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LEPIDOPHTHALMUS MANNINGI, A NEW GHOST SHRIMP FROM THE SOUTHWESTERN GULF OF MEXICO (DECAPODA: THALASSINIDEA: CALLIANASSIDAE)

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ABSTRACT

Lepidophthalmus manningi, new species, is described from intertidal and shallow subtidal margins of estuarine embayments, ephemeral tidal ponds, and river mouths in the states of Veracruz, Tabasco, and Campeche, eastern Mexico. This apparent endemic of the southwestern Gulf of Mexico is ornamented by conspicuous sclerotized plates on ventral surfaces of the abdomen, a feature it shares with several other tropically distributed species in the western Atlantic and eastern Pacific. *Lepidophthalmus manningi* is very close in morphology to the recently described *L. richardi* from Belize, its apparent sibling, but can be distinguished by unique features in sculpture and shape of not only the ventral abdominal plating, but also in structures such as the eye tubercles, major chelipeds, and the anterior two pleopod pairs, dorsal abdominal tergites, and the uropods. It is readily distinguishable from two other Gulf of Mexico species, both of which lack ventral sclerotized plates on the abdomen. The latter include the widely distributed warm-temperate species, *L. louisianensis*, which ranges throughout the northern Gulf of Mexico and into Tamaulipas, Mexico, and a second southwestern Gulf endemic form that remains undescribed and is currently under study. Disjuncture of appropriate habitats in the northern Yucatan Peninsula and limited dispersal ability in the genus appear to account for isolation of *L. manningi* from its Caribbean sibling.

In the course of revising callianassid genera of the Americas (Manning and Felder, 1991), some characters formerly ascribed to separate American species within the broadly applied genus *Callianassa* s.l. (= *sensu lato*), were found to be of generic significance. The genus *Callianassa* Leach, 1814, was restricted to *C. subterranea* (Montagu, 1808) and *C. subterranea australis* Kensley, 1974, from the eastern Atlantic, while the American species were all assigned to alternative genera. Subsequent examinations of the American callianassids composing those genera have in turn revealed a host of characters for use in further systematic subdivisions of these taxa, and have led to the discovery of a remarkable number of undescribed species in American waters, many of these within the highly endemized genus *Lepidophthalmus* Holmes, 1904 (Lemaitre and Rodrigues, 1991; Felder and Rodrigues, 1993; Felder and Manning, 1997, 1998).

Among western Atlantic members of *Lepidophthalmus*, it appeared that tropically distributed species tended to have dense patterns of ventral sclerites on anterior somites of the abdomen, while antitropically distributed warm-temperate species tended to lack this armor (Felder and Manning, 1997, 1998). Within the western Gulf of Mexico, distribution of the unarmored northern Gulf endemic, *L. louisianensis* (Schmitt, 1935), extends south to estuaries of Tamaulipas, Mexico (Felder and Rodrigues, 1993). However, sampling in more southerly tropical estuaries in the states of Veracruz, Tabasco, and Campeche have revealed two additional forms, one of which is ventrally armored and the other of which is not. Both are apparently endemic to coastal estuaries of the southwestern Gulf of Mexico where they commonly occur in sympatry. Affinities of the ventrally unarmored form remain to be resolved, and are currently under study by comparative allozyme and morphological analyses (Staton *et al.*, 2000; Felder, in preparation); the ventrally armored form is the subject of the present work.

The ventrally plated Mexican populations are very similar in morphology to *L. richardi* Felder and Manning, 1997, from Belize and were initially thought to represent additional

materials of that species. However, members of this genus generally prefer muddy or highly organic oligohaline habitats uncommon in Yucatan and exhibit abbreviated larval development with limited dispersal, favoring estuarine retention of larvae (Felder *et al.*, 1986; Nates *et al.*, 1997; Nates and Felder, 1998, 1999). Throughout semiarid northern Yucatan, coastal transitions between calcareous platform shorelines, extensive hypersaline lagoon systems, and high-energy beach environments provide little in the way of colonizable habitat, especially for larvae with such a brief planktonic history as those of *Lepidophthalmus*. Strong west and northwest bound coastal current patterns of the Yucatan Straits also potentially contribute to isolation of these two closely related populations. Thus, disjuncture of these populations across the northern peninsula seemed likely, which led us to undertake careful comparisons between them. The present paper describes the ventrally armored population from the southwestern Gulf as *L. manningi*, new species, and documents morphological differences between the sibling populations. Characters for distinction of the new species from all known western Atlantic and eastern Pacific congeners are also provided.

Materials and Methods

Material examined is listed by location followed by date, collector, number of specimens by sex and condition (ovigerous = ov; mutilated = mutl), size (in parenthesis, when given), and museum catalog number. Notations also indicate those specimens that were used as subjects for line illustrations in the text figures and those that were archived as voucher specimens for 35-mm color photographic slides (used herein as source materials for color descriptions) or genetic tissue extractions (for analyses in Staton *et al.*, 2000, or other ongoing projects) prior to preservation. Size is expressed as postorbital carapace length (CL) or total length (TL) measured in millimeters (mm), both of which exclude the rostrum. Materials, including the holotype male and the illustrated paratype female, along with a number of additional paratypes, have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); additional paratype males and females from all three Mexican states have been deposited in the Colección Nacional de Crustáceos, Instituto de Biología (CNCR-IB) of the Universidad Nacional Autonoma de México (UNAM) and zoological collections of the University of Louisiana- Lafayette (ULLZ, formerly USLZ). Holdings of the USNM and ULLZ were the source for comparative materials of *L. louisianensis* from the Gulf of Mexico; *L. richardi* Felder and Manning, 1997, from Belize; *L. jamaicense* (Schmitt, 1935) from Jamaica and Tobago; *L. sinuensis* Lemaitre and Rodrigues, 1991, from Colombia; and *L. siriboia* Felder and Rodrigues, 1993, from Brazil, as well as most examples of congeneric populations from the eastern Pacific. Comparison was made to the male holotype of *L. bocourti* (A. Milne Edwards, 1870) lent to us from the Muséum national d'Histoire naturelle, Paris (MNHN Th. 64). What are most likely the eastern Pacific type specimens of *L. eiseni* Holmes, 1904, were obtained for examination from the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ 4370).

Lepidophthalmus Holmes, 1904 (For diagnosis, see Manning and Felder, 1991) ***Lepidophthalmus manningi***, new species Figs. 1 a–j, 2 a–s

Lepidophthalmus spp.—Staton *et al.*, 2000: figs. 1, 2, table 1.

Lepidophthalmus sp. "a".—Staton *et al.*, 2000: 161–168, fig. 3, tables 3–5.

Material Examined.—HOLOTYPE.—intertidal and shallow subtidal muddy sand adjacent to red mangrove and cordgrass lined banks of Laguna San Augustín, seaward of bridge (Puente San Augustín) near village of Palma Sola on coastal Highway 180 (19°55.23′N; 96°31.85′W), Veracruz, Mexico, 9 February 1999, collected by D. L. Felder, C. F. Gurgel, S. C. Rabalais, and C. D. Schubart, 1 male photographic voucher and illustrated (CL 14.1 mm), USNM 268595.—PARATYPES: same locality, date, and collectors as holotype, 1 male photographic voucher and illustrated (CL 16.1 mm), ULLZ 4032, parts of 8 mutl unsexed dissected for tissue samples, vouchers for genetic studies, ULLZ 4033.—intertidal and shallow subtidal muddy sand of backbeach pond fed by ephemeral runoff between dunes, about 2 km NW of village of Anton Lizardo (19°03.31′N; 96°00.44′W), Veracruz, Mexico, 29 March 1991, collected by D. L. Felder, R. B. Griffis, J. L. Staton, and T. L. Zimmerman, 4 male including 3 illustrated (CL 15.1, 15.4, and 16.1), 2 ov female, UNAM 18571, parts of 32 mutl unsexed including ov, dissected for tissue samples, vouchers for genetic studies, ULLZ 4030; same locality, 10 February 1999, collected by D. L. Felder, C. F. Gurgel, S. C. Rabalais, and C. D. Schubart, 3 female including 1 ov, USNM 268596, parts of 7 unsexed dissected for tissue samples, vouchers for genetic studies, ULLZ 4034.—sandy mud shoreline at low tide extreme at break in dense mangroves lining shoreline, Rio Seco estuary, just W of Puerto Ceiba (18°25.5′N; 93°07.0′W), Tabasco, Mexico, 6 March 1981, collected by D. L. Felder, W. W. Forman, and S. Snatic, 2 male including 1 mutl, 1 photographic voucher (CL 16.5), ULLZ 3998.—shallow subtidal coarse quartzite sand overlying deeper muddy sand and alluvial muddy clay, where shoreline red mangroves cleared for small marina and dock just NE of Puerto Ceiba (18°26.6′N; 93°05.5′W), Tabasco, Mexico, 28 March 1991, collected by D. L. Felder, R. B. Griffis, J. L. Staton, and T. L. Zimmerman, 10 small male, 9 small female including 2 ov, 1 unsexed juvenile, USNM 268597, parts of 8 mutl unsexed including ov, dissected for tissue samples, vouchers for genetic studies, UNAM 18572; same locality, 14 February 1999, collected by D. L. Felder, C. F. Gurgel, S. C. Rabalais, and C. D. Schubart, 1 juv male, ULLZ 4036, parts of 12 unsexed including ov, dissected for tissue samples, vouchers for genetic studies, ULLZ 4035.—sandy mud flat largely exposed at low tide among partially cleared red mangroves and stilted huts, east bank of Rio San Pedro, just upstream from mouth and seaward of Highway 180 bridge, village of Nuevo Campechito (18°34.85′N;

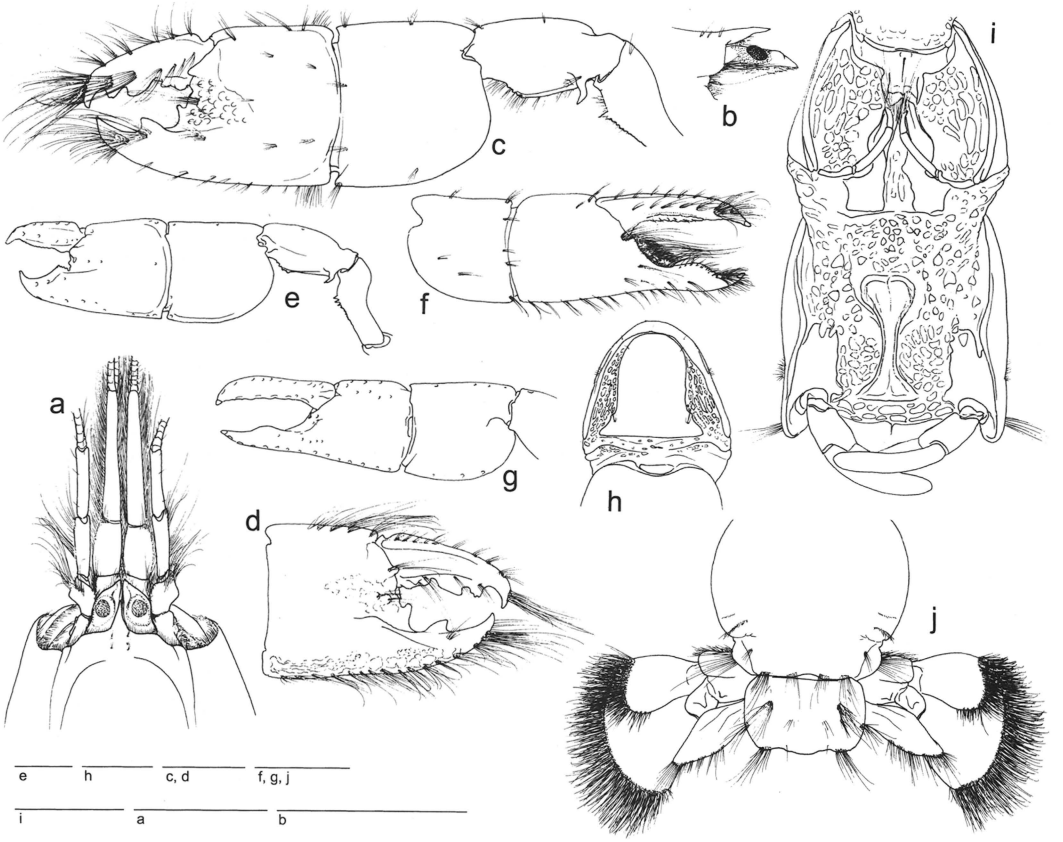

Fig. 1. *Lepidophthalmus manningi,* new species, holotype male (CL 14.1 mm) from Laguna Augustín, southwestern Gulf of Mexico, state of Veracruz, Mexico, USNM 268595: a, anterior carapace, eyestalks and antennae, dorsal surface; b, right eyestalk and rostrum, lateral surface; c, major cheliped, external surface; d, major chela, internal surface; f, minor cheliped, external surface; h, first abdominal somite, dorsal surface; i, anterior abdominal somites, ventral surface; j, sixth abdominal somite, telson and uropods, dorsal surface. Paratype female (CL 14.9 mm) from mouth of Rio San Pedro, southwestern Gulf of Mexico, state of Campeche, Mexico, USNM 268598: e, major cheliped, external surface, setae not shown; g, minor cheliped, internal surface, setae not shown. Scale lines indicate 5.0 mm.

92°27.87′W), Campeche, Mexico, 27 March 1991, collected by D. L. Felder, R. B. Griffis, J. L. Staton, and T. L. Zimmerman, 1 male, 2 female including 1 photographic voucher and illustrated (CL 14.9 mm), 1 ov, USNM 268598, 1 male, 1 ov female, UNAM 18573, 2 male including 1 illustrated (CL 9.0 mm), 3 female, ULLZ 4031, parts of 17 mutl unsexed including ov, dissected for tissue samples, vouchers for genetic studies, UNAM 18574.

Diagnosis.—Rostrum acute, inclined more or less upwards or forming an elevated arch, flanked by low shoulders lateral to eyestalks. Dorsomesial margin of eyestalk thickened to form rounded tubercle in distal 1/3. Ventral margin of cheliped merus bicarinate, internal carina with blunt denticles. Dactyl of major chela in male with rounded or subrectangular prehensile tooth near midlength, separated by notch from broad, subtriangular distal tooth. Merus of major chela with distinct proximal notch. Second abdominal somite ventrally with sclerotized medial plate bearing broad longitudinal furrow, bifurcate posteriorly, terminal posterior furrows directed laterally. Male first pleopod (gonopod) long, narrow, with subterminally broad distal article, bearing weak bifurcation. Appendix interna of male second pleopod small, subtriangular, not reaching to end of endopod. Second through fifth pleopods lacking distolateral spine on anterior surface of basis. Telson broad, posterior margin distinctly trilobate. Uropodal endopod narrow, elongate subrhomboid, broadest at or anterior to midlength, more than twice as long as broad.

Description.—Frontal margin of carapace with acute, narrow rostral spine flanked laterally by low, subangular to rounded shoul-

ders (Fig. 1a) lateral to eyestalks; rostral spine usually directed slightly upward or weakly arched in mature specimens (Fig. 1b), extending about 2/3 to 3/5 length of eyestalks in dorsal view, base of spine ventrally with tuft of setae, longest of which extend anteriorly between eyestalks beyond cornea. Carapace anterior to dorsal oval with several pairs of short setose punctae on either side of midline and scattered smaller punctae laterally, some longer setae plumose; dorsal oval well defined, smooth, usually with pair of widely separated setal punctae just anterior to midlength, length of oval slightly more than 6/10 of postrostral carapace length; marginal suture of oval diminished at anterior midline, stronger and with sclerotized articulation to bulbous cardiac region at posterior midline; branchiostegite with low, sclerotized boss bearing several compound setal punctae in anterior 1/3.

Eyestalks subtriangular in dorsal view, reaching well beyond 3/4 length of basal antennal article; anterolateral margins distinctly sinuous, tapered to arcuate margin in distal half; dorsomesial margin thickened to form a distinct rounded tubercle in distal 1/3, ridge extending to acute or subacute terminal protuberance of eyestalk (Fig. 1a, b); distinct, pigmented cornea centered on dorsal surface, area of pigmentation often broader than faceted surface. Antennular peduncle longer and heavier than antennal peduncle; basal article dorsally invaginated to form statocyst occluded by setae, overlain by eyestalk; second article slightly longer than basal article, third article about 2.6 times length of second; second and third articles with dense, ventromesial and ventrolateral rows of long, distoventrally directed setae; rami of flagellum longer than third article of peduncle, ventral ramus slightly longer, and with much denser, longer setation than dorsal ramus, heavier than dorsal ramus except in distal 1/3 where subterminal articles of dorsal ramus much broader than those of ventral ramus and fringed with short, dense ventral setae. Antennal peduncle reaching to about midlength of third article of antennular peduncle; basal article with dorsolateral carina arched to form lip above excretory pore, ventrally with setose distomesial protuberance; second article with distal field of long setae on lateral boss; third article subequal to combined lengths of first two, slightly shorter than fourth, laterally with few long setae; fourth article narrower than others, setation limited to few long subterminal setae; flagellum with sparse short setae, about 3 times length of antennular flagella.

Mandible (Fig. 2a) with large, setose, 3-segmented palp, elongate third article of palp compressed distally, becoming subspatulate, weakly truncate terminally; gnathal lobe of mandible subquadrate, with weakly angular distolateral shoulder, incisor process with well-defined corneous teeth on cutting margin, concave internal surface with strong lip giving rise to molar process bearing weakly subdivided corneous tooth proximal and internal to incisor teeth; thin, rounded paragnath set against proximal convex surface of molar process. First maxilla (Fig. 2b) with endopodal palp narrow, terminal article deflected at poorly defined articulation; proximal endite with mesial margin sinuous, proximal endite with dense, close-set setation lining sinuous mesial margin, becoming spiniform distally; distal endite elongate, terminally broadened with dense long setation, several rows of which are strongly spiniform; exopodite low, rounded. Second maxilla (Fig. 2c) with margins setose, endopod constricted to narrow terminus, first and second endites each longitudinally subdivided, exopod forming large, broad scaphognathite.

First maxilliped (Fig. 2d) with margins setose, endopod rudimentary, overlain by distal endite; blunt terminus of proximal endite coarsely setose and positioned internomesial to rest of endite; distal endite ovoid, narrowed distally, proximal 2/3 of external surface with densely setose longitudinal elevation; exopod incompletely divided by oblique suture on external surface, on internal surface transverse suture complete, sinuous across most of internal surface except where abruptly deflected proximolaterally near lateral margin to intersect marginal incision; margin with line of long setae and broadly arched proximal and distal to incision, mesial margin with comb of close-set very long setae, external face with dense field of mesially directed setae distal to oblique suture; epipod large, broad, anterior end strongly tapered. Second maxilliped (Fig. 2e) with margins setose, endopodal merus and propodus arcuate, especially proximal half of propodus, flexor margin of merus with comb of long setae, internal surface produced distally to form rounded lobe extending over internal surface of short carpus; merus length

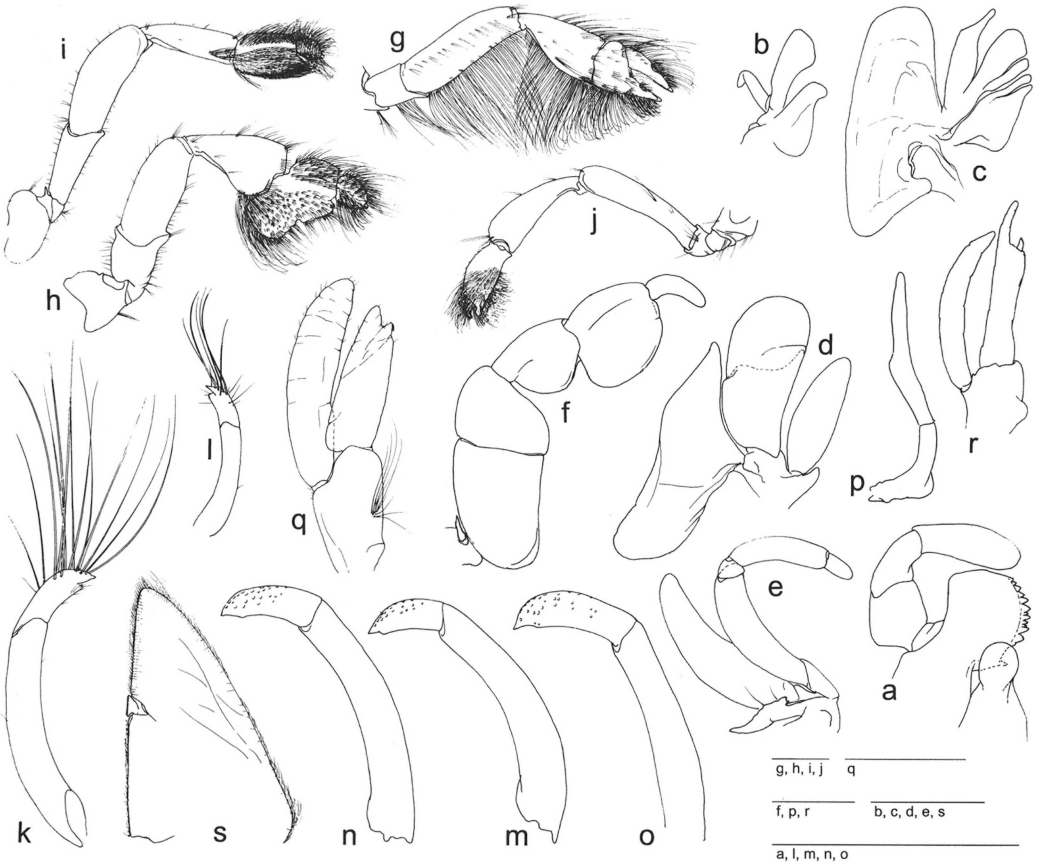

Fig. 2. *Lepidophthalmus manningi*, new species, holotype male (CL 14.1 mm) from Laguna San Augustín, southwestern Gulf of Mexico, state of Veracruz, Mexico, USNM 268595: a, right mandible and paragnath, external surface, setae not shown; b, right first maxilla, external surface, setae not shown; c, right second maxilla, external surface, setae not shown; d, right first maxilliped, external surface, setae not shown; e, right second maxilliped, external surface, setae not shown; f, right third maxilliped, external surface, setae not shown; g, right second pereiopod, external surface; h, right third pereiopod, external surface; i, right fourth pereiopod, external surface; j, right fifth pereiopod, external surface; k, right first pleopod (gonopod), mesial surface; q, right second pleopod, posterior surface; s, endopod of right third pleopod, anterior surface. Paratype male (CL 9.0 mm) from Rio San Pedro, southwestern Gulf of Mexico, state of Campeche, Mexico, ULLZ 4031: l, right first pleopod (gonopod), lateral surface. Paratype males (CL 15.1, 15.4 and 16.1 mm, respectively) from Anton Lizardo, southwestern Gulf of Mexico, state of Veracruz, Mexico, UNAM 18571: m–o, variation in right first pleopod (gonopod), lateral surface, setae not shown. Paratype female (CL 14.9 mm) from mouth of Rio San Pedro, southwestern Gulf of Mexico, state of Campeche, USNM 268598: p, right first pleopod, lateral surface, setae not shown; r, right second pleopod, posterior surface, setae not shown. Scale lines indicate 3 mm.

about 4 times width; propodus length about 2/3 length of merus, longest setae originating on extensor margin and distal half of external surface; dactylus twice as long as broad, rounded terminally, distal half bearing stiff setae; exopod broad, bladelike, narrowing distally, width at 3/4 length more than 1/2 of width at 1/4 length, distinctly overreaching endopodal merus, arcuate, terminally rounded; bilobed epipod originating from peduncle with short, truncate basal lobe, elongate narrowly tapered, arcuate distal lobe. Third maxilliped (Fig. 2f) with small, terminally acute, lightly setose rudimentary exopod and large setose endopod; endopodal ischium subrectangular, maximum diagonal length distinctly less than 2 times width at midlength, internal surface with rudimentary unarmed longitudinal carina on proximal half; merus subtriangular, broader than long, mesial margin forming distinct, rounded lobe; carpus subtriangular, longer than broad;

propodus large, subovoid to subrhomboidal, about as long as broad; low, setose, arcuate lobe on flexor margin immediately below articulation of dactylus, demarcated from rest of inferior margin by slight offset extended onto external surface; dactylus narrow, arcuate proximally, long setae of extensor and distal margins including a few long stiff bristles at slightly truncate terminus.

Branchial formula as reported for congeners (Lemaitre and Rodrigues 1991: 625, Felder and Rodrigues 1993: 363, 369, 370); endopods and epipods as described above, branchiae limited to single rudimentary arthrobranch on second maxilliped, pair of arthrobranchs on third maxilliped, and pair of arthrobranchs on each of the first through fourth pereiopods.

Major cheliped located on either right or left side, shape and ornamentation sexually dimorphic. Major cheliped of male (Fig. 1c, d) massive, more strongly armed than that of female; ischium slender, superior margin sinuous, row of very small distally inclined denticles on proximal 2/3 of inferior (flexor) margin, row usually terminated distally with 1–4 much longer, sharp, narrow, straight teeth, some of which may be compound; merus with distinct, U-shaped notch in proximal 1/4 of superior margin, inferior (flexor) margin arcuate distally, with strong proximal hook at base of bicarinate keel, hook strongly developed to single spiniform tip and usually with weak subterminal lobe, external carina unarmed, divergent from internal keel and sometimes ill-defined proximally, internal carina forming inferior margin bearing (usually 3–5) small blunt denticles, largest of which are positioned at or distal to most arcuate part of inferior margin; external surface of article sometimes weakly eroded immediately distal to base of proximal hook; carpus broad, subquadrate, superior and inferior margins keeled, near parallel in distal half, terminated distally in subacute angular superior corner, truncate inferior corner. Propodus of male major chela broad, heavy, length of fixed finger markedly exceeding 1/2 length of palm; inner surface of palm (Fig. 1d) proximally smooth, with rounded swollen boss centered near midline, rounded carina and shallow adjacent furrow extending proximal from fixed finger below subtriangular field of rounded tubercles proximal to gape of fingers and above irregularly punctuate and eroded lower surfaces of palm and fixed finger (most eroded in large individuals); outer surface (Fig. 1c) with short unarmed longitudinal carina forming inferior border for dense triangular field of rounded tubercles extending proximally from gape of fingers; distinct keel of superior propodal margin restricted to proximal half, keel of inferior margin distinct proximally, extending onto fixed finger, less defined distally, merged into row of weak lobes on inferior inner surface where obscured by setose punctae (Fig. 1d); weakly hooked, superiorly directed tooth at proximal end of gape, terminally microdenticulate, separated by broad U-shaped notch from strong, distally inclined, triangular tooth derived from outer prehensile margin (Fig. 1c) and centered near 2/5 to 1/2 length of fixed finger; fixed finger with well-defined separation of inner and outer prehensile margins, inner margin unarmed but forming thick rounded carina extended slightly onto palm; dactylus with hooked tip, superior margin forming short, rounded proximal carina, inner surface with longer, stronger rounded proximal carina, inferior surface with weakly defined rounded carina forming unarmed inner prehensile margin, outer prehensile margin usually with 3 heavy, distally inclined prehensile teeth, basal tooth a broad low bilobate molar, usually abutted on its inner surface by strong tubercle, bearing microdenticulation on posterior prehensile lobe, middle tooth bladelike, centered near midlength of finger, separated by U-shaped notch from narrow terminally truncate or weakly multilobate distal tooth centered near 3/4 length of finger.

Major cheliped of female (Fig. 1e) less massive, less strongly armed and sculpted than that of male; prehensile margins on fixed finger and most of dactylus weakly serrate, dactylus relatively less massive, fixed finger basally broader than in males, notch at base of fixed finger narrow, U-shaped, bordered distally by small denticles on proximal slope of prehensile tooth; superior and inferior margins of propodus slightly convergent distally; when fingers closed, tip of dactylus usually overreaching more strongly hooked fixed finger and gape filled except for notch at base of fixed finger.

Minor cheliped (Fig. 1f, g) sparsely armed; ischium weakly serrate on most of flexor margin; merus unarmed; carpus with blunted, angular distal corners; proximal 1/2 of fixed finger with broad excavation in proximal half of

prehensile margin, broad swelling or tooth centered near midlength of finger, dactylus with dentition of inferior (prehensile) surface limited to few weak tubercles among setal punctae in proximal 3/4, subterminally with broad tooth on outer prehensile margin, distal to which margin sometimes weakly serrate; each finger terminating in corneous tubercle; in males, dense, elongate setation of excavation in fixed finger largely filling gape between fingers, setation of excavation much less developed in gape between fingers of females; excavation in fixed finger, size of gape, and relative size of propodus compared to carpus, all slightly larger in males than females.

Second pereiopod (Fig. 2g) chelate, flexor margins of merus and carpus lined with evenly spaced long setae, inferior margin of propodus slightly concave, with long setae proximally, stiffened and reduced in length to become dense field of short bristles distally; middle 1/3 of fixed finger with patch of short stiff bristles just outside prehensile margin; prehensile margins of both fingers corneous distally, with heavy translucent cornification at tips; superior margin of dactylus with long stiff setae grading to short stiff bristles distally. Third pereiopod (Fig. 2h) merus length about 2.2 times width; propodus with inferodistal margin bilobate, lobes demarcated by furrows on internal surface, distal margins of both lobes with dense fringe of bristles, fringing bristles absent between lobes and between prominences of scalloped margin on lower lobe, those in distal half of upper lobe partially concealing 1 or 2 prominent, corneous, distally directed teeth arising from margin; longest setae on inferior margin of lower lobe, patterned tufts of lighter setae on outer face of article; dactylus tear-shaped, superior margin scalloped or sinuous, narrowed distally, terminating in short, narrow, ventrolaterally directed corneous tooth, outer surface with fields of setae and shorter stiff bristles lining inferior margin, grading to fields and poorly defined rows of finer setae above. Fourth pereiopod (Fig. 2i) weakly subchelate, inferodistal process of propodus (= fixed finger) a rounded, terminally cornified lobe extended distally about 1/3 length of dactylus, lower margin of lobe with one or more corneous spines obscured by dense brush of setae, setae originating from inferior margin and lower internal surface strongly serrate; dactylus an elongate tear-shape, superior margin arched, narrowed distally, terminating in short ventrolaterally directed corneous tooth. Fifth pereiopod (Fig. 1j) minutely chelate, opposable surfaces of both fingers spooned, terminally rounded; propodus with dense field of long, close-set setae on internal surface, fixed finger deflected, terminally pectinate; dactylus terminally narrower than fixed finger, distally hooked to form beak-like chela obscured by dense fields of setation on distal 2/3 of propodus and superior surface of dactylus.

Abdominal somites mostly smooth dorsally, glabrous; first abdominal tergite (Fig. 1h) with thickened, translucent, bell-shaped middorsal sclerite, flaring of sclerite to form flange of bell-shaped sclerite developed mostly in posterior 1/4 of length, beginning of flaring usually marked on either side by small offset in margin of sclerite, membranous areas to either side with scattered, small sclerites, membranous areas enclosed laterally by arms of anterolateral sclerite diverging toward posterior of somite; second tergite with posterolateral lobe below suture sclerotized like remainder of tergite, lobe with sparse, well-defined anterior and short, less-defined, broken posterior transverse lines of inconspicuous setae, ventrolateral lobe of tergite centered anterior to midlength of tergite; third to fifth tergites each encompassing a finely setose, lateral, membranous subcircular or suboval area below a weak posterolateral suture, that of third tergite more posterolaterally positioned than in fourth and fifth tergites, that of fifth tergite smallest, most circular; sixth tergite (Fig. 1j) with 2 posterolateral lines of short setae anterior to posterolateral groove from which transverse and posterior sutures originate, longest line adjacent, subparallel to transverse suture, transverse suture terminating mesially in 2 to 3 small branches, posterior suture arched to posterior margin, tufts of stiff setae mesial to each posterior suture, on posterolateral corners, and usually as 4 short lines or tufts of stiff setae on posterior margin. Ventral surfaces of abdominal somites (Fig. 1i) armored extensively with sclerotized plates and tubercles; heavy ridges at base of, alongside, and anterior to first pleopods; complex pattern of multiple plates and tubercles arming most of ventral cuticle on second somite, this somite bearing large, elongate, longitudinally furrowed median plate, furrow bifurcating

posteriorly into laterally directed furrows; sclerites anterior and anterolateral to median plate often lobiform or dentiform, sometimes erect and fingerlike, occasionally with tubercles as prominences but lacking distinct sets of terminal bristles.

First pleopod of male and female uniramous, composed of 2 articles; in male, originating just anterior to lateral flange of broad, corneous plate, appendage length slightly less than 1/2 that of second pleopod, proximal article more than 2 times length of terminal article (Fig. 2k–o), terminal article slightly compressed, subspatulate distally, arched subterminal surface bearing long setae, article bifurcate but weakly so in large mature individuals, anterolaterally directed tip slightly cornified; in female (Fig. 2p), total extended length subequal to that of second pleopod, proximal article bearing strong lobe at midlength and slightly shorter than terminal article, terminal article forming narrow spatulate blade beyond midlength, both articles bearing long setae. Second pleopod of male and female biramous, with appendix interna on endopod; appendix interna in both sexes (Fig. 2q, r) small, markedly overreached by terminus of endopod, terminally subacute, terminus and mesial subterminal shoulder with field of minute, rudimentary hooked setae; in male, appendix interna distinctly offset from endopod by proximal and distal sutures, overall setation of appendage sparse, short; in female, appendix interna separated from endopod by weak transverse suture, terminus of endopod very narrow, both rami of appendage setose. Basis of second through fifth pleopods with, at most, a low tubercle or tooth on anterior surface at condylar articulation with exopod. Third to fifth pleopod pairs forming large, posteriorly cupped fans when cross-linked by hooked setae of appendices internae on opposed margins of endopods; endopod of each subtriangular (Fig. 2s), stubby appendix interna demarcated by sutures where embedded in endopod, offset slightly from mesial margin of endopod.

Telson (Fig. 1j) broad, subovoid, width about 1.6 times length, broadest near midlength, posterior margin distinctly trilobate, median lobe broadest, sometimes forming slightly upturned lip; dorsal surface usually with 2 pairs of setal tufts, anteriormost of which are largest fields, originating anterior to midlength, well lateral of midline, smaller pair nearer midline, just posterior to midlength, with additional small tuft sometimes lateral to these on one or both sides, when present overlain by long setae of large anterior tufts; lateral margins typically surmounted by pair of setal tufts just posterior to midlength, posterior margin with distinct tuft surmounting each of the produced posterolateral lobes. Uropod (Fig. 2j) with strong, triangular, posterodorsally directed tooth on protopod and thick, blunt, posteriorly directed tooth on proximal article of exopod, both positioned to abut or overreach anterior margin of extended endopod; endopod elongate, sinuous, ovoid to subrhomboidal, about twice as long as broad, posteromesial margin surmounted with broken fringe of setae, tapering to rounded terminus bearing marginal fringe of long setae, distal end distinctly overreaching distal end of anterodorsal plate on flexed exopod; exopod with anterodorsal plate falling well short of distal margin, posterodistal edge of plate with short, thick, spiniform setae grading to thinner, dense, elongate setae of exopod margin; distal margin of exopod with dense fringe of setation, longest posteriorly.

Size.—On the basis of postorbital length, the largest male among present materials is CL 18.0 mm, TL 82.5 mm, and the largest female CL 14.1 mm, TL 77.5 mm, both from the mouth of the Rio San Pedro, Campeche, in March 1991. The smallest ovigerous female CL 7.6 mm, was taken near Puerto Ceiba, Tabasco, in March 1991, with eggs measuring 1.5 to 1.6 mm in maximum diameter that were in the process of hatching. Maximum diameter of mature, immediate prehatch eggs ranged from 1.3 to 1.7 mm on live ovigerous females, and from 1.2 to 1.5 mm in alcohol preserved specimens. Specimens taken from Puerto Ceiba, Tabasco, during both the March 1991 and February 1999 collecting trips, were smaller on average that those from any other site and included some specimens with CL < 4 mm.

Color (based upon 35-mm color slides, taken before specimen preservation, for holotype male USNM 268595, paratype males ULLZ 4032 and ULLZ 3998 and paratype female USNM 268598).—Overall colors and patterns very similar to those of *L. richardi,* as described by Felder and Manning (1997). Dark pigmentation beneath cornea and often

extensively occupying most of eyestalk, and as small crescent under articular membrane near midlength of antennal peduncle. Much of integument translucent, excepting opaque white over most of third maxillipeds, chelipeds, remaining pereiopods, thicker portions of abdominal tergites 2–6, and thicker sclerites arming ventral membranes of abdomen; faint whitish opacity in anterior of carapace, anterior and posterior of dorsal oval, and dorsal extreme of cervical groove; midportion of oval sometimes with faint, broad weak band or two of translucent yellow; translucent pale olive-cream to yellow-white on bell-shaped dorsal sclerite of first abdominal tergite, tergite least pigmented medially, anteromedially and at tips of bell flanges. Small yellow, yellow-green, or yellow-brown chromatophores forming faint dorsal cover on posterior half of thin, translucent second abdominal tergite and distinct, complex dorsal pattern on slightly translucent cuticle of abdominal tergites 3–6 and telson, pigment arranged in 5 primary areas on each of somites 3–5, much as previously described for congeners (see Williams *et al.,* 1989: fig. 4 of second color plate; Felder and Manning, 1997: 327), medial pigmented area of abdominal tergite 3 often especially large, yellow; on abdominal somite 6, dorsal chromatophores in midlength and posterior forming thin pair of stripes to either side of midline, stripes merging anteriorly, inner stripe the broader, but not as broad as the intervening unpigmented area, posterolateral area of somite with broad area of yellowish pigment which may, especially in females, include rose to reddish-brown fields of chromatophores along posterolateral margins; rich yellow to brownish-yellow dorsal pigment on exposed integument of uropods and posteriorly on telson. Larger of the setal tufts here and on abdominal tergites pale brown to yellow brown.

Known Range and Habitat.—Known from intertidal and shallow subtidal muddy sand and sandy mud substrates in coastal lagoons and river mouths in the southwestern Gulf of Mexico (from states of Veracruz, Tabasco, and western Campeche, Mexico), including small clearings among shoreline mangroves and flats adjacent to stands of cordgrass. Sometimes in brackish to saline coastal ponds with ephemeral connections to the sea. Salinities for present collections ranged from 2.5 to 23 ppt. At one site near Puerto Ceiba, Tabasco, apertures to muddy clay-lined burrows were difficult to discern among coarse quartzite surface sands. Clayey materials for burrow wall construction were apparently transported vertically by the animals from deeper alluvial deposits, an observation also reported for other members of the genus (Felder and Griffis, 1994; Nates and Felder, 1998). Dense populations sampled by us from tidal flats just upstream from the mouth of the Rio San Pedro (village of Campechito, western Campeche) in 1991 were no longer in evidence in 1999, perhaps because of urbanization on this eastern bank of the river or phasic recruitment and colonization in these flood-prone habitats.

Remarks.—The original collections of this species by one of us (DLF) in 1981 consisted of two specimens among a lot of four assignable to *Lepidophthalmus* from a single site near Puerto Ceiba, Tabasco; of this lot, two bore ventral sclerites and two did not. As all specimens fell within varietal forms described by Schmitt (1935) for *Callianassa jamaicense* s.l., and the occurrence of ventral sclerotization had been reported previously as a possible effect of parasitism for that species (Biffar, 1971), all four specimens were tentatively identified as that taxon. Subsequent to revisions of the American Callianassidae and assignment of *C. jamaicense* s.l. and its near relatives to *Lepidophthalmus* by Manning and Felder (1991), members of this genus were targeted by us for population genetic studies in the Gulf of Mexico (Felder *et al.,* 1991; Staton *et al.,* 2000). In addition to collection of materials from throughout the Gulf for initiation of allozyme studies, all specimens of the genus were submitted to additional morphological study. This revealed that presence, absence, and sculpture in ventral sclerotization patterns was not a symptom of parasitization but rather a species-specific character of extreme utility for separation of populations among congeners (Felder and Rodrigues, 1993; Felder and Manning, 1997). The subsequent allozymic analyses clearly supported separations of *L. louisianensis* from the northern Gulf and those populations from the southwestern Gulf that were thereafter assigned to *Lepidophthalmus* sp. "a" (Staton *et al.,* 2000). The latter group is herein described as *L. manningi,* new species, and is also distinguishable from the ventrally unplated

L. louisianensis by its ventral sclerotization. However, allozymic analyses also revealed the existence of a ventrally unplated southwestern Gulf form, of close relationship to *L. louisianensis* and occurring sympatrically with *L. manningi*, new species. Recent morphological examinations of this second, undescribed, southwestern Gulf endemic form, herein treated as *Lepidophthalmus* sp. "b" in accord with Staton *et al.* (2000), have revealed subtle morphological characters that also can be used to distinguish it (Felder, in prep.).

At all five of the collecting sites from which it was taken, *L. manningi*, new species, occurred sympatrically with the above-mentioned undescribed, ventrally unplated congener, *Lepidophthalmus* sp. "b". Specimens of pink wormfish (*Microdesmus* sp.) and a commensal alpheid shrimp (*Leptalpheus* sp.) were also taken with some of these collections and were associated with either or both of these congeneric callianassids. Ovigerous specimens of both *Lepidophthalmus* species occurred at most sites from which collections were made, in both March 1991 and February 1999, and pink wormfish appear to prey upon eggs carried by the females of this genus (Felder and Rodrigues, 1993). Most specimens of *Leptalpheus* sp. appear to be conspecific with an undescribed form previously reported to occur in association with *L. richardi* in Belize and with yet-to-be-determined hosts in southeastern Florida (see Felder and Manning, 1997: 329).

The presence of sclerites or plates forming a ventral armor on the abdominal somites, especially evident in the median plate of the second abdominal somite, will readily separate *L. manningi*, new species, from its ventrally unarmed congeners. In the western Atlantic these include the yet-to-be-described southwestern Gulf of Mexico endemic, *Lepidophthalmus* sp. "b", with which it occurs sympatrically, the well-known northern Gulf endemic, *L. louisianensis*, and the recently described Brazilian species *L. siriboia*, all three of which also lack the strongly trilobate telson characteristic of *L. manningi*, new species. In the eastern Pacific, these include the recently described Colombian species *L. rafai* Felder and Manning, 1998, and other ventrally unarmed materials, yet to be described. The presence of a distinct, median longitudinal furrow in the median plate separates *L. manningi* from all known ventrally armed congeners, except for *L. richardi* from Belize and some individuals of *L. sinuensis* from the Caribbean coast of Colombia. All evidence of this furrow is lacking in specimens of *L. jamaicense* from the Caribbean, and Pacific specimens of *L. bocourti*, *L. eiseni*, and another, yet-to-be-described, ventrally plated species from the Pacific (Felder, in prep.).

Lepidophthalmus sinuensis differs markedly from both *L. manningi*, new species, and *L. richardi* on the basis of its unique development of frontal lobes on the carapace, flanking the rostrum; but it also has a much less-developed ventral armor than do either of the latter two species. Few accessory sclerites surround the median ventral plate of the second abdominal segment, and the longitudinal furrow of the median plate is for the most part closed, sometimes limited to only a medial suture (see Felder and Manning, 1997: fig. 7). Both *L. manningi*, new species, and *L. richardi* have numerous, similarly shaped accessory sclerites surrounding this median ventral plate and exhibit similar development in its median longitudinal furrow. In mature specimens, the furrow in this plate differs between these two closely related species primarily in that it is relatively wider in *L. manningi*, new species, whereas furrows resulting from its posterior bifurcation are deflected less strongly to either side in *L. richardi*.

Other characters that separate apparently mature individuals of these closest known relatives include the less acute and less produced anteromesial eye tubercles of *L. manningi*, new species, which are not excavate or undercut on their anterior margins as in *L. richardi*; the commonly upwardly inclined or upwardly arched rostral spine in *L. manningi*, new species, which tends to be less elevated and weakly arched into an anteriorly directed tip in *L. richardi*; a deflection of the internal suture near the lateral margin on the exopod of the first maxilliped in *L. manningi*, new species, unlike the more graduate deflection of this suture beginning at a more medial position in *L. richardi*; the broad arch of the proximolateral expodal margin on this appendage in *L. manningi*, new species, a margin that is weakly arched or more nearly straight in *L. richardi;* the presence of a small subdactylar setose lobe on the margin of the third maxilliped propodus in *L. manningi*, new species, a structure that is smaller and

restricted to the submarginal external surface in *L. richardi*; lateral flaring of the flange on the bell-shaped first abdominal middorsal sclerite mostly in the posterior 1/4 of its length in *L. manning*, new species, while flaring usually originates at the narrowest portion of the bell-shaped sclerite and encompasses about the posterior 2/5 of this plate in *L. richardi*; a subterminally broad distal article, in lateral perspective, on the mature male gonopod in *L. manningi*, new species, while lateral perspective of this article is narrower subterminally in *L. richardi*; and a uropodal endopod that is broadest at or anterior to midlength in *L. manningi*, new species, while it is broadest posterior to midlength in *L. richardi*.

Comparisons of available materials for the two species also suggest that *L. manningi*, new species, typically has the deeper proximal meral notch on the superior margin of the major cheliped, the larger lobe on the proximal article of the female first pleopod, the larger appendix interna on the male second pleopodal endopod, the narrower distal lobe on the female second pleopodal endopod, and the less strongly developed carination on mesial margins of the lateral ventral plates on the second abdominal somite of mature males. *Lepidophthalmus manningi* also appears to reach larger size than does *L. richardi*, the type series of which consists of small specimens. However, ovigerous specimens of *L. richardi* remain unknown to date, and larger examples of both sexes may remain to be discovered.

Etymology.—The species is named for our friend, mentor and colleague, Raymond B. Manning, in recognition of his dedication to the study of decapod crustaceans. His publications and generous assistance have contributed tremendously to our systematic understanding of many decapod taxa, including the Callianassidae. Especially for one of us (DLF), his collaboration and advice over many years have given perspective on the urgent need for additional systematic study and taxonomic revision of even familiar marine decapod groups.

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