajas (Consejo Nacional de Areas Protegidas de Guatemala) for his support with the collection and export permits. We also thank Christian Birkel (Escuela de Geografía, Universidad de Costa Rica) for helping with the maps. We would like to express our gratitude to Margarita Palmieri and Gabriela Palomo (Biology Department, Universidad del Valle de Guatemala (UVG)), who facilitated the study of the UVG collection, and to Stefania Rodríguez and Christine LeBeau (AMNH), Jochen Gerber (FMNH), Laure Corbari, Paula Martin-Lefrève, and Sébastien Soubzmaigne (MNHN), Peter Dworschak and Martin Schwentner (NHMW), Angelika Brandt, Torben Riehl, Andreas Alspach, Bianca Trautwein, the late Michael Türkay (SMF), Hank Bart Jr. and Nelson Rios (TMNH), as well as Rafael Lemaitre and Karen Reed (USNM) for their assistance during the visits of CM to their respective institutions. A special thanks goes to Mónica Orozco who organized and accompanied us during different field trips in Guatemala, which allowed us collecting specimens reported in this contribution. We also acknowledge the constructive comments of Peter Ng, Paula Martin-Lefèvre, two anonymous referees, and the editors, Laure Desutter-Grandcolas and Anne Mabille, that greatly contributed to improve the manuscript.

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Submitted on 24 September 2024;
accepted on 12 March 2025;
published on 23 October 2025.