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A new genus and species of mud crab (Crustacea, Brachyura, Panopeidae) from shoreline waters of the western Gulf of Mexico

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Abstract

Several specimens of a small panopeid crab from coastal waters of the western Gulf of Mexico were long suspected to represent an undescribed species and are herein designated as representatives of a new genus. While the originally collected specimens from over four decades ago were not of gene-sequence quality, later collections from the same locality produced materials that yielded sequence data for inclusion in molecular phylogenetic studies. Building on results of those analyses, the present taxonomic description draws upon morphology to support the description of a unique species in which especially the male first gonopods differ from those of all other described panopeid genera. To date, the species remains known from only two western Gulf of Mexico sites, both of which are wave-washed intertidal rocky habitats where substrates are heavily burrowed by boring bivalves and sipunculans. While we cannot exclude the possibility that the species was introduced, recurrent collections show its populations to be at very least persistent, the species most likely being a long-overlooked among a confusing hard-substrate assemblage of small panopeid crabs.

Key words: Xanthoidea, mud crab, western Atlantic, shoreline

Introduction

In late spring through summer of 1979, field collections were undertaken in coastal habitats of the northwestern Gulf of Mexico to obtain embryo-bearing female panopeid crabs from which larvae were reared for studies later published by Martin *et al.* (1984, 1985). Excluded from mention in those studies, an unusually colored male and two ovigerous females, initially thought to represent variants of *Acantholobulus bermudensis* (Benedict & Rathbun, 1891) (at the time, *Panopeus bermudensis*), were collected along with *A. bermudensis* from jetties bordering the Brazos Santiago Inlet at the southern end of South Padre Island, Texas. Upon further examination, the male was found to have a unique first gonopod, unlike that of any known panopeid crab. In addition, larvae (no longer extant) reared from one of the ovigerous female clutches were noted (J.W. Martin, personal communication) to differ markedly from those of *A. bermudensis* and other regional panopeid crabs that were at the time under study, so the specimens were set aside in expectation that a larger series would eventually be obtained for examination.

Further collecting efforts at the site did not produce additional specimens until 1998, when three juvenile specimens were found and carefully preserved to facilitate use of tissues in subsequent gene-sequence studies. Initially thought to represent a new species of *Hexapanopeus*, the undescribed species was included in a preliminary molecular phylogenetic analyses of that genus by Thoma *et al.* (2009), which concluded that neither it nor *H. lobipes* (A. Milne-Edwards, 1880) was assignable to *Hexapanopeus* s.s. *Hexapanopeus lobipes* itself was subsequently assigned to the a genus *Milnepanopeus* Thoma & Felder, 2012, but the generic placement of the undescribed species was deferred pending further clarification of its relationships. A robust molecular phylogenetic analysis of panopeid and pseudorhombilid genera has now further substantiated that a generic-level separation of this undescribed panopeid species is warranted (Thoma *et al.* 2014). The present work undertakes formal morphological description and naming of the new genus and species on the basis of the aforementioned long-held materials, while also including one additional specimen that was more recently collected from coastal waters of Veracruz, Mexico.

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Materials and methods

The materials examined include holdings from the University of Louisiana at Lafayette Zoological Collection, Lafayette, LA (ULLZ) currently being transferred to the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). As that lengthy process is incomplete, both catalog numbers are used (all specimens will be permanently cross-referenced under both numbers at the USNM). Measurements were determined with a calibrated ocular micrometer or dial calipers. Specimen size (± 0.1 mm) is reported as carapace width (cw), measured at the widest point including anterolateral teeth. Ovigerous females (ov) were noted; embryonated egg size was measured as the greatest dimension (± 0.01 mm), and reported as a range for 8 embryonated eggs taken *ad libitum* from two different alcohol-preserved females. For all specimens, the collectors (coll) are indicated and the collection depth is shown in meters (m). Digital color photographs of fresh and preserved 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. GenBank accession numbers, previously published by Thoma *et al*. (2014), are included at the end of the species diagnoses with the addition of the equivalent USNM catalog numbers for the archived source specimens of extracted tissues.

Taxonomy

Superfamily Xanthoidea MacLeay, 1838

Family Panopeidae Ortmann, 1893

Lithopanopeus n. gen.

Type species. *Lithopanopeus truesdalei* **n. sp.**, by present designation.

Diagnosis. Carapace outline ovoid to subhexagonal, length about ¾ greatest width (including lateral extremes of anterolateral teeth, slightly less in large females), fronto-orbital width less than ¾ greatest carapace width, front more than twice width of orbit, with deep median V-shaped notch, laterally forming lobiform tooth; dorsal surface appearing nearly smooth with scattered fine granules, coarser near margins, across front, or where forming rows across anterior carapace regions; areolations weakly marked, separated at most by shallow depressed furrows anteriorly, anterior regions surmounted by elongate ridges of low granules; anterolateral margin with five distinct anterolateral teeth (counting as first the outer orbital), second anterolateral tooth rounded subtriangular to lobiform, partially coalesced to first tooth, third and fourth teeth subtriangular, acute to subacute tips directed anteriorly to anterolaterally, fifth tooth smallest, distinctly developed, subtriangular; lacking subhepatic tubercle below margin. Eyestalk short, ending in globular cornea about width of eyestalk shaft. Distalmost article of antennal peduncle elongate, rectangular in outline, reaching to and filling orbit hiatus. Chelipeds unequal, dorsal surface finely granulate with some enlarged granules in short rows and ridges; carpus dorsal surface irregular, distal furrow extending from superior to distolateral surface, deeply depressed, inner corner marked by enlarged blunt, distally directed tooth; propodus upper surface weakly convex longitudinally, granulation slightly coarser, some in short transverse rows dorsally, weakly defined broken dorsal furrow between very low to obsolete longitudinal ridge to internal side and stronger rounded longitudinal ridge to external side; major chela dactylus opposable margin bearing enlarged, lobiform, basal tooth. Ambulatory pereopod merus, carpus, and propodus superior margin bearing narrow tract of subacute granules or small tubercles, superior margin of merus including row of long, closely set, plumose, feathery setae, these less dense on more distal articles, distalmost articles bearing broad tracks of very short, densely plumose setae on margins, densest on inferior and especially superior surface of dactylus; dactylar-propodal locking mechanism not developed, dactyl inferior margin lacking calcareous prehensile tooth. Male thoracic sternum length from apex to suture between fourth and fifth sternites (measured at edge of pleon near or exceeding 0.7 greatest width of fourth sternite (including episternites), sternopleonal cavity in fourth sternite not sculpted or excavate to accommodate first gonopod tips; fifth sternite with granulate press button to each side of sternopleonal cavity; male pleonal margins

thick, reflected toward thoracic sternum, edges appearing heavy, press-button depression deep, thick; third to fifth somites of male pleon fused, second somite spanning almost full width of sternum, narrow tract of eighth sternite exposed between lateral margin and condyle of fifth pereopod coxa, third somite about 1.2 width of second, lateral flange reaching to base of fifth peropod condyle. Male first gonopod tip of modified trifid panopeid form, sternomesial side of trunk lined by heavy teeth in distal half and subterminally with broad, acute, bladelike subterminal tooth. Male second gonopod less than 1/3 length of first. Female gonopore (including opening and surrounding lips or vulva) centered in anterior half of sixth thoracic sternite, in spanning more than half of sixth thoracic sternite adjacent length.

Etymology. The generic name *Lithopanopeus* merges the prefix "litho", for its rocky habitat, with the suffix "panopeus", derived from the type genus of Panopeidae. The gender is masculine. The few known specimens all have been found in association with calcareous intertidal rocks eroded by burrowing molluscs and sipunculan worms. Appropriately, the species bears close general resemblance to a number of other small panopeid crabs.

Assigned species. *Lithopanopeus truesdalei* **n. gen., n. sp.** (monotypic)

Lithopanopeus truesdalei n. gen., n. sp.

(Figs 1A–I; 2A–J; 3A–D; 4A, B)

Hexapanopeus nov. sp.—Thoma *et al.* 2009: 554, table 2, 558, fig. 1, 559, fig. 2, 560.
Nov. gen. nov. sp. near *Acantholobulus schmitti*.—Thoma *et al.* 2014: 92, fig. 1.
Gen. nov., sp. nov. near *A. schmitti*.—Thoma *et al.* 2014: 90, table 1, 98.

Type material. Holotype (northwestern Gulf of Mexico): male, cw 9.6 mm, eroded wave-washed limestone rocks among larger granite boulders of north jetty, Brazos Santiago Inlet, South Padre Island, Texas, 26° 04.044′ N, 97° 09.229′ W, < 1 m, 28 May 1979, coll D.L. Felder & J.W. Martin, USNM 1611097 (= ULLZ 17919, photograph voucher). Paratypes (northwestern Gulf of Mexico): 1 ov female, cw 8.9 mm, collection data same as for holotype, USNM 1611098 (= ULLZ 18400); 1 ov female, cw 9.3 mm, collection data same as for holotype, USNM 1611099 (= ULLZ 18401); 2 males, cw 4.4, 5.6 mm, 1 female, cw 6.0 mm, collection site and setting same as for holotype, 12 January 1998, coll D.L. Felder, USNM 1543794 (= ULLZ 8646, genetic vouchers). Paratype (southwestern Gulf of Mexico): male, cw 6.3 mm, eroded wave-washed rocky ledge with old sabellarid worm accumulations off beach at Playa de la Mancha, Veracruz, Mexico, 19° 35.821′ N, 96° 22.446′ W, < 1 m, 2 July 2002, coll. D.L. Felder, T.M. Rodriguez, & R. Robles, USNM 1541468 (= ULLZ 6447, photograph voucher).

Diagnosis. Carapace weakly convex, ovoid to weakly subhexagonal in outline, length about 0.75 greatest width (including anterolateral teeth), fronto-orbital width about 0.6 carapace width; front with single margin, not bimarginate, with distinct median V-shaped notch, lateral corner forming lobiform tooth; dorsal regions weakly defined, sparsely setose, transverse rows of granules marking most raised surfaces; five anterolateral teeth, angular first and lobiform second teeth distinctly separated by shallow sinus, fifth tooth small but distinct, acute to subacute; lower posterolateral margin and posteroventral branchiostegite with cover of elongate, feathery, plumose setae. Third maxilliped merus distal margin sinuous, produced mesially to form distinctly raised prominence near articulation with carpus. Cheliped merus without enlarged marginal teeth or spines; carpus superior and lateral surfaces covered by rounded to subacute granules, some forming rows or surmounting elevations, supero-external surface with distinctly depressed distal groove parallel to distal margin, groove proximally bordered by two tuberculiform elevations and less prominent granular ridges of supero-external surface, carpus with proximal internal angle low, rounded, distal angle forming blunt, distally directed tooth. Major chela propodus mostly smooth, superior longitudinal crest bordered by broadly depressed supero-external furrow and weak internal furrow defined by longitudinal row of slight depressions in fine granulation, upper external surface of palm with few rows of granules arranged in short diagonal to vertical lines below supero-external furrow. Ambulatory pereopods 2–4 relatively short, merus length about 0.5 carapace length; all ambulatory pereopods with merus superior margin lined by conspicuous elongate plumose setae; propodus superior margin with cover of short plumose setae forming dense pubescence, most developed on posteriormost pereopods, dactylar-propodal locking mechanism not developed; dactyl inferior margin lacking subterminal, prehensile tooth, inferior and superior margins densely covered by short plumose setae forming broad tract of thick pubescence, setal cover of dactylus least in pereopod 2, most in pereopod 5. Male thoracic sternum length from apex to suture between fourth and fifth sternites (measured at edge of pleon) 0.70–0.74 times

greatest width of fourth sternite (including episternites), eighth sternite exposed only as narrow gap between lateral margin of flexed second pleonite and condyle of fifth pereopod coxa. Pleon of male with third through fifth somites fused, telson subtriangularly rounded, widest in proximal third. Male first gonopod tip obscurely trifid, trunk distal half with longitudinal row of very heavy, broad, subacute teeth on sternomesial side, row ending short of acute distal process forming bladelike subterminal tooth. Male second gonopod less than one-third length of first gonopod. Female gonopore (including opening and surrounding lips or vulva) centered on anterior half of sixth sternite, opening broadly crescentic. Applicable GenBank sequence accession numbers from Thoma *et al.* (2014) are as follow for ULLZ 8646 (paratype) = USNM 1543794: (12S) EU863295; (16S) EU863361; (COI) KF682761; (ENO) KF682684; (H3) KF682563.

Description. Carapace (Figs 1A, B; 3A; 4A, B) very weakly convex, distinctly wider than long, frontal width about 0.55 fronto-orbital width, fronto-orbital width about 0.6 greatest carapace width, dorsal outline subovoid to weakly subhexagonal, dorsal regions weakly defined by shallow grooves, strongest anteriorly near margins, most raised surfaces marked by a transverse ridge of small granules, sometimes with few setae along lines, ridges strongest on protogastric, hepatic, and branchial regions, surface otherwise appearing mostly smooth with low cover of small granules, densest and largest near margins; front bilobed, separated by distinctly V-shaped median fissure, lobes broadly convex, single edge of low granules forming margin, lateral tooth distinct, lobiform, terminated laterally at antennal sinus below mesial end of supraorbital margin; supraorbital margin granulate, forming distinct tooth above antennal sinus, median and lateral fissures forming distinct breaks in marginal granulation, margin slightly convex between fissures. Anterolateral teeth well developed along distinctly convex arch of margin, first (outer orbital) acutely angular, separated by distinct sinus from lobiform second; third and fourth broadly triangular, margins granulate, sharply angular tips, tip of fourth more acute than third; fifth tooth distinctly developed though much smaller than preceding, tip acute to subacute. Posterolateral margin marked by broken line of small granules above dense field of feathery plumose setae. Pterygostomial and subhepatic regions (Fig. 1B) with scattered low granules, coarsest near margins, lacking subhepatic tubercle, pterygostomial ridge slightly raised, granulate. Branchiostegite posterolaterally with dense cover of elongate, feathery, plumose setae, extending to and fully concealing ventrolateral margin above coxae of ambulatory legs.

Eyestalk stout, bulbous basally, anterior crest granulate, slightly raised to form short, granulate precorneal crest. Antenna with long flagellum, peduncle with distalmost fused basal article elongate, rectangular, extending into orbital fossa, article proximally separated from parallel margin of suborbital carapace by small ossicle inserted distal to operculum of nephridiopore.

Third maxilliped (Fig. 1B–D) protopod elongate, narrowing laterally, distal surface grooved to intersect ventral edge of carapace, bearing two unequal projections along margin internal to groove, proximal to tight bundle of lamellae forming small podobranch gill positioned above pair of much longer, lamellate, arthrobranch gills. Epipod thin, flattened, strap-like, bearing long simple setae along length. Endopod basis subtriangular; ischium broadly subrectangular, proximal end curved laterally to intersect suture with basis, external surface mostly smooth, weak longitudinal furrow medially, mesial margin with fringe of simple setae; merus subquadrate, lateral margin near straight to very weakly concave, distolateral margin rounded, distal margin sinuous, weakly convex laterally, produced mesially to form distinctly raised tooth-like prominence near articulation with carpus, distomesial corner obliquely excavate to accommodate articulation of carpus; carpus subcylindrical, internal surface with distal submarginal field and distal fringe of elongate stiff setae overlying propodus; propodus cylindrical, internal surface distally with submarginal and distal rows of elongate, stiff setae; dactlyus subcylindrical to coniform, tapering distally, length about 1.3 to 1.4 times that of propodus, inferior margin with few tufts of short, fine setae, tip bearing dense tuft of long stiff setae exceeding length of dactylus. Exopod subrectangularly elongate, slightly narrowing distally, comparatively short, stout, internal edge of mesial margin produced to form strong rounded subtriangular projection in distal third, small tuft of plumose setae distally at articulation of flagellum, flagellum multi-articulate, bearing numerous long, distally directed setae.

Chelipeds (first pereopods) (Figs 1E–I) unequal, sparsely setose over most surfaces except for some margins of merus and carpus, fields of subacute granules on superior and supero-external surfaces of carpus and propodus, some congregated into lines and low ridges or surmounting elevations to form granular tubercles; ischium and merus with line of plumose setae adjacent to tracts of low rounded granules along inner margins, granules extending as fields onto inferior surfaces; merus superolateral margins similarly lined by plumose setae and closely set blunt granules that extend as field onto lateral surface, margin lacking enlarged teeth or spines; carpus superior and lateral

surfaces densely covered by rounded to subacute granules, slightly larger of which form variably defined lines and ridges or surmount elevations, supero-external surface marked by distinct groove parallel to distal margin, proximal to which are two elevated granular tubercles and lower granular ridges of supero-external surface, internal margin with proximal angle low, rounded, unarmed, distal angle much stronger, produced to form heavy, blunt, somewhat distally directed tooth, distal to which margin is defined by tract of slightly enlarged granules.

Major chela propodus mostly smooth to microgranulate, superior longitudinal rounded crest well defined between broadly depressed supero-external furrow and weakly defined internal furrow, the latter marked primarily by longitudinal line of dimples or depressions in fine granulation; coarsest granules atop condyle at proximal end on superior crest and on proximo-superior external surface of palm where some arranged in short diagonal to near vertical lines below supero-external furrow; fixed finger of major chela short, subtriangular, inferior margin weakly sinuous, tip curved upwards, opposable margin bearing three to four prominent subtriangular to rounded teeth with smaller subacute teeth between, largest tooth centered just proximal to midlength, row of teeth set between shallow grooves bearing few setal punctae to internal and external sides; dactylus arched, slightly longer than fixed finger, opposable margin with strong, lobiform, enlarged basal tooth proximally, distally with four somewhat rounded teeth separated by smaller denticles, subacute tip strongly curved to cross to internal side of fixed finger tip when flexed.

Minor cheliped propodus similar to that of major, including in form and granlation of superior longitudinal crest bordered by broadly depressed supero-external furrow and weak internal longitudinal furrow marked by series of weakly defined depressions in fine granulation; fixed finger of minor chela basally narrower than that of major, opposable margin with five enlarged subtriangular teeth; dactylus of minor chela appearing slightly more elongate, less arched than that of major, longer than fixed finger, opposable margin lacking enlarged basal lobiform tooth, cutting edge dentition weaker than in major chela, consisting of five or six low, broadly rounded, subtriangular teeth, subacute tip crossing to internal side of fixed finger tip when flexed.

Ambulatory pereopods 2–5 relatively short, robust, all of similar in general form (Fig. 2A–D), merus length in each less than three times greatest width; pereopods 2–4 subequal in size, length of meri 0.48–0.54 carapace length; pereopod 5 smaller, with relatively shorter merus near 0.4 carapace length, relatively broader, more flattened propodus; ambulatory pereopod meri all with superior margin lined by broken row of low, dentiform granules variably concealed by row of elongate, plumose setae, distal superior margin ending in low, blunt angle beyond subdistal notch, inferior margin finely granulate, at most with few long simple or plumose setae; carpus superior margin with scattered long and short setae, some plumose, along surmounted by granules, ridge roughly parallel to second ridge on superoposterior surface, sulcus between ridges shallow; propodus superior margin weakly granulate, bearing several long plumose setae and much denser, broader cover of short plumose setae forming dense pubescence, most so distally, densest and most broadly developed on posteriormost pereopods, inferior margin with similar setation as superior, less developed in pereopods 2 and 3 than in pereopods 4 and 5, the latter similarly pubescent on both margins; dactylar-propodal locking mechanism not developed; dactylus stout proximally, narrowing in distal half to weakly falciform corneous tip, inferior margin lacking subterminal, calcareous, pehensile tooth, inferior and superior margins with scattered long simple or plumose setae, more densely covered by short plumose setae forming broad tract of thick pubescence, pubescence of dactylus ranging from least in pereopod 2 to most in pereopod 5.

Thoracic sternum of male (Fig. 2E) broader than long, length from acute anterior apex to suture between fourth and fifth sternites (measured at edge of pleon) 0.70–0.74 times greatest width of fourth sternite (including episternites), sternopleonal depression in fourth sternite not unusually sculpted or excavate to accommodate first gonopod tips below flexed pleon; fifth sternite with granulate press button to each side of sternopleonal depression; fourth and fifth episternites narrowly angular, terminally subacute posteriorly, sixth episternite slightly broader and subacute posteriorly, seventh broadly rounded posteriorly, eighth sternite exposed only as narrow gap between lateral margin of flexed second pleonite and condyle pereopod 5 coxa.

Pleon of male (Fig. 2E, F) with third through fifth somites fused, first somite widest at articulation with carapace, rounded to articulation with second somite; second somite widest proximally near articulation with first somite, narrowing distally; fused third through fifth somites widest at lateral flange of third, weakly sinuous laterally, narrowing distally, width at articulation with sixth somite about half that at wide flange of third, sutures between fused somites obscure: sixth somite subrectangular, slightly broadened distally near articulation with telson subtriangularly rounded, widest in proximal third. Pleon of female (Fig. 3D) with first somite narrowing distally, margins distinctly convex, second somite widening distally, margins concave; third with convex margins, widening distally, lengths of third through sixth somites incrementally increasing, telson exceeding length of sixth; fourth somite wid-

est though third very nearly as wide, widths of fourth through sixth somites decreasing, all with convex lateral margins, sixth much wider than telson greatest width, telson subtriangular, terminally rounded, length about 2/3 width.

Male first gonopod tip (Fig. 2G–I) of modified panopeid form, obscurely trifid, trunk in distal half of sternomesial side bearing longitudinal row of very heavy, broad, subacute teeth, row ending well short of larger acute distal process forming bladelike, somewhat flattened, weakly hooked subterminal tooth, distal third of abdomino-lateral margin bearing longitudinal row of smaller subacute teeth. Male second gonopod less than one-third length of first gonopod, terminating in simple spiniform tip (Fig. 2J). Female gonopore (including opening and vulvar cover) (Fig. 3C) large, centered on anterior half of subpleonal sixth sternite, occupying most of sixth thoracic sternite length, gonopore opening broadly crescentic, slightly raised convex lip defining lateral concave opening of pore.

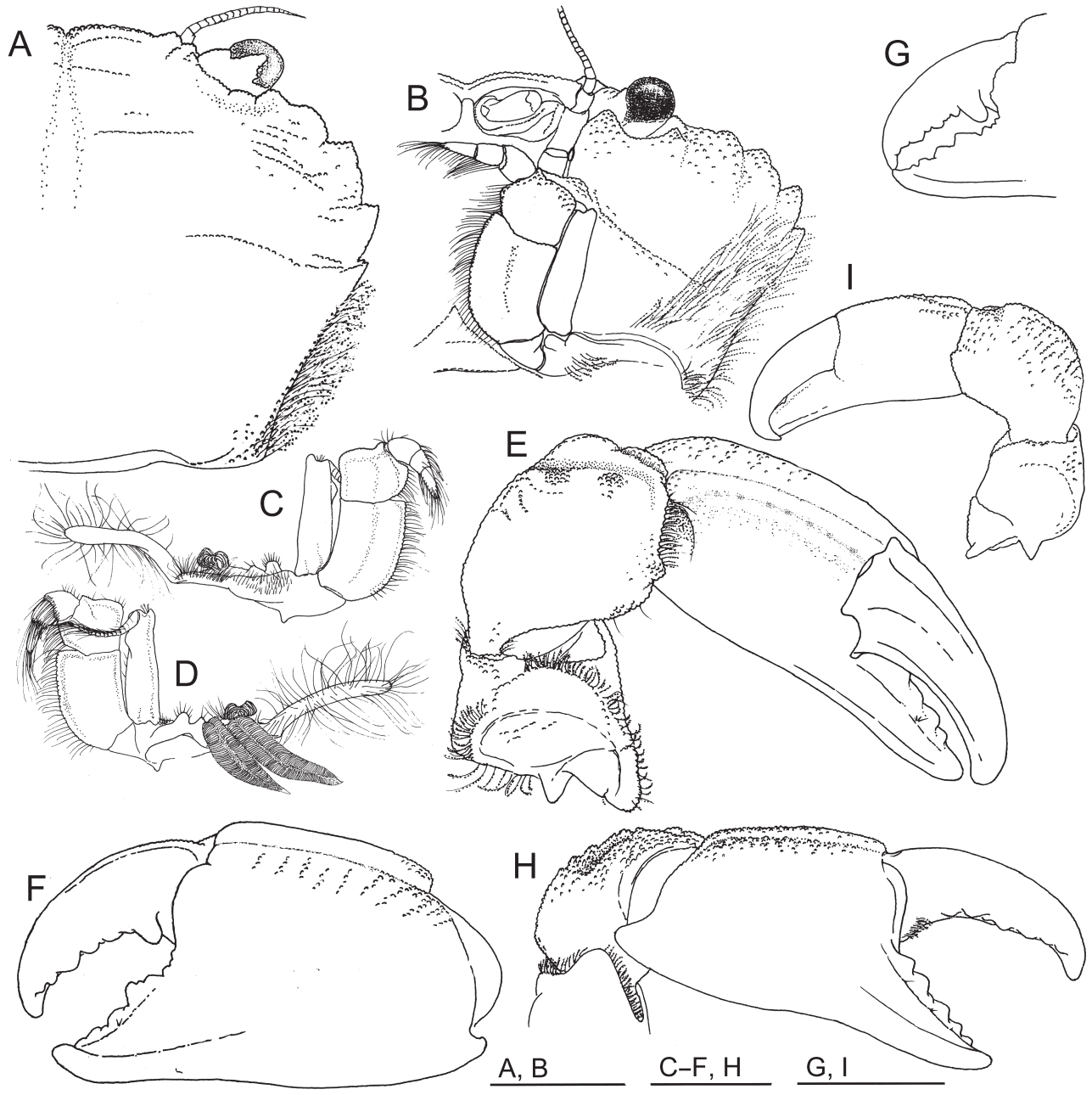

FIGURE 1. *Lithopanopeus truesdalei* **n. gen., n. sp.**, male holotype (USNM 1611097 = ULLZ 17919) A–F, H; male paratype (USNM 1541468 = ULLZ 6447) G, I. A, right side of carapace, dorsal surface; B, left side of carapace, ventral surface; C, right third maxilliped detached, external surface, (arthrobranch gill pair not shown); D, right third maxilliped detached, internal surface; E., major (left) cheliped, supero-internal surface; F, major (left) chela, external surface; G, major (left) chela fingers, external surface; H, minor (right) cheliped, infero-external surface; I, minor (right) cheliped, supero-internal surface. Scale bars = 2.0 mm.

Color. The highly variable color patterns, where known for fresh specimens, overall range from densely mottled reddish brown overlying off white to large unbroken areas of orange on the carapace (Fig. 4A, B). Upper surfaces of the cheliped palms vary from mostly off white to broken reddish brown above, the latter sometimes with a pair of large, solid, darker spots on the supero-internal surface of the palm. Fingers of the chelae vary from pale horn to brown. The merus of the ambulatory legs may have a near solid or broken band of white marking the distal quarter, while the distal half of propodus and dactylus are typically of lighter coloration that more proximal articles.

Etymology. The species name is assigned in recognition of Frank M. Truesdale for his many contributions to crustacean biology through his personal research and training of students, but also in gratitude for many years of supportive assistance and collaborations with DLF and his students. In addition to his renowned compilations on the history of carcinological research, his special expertise in the rearing of decapod larvae has contributed substantially to understanding of decapod crustacean life histories, including those of panopeid crabs.

Size. Carapace widths ranged from 4.4 mm in the smallest male paratype to 9.6 mm in the male holotype. The largest female was one of two ovigerous specimens, 9.3 mm in carapace width. Embryonated eggs (most showing eyespots) in sampled clutches of alcohol-preserved ovigerous females ranged from 0.33 to 0.39 mm in greatest dimension.

Distribution. Brazos Santiago Inlet in extreme south Texas and a natural rocky shoreline platform along Playa de la Mancha, Veracruz, Mexico.

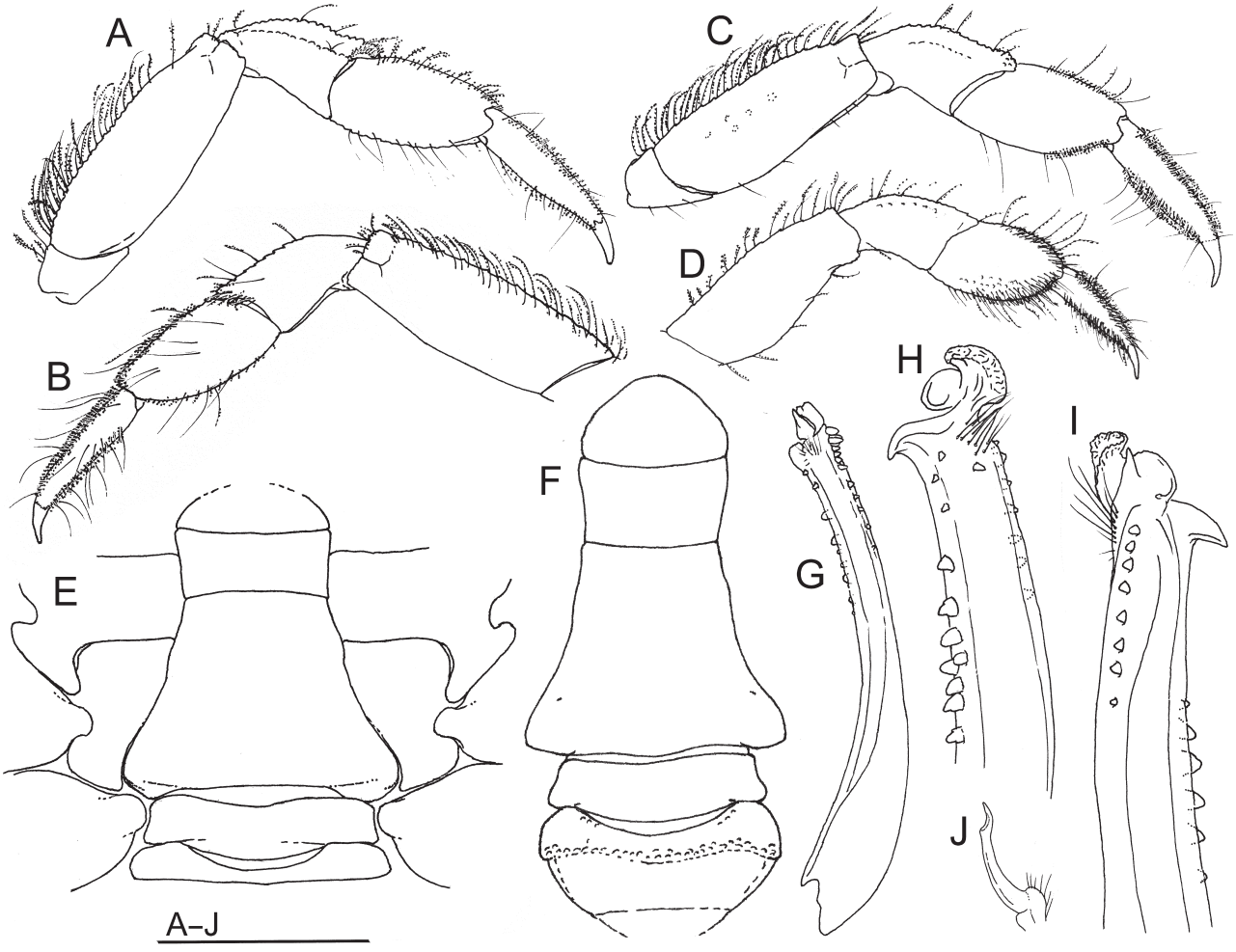

FIGURE 2. *Lithopanopeus truesdalei* **n. gen., n. sp.**, male holotype (USNM 1611097 = ULLZ 17919) A–C, E–I; male paratype (USNM 1541468 = ULLZ 6447) D, J. A, right second pereopod, upper surface; B, right third pereopod, lower surface; C, right fourth pereopod, upper surface; D, right fifth pereopod, upper surface; E, pleon, sternum, and pereopod coxae, posteroventral surfaces; F, pleon disarticulated; G, right first gonopod, lateral surface; H, right first gonopod, sternal surface; I, right first gonopod, abdomino-mesial surface; J, right second gonopod, pleonal surface. Scale bar = 3.0 mm (A–C); 2.0 mm (D–F); 1.0 mm (G, J); 0.5 mm (H, I).

Habitat. Thus far known only from intertidal to shallow subtidal wave-washed rocky substrates (0–1 m depth), including man-made jetties, especially from porous rocks eroded by sipunculans, burrowing bivalves, or boring sponges, there among (or in cavities beneath) epibiota dominated by calcareous and fleshy macroalgae, barnacles, or encrusting sponges.

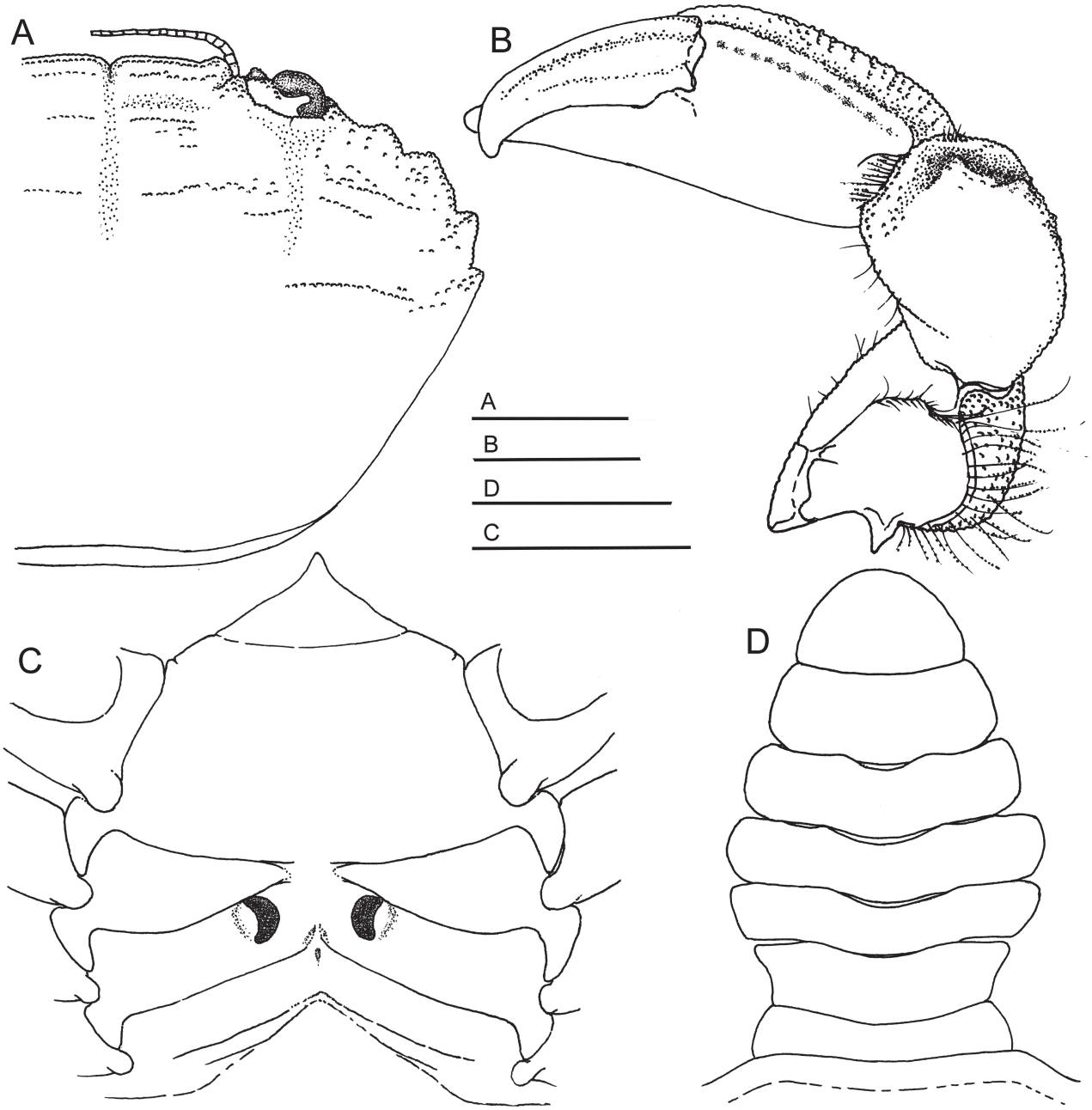

FIGURE 3. *Lithopanopeus truesdalei* **n. gen., n. sp.**, female paratype (USNM 1611099 = ULLZ 18401). A, right side of carapace, dorsal surface (setae not shown); B, major (right) cheliped, supero-internal surface; C, thoracic sternum, pleon lifted away to expose gonopores; D, pleon, external surface. Scale bars = 2.0 mm.

Remarks. Specimens herein assigned to *Lithopanopeus* **n. gen.** have in some previous molecular phylogenetic analyses shown affinities to *Glyptoplax smithii* A. Milne-Edwards, 1880 on the basis of 12S rRNA sequences (Thoma *et al*., 2009: fig. 2) or to *Hexapanopeus* s.s. on the basis of 16S rRNA sequences (Thoma *et al*., 2009: fig. 1). However, neither of those arrangements was well supported in later and much more robust analyses by Thoma *et al.* (2014: fig. 1), where the specimen of *Lithopanopeus* **n. gen.** (therein treated as "gen. nov., sp. nov. near *Acantholobulus schmitti*—ULLZ 8646") was resolved with low Bayesian support as one of three well-separated lineages. Two other lineages formed a modestly supported subclade grouping *Eucratopsis* along with most members of *Pano-*

peus (i.e., *Panopeus* s.s. of Thoma, *et al.* 2014) and a well-supported subclade grouping of several (though not all) species currently assigned to *Eurypanopeus*. Other than for this basal grouping, there was no significant support for close genetic relationship between the specimen of *Lithopanopeus* **n. gen.** and any of the three genera represented in these topologically joined subclades.

Morphologically, all members of *Panopeus* s.s. have a similar male first gonopod tip of a familiar trifid panopeid form with three divergent, clearly separated terminal processes, this feature also being shared with *Eucratopsis* as well as some other panopeid genera (see Martin & Abele 1986). In contrast, the three members of *Eurypanopeus* that were grouped into an adjacent subclade (*E. planissimus*, *E. abbreviatus*, and *E. ater*) share a male first gonopod tip of modified panopeid form with less pronounced separation of three terminal processes, perhaps expected given shallow lobiform to subquadrate anterolateral teeth that differ strikingly from those in both *Panopeus* s.s, and members of *Eurypanopeus*, as well as *Lithopanopeus* **n. gen.** The terminal configuration of the male first gonopod in *Lithopanopeus* **n. gen.** is of yet another highly modified panopeid form, but the gonopod trunk is also armed by a unique row of strikingly large teeth along much of its sternomesial margin, a feature found in no other known panopeid genus. While the general habitus of *Lithopanopeus* **n. gen.** resembles that in some species of *Glyptoplax*, *Hexapanopeus*, and *Acantholobulus*, this character of the first gonopod trunk, along with striking differences in its terminal configuration, readily distinguishes it from all known members of these genera (see Martin & Abele 1986; Felder & Martin 2003).

So far as known, the habitat of *Lithopanopeus truesdalei* **n. gen., n. sp.**, is restricted to eroded rocky or other hard substrates of intertidal and shallow subtidal warm-temperate to tropical waters of the western Gulf of Mexico, particularly where date mussels identified as *Leiosolenus bisulcatus* (d'Orbigny, 1853) (Mytilidae), sipunculans assignable to *Antillesoma antillarum* (Grube & Oersted, 1858) (Phascolosomatidae) and unidentified boring sponges have heavily eroded limestone or other penetrable substrates. While it is unknown whether the association of *L. truesdalei* **n. gen, n. sp.** with these burrowers is to any degree obligate, most specimens of this new species were taken from cavities abandoned or occupied by these burrowers beneath epibiota covering rock surfaces. Other small panopeid crab species broken from such porous jetty rocks at Brazos Santiago, Texas, where the sampled substrates were limestone rocks serving as fill between large granite boulders, included *Acantholobulus bermudensis* and *Hexapanopeus paulensis* Rathbun, 1930, along with occasional juvenile specimens of *Eurypanopeus ater* Rathbun, 1930 (though the latter were more commonly found as adults burrowed beneath shoreward intertidal stones on sand). Small non-panopeid brachyurans also broken from these cavities or found to occupy lower strata of overlying epibiota included *Pseudomedaeus agassizii* (A. Milne-Edwards, 1880) (Xanthidae), *Pilumnus dasypodus* Kingsley, 1879, *Pilumnus pannosus* Rathbun, 1896 (Pilumnidae), and juveniles of *Menippe adina* Williams & Felder, 1986 (Menippidae). Other small brachyurans that were usually more broadly distributed and less commonly found in this microhabitat were the majoid *Acanthonyx petiverii* H. Milne Edwards, 1834 (Epialtidae) along with the grapsoids *Pachygrapsus gracilis* (de Saussure, 1858) and *Pachygrapsus transversus* (Gibbes, 1850) (Grapsidae).

Given that *Lithopanopeus truesdalei* **n. gen., n. sp.** occurs in shoreline habitats that have been the subject of varied regional surveys since the 1930s (for example, Whitten *et al.* 1950) it may seem remarkable that this species has gone unreported to date, which thus suggests it could possibly represent a recent introduction. While we cannot exclude this possibility, the species has clearly been established in south Texas for over four decades, and has over that time period remained a minor but persistent component of the assemblage of small brachyurans that populates fouled shoreline hard substrates of anthropogenic origin. More probable than an introduction, we suspect the species colonized south Texas rock jetties that were maintained over the last century to buttress margins of inlets along what are otherwise uninterrupted sandy beaches that line almost all of the Texas shoreline. As the species also occurs further to the south on natural rocky ledges at Playa de la Mancha, Veracruz, Mexico, northbound longshore currents could easily have provided larval recruits to the more northerly jetties. As to why this xanthoid was not previously recognized at either extreme of the range, specimens from western Gulf of Mexico shoreline waters of south Texas and northeastern Mexico were not well represented in Rathbun (1930), and little other contemporary taxonomic expertise was focused on small xanthoid crabs of hard substrates. For example, the sympatric and now regionally familiar *Acantholobulus bermudensis* was not reported from the northwestern Gulf of Mexico until tentative identification by Felder (1973), that report being from a commonly sampled rock jetty fronting on long-establish marine laboratory. When the identity was later confirmed by synoptic comparison to the type (DLF, 1974), a single prior collection was found to have been taken from Texas in 1966 (USNM 113636) and identified by H.B. Roberts, though never published. The species is, however, now widely documented from throughout appropriate habitats in coastal waters of the Gulf of Mexico (Felder & Martin 2003; Felder *et al*. 2009). Most likely it was overlooked or unrecognized in the course of early studies, much as in the case of present newly described species.

Among its ecological associates, *Lithopanopeus truesdalei* **n. gen., n. sp.** most resembles *A. bermudensis* in habitus, especially in terms of general carapace surface appearance and proportions, relative pereopod lengths and weights, presence of a distal furrow on the cheliped carpus, and (typically) presence of a lobiform basal tooth on the dactylus of the major chela. While differences in color for some specimens originally suggested that a second species was mixed among collections thought to all represent *A. bermudensis*, the ranges of color variation in the two species, as now understood, are too great for color-based separations. However, distinguishing males of *L. truesdalei* **n. gen., n. sp.** is, as previously noted, easily based on the unique heavy dentition of its first gonopod trunk**,** as well as its lack of the distinctive thorny median lobe of the of the gonopod tip found in *A. bermudensis*, diagnostic for members of the latter genus (Felder & Martin 2003). Additionally, specimens of either sex for these species can be distinguished by the degree of separation between the first and second anterolateral teeth. In *L. truesdalei* **n. gen., n. sp.** the first tooth (outer orbital angle) is separated from the lobiform second tooth by a distinct sinus, much deeper than the shallow to all but absent depression in *A. bermudensis*, which usually has these teeth closely merged if not all but entirely fused. Furthermore, the carapace front in *A. bermudensis* is typically bimarginate, not the case in *L. truesdalei* **n. gen., n. sp.** The species can also be distinguished by upper surface sculpture of the cheliped carpus, which in *L. truesdalei* **n. gen., n. sp.** has a variably defined pair of tuberculiform elevations aligned along the proximal limits of the distal furrow, these being absent from the proximal border of the furrow in *A. bermudensis*.

Characters other than the distinctive male first gonopods also separate the often sympatric panopeid *Hexapanopeus paulensis* from *L. truesdalei* **n. gen., n. sp.,** even though both have the sinus between the first and second anterolateral teeth well-defined, a distal furrow present on the cheliped carpus, and a lobiform basal tooth on the dactylus of the chela. In *H. paulensis*, the second anterolateral tooth is typically more angular than lobiform and the carpus of the cheliped very uniquely has 8–15 tubercles on its upper surface proximal to the distal furrow (Williams 1965, 1984).

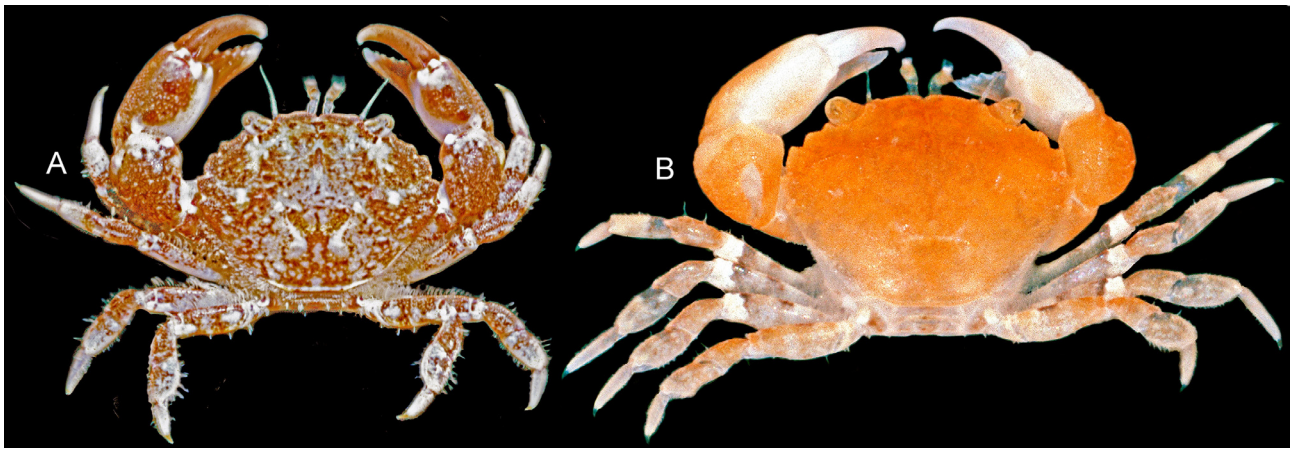

FIGURE 4. *Lithopanopeus truesdalei* **n. gen., n. sp.** A, male holotype (USNM 1611097 = ULLZ 17919) cw 9.6 mm, northwestern Gulf of Mexico; B, juvenile male paratype (USNM 1541468 = ULLZ 6447) cw 6.3 mm, southwestern Gulf of Mexico.

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