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Célio Magalfães Pesquisador INPA/CPBA

# SIX NEW SPECIES OF FRESH-WATER CRABS (BRACHYURA: PSEUDOTHELPHUSIDAE) FROM CHIAPAS, MEXICO

### Fernando Alvarez and José Luis Villalobos

#### ABSTRACT

Six new species of fresh-water crabs of the family Pseudothelphusidae from Chiapas, Mexico, are described. Two of the new species belong to the genus *Phrygiopilus*, which is reported from Mexico for the first time; 1 new species of *Potamocarcinus* is recognized; and 3 new species are placed in the genus *Odontothelphusa*. With the description of these new taxa, Chiapas, Mexico, can be considered as one of the areas of highest diversity for pseudothelphusid crabs.

The humid tropical region of Mexico, which includes a major portion of the State of Chiapas, has been recognized as one of the richest zones of biodiversity in the world (Toledo and Ordoñez, 1993). The fresh-water decapod fauna in the area is very diverse, especially the fresh-water crabs of the family Pseudothelphusidae (Alvarez et al., 1996). Rodríguez, in his monograph on the Pseudothelphusidae (Rodríguez, 1982) recorded four species in Chiapas, namely, Raddaus bocourti Milne Edwards, 1866; Potamocarcinus magnus Rathbun, 1896; Typhlopseudothelphusa mocinoi Rioja, 1952; and Epithelphusa chiapensis Rodríguez and Smalley, 1969. Three new species have been described since, namely, Typhlopseudothelphusa hyba Rodríguez and Hobbs, 1989; Odontothelphusa toninae Alvarez and Villalobos, 1991; and Tehuana lamothei Alvarez and Villalobos, 1994. Six new species are described in this study, bringing the total to 13, in seven genera. In spite of the noticeable increase in the number of species for the region in the last 15 years, it is anticipated that more new species will be found, since vast areas within Chiapas still remain unexplored (Fig. 1). From the biogeographical perspective, the presence of genera from three different tribes of Pseudothelphusidae in the same region raises important questions about the time and place when and where the family originated and the processes involved in shaping the present distribution of species.

Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (CNCR), are the result of a number of collecting trips and donations. The gonopod terminology used is that proposed by Smalley (1964, 1970). Carapace width and carapace length are abbreviated as "cw" and "cl."

#### RESULTS

#### Tribe Hypolobocerini

### Phrygiopilus yoshibensis, new species Fig. 2

Holotype.—., cw 27.8 mm, cl 16.4 mm; Sumidero Yoshib, Yoshib, Municipio de Oxchuc, Chiapas (16°51 N, 92°27 W); March 1977, colls. G. Davis and B. Liebmann; USNM 332309.

Description.—Dorsal surface of carapace slightly convex, covered by minute rounded granules, in frontal view branchial regions more elevated than cephalic region; branchial regions sparsely covered with setae. Superior frontal border absent; inferior frontal border low and smooth. Postfrontal lobes discernible. Median groove shallow. Cervical groove straight, not reaching anterolateral margin. Anterolateral margin bearing blunt tubercles. Posterior margin of carapace, between coxae of fifth pair of legs, strongly sinuous. Opening of branchial efferent channel rounded in section. Third maxilliped with ischium rectangular, ratio of exopod/ischium 0.86. Major chela right, palm inflated, fingers gaping, movable finger with teeth decreasing in size distally, fixed finger with 3 large teeth and rest smaller, similar in size. Gonopod compressed lateromesially. In total cephalic view, gonopod slender, proximal half straight, distal half bent laterally. In total lateral view, basal portion of gonopod slightly inclined cephalically, distal portion formed by marginal process, supra-apical process, and cephalic lobe. Marginal process oval

#### MATERIALS AND METHODS

The species treated in this study came from two sources. The specimens of *Phrygiopilus* from Sumidero Yoshib were recognized as a new species by the second author while visiting the Crustacean Collection at the National Museum of Natural History, Washington, D.C. (USNM). The rest of the specimens, which are part of the



Fig. 1. Map of the State of Chiapas, Mexico, with all known localities for pseudothelphusid crabs.

in caudal view, approximately triangular in lateral and mesial views, with caudal surface covered with strong spines. Opening of sperm channel between marginal and supra-apical processes. Space between marginal and supraapical processes hooklike in lateral view. Length of supra-apical process one-third that of gonopod, oval in lateral and mesial views, with dense field of strong spines on cephalic surface; appearing as rounded lobe in caudal view. In lateral view, cephalic lobe extending obliquely from base of marginal process to cephalic surface, overreaching cephalic margin of supra-apical process; in mesial view, appearing as a thick, large tooth. mann, 1965); *P. chuacusensis* Smalley, 1970; *P. acanthophallus* Smalley, 1970], and from *P. montebelloensis* described below, by a gonopod which has a marginal process extending beyond the apex cavity forming part of the supra-apical structures, and by two conspicuous fields of spines, one on the caudal surface of the marginal process and a second on the cephalic surface of the supra-apical process.

*Etymology.*—The specific name is derived from "Yoshib," the name of the cave system where the species was collected.

*Remarks.*—The presence of *Phrygiopilus* yoshibensis in a cave is probably accidental, since it has no obvious morphological adaptations to the troglobitic habitat. The species exhibits well-developed ocular peduncles with pigmented corneas, short pereiopods like those of epigean species, and a pigmented carapace. This new species can be distinguished from the other three species described for the genus [*P. strengerae* (Pretz-

# Phrygiopilus montebelloensis, new species Fig. 3

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Holotype.—ć, cw 24.4 mm, cl 15.0 mm; Gruta del Arco, San Rafael del Arco, Municipio de La Trinitaria, Chiapas (16°9´N, 91°39´W); 23 May 1952, coll. A. Villalobos; CNCR 448.

Description.—Carapace slightly convex, gastric region higher than rest of carapace, surface covered by minute, regularly distributed rounded granules. Superior frontal border absent; inferior frontal border low and smooth, sinuous in frontal view, extending into internal portion of orbits. Superior internal margin of orbits higher, descending laterally. Postfrontal lobes discernible. Anterolateral margin with smooth section next to orbits, then armed with blunt tubercles. Median groove absent. Cervical groove slightly arched, not reaching anterolateral margin. Posterior margin of cara-



Fig. 2. *Phrygiopilus yoshibensis*, new species, male holotype. Left gonopod: a, caudal view; b, mesial view; c, cephalic view; d, lateral view; e, left third maxilliped; f, right chela. Scale bars: a-e = 1 mm, f = 1 cm.

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Fig. 3. Phrygiopilus montebelloensis, new species, male holotype. Left gonopod: a. cephalic view; b, caudal view; c, mesial view; d, lateral view; e, right third maxilliped. Scale bars: a-e = 1 mm.

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pace, between coxae of fifth pair of legs, slightly sinuous. Third maxilliped with ischium rectangular, outer margin of merus rounded, ratio of exopod/ischium 0.76. Opening of branchial efferent channel rounded in section. Chelae missing.

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Gonopod compressed lateromesially. In cephalic view, gonopod strongly sinuous, bent laterally below apex cavity at 90° angle, opening of apex cavity oriented proximally toward base of gonopod, supra-apical process extending from mesial crest and oriented distally. In mesial view, gonopod wide, marginal suture arched, serrate projection below marginal process, cephalic lobe composed of 2 projections, and supra-apical process broadly rounded with large spines along its crest. In caudal view, gonopod strongly bent, marginal process curved, forming 90° angle with rounded end, supra-apical process appearing as cap on top of apex cavity. In lateral view, gonopod wide, setae of apex cavity and apex cavity visible.

*Etymology.*—The specific name is derived from "Montebello," the region of the state of Chiapas where the species occurs.

Remarks.—As in the case of P. yoshibensis, described above, and P. acanthophallus, P. montebelloensis was collected inside a cave, but it does not exhibit any visible adaptation to the cave environment; the single specimen of this new species was collected with the troglobitic palaemonid shrimp Cryphiops (Bythinops) luscus Holthuis. Phrygiopilus montebelloensis exhibits an extremely modified gonopod morphology within the genus. It can be distinguished from the three known congeneric species and from P. yoshibensis by the noticeable twisting of the gonopod below the apex cavity, which leaves the apex cavity exposed toward the proximal portion of the gonopod, and the supra-apical process placed off the main axis of the basal portion of the gonopod. Additional distinguishing characters are a cephalic lobe composed of two projections, a serrate margin on the distal portion of the marginal process, and a field of spines along the crest of the supra-apical process.

*Material Examined.*— $^{\circ}$ , cw 51.6 mm, cl 34.9 mm; designated as allotype; same locality, date, and collector as holotype; CNCR 12586.

Description.—Superior frontal border of carapace divided by median groove into 2 laminar lobes, these further subdivided in two by shallow notches. Margin of border densely armed with small spines. Inferior frontal border fused to superior one. In dorsal view, internal portion of orbit deeper than external one. Anterolateral margin armed with 11 strong, sharp spines, followed posteriorly by 4 or 5 smaller spines. Spines on widest portion of carapace longest. Ratio of exopod/ischium of third maxilliped 0.38; exopod triangular.

Gonopod similar to that of *P. hartmanni* Pretzmann from Tabasco, differing in: (a) setae on cephalic surface limited to small field on hump under cephalic spine, (b) lower caudal crest of apex, formed by projection of lateral process, and (c) apical crests of marginal and mesial processes directed laterally.

Remarks.—Due to noticeable differences in several morphological characters and to the considerable distance, 280 km, between Río Puyacatengo, near Teapa, Tabasco, where P. hartmanni occurs, and Chajul, Chiapas, the specimens from Chiapas are regarded as belonging to a new species. The specimens of P. chajulensis differ from P. hartmanni from Tabasco in only minor details of gonopod morphology, such as the density of setae in some areas or the orientation of the apical crests. However, important differences are noted in their external morphology. In the specimens from Tabasco, the superior frontal border of the carapace is smooth and laminar, divided by the median groove into two lobes; the inferior frontal border is present with fewer spines along the anterolateral margin; and the ratio exopod/ischium of the third maxilliped is 0.47. In the specimens from Chiapas, the superior frontal border is divided by the median groove, but further subdivided by two shallow notches; the inferior frontal border is fused to the superior one with more anterolateral spines; and the ratio exopod/ischium of the third maxilliped is 0.38.

### Tribe Potamocarcinini

# Potamocarcinus chajulensis, new species Fig. 4

Holotype.—d, cw 59.0 mm, cl 39.2 mm; Chajul, Chiapas (16°7'N, 90°55'W); 28 July 1993, coll. M. Palma; CNCR 12586.

# Odontothelphusa lacandona, new species Fig. 5

Holotype.—., cw 26.7 mm, cl 18.2 mm, small stream 8 km from Benemérito de las Américas, Municipio de



Fig. 4. Potamocarcinus chajulensis, new species, male holotype. Left gonopod: a, lateral view; b, caudal view; c, cephalic view; d, carapace, dorsal view; e, right third maxilliped. Scale bars: a-c = 5 mm, d = 1 cm, e = 5 mm.

Ocosingo, Chiapas (16°25′N, 90°30′W); 26 April 1991, coll. J. L. Villalobos; CNCR 11204.

Material Examined.—3  $\Im$ , cw 30.5, 29.0, 28.7 mm, cl 20.9, 20.0, 20.0 mm; same locality, date, and collector as holotype; CNCR 11204.

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Description.—Dorsal surface of carapace slightly convex, covered with minute rounded granules. Superior frontal border well marked, formed by small tubercles; inferior frontal border continuous, in dorsal view extending beyond superior one. Median groove short, deep, dividing superior frontal border. Postfrontal lobes discernible. Cervical grooves wide, shallow, and straight. Notch on anterolateral margin between orbit and cervical groove. Anterolateral margin bearing distinct denticles, decreasing in size posteriorly. Posterior margin of carapace between coxae of fifth pair of pereiopods straight. Opening of branchial efferent channel square in section. Ischium of third maxilliped rectangular, merus with outer margin broadly rounded; ratio of exopod/ischium 0.86. Pterygostomian region densely covered with setae. Major chela right, fingers not gaping.

Gonopod straight, wider proximally. Apical region, formed by lateral and mesial crests, wider than taller. Distal margin of apical crests straight. In lateral view, triangular spine on middle portion of lateral surface oriented proximally, reaching beyond inferior margin of lateral surface. In mesial view, large proximomesial spine oriented cephalically, distomesial spine absent; marginal process not reaching distal margin of apical

### Odontothelphusa lacanjaensis, new species Fig. 6

Holotype.—d, cw 78.0 mm, cl 48.8 mm; small tributary of Lacanjá river, town of Lacanjá Chansayab, Chiapas (16°46'N, 91°6'W); 30 July 1990, colls. H. Espinosa, P. Fuentes, and L. Huidobro; CNCR 12920.

Material Examined.—9, cw 86.4 mm, cl 55.0 mm; same locality, date. and collector as holotype; CNCR 12920. 3, cw 64.5 mm, cl 41.0 mm; 9, cw 78.5 mm, cl 51.4 mm; Cedros stream, near Bonampak, Municipio de Ocosingo, Chiapas (16°47'N, 91°6'W), 28 April 1991, coll. J. L. Villalobos; CNCR 11199.

Description.—Dorsal surface of carapace convex. Superior frontal border thick, divided by median groove. Median groove deep and short, not reaching postfrontal lobes. Postfrontal lobes indicated anteriorly by shallow depressions. Cervical grooves shallow and straight, reaching anterolateral margin. Cardiac and gastric regions indicated by shallow grooves. Anterolateral margin formed by small tubercles between orbit and cervical groove, tubercles increasing in size posterior to cervical groove. Merus of third maxilliped with external margin rounded and rounded notch on superior margin; ischium becoming broader distally, ratio of exopod/ischium 0.68. Major chela left, fingers gaping, fixed finger with largest tooth in middle portion. Opening of branchial efferent channel square in section.

Gonopod straight, thick, slightly bent cephalically. In mesial view, large proximomesial spine oriented proximally, in apical view oriented laterally. Superior margin of mesial crest sinuous, curved downward, ending distally in rounded lobe. Distomesial spine triangular, oriented mesially. Large, conical spine on lateral surface oriented proximally. Marginal process reaching same height as lateral and mesial crests. Rounded hump on caudal portion of lateral surface.

crests, tip of lateral spine visible. Rounded hump on caudal portion of lateral surface.

*Etymology.*—The specific name is derived from "Lacandona," the region where the type locality is situated.

*Remarks.*—Although the holotype of this new species is small compared to congeners, it is clearly a valid species, with well-defined diagnostic characters. *Odontothelphusa lacandona* can be distinguished from the rest of the species in the genus, especially from the related *O. monodontis* Rodriguez and Hobbs, by a gonopod with a lateral spine oriented proximally, reaching beyond the inferior margin of the lateral surface, by the absence of a distomesial spine, and by a robust proximomesial spine. This new species represents the most easterly occurrence of the genus.

*Etymology.*—This species is named after the Lacanjá River region, Chiapas, the type locality.

Remarks.—Odontothelphusa lacanjaensis has an intermediate gonopod morphology between those of O. maxillipes (Rathbun, 1898) and O. toninae. The new species can be distinguished from O. maxillipes and O. toninae in the orientation of the proximomesial spine of the gonopod; in O. lacanjaensis it appears at a  $45^{\circ}$  angle with respect to the



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Fig. 5. Odontothelphusa lacandona, new species, male holotype. Left gonopod: a, lateral view; b, cephalic view; c, mesial view; d, apical view; e, left third maxilliped; f, right chela. Scale bars: a-e = 1 mm, f = 5 mm.



Fig. 6. Odontothelphusa lacanjaensis, new species, male holotype. Left gonopod: a, lateral view; b, cephalic view; c, mesial view; d, apical view; e, left third maxilliped: f, right chela. Scale bars: a-c = 5 mm, d = 1 mm, e, f = 1 cm.

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Fig. 7. Odontothelphusa palenquensis, new species, male holotype. Left gonopod: a, mesial view; b, lateral view; c, cephalic view; d, apical view; e, left third maxilliped; f, right chela. Scale bars: a-c = 2 mm, d = 1 mm, e = 5 mm, f = 1 cm.

main axis of the gonopod, in O. maxillipes it is at a 90° angle, and in O. toninae it is oriented proximally, being parallel to the main axis of the gonopod (Rodríguez, 1982; Alvarez and Villalobos, 1991). Odontotothelphusa lacanjaensis also differs from O. maxillipes and O. toninae in the profile of the mesial crest of the gonopod, which in the new species is distinctly curved, being lower in the cephalic portion; in the orientation of the distomesial spine, which is oriented mesially in O. lacanjaensis; and in the height of the marginal process.

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# Odontothelphusa palenquensis, new species Fig. 7

Holotype.—d, cw 39.0 mm, cl 26.0 mm; small stream in Palenque archeological site, Municipio de Palenque, Chiapas (17°29'N, 92°3'W); 9 April 1986, colls. J. L. Villalobos, D. Valle, J. C. Nates, and A. Cantú; CNCR 5589.

*Material Examined.*— $\delta$ , cw 24.4 mm, cl 16.3 mm;  $\circ$ , cw 27.3 mm, cl 18.2 mm; same locality, date, and collector as holotype; CNCR 5589.

Description.—Carapace slightly convex. Superior frontal border formed by blunt tubercles, straight in dorsal view, divided by median groove; inferior border continuous, smooth, and straight. Median groove deep, narrow, and short. Postfrontal lobes discernible. Cervical grooves arched and wide, not reaching anterolateral margin. Anterolateral margin armed with small blunt, triangular tubercles. Merus of third maxilliped with external margin rounded; ratio of exopod/ischium 0.85, distal tip of exopod acute. Major chela right, with fingers not gaping, fixed finger with 3 large and 4 small teeth, movable finger with 6 large teeth of similar size and 5 small teeth. Gonopod straight, slightly decreasing in thickness distally. Large proximomesial spine directed cephalically at 90° angle with respect to main axis of gonopod, in apical view pointing laterally. Cephalic margin of mesial crest ending in rounded laminar lobe. Distocephalic margin of lateral surface ending in triangular distomesial spine. Sharp, conical spine arising from lower portion of lateral surface. Protuberance on lateral surface at base of apical region, broadly triangular in apical view. Caudodistal portion of lateral surface with distinct, elevated margin. Marginal process with distal end rounded, ending below maximum height of mesial crest.

*Etymology.*—This species is named after the Mayan ruins of Palenque, Chiapas, where it was collected.

Remarks.—The gonopod morphology of O. palenquensis is very similar to that of O. maxillipes. However, the form and position of the spine on the lateral surface, the shape of the distomesial spine, the orientation of the mesial spines, and the height of the lateral and mesial crests relative to the length of the gonopod clearly differentiate the two species. In addition, O. palenquensis exhibits on the lateral surface of the gonopod a distinct protuberance at the base of the apical region and an elevated margin of the distal portion, traits not present in O. maxillipes.

#### DISCUSSION

With the description of the six new taxa included in this study, the Mexican pseudothelphusid fauna now comprises 13 genera and 49 species (see Alvarez *et al.*, 1996). The genus *Phrygiopilus* was previously restricted to the highlands of south-central Guatemala (Rodríguez, 1982). With the two new species in Mexico reported here, the geographic range of the genus increases to 335 km in a straight line, from the vicinity of Guatemala City to the environs of San Cristóbal de Las Casas, Chiapas. Interestingly, three of the five species in the genus have been found in caves,

although no obvious adaptations to a troglobitic life style are evident in any of them.

The description of *Potamocarcinus chajulensis* as a new species is based on: (a) strong differences in the external morphology from the related *P. hartmanni* from Tabasco, and (b) the considerable distance that separates the two populations. The most significant morphological difference between the two species is the absence of a front of the carapace in *P. chajulensis*, resulting from the fusion of the two frontal borders.

The genus Odontothelphusa erected by Rodríguez (1982), was proposed for Potamocarcinus (Zilchia) maxillipes (Rathbun, 1898), which differed from the typical Potamocarcinus morphology in that the apex of the gonopod is flattened and bears two distomesial and one proximomesial spines. Rodríguez and Hobbs (1989) and Alvarez and Villalobos (1991) described two new species, extending the range of the genus from Los Tuxtlas, Veracruz, to the central highlands of Chiapas. With the three new species included in this study, the range of *Odontothelphusa* now covers the northern and eastern portions of Chiapas.

In Chiapas, as well as in the neighboring states of Oaxaca and Veracruz, there are representatives of three of the five tribes that compose the Pseudothelphusidae (Hypolobocerini, Potamocarcinini, Pseudothelphusini), establishing a unique area of high diversity within the range of the family. The Isthmus of Tehuantepec, which encompasses most of these three states, has already been recognized as a high diversity area for pseudothelphusid crabs, but has not been regarded as a primary center of radiation for the family, since the more primitive forms occur in the Greater Antilles and in northern South America (Rodríguez, 1986, 1992). However, the adoption of Rodríguez's scheme of dispersal to Central America and Mexico from northern Colombia, to explain the richness of forms in the Isthmus of Tehuantepec, raises a problem with timing, since this migration could only have taken place after the closing of the Isthmus of Panama around 3 million years before the present. This scenario seems unlikely, since it would leave a very brief period of time for the invasion of Central America and Mexico and the speciation of more than 15 genera and 60 species, including very specialized forms such as the troglobitic genera Typhlopseudothelphusa and Stygothelphusa.

Llorente, A. N. García-Aldrete, and E. González, eds., Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento. Pp. 103–129. Instituto de Biología, Universidad Nacional Autónoma de México–CONABIO, México.

- Milne Edwards, A. 1866. Description de trois nouvelles espèces du genre *Boscia*, Crustacés Brachyures de la tribu des Thelphusiens.—Annales de la Societé Entomologique Française 4: 203–205.
- Pretzmann, G. 1965. Vorläufiger Bericht über die Familie Pseudothelphusidae.—Anzeiger der Oesterreichischen Akademie der Wissenschaften mathematisch naturwissenschaftliche Klasse 1: 1–10.

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- Rathbun, M. J. 1896. Descriptions of two new species of fresh-water crabs from Costa Rica.—Proceedings of the United States National Museum 18: 377–379.
- Rioja, E. 1952. Estudios carcinológicos. XXVIII. Descripción de un nuevo género de Potamónidos cavernícolas y ciegos de la Cueva del Tío Ticho, Comitán, Chis.—Anales del Instituto de Biología, Universidad Nacional Autónoma de México 23: 217-225.
- Rodríguez, G. 1982. Les crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae.—Faune Tropicale 22: 1–224. ORSTOM. Paris.
- ——. 1986. Centers of radiation of freshwater crabs in the neotropics.—In: R. H. Gore and K. L. Heck, eds., Biogeography of the Crustacea. Crustacean Issues 4: 51-67.

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# LITERATURE CITED

Alvarez, F., and J. L. Villalobos. 1991. Two new freshwater crabs from México, Odontothelphusa toninae and Stygothelphusa lopezformenti (Crustacea, Brachyura, Pseudothelphusidae).—Proceedings of the Biological Society of Washington 104: 288-294.

, and ——. 1994. Two new species and one new combination of freshwater crabs (Brachyura, Pseudothelphusidae) from Mexico.—Proceedings of the Biological Society of Washington 107: 729-737.
, —, and E. Lira. 1996. Decapoda.—In: J.

ología, Universidad Nacional Autónoma de México 40: 69–112.

- Smalley, A. E. 1964. A terminology for the gonopods of the American river crabs.—Systematic Zoology 13: 28-31.
- ———. 1970. A new genus of freshwater crabs from Guatemala, with a key to the Middle American genera (Crustacea, Decapoda, Pseudothelphusidae).—American Midland Naturalist 83: 96–106.
- Toledo, V. M., and M. J. Ordoñez. 1993. The biodiversity scenario of Mexico: a review of terrestrial habitats.—In: T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, eds., Biological diversity of Mexico. Pp. 757–778. Oxford University Press, Oxford, England.

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Address: Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70–153, México 04510, D. F. México. (e-mail: falvarez@servidor.unam.mx)