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A new mud shrimp of the genus *Pugnatrypaea* from outer continental shelf waters of the northern Gulf of Mexico, commonly associated with hydrocarbon seeps (Crustacea: Decapoda: Callianassidae)

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Abstract

A new species of callianassid mud shrimp is described from outer continental shelf waters of the northwestern Gulf of Mexico, where it appears to commonly live in close association with sediments on or near natural hydrocarbon seeps. Recent genus-level taxonomic revisions of the Callianassidae, based on gene sequence analyses and comparative morphological studies, included specimens representing this new species, assigning it with strong support to the genus *Pugnatrypaea* Poore *et al.*, 2019. The other known species of this genus are also typically found in offshore waters of continental shelves, but are all restricted in distribution to the Indo-West Pacific and are known from relatively few specimens. Collections of this new Gulf of Mexico representative of the genus are all from slightly deeper waters than for other known congeners, and commonly occur near hydrocarbon seeps, on some occasions being directly associated with sulfidic substrates that include waxy crude oil globules.

Introduction

Benthic sampling with dredges, skimmers, and corers in offshore waters of the northern Gulf of Mexico over the last five decades has yielded a number of mud shrimps, though most specimens of these soft-bodied burrowers have been somewhat mutilated in the collection process. In addition, none of the commonly applied collection methods deeply penetrate benthic sediments, which appears to somewhat bias captures to shallower burrowed juvenile and sub-mature individuals. Nonetheless, there are a few accounts of callianassids from outer continental shelf waters in the northern Gulf of Mexico (Heard & Reames 1979; Rabalais *et al.* 1981), along with some updates of taxonomy and distributions (Felder *et al.* 2009; Felder 2019). However, fragmentary specimens from the region have been little represented in publications to date, and taxonomic resolution remains questionable for a number of reported species.

Our collections over the last two decades have focused on obtaining intact specimens of offshore callianassids from carefully processed sediment samples, while also documenting color in these fresh specimens and obtaining sequence-quality tissue subsamples for use in molecular phylogenetic analyses. Regional specimens have been included in several molecular phylogenetic analyses (Robles *et al.* 2009; Felder & Robles 2009; Robles *et al.* 2020), somewhat clarifying relationships of these materials to world members of the family and, in several cases, documenting the need for descriptions of new taxa. One such new species found most commonly near hydrocarbon seeps is herein formally described, named, and compared to morphologically similar taxa.

Materials and Methods

Ship-based collections were made by deploying a 0.25-m² box corer, a multi-corer array, or a benthic skimmer (for the latter, see Pequegnat *et al.* 1970). Bottom depths at collection sites are shown in meters (m). Collections from

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2002 and later were flash frozen briefly aboard ship in seawater or glycerine before being photographed and then either fixed directly in 75% ethyl alcohol or returned to the lab frozen before alcohol fixation. Digital color photographs were made with subjects immobilized below the water surface of a shallow tray lined with black felt for framing of the exposure. Procedures for tissue extraction and sequence analysis were as previously described by Robles *et al.* (2009). Line illustrations were prepared with a Wild M5 dissecting microscope equipped with a camera lucida. Postorbital carapace length (pocl) was measured in millimeters (nearest 0.1 mm) from the posterior orbital margin at the base of the rostrum to the posterior margin of the carapace (= postrostral carapace length); embryo diameter size range indicates variation in the greatest dimension of five randomly selected embryos (to nearest 0.01 mm) from each ovigerous female. All measurements were determined with a calibrated ocular micrometer. Specimens were archived in the Smithsonian Institution National Museum of Natural History (USNM), Washington, D.C., USA or Texas A&M University Biodiversity Collection (TAMU-TCWC), formerly known as the Texas Cooperative Wildlife Collection, College Station, Texas. As holdings of the University of Louisiana's Lafayette Zoological collection (ULLZ), Lafayette, Louisiana, are currently being transferred permanently to the USNM, where they will remain cross-referenced under both catalog systems, a number of specimens are shown with both numbers indicated.

Taxonomy

Infraorder Axiidea de Saint Laurent, 1979

Superfamily Callianassoidea Dana, 1852

Family Callianassidae Dana, 1852

Pugnatrypaea Poore, Dworschak, Robles, Manetlatto & Felder, 2019

Pugnatrypaea emanata n. sp.

(Figs 1A–J, 2A–M, 3A–E)

Callianassidae (an undescribed genus).–Martin & Haney 2005:500.
Callianassa ? sp. GMX-1, GMX-2.–Felder & Robles 2009: 336, 339, fig. 1 (part), table 1 (part).
Pugnatrypaea GMX.–Robles *et al.* 2020 (in press: proof pages D, F), figs 1, 3, suppl. tables 1, 2.
Pugnatrypaea GMX.–Poore *et al.*, 2019: 35, fig. 6j.

Type material. Off Louisiana and Texas, U.S.A. (northwestern Gulf of Mexico). **Holotype:** male (photograph voucher), pocl 8.6 mm (USNM 1559553 = ULLZ 17962), near Bush Hill hydrocarbon seep, 0.25-m² box corer sample, 560 m depth, 27° 46.829' N; 91° 30.387' W, soft silty sulfurous mud releasing globules of waxy crude oil and oily surface sheen, 1 August 2002, D.L. Felder & R. Robles. **Paratypes**: 1 male, pocl 4.7 mm (USNM 1559376 = ULLZ 17961), near Bush Hill hydrocarbon seep, sieved from multi-corer sample, 590 m depth, 27° 46.829' N; 91° 30.387' W, soft silty mud, 31 July 2002, C. Allan, S. Brooke, D.L. Felder, & R. Robles; 1 male (photograph voucher), pocl 6.6 mm (USNM 1541301 = ULLZ 6058), near Bush Hill hydrocarbon seep, 0.25-m² box corer sample, 560 m depth, 27° 46.829' N; 91° 30.387' W, soft silty sulfurous mud releasing globules of waxy crude oil and oily surface sheen, 1 August 2002, D.L. Felder & R. Robles; 1 ovigerous female, pocl 8.8 mm, embryo diameter 0.50–0.54 mm (USNM 1543631 = ULLZ 8279) benthic skimmer, 610–850 m depth, station NSF-III-074, 28° 06.52' N; 89° 46.57' W, mud, 8 July 2006, D.L. Felder, S. Fredericq, *et al.*; 1 ovigerous female (photograph voucher), pocl 7.8 mm, embryo diameter 0.61–0.68 mm (USNM 1543633 = ULLZ 8280) benthic skimmer, 610–850 m depth, station NSF-III-074, 28° 06.52' N; 89° 46.57' W, mud, 8 July 2006, D.L. Felder, S. Fredericq, *et al.*; 1 ovigerous female (photograph voucher), pocl 8.1 mm, embryo diameter 0.47–0.64 mm (USNM 15433634 = ULLZ 8281) benthic skimmer, 610–850 m depth, station NSF-III-074, 28° 06.52' N; 89° 46.57' W, mud, 8 July 2006, D.L. Felder, S. Fredericq, *et al.*; 1 male (photograph voucher), pocl 8.6 mm (USNM 1543632 = ULLZ 8282) benthic skimmer, 610–850 m depth, station NSF-III-074, 28° 06.52' N; 89° 46.57' W, mud, 8 July 2006, D.L. Felder, S. Fredericq, *et al.*; 1 male, pocl 6.7 mm (TAMU/TCWC 2-3269) benthic skimmer, 732 m depth, 27° 35' N; 95° 23' W, 20 November 1968, W.E. Pequegnat & L.H. Pequegnat.

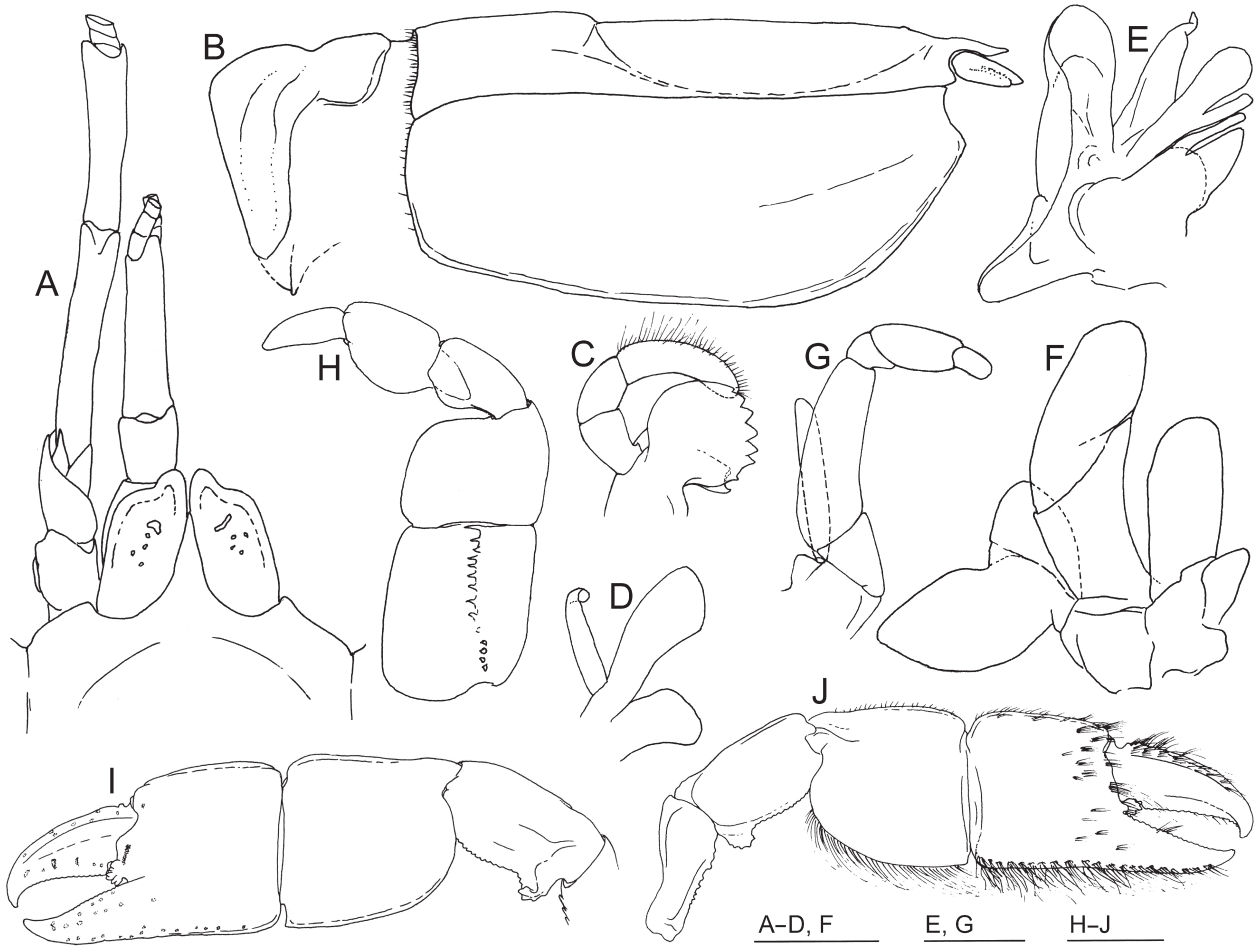

FIGURE 1. *Pugnatrypaea emanata* **n. sp.** A–J, male holotype, pocl 8.6 mm, northwestern Gulf of Mexico, near Bush Hill hydrocarbon seep, 560 m depth (USNM 1559553 = ULLZ 17962): A, anterior carapace and peduncles, dorsal; B, carapace and first pleonal somite, lateral; C, right mandible, external; D, right first maxilla, without setae, external; E, right second maxilla, without setae, external; F, right first maxilliped, without setae, external; G, right second maxilliped, without setae, external; H, right third maxilliped, without setae, external; I, major cheliped (left), without setae, external; J, major cheliped (left), internal. Scale bars = 1.0 mm (A–G), 2.0 mm (B, H–J).

Diagnosis.–Carapace with narrow triangular spiniform rostrum, low rounded shoulders lateral to eyestalks forming orbits; dorsal oval well defined. Eyestalk elongate, subrectangular, distomedial corner produced into rounded prominence, cornea poorly defined. Antennular peduncle much shorter than antennal. Second maxilliped small, narrow, straplike exopod carried closely against internal surface of endopod, distinctly shorter than endopodal merus. Third maxilliped lacking exopod, row of spiniform teeth forming distinct crista dentata on internal surface of ischium. Major chela with inferior keel of merus bearing proximal hooked spine or spined lobe, propodus external surface with multidenticulate lobe or tubercle extending over base of gape between fingers. Pleonal tergites mostly glossy smooth, enamel-like, first crossed by dorsal transverse furrows, broad oblique furrow on ventrally directed posterolateral lobe, second somite almost twice length of first. Male first and second pleopods uniramous, each composed of two articles, terminal article of first elongate, suboval, vestigial second male pleopod narrowly straplike. Female first and second pleopods biramous. Third through fifth pleopodal endopods each with short stubby appendix interna extending clearly beyond margin. Telson elongate subrectangular, posterior margin distinctly bilobate, lobes posteriorly separated by deep incision accommodating distinct median spine. Uropodal endopod broad, about 1.5 times longer than broad, dorsally with several stiff bristles distributed along longitudinal median ridge and posterolateral surface; exopod anterodorsal plate not reaching to distal endopod margin, elongate setae of exopod distal margin grading distomesially to dense line of heavy spiniform bristles. GenBank Accession numbers for paratypes, USNM 1541301 = ULLZ 6058: (16S) EU882915, (12S) EU875025, (H3) MN238262; USNM 1543631 = ULLZ 8279: (16S) EU992932, EU882933; (12S) EU87542, EU87543, (H3) MN238300.

Description.–Carapace frontal margin with acute, narrowly triangular rostrum, flexure weakly sinuous in lateral view, terminally spiniform, tip slightly upturned, reaching at least 2/3 length of eyestalks in dorsal view, rostral base flanked laterally by low, rounded shoulders forming orbits (Figs 1A, B; 3A, B, D, E); dorsal oval well defined, weak median tubercle in anterior 1/5, oval length about 2/3 total post-rostral carapace length; marginal furrow of oval becoming obscure at post-rostral midline, strong posteriorly at sclerotized articulation to inflated cardiac region.

Eyestalks elongate, tips reaching to penultimate article of antennular peduncle, strap-like, carried slightly deflected, subrectangular in dorsal view; distomedial corner produced into rounded prominence (Fig. 1A); medial borders of stalks meeting along straight line, closely opposed; dorsal surface with very shallow longitudinal sulcus, corneal pigment variably defined, poorly faceted, dark pigmentation dispersed into multiple spots or somewhat coalesced.

Antennular peduncle shorter and not strikingly heavier than antennal peduncle, reaching to or almost to proximal end of distal article of antennal peduncle (Fig. 1A); second article much shorter than basal, third article about 2.5 times length of second; second and third articles with ventromesial and ventrolateral rows of long, distoventrally directed setae. Antennular flagellum dorsal and ventral rami much longer than third article of peduncle, ventral with much longer setation than dorsal ramus; dorsal ramus heavier than ventral, especially in distal 1/3 where subterminal articles much broader than those of ventral ramus, articles there fringed with, dense ventral aesthetascs. Antennal peduncle reaching about to midlength of antennular flagellum rami; basal article dorsolateral carina arched to form lip above excretory pore; length of second article about twice width, distal articulation to third article overreached dorsally by strong spiniform scaphocerite; fourth article slightly exceeding combined lengths of first two, slightly longer than fifth, fourth and fifth very sparsely setose; fifth article slightly narrower than others. Antennal flagellum more than 3 times longer than rami of antennular flagellum, antennal flagellum setation sparse, setae very thin, 2–3 articles in length.

Mandibular palp 3-segmented, elongate third article narrow, arched, setose (Fig. 1C); gnathal lobe of mandible weakly subquadrate, distolateral shoulder rounded, incisor process with well-defined triangular corneous teeth on cutting margin, one or more minute teeth proximally, concave internal face with heavy thickened lip giving rise to terminally bifurcate molar process positioned proximal and internal to incisor teeth, a few small accessory denticles between primary teeth of molar process. First maxilla endopodal palp narrow, terminal article deflected, fringed by long thin setae (Fig. 1D); proximal endite forming rounded mesial lobe densely fringed by long setae; distal endite elongate, terminally broadened with dense setation, several closely set rows strongly spiniform, innermost row weakly hooked. Second maxilla margins setose, endopod constricted distally to form narrow deflected terminus (Fig. 1E); first and second endites each longitudinally subdivided, exopod forming large, broadly cupped scaphognathite.

First maxilliped margins setose, endopod very small, rudimentary, ovoid, concealed between base of distal endite and exopod (Fig. 1F); proximal endite rounded, surface at right angle to that of distal endite, densely setose terminally; distal endite straplike, subrectangular, margins and most of external surface densely setose; exopod straplike, elongate, arcuate, completely divided by oblique suture, close-set comb of very long plumose setae on mesial margin, those immediately proximal to oblique suture longer than others, overreaching distal end and setation of distal endite; epipod shorter than exopod, broad, anterior and posterior lobes subtriangular.

Second maxilliped small, margins of both rami setose; endopod merus weakly arcuate, broadest proximally, length about 3 times width, length exceeding combined length of short subcylindrical propodus and dactylus, propodus length slightly less than 1/2 length of merus (Fig. 1G); dactylus about twice as long as broad, rounded terminally; exopod narrow, straplike, carried closely against internal surface of endopod, distinctly shorter than endopodal merus, terminally rounded; epipod and vestigial branchiae lacking.

Third maxilliped lacking exopod, coxa bearing short spine on inner surface just proximal to articulation with ischium (Fig. 1H); endopod fringed by long setae, especially on mesial margins of ischium and merus, along with most of palp articles; ischium subrectangular, length about 1.25 times breadth, internal surface with slightly angled longitudinal row of spiniform teeth forming strong crista dentata, line ending in strong distal spine; merus subquadrate, slightly broader than long, about 3/5 length of ischium, internal surface with longitudinal fields of long setae proximal to articular with carpus; carpus almost as broad as propodus, both longer than broad, both with dense field of setae on internal surface, propodus distinctly ovoid; dactylus heavy, somewhat pyriform, weakly arcuate, terminally bearing long, stiff, serrate bristles.

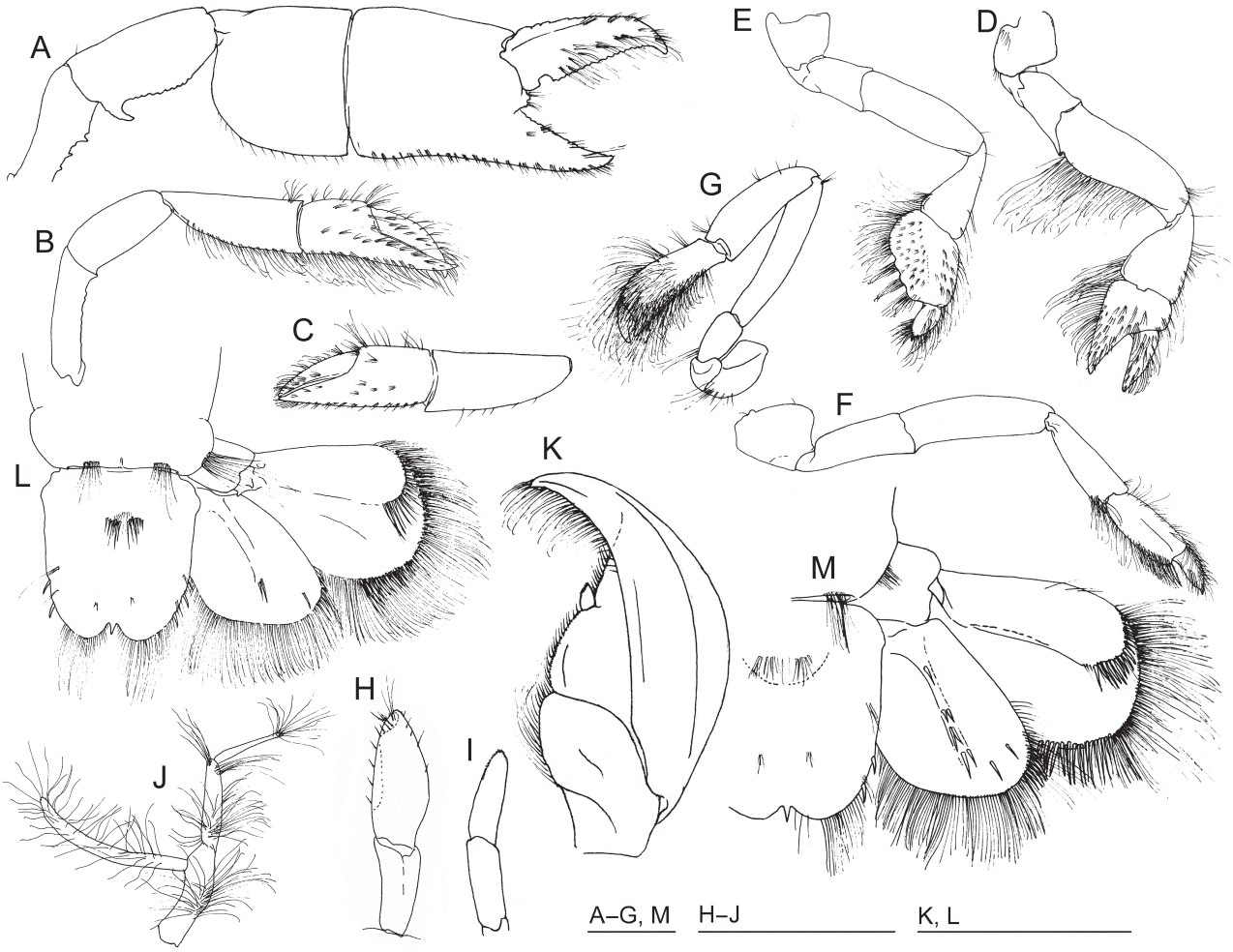

FIGURE 2. *Pugnatrypaea emanata* **n. sp.** A, ovigerous female paratype, pocl 8.1 mm, northwestern Gulf of Mexico, 610–850 m depth (USNM 15433634 = ULLZ 8281); B, D–I, K, L, male holotype, pocl 8.6 mm, northwestern Gulf of Mexico, near Bush Hill hydrocarbon seep, 560 m depth (USNM 1559553 = ULLZ 17962); C, J, ovigerous female paratype, pocl 8.8 mm, northwestern Gulf of Mexico, 610–850 m depth (USNM 1543631 = ULLZ 8279); M, male paratype, pocl 6.6 mm, northwestern Gulf of Mexico, near Bush Hill hydrocarbon seep, 560 m depth (USNM 1541301 = ULLZ 6058): A, major cheliped of female (right), external; B, minor cheliped of male (left), external; C, minor cheliped of female (left), external; D, right second pereopod, external; E, right third pereopod, external; F, right fourth pereopod, external; G. right fifth pereopod, external; H, right male first pleopod, anterior surface; I, right male second pleopod, anterior surface; J, right female second pleopod, posterior surface; K, right third pleopod, anterior surface; K, L, telson and uropod variants. Scale bars = 2.5 mm (A, B), 2.0 mm (C–G), 1.0 mm (H), 0.33 mm (I, J), 4.5 mm (K), 5.0 mm (L), 0.75 mm (M).

First pereopods strongly heterochelous in both sexes (Figs 2A–C; 3A, B, D), major cheliped located on either right or left side, shape and ornamentation sexually dimorphic, all articles typically heavier, stouter, more coarsely ornamented in mature male than in female (Figs 1I, J; 2A; 3A–E); ischium slender, superior margin sinuous, inferior marginal carina armed by row of small spines or denticles, distal third of which is offset from proximal by slightly enlarged tooth or spine; merus superior margin with evidence of shallow depression in proximal 1/3, with or without one or more small denticles proximal to depression, inferior (flexor) margin forming microdenticulate keel, weakly bowed in distal half, variable heavy proximal hooked spine or sculpted lobe at base of keel, terminated in single acute tip or with ancillary subterminal spine or small denticles; carpus broad, subquadrate, superior and inferior margins keeled, superior margin lined by short setae, terminating distally at rounded corner, inferior margin lined by close-set row of long setae, terminating distally in acutely to subacutely angular corner; propodus broad, heavy, length of postdactylar palm subequal to or greater than length of carpus, length of fixed finger about 2/3 to 3/4 length of palm, superior and inferior margins forming keel proximally, inferior margin with rows of punctae to internal and external

FIGURE 3. *Pugnatrypaea emanata* **n. sp.** A, male holotype, pocl 8.6 mm, northwestern Gulf of Mexico, near Bush Hill hydrocarbon seep, 560 m depth (USNM 1559553 = ULLZ 17962); B, C, male paratype, pocl 8.6 mm, northwestern Gulf of Mexico, 610–850 m depth (USNM 1543632 = ULLZ 8282); D, E, ovigerous female paratype, pocl 7.8 mm, northwestern Gulf of Mexico, 610–850 m depth (USNM 1543633 = ULLZ 8280).

sides bearing tufts of long setae, much more so than along superior margin, palm externally bearing distal multidenticulate lobe or heavy tubercle extended over base of gape between fingers (strongest in mature male), prehensile edge of fixed finger lined by distally diminishing row of uniform low denticles, submarginal longitudinal depression to internal side of edge, separating edge from weak low secondary margin, tip very weakly upturned; dactyl superior margin with raised proximal tubercles and array of large punctae bearing tufts of long setae extending to near tip, prehensile edge with conspicuous U-shaped proximal notch, remainder lined by uniform low denticles diminishing in size distally, deep submarginal longitudinal depression to internal side of edge, separating edge from strong secondary margin, external side marked by row of large punctae bearing tufts of long setae, tip strongly hooked.

Minor cheliped ischium narrowly elongate (Fig. 2B), inferior margin at most weakly serrate; merus subrectangular, unarmed; carpus narrow at proximal articulation, elongate with parallel superior and inferior margins distally, length slightly less than twice length of palm (Fig. 2B, C); inferior margins of carpus and propodus bearing much longer, denser setae than superior; fixed finger length subequal to or greater than length of palm, fixed and movable fingers basally broad, closely opposed, minimal gape, tips acute.

Second pereopod chelate, flexor margin of merus, distal flexor margin of carpus, inferior margin of propodus lined by long regularly spaced setae, those of fixed finger becoming distally shorter and more hooked (Fig. 2D); outer surface of dactylus and distal propodus covered by tufts of long setae.

Third pereopod merus length about 3 times width; propodus with inferodistal margin trilobate distal to broad proximal heel, distal lobe broadest, distal margins of lobes and heel densely lined by elongate setae (Fig. 2E), most of external surface covered by tufts of short setae; dactylus tear-shaped, superior margin concealed by long dense setae on outer surface, internally evident as slightly sinuous, article terminating in elongate, narrow, laterally directed corneous spine.

Fourth pereopod very weakly subchelate, inferodistal process of propodus (= fixed finger) developed as a low densely setose rounded lobe extending distally less than 1/5 length of dactylus, lobe terminally including several very coarse, marginally serrate bristles among dense setae, these somewhat flattened and weakly channeled along one side, at least one larger than all others (Fig. 2F); dactylus elongate, weakly sinuous, tapering distally, tip twisted to terminate in well developed ventrolaterally directed triangular corneous tooth.

Fifth pereopod minutely chelate terminally amid dense setation, opposable surfaces of fingers slightly spooned, terminally rounded (Fig. 2G); propodus with dense field of long, close-set setae on internal surface.

Branchiae limited to pair of arthrobranchs on third maxilliped and each of first through fourth pereopods.

Pleonal tergites glossy smooth, enamel-like dorsally (Fig. 3A, B, D, E). First pleonal tergite well sclerotized dorsally, crossed by distinct transverse furrow in anterior half, sclerite extended posteroventrally as broadly furrowed linguiform lobe (Fig. 1B). Second tergite almost twice length of first, anterior quarter cut by deeply incised furrow running dorsoventrally, furrow dorsally becoming obsolete, tergite ventral margin almost straight, weakly bowed, posterolateral lobe with scant setation limited to linear tuft. Third to fifth tergites each with very broad field of very fine soft setae overlying posterolateral lobe, that of third more posteriorly restricted than those on fourth and fifth, which originate near midlength. Sixth tergite with distinct posterolateral groove and short suture defining posterolateral lobe, suture not extending across tergite, lobe with submarginal tuft of stiff setae posterolaterally, separated from remaining posterior margin of tergite by similar tuft to mesial side of lobe (Fig. 2L, M). Ventral surfaces of pleonal somites mostly membraneous, lacking extensive armor of sclerotized plates or dense tubercles embedded in integument.

First and second pleopods of male uniramous, each composed of 2 articles (Fig. 2H, I); first less than 1/5 length of third, elongate terminal segment subovoid, sparsely setose with few elongate setae distally; second minute, vestigial, narrower, about ¾ length of first. Second pleopod of female biramous (first not intact in available preserved specimens); exopod with scattered elongate setae, very narrow, bowed, reaching about to end of endopod when flexed against it, endopod with tuft of elongate setae, including at tip of very narrow appendix interna (Fig. 2J). Third to fifth pleopods forming large, posteriorly cupped fans, endopod of each subtriangular with short heavy appendix interna projecting distinctly from mesial margin, opposed surfaces on appendix internae of two sides each with small field of microscopic hook setae (Fig. 2K).

Telson elongate subrectangular, length slightly exceeding width Figs 2L, M; 3A, D), lateral margins with weakly projecting lateral lobes in anterior 1/4, margins weakly converging posteriorly, posterior 1/3 of margin bearing pair of weakly hooked corneous spines on each side; posterior margin distinctly bilobate, lobes separated by deep posterior incision accommodating distinct median spine; dorsal surface with weak median elevation in anterior 1/3, bearing somewhat bilaterally separated fields of stiff setae or spiniform bristles.

Uropodal endopod broad, subrectangular, about 1.5 times longer than broad, posterior margin with continuous fringe of long setae replaced distolaterally by line of stiff spiniform bristles, dorsally with several stiff bristles distributed along longitudinal median ridge and posterolateral surface (Fig. 2L, M); exopod anterodorsal plate well developed, distally not reaching to endopod margin, posterodistal edge of plate lined by short, thick, spiniform bristles grading distolaterally to thinner, dense, elongate setae of exopod distal margin, very long distal setation grading distomesially to dense line of heavy spiniform bristles.

Color.–Little coloration in life (Fig. 3A–E), sclerotized major cheliped mostly opaque white, antennal peduncles, rostrum, eyestalks, minor cheliped, and proximal articles of other pereopods translucent whitish. Body otherwise mostly translucent horn to pale olive, with narrow tracts of translucent whitish along sclerotized margins of somites. Embryos pale orange to yellow.

Size.–Largest male pocl 8.6 mm; largest female pocl 8.7 mm; range of embryo diameters, measured as greatest dimension, 0.50–0.68 mm.

Habitat.–Soft muds and silts (Fig. 4A, C, D), including those in immediate vicinity of hydrocarbon (methane) cold seeps, outer continental shelf and upper slope, 560 to at least 732 m depth.

Distribution.–Western Atlantic Ocean, northwestern Gulf of Mexico, outer continental shelf off Louisiana and Texas.

Etymology.–The species name "*emanata*" is an adjective derived from the Latin "emanare", meaning to ooze or flow out, alluding to the hydrocarbon seeps with which this species is often associated.

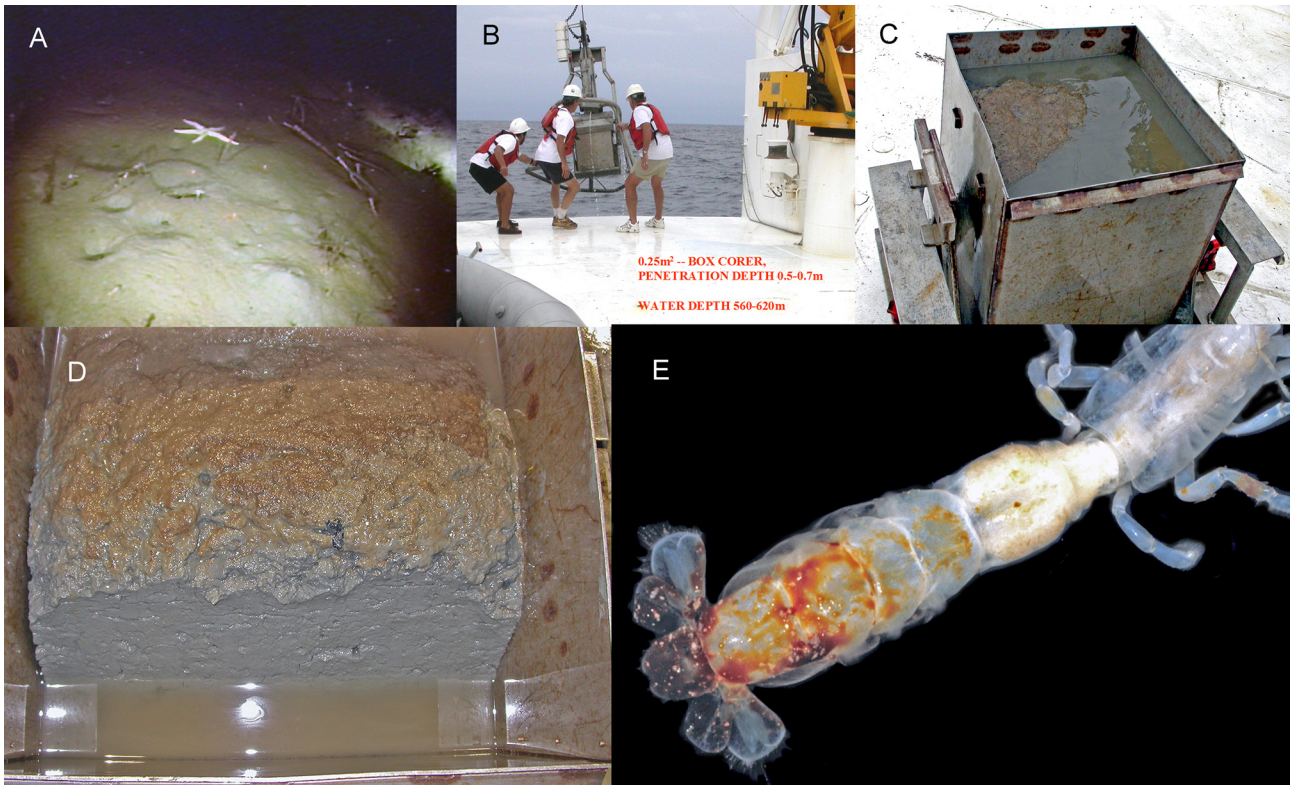

FIGURE 4. *Pugnatrypaea emanata* **n. sp.** collections at type locality. A, heavily burrowed sediments previously photographed near Bush Hill hydrocarbon seep (provided by R. Carney); B, retrieval of 0.25-m² box corer; C, surface of recovered core sample with oily sheen on included water; D, burrows in recovered core sample with oily sheen on draining water; E, waxy oil on body of live holotype specimen (USNM 1559553 = ULLZ 17962) immediately after being sieved from core sample.

Remarks.–Preliminary molecular genetic analyses (Felder & Robles 2009) provided evidence that this unnamed species might warrant a generic assignment other than *Callianassa* s.s., though no obvious alternative assignment was at the time available. More recently, comprehensive molecular phylogenetic analyses supported by morphological re-evaluations (Robles *et al.* 2020), have underpinned major taxonomic revisions of Callianassidae at the generic level (Poore *et al.* 2019). Among several new callianassid genera established in the latter work, *Pugnatrypaea* was shown to include "*Pugnatrypaea* sp. from the Gulf of Mexico", the species herein named as *P. emanata* **n. sp.** Additionally, this genus now includes, under revised name combinations, *Pugnatrypaea bicauda* (Sakai,

2010) from 73 m depth in the Gulf of Tonkin, Vietnam; *Pugnatrypaea intermedia* (De Man, 1905) from 330 m depth in the Bali Sea, Indonesia; *Pugnatrypaea iranica* (Sepahvand, Momtazi, & Tudge, 2015) from 40–50 m depth in the Persian Gulf, Iran; *Pugnatrypaea lobetobensis* (De Man, 1905) from 247 m depth in the Banda Sea, Indonesia; *Pugnatrypaea orientalis* (Spence Bate, 1888) from 28 m depth on the Arafura Shelf, Indonesia; and *Pugnatrypaea pugnatrix* (De Man, 1905) from 75–330 m depths in Indonesia and India, 75–330 m. Most of these congeners are known from very few specimens, often only a holotype, and all are known to occur only in the Indo-West Pacific. Like *P. emanata* **n. sp.**, all are also found only in relatively deep subtidal habitats of continental shelves, though *P. emanata* **n. sp.** appears restricted to somewhat deeper waters than reported for any of its congeners.

Species of the genus represented in the molecular phylogenetic analyses of Robles *et al.* (2020), included only *P. emanata* **n. sp.** (therein = "*Pugnatrypaea* GMX") and *P. pugnatrix*, which shared a clade. The other species grouped into *Pugnatrypaea* were so placed on the basis of morphological characters shared with these two species (Poore *et al.* 2019). Among the more diagnostic of these characters are the shapes of the third maxilliped merus, third pereopod propodus, uropodal exopod, and telson. Perhaps most strikingly, the telson tapers gradually toward a bilobate posterior margin, bears a strong pair of spiniform setae on each posterolateral margin, has a deep median excavation on the posterior margin, and has a medial spine or spinule centered in the posterior excavation. While the excavate margin of the telson is obvious in all species presently assigned to the genus, yielding the bilobed shape, the median posterior spine or the pair of spiniform posterolateral setae may not be evident in all fragmentary or mutilated specimens. This is assumed to be the case in *P. bicauda* and *P. orientalis*, both known from only single, apparently incomplete, specimens lacking evidence of these features.

Morphological separation of *P. emanata* **n. sp.** from its congeners draws upon the work of De Man (1928a, b), Sakai (1999; 2010; 2011), and Sepahvand *et al.* (2015). Distinctions can be based upon a combination of characters, including in part the relative lengths of the antennal and antennular peduncles. With the exception of *P. pugnatrix*, in which the antennal and antennular peduncles are of almost the same length, known members of the genus have an antennal peduncle that distinctly over-reaches the antennular. This includes *P. emanata* **n. sp.**, wherein the terminal article of the antennular peduncle reaches roughly to or almost to the articulation with the penultimate article of the antennal peduncle. According to the text description of De Man (1928), this is similar to the case in *P. lobetobensis*. However, in *P. intermedia*, the end of the antennular peduncle falls distinctly short of this articulation and in *P. bicauda* and *P. iranica* it reaches beyond this articulation. When the major cheliped is available for comparisons, an enlarged proximal hook or hook-like process of the merus inferior margin immediately separates *P. emanata* **n. sp.**, *P. pugnatrix*, and *P. iranica* from both *P. intermedia* and *P. lobetobensis* in which the merus inferior margin instead bears multiple spiniform teeth and the proximal superior margin bears a distinct distally directed spine not known in other species of the genus. Despite cheliped similarities, *P. iranica* can be readily separated from *P. emanata* and *P. pugnatrix*, as well as all other known congeners, by its distally spined eyestalks, while *P. pugnatrix* is separated from *P. emanata* **n. sp.** by the aforementioned antennular and antennal comparisons. Finally, the major chelipeds of *P. emanata* **n. sp.** and *P. pugnatrix* appear to uniquely share a distinct tubercle or tooth extending from the distal border of palm external surface, slightly over-reaching the proximal end of the gape just above the fixed finger.

The present description of *P. emanata* **n. sp.** adds to a growing list of extant and fossil axiidean decapods reportedly associated with sediments near hydrothermal vents, cold hydrocarbon seeps, mud volcanos, and similar environments (see Türkay & Sakai 1995; Peckmann *et al.* 2002; Lin *et al.* 2007; Dworschak & Cunha 2007; Karasawa 2011; Dworschak *et al.* 2012; Kiel & Hansen 2015; Kim *et al.* 2016; Ahn *et al.* 2017; Hyžný *et al.* 2018). Predating most of these reports was a world summary of vent and seep associated decapods by Martin & Haney (2005) that included the eastern Atlantic and Mediterranean *Callianassa truncata* Giard & Bonnier, 1890 (now *Necallianassa truncata*) as the only listed callianassid, along with the western Atlantic *Calaxius carneyi* Felder & Kensley, 2004 as the only axiid. However, mention was made of an undescribed species of calocaridid (now merged into Axiidae, sensu Robles *et al.* 2009) and a callianassid of what was at the time an "undescribed genus" from the northern Gulf of Mexico. While the mentioned calocaridid remains undescribed, and may prove to be a variant of *Calocaris caribbaeus* Kensley, 1996, the undescribed callianassid refers to what is herein established as *Pugnatrypaea emanata* **n. sp.** It is notable that this new species, along with the previously described *Calocaris carneyi* and the referred to calocaridid were all found to occur in sediments on or immediately adjacent to the Bush Hill hydrocarbon seep site, even though the latter two have also now been taken from other sites of similar depth in the northwestern Gulf of Mexico.

The association of an infaunal burrowing decapod with a hydrothermal vent or cold hydrocarbon seep can be difficult to establish, especially for species described on the basis of one or few specimens, sometimes in dated

taxonomic literature lacking mention of collection methods, sediments, and bottom topography. To varied degrees, this is the case for many species of *Pugnatrypaea*, though box-core collections for several specimens of *P. emanata* **n. sp.** clearly showed them to be living in strongly odiferous sulfidic sediments that presented an oily sheen upon return to the surface (Fig. 4A–D). Sieving of these collected sediments produced live specimens of *P. emanata* **n. sp.** that became smeared with the waxy oil globules that were also retained in the process (Fig. 4E). While a few collections from other sites infer a less than obligate association of this species with cold hydrocarbon seeps, our observations at very least suggest a remarkable ability of this species to live in close association with some forms of crude oil seepage.

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