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Redescription of the mole crab *Emerita portoricensis* Schmitt, 1935 (Crustacea: Decapoda: Hippidae), based on Caribbean populations from Puerto Rico, Belize, Costa Rica, and Panama

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Abstract

The mole crab Emerita portoricensis Schmitt, 1935 was originally described solely on the basis of few key characters that were not precisely defined, giving reason to question subsequent reports of its distribution. The present study, prompted by recent collections documenting coloration in life, undertakes a comprehensive redescription of the species based on specimens of varied sizes from Puerto Rico, Belize, Costa Rica, and Panama. Collections from the northern Caribbean that at first take appear to represent a northernmost record of E. brasiliensis Schmitt, 1935 or southernmost occurrence of E. talpoida (Say, 1817), may be assignable E. portoricensis as now recognized. Among western Atlantic species, E. portoricensis and E. benedicti have to date been considered to have the dactylus of the first percopod terminally subacute or sharply pointed, which purportedly separates them from E. brasiliensis and E. talpoida, western Atlantic species in which this article is terminally rounded. However, in E. portoricensis this character varies with specimen size and the magnification at which the distal extreme of the dactylus is examined, being rounded to varying degrees in all but the largest specimens. Even in sexually mature specimens of less than maximum size, this rounded tip is armed by a minute corneous spine in E. portoricensis, although it is less prominent than the terminal spine on the consistently more acute dactylus of E. benedicti at all adult sizes. Also, the carapace color in live specimens of E. portoricensis, as documented for specimens collected in both Belize and Panama, differs from that of E. brasiliensis, E. talpoida, and E. benedicti by typically including longitudinal and diagonal dark bars of olive brown on the branchial regions and a light longitudinal bar marking the posterior quarter of the median line. Posterior to the cervical groove, fine rugae of the carapace that form broken transverse lines are at most little diminished across the mid-dorsal longitudinal line in *E. portoricensis* and E. benedicti, somewhat more broken in E. brasiliensis, and distinctly diminished to all but absent at the midline in E. talpoida. Previously reported BINs in the Barcode of Life database include sequenced specimens from Costa Rica herein accepted as *E. portoricensis*. We exclude populations from Brazil that have been mis-assigned to *E. portoricensis*.

Key words: Anomura, beach fauna, Caribbean, Taxonomy

Introduction

The description of *Emerita portoricensis* by Schmitt, 1935 and an account of features to distinguish it from *E. benedicti* Schmitt, 1935 were based solely upon the few diagnostic characters used in Schmitt's (1935) identification key, supported by several photographs of limited quality and a few footnotes. Among western Atlantic species, *E. portoricensis* and *E. benedicti* were grouped primarily by having the dactylus of the first pereopod "distally subacute or sharply pointed" in order to separate them from *E. brasiliensis* and *E. talpoida* in which this article is "distally rounded off, obtuse". No detailed illustrations were provided to clarify what range of variation might be encompassed by "distally subacute" compared to distally "rounded off". In addition,

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E. portoricensis and *E. benedicti* were noted to share transverse crenulate lines (hereafter termed rugae) of the carapace that were more or less continuous, close set, and "crossing dorsum for the whole of its extent", as opposed to *E. brasiliensis* and *E. talpoida* having the "lateral or epimeral expansions of the carapace for the greater part smooth and punctate". Yet, the same key somewhat confusingly distinguished *E. portoricensis* as having the lateral epimeral expansion of the carapace "smooth and punctate, merest traces of transverse lines of dorsum showing on upper part of epimeral portion". To date, no more comprehensive morphological descriptions or line illustrations have been provided that might further support distinction of *E. portoricensis* from the other western Atlantic species, with the exception of that by Calado (1990) based strictly on a Brazilian population. As noted in our following treatment, we exclude that Brazilian population as well as Brazilian specimens previously reported as *E. portoricensis* by Schmitt (1935) and Efford (1976) from *E. portoricensis* s.s., reserving taxonomic treatment of that population for a paper in preparation that will include molecular phylogenetic analyses of all American congeners.

Color photography of a freshly collected mole crab from Belize revealed a unique light and dark dorsal color patterning not previously noted among other similarly photographed regional specimens of *Emerita*. Morphologically, the specimen was found to have a first percopod dactylus that tapered to a terminally rounded tip at its distal extreme, suggesting it could represent either of the two known western Atlantic species that share this character, E. brasiliensis and E. talpoida. Schmitt (1935) reported the northern limit of range for Emerita brasiliensis to be Yucatán. However, the only material appearing to support that record (USNM 21733), originally identified as such by J.E. Benedict, was later examined by Efford (1976) who with some reservation labelled it instead as E. talpoida. Further collections and photography of fresh specimens from the Caribbean coast of Panama have revealed specimens of *Emerita* very similar in general color patterning and morphology to those from Belize (Fig. 1A–C). Gene sequences of these specimens, labelled only as *Emerita* sp. and cited from the Barcode of Life Database by Venera-Ponton et al. (2020), showed them to be distinct from both E. brasiliensis and E. talpoida, while also indicating they grouped with additional previously sequenced specimens from the Caribbean coast of Costa Rica and Puerto Rico, though they did not group with a Brazilian population that has long been treated as E. portoricensis by several authors (Schmitt 1935; Efford 1976; Calado 1990; Melo 1999). It was thus questioned which of these materials might represent E. portoricensis s.s., how morphological variation must perhaps be accounted for, and how distributional reports may require redefinition.

We here undertake morphological study of materials from Belize, Costa Rica, and Panama along with examination of the holotype and other representative collections of *E. portoricensis* from Puerto Rico. As the holotype of this species is larger than most specimens representing compared populations, we attempt to represent adults of varied sizes in our illustrations and to do not bias character states to those of the unusually large holotype. As comprehensive descriptions are in general lacking for congeners, the notable exception being those for *E. talpoida* (Smith 1877; Snodgrass 1952), we include full dissection and illustration of mouthparts and other appendages as baselines for future comparative studies. Our morphologically based diagnosis makes reference to GenBank accession numbers for mt COI and 16S sequences, but complete molecular phylogenetic analyses are deferred for robust representation of the genus in a pending study.

Materials and methods

The specimens examined include holdings of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) as well as former holdings from the University of Louisiana at Lafayette Zoological Collection, Lafayette, LA (ULLZ) that were recently transferred there, where they are now cross-referenced under both catalog systems. For a few cases in which specimens have been previously reported under ULLZ catalog numbers both numbers are herein indicated. In most other cases, only the USNM catalog numbers are referenced. A single comparative illustration was based on material examined at the Texas A&M University Biodiversity Research and Teaching Collection (TAMU/TCWC), College Station. Additional specimens from the Crustacean Collection of the Department of Biology (CCDB) at the Faculty of Philosophy, Sciences and Letters at Ribeirão Preto, University of São Paulo were used in both morphological comparisons and referenced molecular genetic analyses. Measurements were determined with a calibrated ocular micrometer or dial calipers. Specimen size (± 0.1 mm) is reported as carapace length (cl) measured along the dorsal median line including the rostrum. Digital color photographs of fresh

specimens were made with subjects immobilized below the water surface of a shallow tray lined with black felt for framing of the exposure. Line illustrations were prepared on a Wild M5 dissecting microscope equipped with a camera lucida, after staining the specimen with chlorazole black E when necessary. Where referred to, sequence data were from the Barcode of Life Database (dataset dx.doi.org/10.5883/DS-CRUSTACE) and GenBank (www. ncbi.nlm.nih.gov/genbank).

Comparative materials examined are as follow. *Emerita benedicti*: ovigerous female, USNM 171402, Tampa Bay, Florida, 1 April 1901; ovigerous female, USNM 171403, collection data same as preceding; ovigerous female, USNM 17919, Pensacola, Florida; ovigerous female, USNM 1542589, Dauphin Island, Alabama; ovigerous female, USNM 1548758, Isles Dernieres, Lousiana; 2 females (one ovigerous), USNM 1550359, Mustang Island, Texas; ovigerous female, USNM 1545950, Anton Lizardo, Veracruz, Mexico. *Emerita brasiliensis*: ovigerous female, USNM 50674, Rio de Janeiro, Brazil; ovigerous female, USNM 1549093, Ubatuba, Lázaro Beach, Brazil. *Emerita talpoida*: ovigerous female, USNM 1540318, Isle of Palms, South Carolina; ovigerous female, USNM 1544838, Ft. Pierce, Florida (Atlantic); ovigerous female, USNM 1542528, Anna Maria Island, Florida; female, USNM 1546662, Ft. Pickens, Gulf Islands National Seashore, Florida; ovigerous female, USNM 1540091, Port Fourchon Beach, Louisiana; female, Padre Island, Texas, TAMU/TCWC 2-8703, Padre Island, Texas; 2 ovigerous females, USNM 267835, Progresso, Mexico (Yucatán).

Taxonomy

Superfamily Hippoidea Latreille, 1825

Family Hippidae Latreille, 1825

Emerita Scopoli 1777

Emerita portoricensis Schmitt, 1935

(Figs. 1A-C; 2A-G; 3A-H; 4A-Q; 5A-C)

Emerita portoricensis Schmitt, 1935: 213 (figs. 72a-b), 215, 217 (part, excluding Florida and Texas).

Emerita portoricensis.—Goodbody, 1965: 195–197; Efford, 1967: 88–90; Abele & Efford, 1972: 506; Efford, 1976: 174 (part, excluding Florida), 175–178, 179 (fig. 7, part, excluding Florida and Brazil), 183; Rodriguez, 1980: 241 (part, excluding Florida and Texas); Abele & Kim, 1986: 38 (part, excluding Florida and Texas), 434 (unnumbered figure); Sastre, 1990: 526–533 (table 1; figs. 1–7); Sastre & Yoshioka, 1992: 456–463 (figs. 1–5); Tam *et al.*, 1996: 489, 490 (fig. 1, part, excluding Brazil), 491 (table 1), 495 (fig. 4); Melo, 1999: 295, 298 (part, excluding Florida and Brazil, excluding 299, fig. 204); Pérez, 1999: 320–326; García *et al.*, 2000: 215–223; Haye *et al.*, 2002: 903, 904 (fig. 1, part, excluding Brazil), 905 (fig. 2), 906, 907 (table 1), 908 (fig. 3), 910 (table 2); Felder *et al.*, 2009: 1068, (1095 footnote 177) (part, excluding Pensacola, NW Florida); Boyko & McLaughlin, 2010: 142; Hsueh, 2015: 254, 255 (table I), 256 (key); Poupin, 2018: 152, 254.

Emerita sp.—Venera-Ponton *et al.*, 2020: 5 (table 1, BINs cluster BOLD:ACU0009).

Type material. *Holotype*: ovigerous female holotype, USNM 65731, Mayaguez, Puerto Rico, 19–20 January 1899. *Paratype*: ovigerous female, USNM 65729, Isla de Vieques, Puerto Rico, 8 February 1899.

Other material examined. Puerto Rico: 18 females, 11 ovigerous, USNM 42209, San Juan Harbor, 13 January 1899. Belize: 9 small females, USNM 22601, Carrie Bow Cay, no date; one lot, USNM 1672672, sta. CB-38, Carrie Bow Cay, 15 May 1977; ovigerous female, USNM 1545049 (= ULLZ 10465), lower intertidal muddy, quartzite, riverine sand off wave-washed beach, 0.5 m, Pelican Beach Hotel, Dangriga, Stann Creek District, 18 April 1983; one lot, USNM 1672671, collection data same as preceding. Costa Rica (Caribbean): ovigerous female, CCBD 4690, Parque Nacional de Cahuita, 13 July 2013; ovigerous female, CCDB 4690, Parque Nacional de Cahuita, 13 July 2013; ovigerous female, CCDB 4690, Parque Nacional de Cahuita, 13 July 2013; ovigerous female, CCDB 4690, Parque Nacional de Cahuita, 13 July 2013; ovigerous female, CCDB 4690, Parque Nacional de Cahuita, 13 July 2013; ovigerous female, CCDB 4690, Parque Nacional de Cahuita, 13 July 2013; ovigerous female, CCDB 4690, Parque Nacional de Cahuita, 13 July 2013; ovigerous female, CCDB 4690, Parque Nacional de Cahuita, Limón, 13 July 2013; ovigerous female, USNM 1672670, Shimmey Beach, Fort Sherman, 10 August 1969; ovigerous female, USNM 1546871 (= ULLZ 13325), swash zone quartzite sand, low energy beach inshore of grassbed, Playa Boca del Drago, Isla Colon, 6 August 2011; ovigerous female, USNM 1546925 (= ULLZ 13456), collection data same as preceding; juvenile female, USNM 1546926 (= ULLZ 13457), collection data same as preceding; juvenile, female, USNM 1546926 (= ULLZ 13457), collection data same as preceding; juvenile, female, USNM 1546926 (= ULLZ 13457), collection data same as preceding; juvenile, female, USNM 1546926 (= ULLZ 13457), collection data same as preceding; juvenile, female, USNM 1546926 (= ULLZ 13457), collection data same as preceding; juvenile, female, USNM 1546926 (= ULLZ 13457), collection data same as preceding; juvenile, female, USNM 1546926 (= ULLZ 13457), collection data same as preceding; juvenile, female, USNM 1546926 (= ULLZ 13457), collection data s

USNM 1547046 (ULLZ 13690), swash zone muddy quartzite sand, Bocas del Toro beach across road from STRI lab, Isla Colon, 9 August 2011. Trinidad: ovigerous female, USNM 65727, Cedros, January 1905.

Diagnosis. Carapace dorsally convex, surface densely covered by transverse microcrenulate rugae not extensively disposed as short lines or short crescentic rows, many elongate and continuous across median longitudinal line of carapace, more than 17 crossing median line posterior to cervical furrow, rugae laterally becoming obsolete over most of broad, punctate, epimeral lobe of carapace; front terminating in three strong subacute lobes, median forming broad angular rostrum less advanced than narrower lateral lobe to each side. Antennular flagellum dorsal ramus comprised of approximately 30 articles. Antennal peduncle with second article terminating in large, distally upturned, median spine, shorter dorsal and ventral spines reaching no more than half length of median spine. Third maxilliped lacking exopod; endopod with merus mesial margin distal end terminating in strongly produced subtriangular lobe, lateral margin sinuous, distal third offset by weakly angular bend, distal end forming acute corner. First percopod merus massive, distal half of flexor margin produced to form broad, truncate lobe; carpus terminating in narrow spine reaching to base of dactylus; propodus approximately three times longer than broad, subequal in length to dactylus; dactylus elongate, length more than two times greatest width, lateral surface narrowly ellipsoid in outline, terminus rounded, margins of article lined by long, plumose setae interspersed with short spiniform setae or spinules of varied sizes, rounded terminus of article bearing slightly enlarged single, short, spine. Pleon with second pleonite larger than all others, its dorsal tergite reaching to full width of carapace, lateral extremes forming broadly rounded flanges to each side of narrower median commissure, flange dorsal surfaces each bearing pair of long largely unbroken transverse rugae extending almost to ventrolateral margin of tergite. Diagnostic DNA sequence data for COI and 16S mitochondrial genes included in the Barcode of Life Database (dataset dx.doi.org/10.5883/DS-CRUSTACE) under BINs cluster BOLD:ACU0009 and in GenBank (www.ncbi.nlm.nih.gov/genbank) under accession numbers MN183852, MN183956, MN184098, and MN189420 for COI, and L43111, MK971283, MK971390, MK971536, and MK971646 for 16S.

Description. Carapace (Figs. 1A–C; 2A, D; 3A; 4A; 5A–C) elongate, subcylindrical, dorsally arched, strongly convex transversely, longitudinal arch strongest in anterior half; carapace surface densely textured by low transverse microcrenulate to microdenticulate rugae, many rugae continuously elongate, not extensively disposed in short lines or as short crescentic rows, many continuous across middorsal regions of anterior and posterior carapace, number extending across postcervical middorsal line typically exceeding 17; ventrolateral rugae of pterygostomial region separating weak anteriorly curved ridges near ventral margin, ridges abbreviated to produce minutely serrate appearance along anterior margin of broad epimeral lobe; front terminating in three strong subacute dentiform lobes (Fig. 2B, E), median forming broad angular rostrum, rostrum less advanced to anterior than narrower, longer, lateral lobe to each side, separated from each lateral lobe by broad U-shaped sulcus overlying ocular plate; transverse frontal groove parallel to frontal margin, incised by weak median notch and short posteriorly directed bend at each lateral extreme, microdenticulate ridge marking posterior lip of frontal groove positioned about 1/5 distance from tip of rostrum to cervical groove, cervical groove just anterior to carapace midlength, posterior lip of cervical groove marked by microdenticulate ridge, overall broadly crescentic with lateral arms extending anteroventrally, obsolete across carapace midline; rugae laterally becoming broken to obsolescent over most of broad lower epimeral lobe otherwise marked by well-separated punctae, rugae weakly evident as short lines on ventralmost margins of lobe.

Eyes at swollen ends of very narrowly elongated peduncles, corneal end reaching anteriorly to near midlength of terminal article of antennal peduncle when extended, exceeding anterior reach of longest spine on penultimate article of antennal peduncle. Antennular flagellum (Figs. 2A, B, D, E; 3A; 4A) dorsal ramus comprised of approximately 30 articles, length near twice that of ventral ramus. Antennal peduncle (Figs. 2A, B, D; 3A; 4B; 5C) with second article terminating distally in large, upturned, median spine, spine originating from lateral crest on article, shorter dorsal and ventral spines reaching no more than half length of median spine, terminal article of peduncle with dense lateral row of elongate setae continuous with row on antennal flagellum; flagellum long, robust, typically comprised of more than 85 densely setose articles.

Mandible (Fig. 3B) membranous, extensively fused with posterior margin of epistome, basally produced to form mesially directed gnathal lobe with long plumose setae along distal and mesial margins; palpus of two articles larger than gnathal lobe, proximal article of palp with line of stiff spiniform setules along lateral margin, terminal article with margins lined by rows of long plumose setae distally and mesially, separated by distomesial row of shorter setae, external surface with scattered short simple setae. First maxilla (Fig. 3C) proximal endite developed as flattened lobe, loosely attached to remainder of appendage, mesial margin lined by row of long plumose setae adjacent to field of long simple setae, field of simple setae extended onto external surface; distal endite elongate with broadened terminal end, lateral slope of terminus bearing very elongate plumose setae, mesial slope of terminus bearing



FIGURE 1. *Emerita portoricensis* Schmitt, 1935: A, B, ovigerous female, cl 11.9 mm, Boca del Drago, Panama Caribbean, USNM 1546871 (= ULLZ 13325); C, ovigerous female, cl 10.3 mm, Dangriga, Belize, USNM 1545049 (= ULLZ 10465).



FIGURE 2. *Emerita portoricensis* Schmitt, 1935: A–C, ovigerous female holotype, cl 17.5 mm, Mayaguez, Puerto Rico, USNM 65731; D–F, ovigerous female, cl 11.5 mm, Dangriga, Belize, USNM 1545049 (= ULLZ 10465). A, carapace, eyestalk, and anterior appendages, right lateral surface; B, carapace front, eyestalks and anterior appendages, dorsal surface; C, G, terminus, dactylus of right first pereopod, lateral surface; D, right lateral surface of carapace front, eyestalks, and anterior appendages; E, dorsal surface of carapace front, eyestalks, and anterior appendages; F, right first pereopod, lateral surface. Scale bars = 3 mm (A, B); 2 mm (D–E); 1 mm (C, G).

narrow field of short, stiff, serrate, spiniform setae, shaft of article setose along lateral and mesial margins, those of lateral margin short, those of mesial margin dense, long, plumose; endopodal palp elongate, sparsely setose, weakly hooked, narrowed to subacute rounded tip. Second maxilla (Fig. 3D) exopod broadly developed as scaphognathite attached to base; proximal endite subdivided, larger lobe broad, flattened with mesial margin bearing overlapped rows of long plumose setae, short simple setae covering most of external surface; distal endite club-shaped, marginal setae longer, plumose laterally, those of distal end forming dense field of short stiff setae, continued as field of short simple setae on external surface; endopod short, stubby, narrowed, subacute tip deflected distally.

First maxilliped exopod (Fig. 3E) arched, crescentic, comprised of two marginally setose articles, proximal article strap-like, subrectangular, distal article subovoid, margin concave laterally, narrowing toward terminus, distal margins lined by long plumose setae; endopod minute and strap-like, membranous, subterminal shoulder with small cluster of plumose setae, tip constricted to narrow shaft; distal endite prominent, elongate, exceeding length of exopod proximal article, strap-like, heavy setation including cover of short setae over external surface, long plumose setae in dense terminal field and along entire mesial margin, proximal half of mesial margin with additional row of longer, coarser, plumose setae overlying others.

Second maxilliped exopod (Fig. 3F) comprised of two articles, proximal article elongate, length subequal to endopod ischiomerus, broadest proximally, tapered over full length to narrow articulation with distal article, sparsely setose, distal article subovoid, spatulate, slightly tapered in distal half to blunt tip, margins densely lined by long plumose setae; endopod comprised of four articles, ischiomerus (proximal article) narrow, distinctly arcuate, rib-shaped, lateral margin densely lined by long plumose setae, mesial margin lined by row of long plumose setae overlain by row of longer, heavier simple setae originating from weakly defined crest along external surface, carpus short, inflated, approximately 1/4 length of ischiomerus, distal and lateral margins covered by dense filed of heavy, elongate, plumose setae, propodus less robust, narrower than but subequal in length to carpus, margins setose but less coarse than on carpus, dactylus narrowly elongate, weakly tapered to rounded tip, length approximately 2/3 that of ischiomerus, margins heavily setose, longest setae coarse, simple, extending as row along entire flexor margin. expanded more broadly onto surface in distal half, comparable to those of ischiomeral surface, which are overlapped when article flexed.

Third maxilliped (Fig. 3G, H) lacking exopod; endopod with merus broad, margin lined by short setae laterally, long plumose setae mesially and distally, length approximately 1.9 times greatest width, mesial margin strongly rounded in proximal third, broadly rounded distally, distal end terminating in strongly produced subtriangular lobe overlying external surface of carpus and proximal propodus, lateral margin sinuous, distal third offset by weak but distinct angular bend, distal end forming acute corner, carpus short, subquadrate, robust, long plumose setae on distal and lateral surfaces, dense field of plumose setae originating on distal half of internal surface, contiguous with field over entire internal and flexor surfaces of propodus and dactylus, propodus length approximately five times greatest width, dactylus subcylindrical, approximately 2/3 propodus length, terminus rounded.

First pereopod (Figs. 2A, C, F, G; 4A, C–H) merus massive, broadly subovate in outline, lateral surface convex, crossed by broken, oblique lines setose rugae, extensor margin most strongly arched proximally, distal half of flexor margin produced to form broad, truncate lobe; carpus elongate, distally terminating in strong narrow spine reaching to base of dactylus, spine offset laterally from proximal portion of article by setose ridge, portion proximal to spine approximately two times longer than broad, lateral surface crossed by few broken oblique setose rugae; propodus approximately three times longer than broad, subequal in length to dactylus, lateral surface with longitudinal ridge along most of inferior margin and strong ridge extending obliquely from articulation with dactylus to near inferior margin, latter ridge marking origin of blade-like distal process, distal process narrowing to rounded terminus, its superolateral surface excavate to cup base of flexed dactylus, stiff bristle-like setation along ridges of article, terminal setation of distal process elongate, plumose; dactylus elongate, length distinctly exceeding two times greatest width, lateral surface narrowly ellipsoid in outline, terminus rounded, weakly arched ridge originating just below superior (extensor) margin proximally, merging with superior margin distally, surface between ridge and inferior (flexor) margin weakly concave, ridge lined by short bristle-like setae, margins of article lined by long, plumose setae interspersed with short spiniform setae or spinules of varied sizes, rounded terminus of article bearing slightly enlarged single, short, spine.

Second through fourth pereopods all heavy, similarly configured (Fig. 4A, I–K); second with merus massive, sub-rectangular, slightly longer than broad, lateral surface convex with scattered short setose rugae, extensor margin most strongly arched distally, distal half of flexor margin produced to form subtriangular lobe, carpus robust,

subtriangular in outline, approximately as long as broad, lateral surface with superior and arched inferior longitudinal ridges, both coarsely setose, propodus heavy, subquadrate, distal extreme produced, tapered to densely setose bluntly tipped process fitted against internal surface of flexed dactylus, dactylus distinctly flattened, articulated to distal end of superior propodal margin, broad proximally, distinctly hooked in lateral outline, concave superior margin lined by coarse short setae, strongly convex inferior (flexor) margin lined by short setae proximally, longer heavy setae distally, narrowing to upturned subacute distal tip; third pereopod overall with similar ridging and setation to second, merus more elongate, lacking subtriangular lobe on flexor margin, carpus more distinctly triangular in outline, dactylus less strongly hooked with less acute tip; fourth pereopod merus similar to that of third, carpus lateral surface subrectangular, propodus lacking tapered distal process fitted against internal surface of dactylus, dactylus heavy, less flattened than in second and third pereopods, indistinctly hooked in lateral outline, with dense longitudinal tract of short heavy setae on lateral surface near superior (extensor) margin; fifth pereopod concealed beneath posterior thorax, typically intruding into branchial chambers, comprised of seven articles, all narrowly elongate except for the very short hooked dactylus opposing a distal process on the propodus to form a minute chela, merus exceeding length of all other articles, long setae disposed primarily in short tracts or patches, especially near distal ends of distal articles.

Pleon (Figs. 2A, D; 4A, M) with first pleonite exposed dorsally as short, transversely narrow sclerite (tergite) fitting into posterior concavity of carapace, second pleonite larger than all others, its dorsal tergite reaching to full width of carapace, lateral extremes forming broadly rounded flanges to each side of narrower median commissure, flange surfaces each bearing pair of long relatively unbroken transverse rugae extending almost to ventrolateral margin of tergite, in addition to raised submarginal lips, flanges framing posterior concavity where smaller third pleonite articulates, tergites of third through fifth pleonites decreasing in size, lateral flanges directed ventrolaterally, lateral flange of third rounded, largely concealed below flange of second, that of fourth triangular, that of fifth narrowly produced, sixth pleonite with tergite elongate to form enlarged plate with subtriangular lateral extremes, width approximating that of telson to which it articulates; pleopods not developed on first and fifth pleonites, each developed as three narrow setose articles on second through fourth pleonites in females; large uropods (Fig. 3G) articulated laterally to ventrolaterally on sixth pleonites, each comprised of elongate basal article attached to flattened endopod and exopod, both elongate ovoid in shape with dense plumose marginal setation, setation longest distally; telson lanceolate, lateral margin setose, weakly convex in outline, longitudinal tract of short setae filling furrow just medial to distinct submarginal ridge, terminus subacute.

Habitat. Shallow infaunal, moving with tidal rise and fall, concealing by shallow burrowing; siliceous, calcareous, and mixed sandy substrates, some with molluscan shell or coral fragments; beach wave swash zones to shallow subtidal flats, some near estuarine tidal outflows; 0–2 m.

Distribution. Tropical sandy island and Central American mainland shorelines of Caribbean Sea, confirmed to include, but not limited to, Puerto Rico, Dominican Republic, Virgin Islands, Jamaica, Belize, Costa Rica, Panama, Colombia St. Lucia, St. Thomas, Venezuela, and Trinidad; western Atlantic Ocean.

Remarks. The variably rounded terminus of the first percopod dactylus in all but the largest specimens of E. portoricensis could perhaps lead to their misidentification as E. brasiliensis or E. talpoida, two western Atlantic species that to some degree share this character, even though their dactyli are usually broader and overall more ovoid in appearance (Fig. 40-Q; see also Williams 1965: fig. 115B). The narrowed, elongate shape of the first percopod dactylus (Figs. 2C, F, G; 4C–G), which is also slightly more tapered distally toward its rounded tip than in E. brasiliensis and E. talpoida, appears to account for its being labelled as a subacute tip (Schmitt, 1935) in E. portoricensis. In only the largest of specimens does it approach the distinctly acute tip of E. benedicti (Fig. 4N; see also Williams 1965: fig. 115A), the only other presently described western Atlantic species that shares the generally narrowed, more elongate shape of the first percopod dactylus overall. While the shape of this article is somewhat alike in *E. portoricensis* and *E. benedicti*, specimens of these two species can be separated at most sizes by examination of the dactylus tip under magnification. In all mature adult specimens, the tip tapers triangularly to become a sharp corneous spine in *E. benedicti*, while the tip is to varying degrees rounded to a terminus at which it bears a short, slightly enlarged corneous spine in *E. portoricensis*. However, in the largest examples of *E.* portoricensis, including the holotype, the terminus tends to be less rounded than in all examined smaller specimens of these species from sampled populations, though it is nonetheless separable from large specimens of E. benedicti when they are compared under magnification.



FIGURE 3. *Emerita portoricensis* Schmitt, 1935: ovigerous female paratype, cl 13.7 mm, Boca del Drago, Panama, USNM 1546925 (= ULLZ 13456): A, right lateral surface of carapace, eyestalk, and anterior appendages; B, right mandible, external surface; C, right first maxilla, external surface; D, right second maxilla, external surface; E, right first maxilliped, external surface; F, right second maxilliped, external surface; G, right third maxilliped, external surface; H, right third maxilliped, internal surface. Scale bars = 1 mm (A, C); 2 mm (D–F); 3 mm (G, H).

Morphological separation of *E. portoricensis* from its western Atlantic congeners can also be based on patterning of the fine dorsal rugae of the carapace and second pleonite. Posterior to the cervical groove, fine broken transverse lines of rugae in *E. portoricensis* are at most little diminished across the mid-dorsal longitudinal line, while they are somewhat more broken into short cusps in adult *E. brasiliensis* and distinctly diminished to all but absent at the midline in adult *E. talpoida*. The pattern and density of transverse rugae are relatively similar dorsally in *E. benedicti* and *E. portoricensis*, but the relative absence of transverse rugae laterally on the epimeral lobe of the carapace in *E. portoricensis* was used as a key character by Schmitt (1935) to separate *E. portoricensis* from *E. benedicti*. This character, based upon Schmitt's (1935) comparisons to the only three specimens of *E. benedicti*

known at that time, was adopted in regional taxonomic references (Felder 1973; Abele & Kim 1986) but appears to be of questionable utility, being somewhat subjective and dependent upon lighting and staining of the examined specimens. In almost all cases, some evidence of transverse rugae can be seen on the epimeral lobe in specimens of *E. portoricensis*, and these often resemble the only slightly denser patterns in specimens of *E. benedicti* of varied sizes. Lengths of rugae on the pleon are also useful in separating western Atlantic species, especially those on the dorsal surface of the lateral flange of the second pleonite, which in *E. portoricensis* (Figs. 2A, D; 4A), much as in *E. benedicti*, is marked by a pair of relatively unbroken transverse rugae that extend almost to the ventrolateral margin of the tergite. In both species, these reach further laterally than in *E. brasiliensis* and *E. talpoida*.

Except for some depictions of third maxillipeds, published illustrations are lacking for other anterior oral appendages of most congeners, limiting potential comparisons to illustrations herein provided (Fig. 3B–F). For the present, it can only be noted that those of *E. portoricensis* in general conform to descriptions and illustrations as provided for *E. talpoida* by Smith (1877) and Snodgrass (1952), adding to a baseline for future interspecific comparisons. From our own examinations it appears that the third maxilliped merus in *E. portoricensis* may bear a slightly more angular bend or shoulder on its lateral margin than in *E. brasiliensis* and *E. talpoida*, though this can be expected to vary somewhat with size and maturation.

It should also be noted that Schmitt (1935), as a footnote to his description of *E. benedicti*, noted that this species was nearest *E. portoricensis* in habitus, though "it tapers appreciably more anteriorly" than does that species. In the course of our examining a full range of sizes for both species, we could not confirm this to be a reliable character supported by either measurements or comparisons of dorsal outlines.

At present, applying diagnostic characters as herein defined, we have seen no vouchers to confirm that E. portoricensis ranges beyond Caribbean waters to the northern coast of Yucatán or onto shorelines of the Gulf of Mexico and southern Florida. Even so, there would seem little obstacle to its perhaps periodic occurrence in the more tropical of these waters, especially with warming of coastal waters, and one might expect it to range widely along shorelines of Cuba. In his descriptive paper, Schmitt (1935) included "South Florida and several Texas localities in the range he reported for E. portoricensis. Efford (1976) concluded these were all misidentifications of E. benedicti, but he confirmed a record of E. portoricensis from Pensacola, Florida (USNM 17919), this being the only one from within the Gulf of Mexico. Applying redefined characters in our own examination of this specimen, we find that this is instead a small representative of *E. benedicti*, with the terminus of its first percopod dactylus being as in other specimens of *E. benedicti* (Fig. 4N) more acute than it would in a specimen of *E. portoricensis* at a comparable size. Thus, we conclude that regional checklists and identification keys for waters of the eastern US and its coastal states (Behre 1950; Felder 1973; Abele & Kim 1986; Camp et al. 1998; McLaughlin et al. 2005; Felder et al. 2009), being based on literature compilations, are in whole or part referring to records for *E. benedicti* within those regions, not to E. portoricensis. Regarding specifically the Gulf of Mexico, there is no basis for concluding that both species occur "throughout the region", though the history of confusion among regional workers might explain why the two are believed by some to be the same species (Britton & Morton 1989: 120).

Coloration in life is documented for only two specimens of *E. portoricensis*, but these conform to one another very closely and are for specimens taken from opposite ends of the known range, suggesting color could represent a relatively stable diagnostic character, at least for specimens of similar size and maturity (Fig. 1A–C). As documented, the pattern includes longitudinal and diagonal dark bars of olive brown on the branchial regions and a light longitudinal bar marking the posterior of the median line. Clearly, this differs from much less striking color patterns in live specimens of *E. benedicti*, *E. brasiliensis*, and *E. talpoida* that we have documented to date (DLF photographic files). However, it remains to be shown whether this pattern is consistently evident in all fresh specimens of *E. portoricensis*. Should comparisons be made, it might also here be noted that the color image of a specimen reported to be *Emerita talpoida* from Guadeloupe, depicted in Poupin (2018: fig. 151), does not represent that species but instead *Hippa testudinaria* (Herbst, 1791). Four related images reported as *E. talpoida*, accessible at http://crustiesfroverseas.free.fr/, also represent *H. testudinaria*. At present, there is no confirmed evidence that the distribution of *E. talpoida* extends into Caribbean waters.

The presently known world membership of *Emerita* Scopoli, 1777 stands at eleven, with a single new species being added since the listing of ten by Boyko & McLaughlin (2010). The addition of *E. taiwanensis* Hsueh, 2015, was accompanied by a key to members of *Emerita*, albeit it apparently compiled from text and illustrations in literature rather than first-hand examinations of specimens representing species in the key (Hsueh 2015: table I). Applying characters used therein, *E. portoricensis* might correctly key to that species depending upon whether the



FIGURE 4. *Emerita portoricensis* Schmitt, 1935: A–D, ovigerous female, cl 14.7 mm, San Juan Harbor Puerto Rico, USNM 42209; E, female, cl 12.8 mm, same lot as previous; F, ovigerous female, cl 15.0 mm, same lot as previous; G–M, ovigerous female, cl 13.7 mm, Boca del Drago, Panama, USNM 1546925 (= ULLZ 13456). *Emerita benedicti* Schmitt, 1935: N, ovigerous female, cl 13.3 mm, Tampa, Florida; O, *Emerita talpoida* (Say, 1817): O, ovigerous female, cl 15.5 mm, Padre Island, Texas, TAMU/TCWC 2-8703. *Emerita brasiliensis* Schmitt, 1935: P, ovigerous female, cl 11.4 mm, Urbatuba, Laxaro Beach, Brazil, ULLZ 15981; Q, ovigerous female, cl 19.4 mm, Rio de Janeiro, Brazil, USNM 50674. A, right lateral habitus; B, right third maxilliped, external surface; C, G, right first pereopod, lateral surface; D–F, H, N–Q, terminus, dactylus of right first pereopod, lateral surface; I, lateral surface of right fifth pereopod; M, external surfaces of telson and uropods. Scale bars = 12 mm (A); 8 mm (B, C, G); 2 mm (D–F, N, O–Q); 4 mm (H–L); 10 mm (M).

first percopod dactylus was in fact interpreted to be "distally subacute in the first couplet. However, as we herein establish, this article in *E. portoricensis* is upon close study clearly rounded at the very terminus in all but the largest of specimens, and thus much less acute than for any of the other four species to which that character applies in the key. Even so, presence of a slightly enlarged terminal spine on the otherwise rounded margin in *E. portoricensis* suggests some degree of acuity if not examined under magnification. It should also be noted that the first key couplet separates members of the genus in large part on the basis of a length to width ratio in the first percopod dactylus, measurement of which is not therein precisely defined. Among western Atlantic members of the genus, the length of the full article is not necessarily or conspicuously less than two times width in all specimens of *E. talpoida* and *E. brasiliensis*, depending on maturity of specimens and whether the length measurement fully encompasses the distance from articulation with the propodus to the distal terminus. Even so, a relatively narrow, elongate first percopod dactylus is found in *E. portoricensis*, consistently longer than twice the greatest width.



FIGURE 5. *Emerita portoricensis* Schmitt, 1935: A, B, ovigerous female holotype, cl 17.5 mm, Mayaguez, Puerto Rico, USNM 65731; C, ovigerous female, cl 14.7 mm, San Juan Harbor, Puerto Rico, USNM 42209.

We also here note that Hsueh (2015) includes an apparent error in both tabular data (table I) and the key (Appendix, couplet 8) regarding relative width of the second pleonite in *E. benedicti*, which is stated to be less than 2/3 the carapace width and thus is used as a distinguishing characters for its identification. The second pleonite actually equals or exceeds 2/3 the carapace width in *E. benedicti* and all other western Atlantic species examined to date, even when allowing for some variation in its width due to different sizes and degrees of maturation. If

judged only from the poorly lighted type specimen photographs of Schmitt (1935: fig. 71a, b) this would not be readily apparent, but it is clear from our direct studies of both the type material and a large series of specimens from throughout the range of *E. benedicti*.

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