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GHOST SHRIMPS OF THE GENUS *LEPIDOPHTHALMUS* FROM THE CARIBBEAN REGION, WITH DESCRIPTION OF *L. RICHARDI,* NEW SPECIES, FROM BELIZE (DECAPODA: THALASSINIDEA: CALLIANASSIDAE)

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ABSTRACT

Lepidophthalmus jamaicense, originally described in limited detail on the basis of two male type specimens from Montego Bay, Jamaica, is redescribed and fully illustrated in the course of our examination of the original types, a large series of recently collected male and female topotypes, and recent collections from the southeastern Caribbean Sea. Comparative morphological studies of all the known western Atlantic species serve to distinguish materials from Belize, which are herein recognized as *L. richardi,* new species. Included in these comparisons and descriptions are detailed studies of ventral cuticular armor in the anterior abdominal somites, an apparent apomorphic character of particular value in segregating tropical western Atlantic populations. The occurrence of *L. jamaicense* in southeastern Cuba is confirmed from reexamination of museum material, and the range of the species is extended to Tobago and coastal Venezuela in the extreme southeastern Caribbean. While there appears to be strong potential for regional endemism in western Atlantic species of the genus *Lepidophthalmus,* the widely separated insular populations of *L. jamaicense* in the Antillean region appear to be undifferentiated. Reproductive history and potential for larval dispersal in this species remains unknown and may not conform to the abbreviated life histories reported for its western Atlantic congeners.

Western Atlantic members of the genus *Lepidophthalmus* appear to be particularly well-adapted to low salinity estuaries and river mouths (Felder, 1978; Felder *et al.,* 1986; Manning and Felder, 1991). Such adaptations can favor larval retention and accumulation of large populations in coastal lagoons and embayments, where these animals may dominate biogeochemical processes with beneficial turbational effects on natural habitats (Felder and Griffis, 1994) or, where populations invade artificial systems, may have detrimental effects on aquacultural operations, such as penaeid shrimp farms (Lemaitre and Rodrigues, 1991; Felder *et al.,* 1995). Reduced larval dispersal and restriction to disjunct estuaries may also have uniquely favored endemism and subsequent speciation in this genus, and the existence of undescribed species in these habitats has been previously noted (Felder *et al.,* 1991). River mouths and estuaries throughout Caribbean coastlines are, as in many developing regions (Day *et al.,* 1989: 537), rapidly succumbing to industrialization, port development, modification for aquaculture, urbanization, and other forms of traumatic habitat modification, and it is urgent that the status of isolated estuarine populations be resolved quickly. Only then can risks for cross-inoculations of species between habitats (Carlton and Geller, 1993) or potential for extinction of endemics be recognized.

The short description and limited illustrations which accompanied naming of *Callianassa jamaicense* Schmitt, 1935, a species now referred to as *Lepidophthalmus jamaicense* (Schmitt, 1935), have contributed to its confusion with undescribed congeners in the western Atlantic (see Felder and Rodrigues, 1993). The original description was based upon only two specimens collected from a brackish pond near Montego Bay, Jamaica, in 1910, and no topotypic materials have been reported since. In addition to the Jamaican types, Schmitt also figured and briefly described *C. jamaicense* var. *louisianensis,* on the basis of a single specimen from the northern Gulf of Mexico which he believed to vary from the types because of injury to the specimen. Subsequent workers, some of whom reexamined the type materials, further explored certain characteristics of the Jamaican materials and putative variant populations of the species from the Gulf of Mexico and Brazil (Biffar, 1971; Rodrigues, 1966, 1971; Tiefenbacher, 1976), but did not diagnose morphology in adequate detail to definitively distinguish the Jamaican materials from other Caribbean populations. A few additional features of the types were figured by Manning and Felder (1991) in the course of assigning the species to *Lepidophthalmus* Holmes, 1904, but morphology was not compared within the genus.

Recently, populations from the Gulf of Mexico and Brazil that were regarded formerly as variants of *L. jamaicense* have been reexamined and accorded species rank (Felder and Rodrigues, 1993). In the course of that work, it was recognized that both of those populations lacked certain distinctive patterns of cuticular armor on ventral surfaces of the anterior abdomen, features which we found to be characteristic in the types of *C. jamaicense* and *L. sinuensis* Lemaitre and Rodrigues, 1991, as well as in our holdings of several unassigned populations from the Caribbean (see Felder *et al.*, 1991; Felder and Rodrigues, 1993: 373). While not used in previous diagnoses for species of *Lepidophthalmus,* and thus not figured in descriptions to date, variation in patterning of ventral armor on the abdominal somites appears to be an apomorphic character of utility in discerning closely related species within other thalassinid genera (see Williams, 1986: 25, 44, 1993: 55, 57; Felder and Manning, 1994: 346–347). Since these features in the types of *L. jamaicense* had been identified previously as possible atypical effects of parasitism (Biffar, 1971), an additional series of comparative topotypic materials was obtained from near Montego Bay, Jamaica, by one of us (DLF) in 1991. Used in conjunction with the type materials, the extensive series of topotypes obtained in Jamaica facilitated not only the present reexamination and redescription of *L. jamaicense* but also detailed comparisons to recently collected populations from Tobago, Venezuela, and Belize, as well as reevaluation of a specimen previously reported from Cuba (Holthuis, 1974).

Thorough morphological description and illustration of *L. jamaicense* from Jamaica were deemed essential for detailed comparisons with the other Caribbean materials here addressed, as well as for works in progress concerning problematic materials from the Gulf of Mexico and the eastern Pacific. On the basis of such comparisons, we herein confirm assignment of materials from Cuba, Tobago, and Venezuela to *L. jamaicense,* while materials of the genus from Belize, which somewhat resemble *L. jamaicense* in ventral ornamention of the second abdominal somite, are distinguished from other Caribbean species as *Lepidophthalmus richardi,* new species. Compilation of a systematic key is deferred to a forthcoming paper which will include Gulf of Mexico members of the genus and conclude treatment of presently available materials from the western Atlantic.

MATERIALS AND METHODS

Other than for the museum types of *L. jamaicense,* the museum specimen from Cuba, and some museum specimens referred to in comparative remarks, all materials used in this study were collected by extraction of specimens from intertidal and shallow subtidal sediments with hand-operated yabby pumps (see Hailstone and Stephenson, 1961; Manning, 1975). Materials from two localities in Belize were collected jointly by the authors in 1983 during an early phase of their on-going survey of decapod crustaceans in that area. Those from Dangriga (referred to on some maps as Stann Creek Town), were taken from a shelly, muddy quartzite sand beach and margins of an adjacent run-off fed cove near the Pelican Beach Hotel. Those from the Monkey River were taken on a tidally exposed, unvegetated mud flat set among mangroves near the mouth of the river. Topotypic materials from Jamaica were collected by D. L. and J. M. Felder in 1991 while also obtaining tissue samples for genetic studies (DLF, work in progress with J. L. Staton and D. W. Foltz). All were taken from flowing but tidally influenced lower reaches of the Mosquito Cove River (referred to on some maps as Miskito Cove River) in northwestern Jamaica, just west of Montego Bay. Animals were obtained with difficulty there, where they were burrowed among stones and gravel into mud and clay mixed with coarse, angular sand. All were taken just upstream of mangroves that vegetate the river mouth, in areas where salinity of the overlying water measured 1 ppt. Materials from Tobago were obtained by R. W. Heard, Gulf Coast Research Laboratory, Ocean Springs, Mississippi, from near the mouth of a small stream near Speyside in eastern Tobago in 1993 during a systematic survey of decapods in that region. Detailed field notes (R. W. Heard, personal communication) indicate that burrows occurred from waters edge to depths of 1.5 m where overlying waters were "fresh or very nearly so'' and were blocked from the sea by a shallow sand bar which crossed and temporarily occluded the stream mouth. Burrows occurred in sediments which graded from largely gravel and stones upstream to primarily sand downstream. Materials from Venezuela were obtained by J. P. Blanco Rambla, Instituto Oceanográfico de Venezuela, Universidad de Oriente, Cumaná, during his survey of thalassinids from the Golfo de Cariaco. Those materials were collected at the mouth of the river Caño Tunantal in muddy sediments overlain by 5–10 cm of estuarine water diluted by river flow.

Material examined is listed by location followed by date, collector, number of specimens by sex and condition (imm = immature, mutl = mutilated), and, if applicable, museum number (RMNH = Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; USLZ = University of Southwestern Louisiana Zoological Collections; USNM = National Museum of Natural History). Size is expressed as postorbital carapace length (CL) or postorbital total length with the abdomen extended (TL) and measured in mm. The holotype and some paratypes of *Lepidophthalmus richardi,* along with topotypic and representative southeastern Caribbean materials of *L. jamaicense,* have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Paratypes of *L. richardi,* along with topotypes and representative southeastern Caribbean materials of *L. jamaicense,* have been deposited in the University of Southwestern Louisiana Zoological Collections, Lafayette, Louisiana. Holdings of two institutions (USNM and USLZ) were also the source for materials of *Lepidophthalmus louisianensis* (Schmitt, 1935) from the Gulf of Mexico, *L. sinuensis* Lemaitre and Rodrigues, 1991, from Colombia, *L. siriboia* Felder and Rodrigues, 1993, from Brazil, and most examples of congeneric populations from the eastern Pacific, where referred to in comparative discussions. Comparison to the probable eastern Pacific type specimens of *Lepidophthalmus eiseni* Holmes, 1904, was based upon our examination of cataloged lot number MCZ 4370, provided on loan from the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. Direct comparison of our illustrations to materials of *L. jamaicense* sensu lato (lot numbers NHWM 6815 and 6897) in the Museum of Natural History, Vienna, Austria, was kindly conducted by P. C. Dworschak.

Lepidophthalmus Holmes, 1904 (for diagnosis, see Manning and Felder, 1991)

Lepidophthalmus jamaicense (Schmitt, 1935) Figs. 1 a–i, 2 a–s, 3 a–j

Callianassa jamaicense Schmitt, 1935: 1, 4 (part of key couplet, Jamaican only), 9–12, pl. 1, fig. 1, pl. 2, figs. 6, 8, pl. 4, fig. 1 (*not* including *Callianassa jamaicense* var. *louisianensis* Schmitt, 1935: 1, 12–15, pl. 1, fig. 2, pl. 2, figs. 4, 7, pl. 4, fig 4).—Rodrigues, 1966: 11, 14, 34–44, 160 (part, Jamaican only).—Biffar, 1971: 650, 654 (part, Jamaican only); 1972: 71 (part, *not* materials "originally described as the variety *C. j.* var. *louisianensis*").—Coelho and Ramos, 1972: 162 (part, Antilhas only).—Abele and Kim, 1986: 27, 295, 296, 302–303, figs. j, k, l (part, Jamaican only).—Manning, 1987: 397.

Callianassa (*Callichirus*) *jamaicense.*—Rodrigues, 1966: ii, 34 (part, Jamaican only).

Callianassa (*Calichirus*) *jamaicensis.*—Rodrigues, 1971: 198 (part, Jamaican only).

Callianassa jamaicensis.—Rodrigues, 1971: 191, 202–204, table 2 (part, Jamaican only).—Holthuis, 1974: 231.—Tiefenbacher, 1976: 314–316 (part, Cuban and Jamaican only).

Callichirus jamaicensis.—Saint Laurent and LeLoeuff, 1979: 67, 96 (part, Jamaican only).—Coelho and Ramos-Porto, 1987: 30 (part, Antilhas only).

Lepidophthalmus jamaicense.—Felder *et al.,* 1991: 101A (part of Caribbean group only).—Manning and Felder, 1991: 778, fig. 13 a–f.—Lemaitre and Rodrigues, 1991: 629.—Felder and Rodrigues, 1993: 357, 358, 367, 373.

Material Examined.—HOLOTYPE.—brackish pond on Montego Bay, Jamaica, 29 June 1910, collected by C. B. Wilson, 1 mult ♂ (carapace missing; Schmitt, 1935, reported CL with rostrum to be near 18 mm), USNM 69363. PARATYPE.—salt pond on Montego Bay, Jamaica, 24 June 1910, collected by A. E. Andrews, 1 ♂ (CL 13.8 mm), USNM 70797. TOPOTYPES.—Mosquito Cove River, immediately upstream of bridge on Highway A1, about 15 km west of Montego Bay, Hanover District, northwestern Jamaica, 30 November 1991, collected by D. L. Felder and J. M. Felder, 6 ♂♂ (1 imm, 2 illustrated), 6 ♀♀ (1 imm, 1 illustrated), USNM 277781, parts of 17 mutl unsexed dissected for tissue samples, vouchers for genetic studies, USLZ 3574.—same locality and collectors, 1 December 1991, 9 ♂♂ (4 imm), 5 ♀♀, USLZ 3573, parts of 11 mult unsexed dissected for tissue samples, vouchers for genetic studies, USNM 277780. OTHER SPECIMENS.—CUBA: coarse sand and coral fragments forming small beach at Playa Siboney, east of Santiago de Cuba, southeastern Cuba, 16 February 1973, collected by L. Botosaneau with the Cuban-Roumanian Biospeological Expedition to Cuba, 1 mutl female, RMNH D–30630. TOBAGO: shallow margins of small river just south of Blue Waters Hotel, near town of Speyside, southeastern Caribbean island of Tobago, 14 January 1993, collected by R. W. Heard, 3 ♂♂ (illustrated), 8 ♀♀ (2 illustrated), USNM 277782, 1 ♂, 1 ♀, USLZ 3575. VENEZUELA: from sediments in waters 5–10-cm depth, mouth of the river Caño Tunantal, southern Gulf of Cariaco, near Cumaná, Estado Sucre, 16 May 1996, collected by J. P. Blanco Rambla, 1 ♂, 3 ♀♀, USLZ 3576.

Description (based on male holotype, USNM 69363, paratype, USNM 70797, and topotypes USNM 277780, 277781, and USLZ 3573, 3574).—Frontal margin of carapace with acute, narrow rostral spine flanked laterally by low, weakly produced rounded shoulders (Fig. 1a), apices of which being immediately lateral to eyestalks; rostral spine usually directed slightly upward in mature specimens (Fig. 2a), less so in juveniles, and extending about one-half to two-thirds length of eyestalks in dorsal view, ventral base of spine with tuft of setae, longest of which extending anteriorly between eyestalks beyond cornea. Carapace anterior to dorsal oval usually with several pairs of short setose punctae on either side of midline and scattered

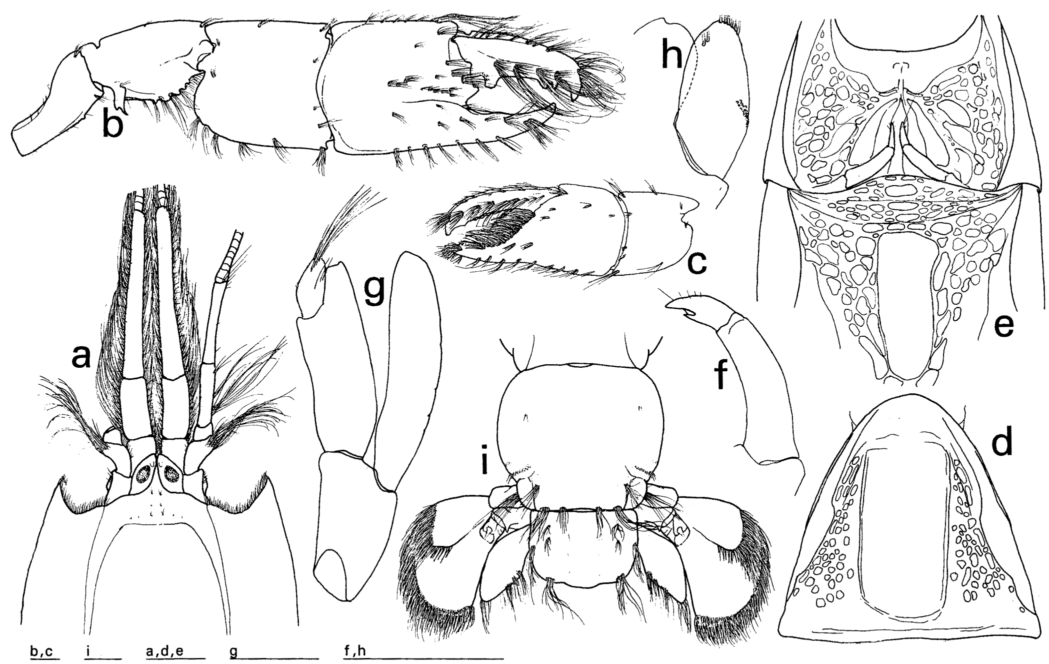

Fig. 1. *Lepidophthalmus jamaicense* (Schmitt, 1935), male paratype from Montego Bay, Jamaica, USNM 70797 (CL 13.8 mm): a, anterior carapace, eyestalks, and antennae, dorsal surface; b, major cheliped, external surface; c, minor cheliped, external surface; d, first abdominal somite, dorsal surface; e, anterior abdominal somites, ventral surface, microsetation of sclerites not shown; f, right first pleopod (gonopod) external surface; g, right second pleopod, anterior surface; h, appendix interna of right second pleopod, posterior surface; i, sixth abdominal somite, telson, and uropods, dorsal surface. Scale lines indicate 2 mm.

smaller punctae laterally; dorsal oval well defined, smooth, usually with pair of widely separated setal punctae just anterior to midlength and short, transverse lateral lines of smaller punctae in posterior third, length of oval about six-tenths of postrostral carapace length; marginal suture of oval diminished at anterior midline, stronger and with cornified tubercular articulation to cardiac region at posterior midline.

Eyestalks subtriangular in dorsal view, reaching to or beyond three-fourths length of basal antennal article; anterolateral margins tapered to thin, arcuate edge, dorsomesial margin with marginal tubercle arising at about two-thirds to three-fourths length, base of which tapering into low marginal ridge and blunt terminal protuberance of eyestalk (Fig. 2a); distinct, pigmented cornea centered on dorsal surface, area of pigmentation often broader than faceted surface. Antennular peduncle heavier, longer than antennal pedun-

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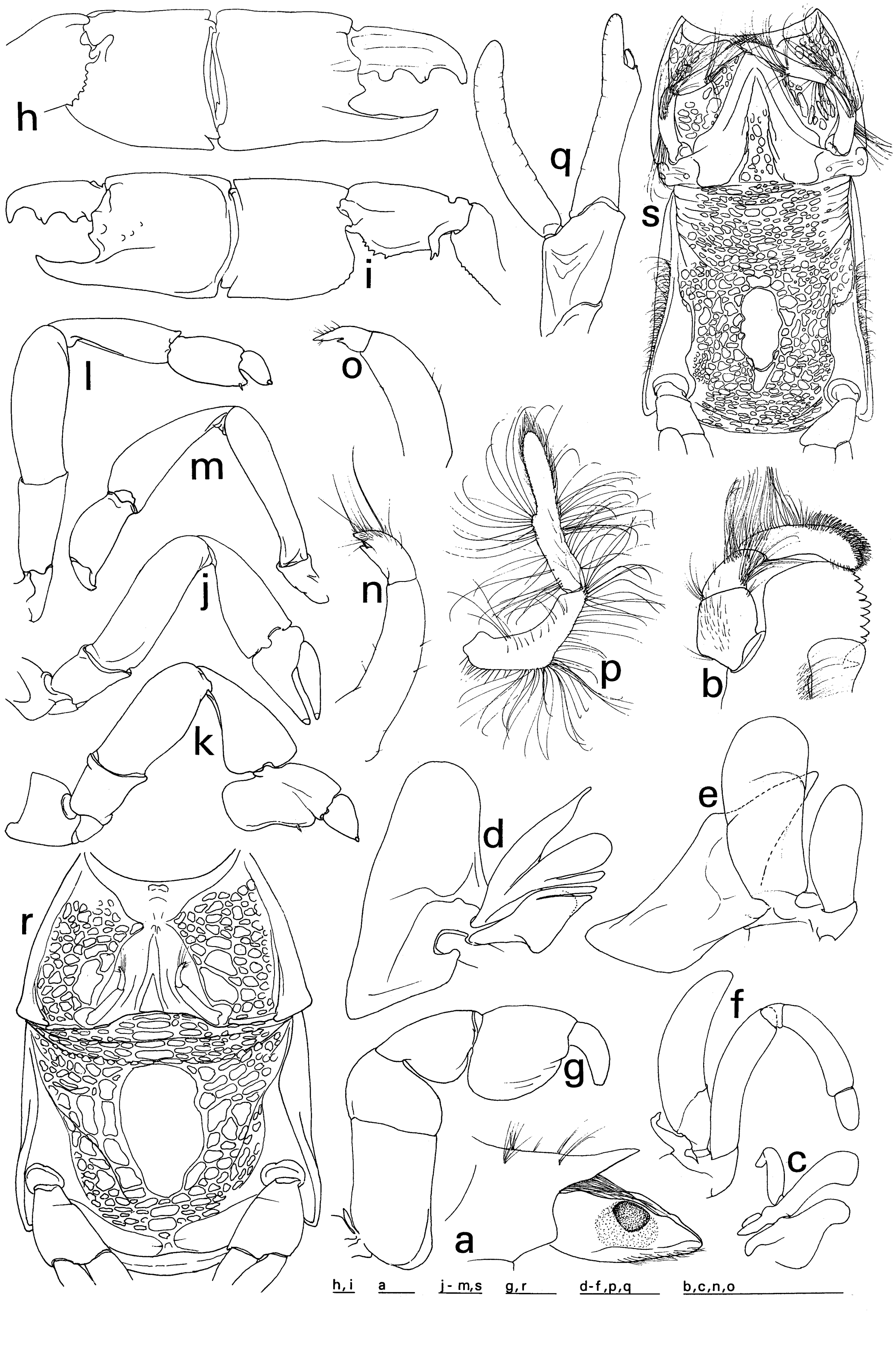
Fig. 2. *Lepidophthalmus jamaicense* (Schmitt, 1935), topotypic males from mouth of Mosquito Cove River, Jamaica, USNM 277781 (CL 16.5 mm for a–h, m, n, and r; 15.7 mm for i–l, o): a, right eyestalk and rostrum, lateral surface; b, right mandible and paragnath, external surface; c, right first maxilla, external surface, setae not shown; d, right second maxilla, external surface, setae not shown; e, right first maxilliped, external surface, setae not shown; f, right second maxilliped, external surface, setae not shown; g, right third maxilliped, external surface, setae not shown; h, major cheliped, internal surface, setae not shown; i, major cheliped, internal surface, setae not shown; j, right second pereiopod, external surface, setae not shown; k, right third pereiopod, external surface, setae not shown; l, right fourth pereiopod, external surface, setae not shown; m, right fifth pereiopod, external surface, setae not shown; n, right first pleopod (gonopod), external surface; o, right first pleopod (gonopod), external surface; r, anterior abdominal somites, ventral surface, microsetation of sclerites not shown. *L. jamaicense* (Schmitt, 1935), topotypic female from mouth of Mosquito Cove River, Jamaica, USNM 277781 (CL 13.6 mm): p, right first pleopod, posterolateral surface; q, right second pleopod, posterior surface, setae not shown; s, anterior abdominal somites, ventral surface, microsetation of sclerites not shown. Scale lines indicate 2 mm.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cle (Fig. 1a); 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, ventrally directed setae; rami of flagellum slightly longer than third article of peduncle, ventral ramus slightly longer and with much denser, longer setation than dorsal ramus, subterminal articles of dorsal ramus heavier than those of ventral ramus, and endowed with short ventral setae. Antennal peduncle reaching to or just beyond midlength of third article of antennular peduncle; basal article with dorsolateral carina strongest proximally, forming lip above excretory pore, ventrally with setose distomesial protuberance; second article ventrally with large longitudinal suture, distally with field of long setae on boss lateral to ventral suture; third article elongate, subequal to combined lengths of first two, slightly shorter than fourth, proximally forming shoulder sutured to small, lateral condylar element, laterally with row of long setae; articulation between third and fourth articles usually with small, persistent, dorsolateral crescent of dark subcuticular pigment; fourth article narrower, less setose than third; flagellum sparsely setose, about 3 times length of antennular flagella.

Mandible (Fig. 2b) with large, heavily setose, 3-segmented palp, elongate, arcuate third article of palp compressed distally, becoming subspatulate, bilobed terminally; gnathal lobe of mandible with weakly angular to rounded distolateral shoulder, incisor process with well-defined corneous teeth on cutting margin, concave internal surface with lip giving rise to molar process with few small corneous teeth proximal and internal to incisor teeth; thin, rounded paragnath set against proximal convex surface of molar process. First maxilla (Fig. 2c, setation not shown) with endopodal palp long, narrow, terminal article deflected at poorly defined articulation; proximal endite with mesial margin sinuous, distal endite elongate, terminally broadened and setose; exopodite low, rounded. Second maxilla (Fig. 2d, setation not shown) with setose margins, endopod narrowed terminally, first and second endites each longitudinally subdivided, exopod forming large, broad, scaphognathite. First maxilliped (Fig. 2e, setation not shown) with setose margins, endopod rudimentary, overlain by distal endite; proximal endite thick, angular, distomesial corner directed to internal side of endite; distal endite ovoid, proximal two-thirds of external surface with broad longitudinal elevation on lateral half, mesial half densely setose; exopod incompletely divided by oblique suture, lateral margin near midlength not markedly offset to form produced corner at intersection with suture, mesial margin with comb of closely set, 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. 2f, setation not shown) with setose margins, endopodal merus and propodus arcuate, both slightly broader distally than proximally, flexor margin of merus with comb of closely set, long setae, internal surface distally produced to form rounded lobe extending over internal surface of short carpus; merus length about 4 times width; propodus length two-thirds to three-fourths length of merus, longest setae originating on extensor margin and distal half of external surface; dactylus at least twice as long as broad, terminally rounded, distal half bearing field of stiff setae; exopod broad over much of length, width at three-fourths length exceeding one-half of width at one-fourth length, overreaching endopodal merus, arcuate, terminally rounded; bilobed epipod originating from short peduncle, with narrow tapered distal lobe. Third maxilliped (Fig. 2g, setation not shown) with small, naked, terminally acute, rudimentary exopod and large setose endopod; endopodal ischium subrectangular, length almost 2 times width, internal surface with low, unarmed longitudinal ridge or elevation, strongest proximally; merus subtriangular, broader than long; carpus subtriangular, slightly longer than broad; propodus large, ovoid, about as broad as long; dactylus narrow, arcuate, long setae of extensor and distal margins including stiff bristles at subtruncate terminus.

Branchial formula as reported for *L. sinuensis* and other 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 first through fourth pereiopods.

Major cheliped located on either right or left side of body, shape and ornamentation sexually dimorphic. Major cheliped of mature male (Fig. 1b, 2h, i, 3a, b) massive and strongly armed; ischium slender, superior margin sinuous, row of small denticles on proximal two-thirds of inferior (flexor) margin, row usually terminated distally with 1–4 stronger, well-separated teeth; merus with distinct, U-shaped or undercut notch in proximal one-fifth of superior margin, inferior (flexor) margin subangular, with strong, sinuous proximal hook offset on inner surface from base of keel, hook variously bifid terminally, usually with sharp tip and weaker subterminal spine or lobe, distal half of inferior margin with several (usually 4–6) strong subtriangular denticles, strongest forming angular bend of inferior margin; carpus broad, subquadrate to subrectangular, superior and inferior margins keeled, nearly parallel to weakly convergent in distal half, terminated distally in angular corners, keel along proximal lobe of arcuate inferior margin variably sinuous; propodus broad, heavy, length of fixed finger subequal to or slightly exceeding one-half length of palm; inner surface of palm swollen proximally, producing smooth boss centered above midline; outer surface with unarmed longitudinal carina and adjacent furrow extending posteriorly from gape of fingers; distinct keel of superior propodal margin restricted to proximal one-half, keel of inferior margin distinct proximally, distally diminished, and overlain by setose punctae; subtriangular, distally directed tooth at proximal end of gape, tooth undercut by broadly U-shaped notch at base of fixed finger, notch terminated distally by low prehensile tooth near two-thirds to one-half length of finger; fixed finger lacking well-defined separation of inner and outer prehensile margins, at most with low outer carina running from single tooth toward upturned tip of finger; dactylus with sharp, hooked tip, superior margin with one or more erect tubercles at proximal end, inferior surface lacking defined separation of inner and outer prehensile margins, usually with 2 large, variously subdivided (sometimes appearing as 3 or more) prehensile teeth, proximal tooth centered near one-third length and sometimes weakly bilobed, knobbed or tuberculate, separated by U-shaped gap from broader more commonly subdivided distal tooth, distal shoulder of which often notched to produce separate tooth or series of small teeth running distally, all of which sometimes with minute tubercles terminally. Major cheliped of female less massive (Fig. 3c–e), less strongly armed and furrowed than that of mature males (as also in juvenile males and males with regenerated major chela), though small sinuations of proximo-inferior margin of carpus usually remaining apparent; outer prehensile margins of fixed finger and dactylus weakly serrate, dactyl relatively less massive and fixed finger broader than in males, notch at base of fixed finger reduced to narrow crevice; superior and inferior margins of propodus distinctly converging distally, inferior margin broadly sinuous; when fingers closed, dactyl usually overreaching fixed finger, tips slightly crossing, gape filled, and entire chela tapered to acute distal end.

Minor cheliped (Fig. 1c, 3f) sparsely armed, ischium with row of minute denticles or tubercles on most of flexor margin; merus usually unarmed, rarely with small denticle on proximo-inferior margin; carpus with blunt, angular or acuminate distal corners, either of which sometimes tipped by spine or turbercle; fixed finger with dense brush of setae on proximal three-fifths of inner and outer prehensile margins, neither of which set in conspicuous excavation, setae largely filling gape between fingers; setation similarly developed in mature males and females, gape slightly larger in males; dactylus with dentition of inferior (prehensile) surface limited to low, rounded tubercles over proximal four-fifths, subterminally with broad tooth on outer prehensile margin opposing similar low tooth or swelling centered near three-fourths length of prehensile margin on fixed finger, each finger terminating in corneous tubercle.

Second pereiopod (Fig. 2j, setation not shown) chelate, flexor margins of ischium, merus, and carpus lined with evenly spaced long setae, inferior margin of propodus with setae long proximally, progressively more reduced in length and stiffened distally, subterminally becoming dense patch of short, stiff bristles; middle one-third of fixed finger with dense patch of short, stiff bristles just outside prehensile margin; tips and distal prehensile margins of both fingers corneous; superior margin of dactylus with stiff, arched bristles reduced in length distally. Third pereiopod (Fig. 2k, setation not shown) merus

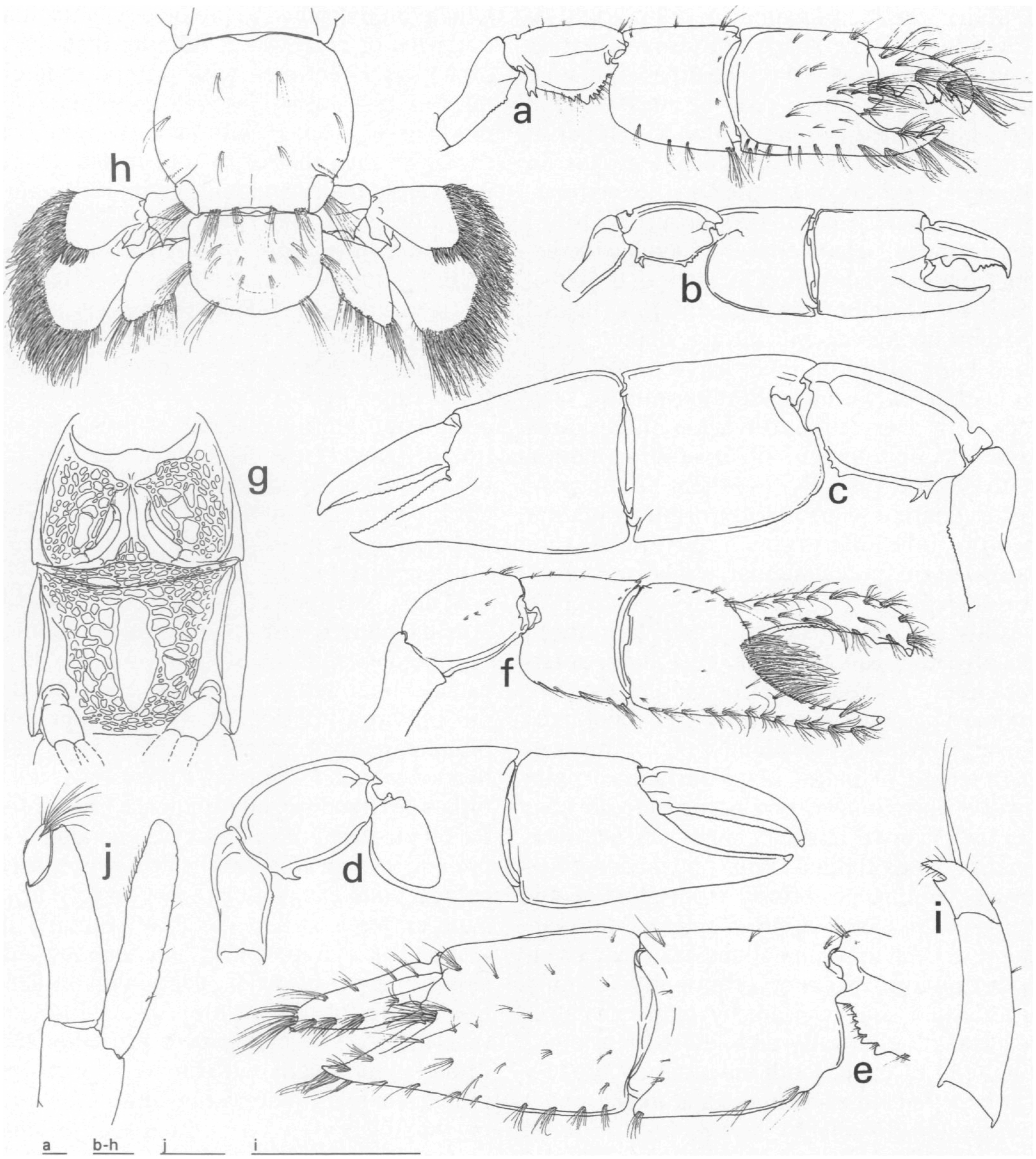


Fig. 3. *Lepidophthalmus jamaicense* (Schmitt, 1935), males from river mouth near Speyside, Tobago, USNM 277782 (CL 14.8 mm for a, f; 9.0 mm for b; 15.0 mm for g–j): a, major cheliped, external surface; b, major cheliped, internal surface, setae not shown; f, minor cheliped, internal surface; g, anterior abdominal somites, ventral surface, microsetation of sclerites not shown; h, sixth abdominal somite, telson and uropods, dorsal surface; i, right first pleopod (gonopod), external surface; j, right second pleopod, anterior surface. *L. jamaicense* (Schmitt, 1935), females from river mouth near Speyside, Tobago, USNM 277782 (CL 15.4 mm for c; 15.7 mm for d): c, major cheliped, internal surface, setae not shown; d, regenerated major cheliped, internal surface, setae not shown. *L. jamaicense* (Schmitt, 1935), female from Playa Siboney, Cuba, RMNH D–30630 (CL 14.8 mm); e, major cheliped, external surface. Scales lines indicate 2 mm.

length about 2.2 times width; propodus with inferodistal margin below articulation of dactylus bilobate, lobes demarcated by furrows on internal surface, distal margins of both lobes with stiff bristles concentrated on prominences and absent from depressions, those near middle of upper lobe partially concealing prominent, corneous, distally directed tooth arising from margin; longest setae on inferior margin of lower lobe, patterned tufts of lighter setae on outer face of article; dactylus subtriangular, most of superior margin sinuous, narrowed distally to short, thick laterally directed neck giving rise to slightly narrower laterally directed corneous tooth, outer surface with lower field of fine stiff setae grading to pattern of setal tufts in upper half. Fourth pereiopod (Fig. 2l, setation not shown) weakly subchelate, inferodistal process of propodus (=fixed finger) distinct angular lobe extended distally at least one-third length of dactylus, lower margin of lobe with usually singular, well-developed, articulated corneous spine, often obscured by dense brush of stiff setae, dactylus subtriangular, superior margin slightly sinuous, narrowed distally to short, thick, laterally directed neck giving rise to slightly narrower laterally directed corneous tooth. Fifth pereiopod (Fig. 2m, setation not shown) minutely chelate, opposable surfaces of fixed finger and minute dactylus spooned, terminally rounded, forming beaklike chela obscured by dense fields of setation on distal two-thirds of propodus and superior surface of dactylus, deflected tip of dactylus narrow, no broader than spooned terminus of fixed finger.

Abdominal somites mostly smooth dorsally, glabrous; first abdominal tergite (Fig. 1d) with thickened, translucent, subrectangular middorsal sclerite, flanked to either side by triangular membranous areas sometimes bearing scattered small, minutely setose plates, membranous areas enclosed laterally by arms of anterolateral sclerite diverging to posterior of somite; second tergite with posterolateral lobe below suture sclerotized much as remainder of tergite, lobe with sparse anterior and posterior transverse lines of inconspicuous setae, except for elongate tuft in posterolateral extreme; third to fifth tergites each encompassing finely setose, lateral, membranous subcircular or suboval area, that of third tergite larger, more circular and more posterolaterally positioned than in fourth and fifth tergites; sixth tergite (Fig. 1i, 3h) with 2 posterolateral lines of short setae anterior to posterolateral groove from which transverse and posterior sutures originating, longest line adjacent and subparallel to transverse suture lacking terminal bifurcation, posterior suture directed from posterolateral groove to posterior margin through 2 angular bends, tufts of stiff setae medial to 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. 1e, 2r, s, 3g) armored extensively with plates and tubercles; heavy ridges at base of, alongside, and anterior to first pleopods in flexed position, pair of broad, thin plates posterior to origins of first and second pleopods (sometimes concealed by intersegmental fold of cuticle); complex pattern of multiple plates and tubercles arming most of ventral cuticle on second somite, bearing large, flat, elongate median plate; larger of surrounding plates and tubercles often surmounted by 1–5 short bristles.

First pleopod of male and female uniramous, composed of 2 articles; in male (Fig. 1e, f, 2n, o, r, 3g, i) originating just anterior to midwidth of broad corneous plate (plate concealed by body folds in figures), length less than one-half that of second pleopod, proximal article more than 2 times length of terminal article, terminal article subspatulate and bifurcate, anteriorly directed tip bearing few long terminal and subterminal setae; in female (Fig. 2p), total extended length subequal to that of second pleopod, proximal article slightly shorter and heavier than terminal article, terminal article narrowed to spatulate blade beyond midlength, both articles bearing long setae. Second pleopod of male and female biramous, with appendix interna on endopod; appendix interna of male (Fig. 1g, 3j) large, ovoid, dense setation restricted to terminus distinctly overreaching tip of endopod, small field of rudimentary hooked setae on posteromesial shoulder (Fig. 1h); in female (Fig. 2q, setation not shown), both rami setose, appendix interna small, elongate. 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, articulation of stubby appendix interna embedded into mesial margin. Telson (Fig. 1i, 3h) broad, subrectangular, width about 1.4 times length, posterior margin weakly trilobate, median lobe of posterior margin extending slightly farther to posterior than posterolateral lobes; dorsal surface usually with 4 pairs of setal tufts, of which 2 anteriormost set well lateral of midline in anterior half, 2 or more short median pairs mostly positioned to posterior of these; lateral margins typically with pair of setal tufts near midlength, posterior margin with tuft on each of weak posterolateral lobes. Uropod (Fig. 1i, 3h) usually with short, posteriorly directed spine on protopod overreaching anterior margin of endopod and short, posterior spine (sometimes nearly bifid; broken in paratype) on proximal article of exopod abutting anterior margin of extended endopod; endopod elongate, ovoid to subrhomboidal, at least twice as long as broad, tapered to rounded terminus bearing marginal fringe of long setae, posteromesial margin with broken fringe of setae; exopod with anterodorsal plate falling well short of distal endopodal margin, distal edge of plate with short, thick, spiniform setae grading to thinner, dense, elongate setae of exopod margin, posterodistal corner of plate bearing dense field of long, stiff, spiniform setae; distal margin of exopod with dense fringe of setation, longest posteriorly.

Size.—On basis of postorbital lengths, measured after preservation, largest male from the Mosquito Cove River, Jamaica (CL 16.8 mm, TL 78.5 mm); largest females from near Speyside, Tobago (CL 16.5 mm, TL 77.8 mm) and mouth of Caño Tunantal, Venezuela (CL 17.5 mm, TL 77.5 mm). Egg size unknown, since no ovigerous specimens collected to date.

Color (based primarily upon 35-mm color slides of live topotypic male, USNM 277781, from Mosquito Cove River site, Jamaica, photographed 30 November 1991; supplemented by field notes on other live specimens from same site).—Integument largely translucent except for varied opaque white over much of third maxillipeds, chelipeds, remaining pereiopods, anterior of carapace, dorsal extreme of cervical groove, and somewhat on dorsal sclerites of first abdominal tergite; brown to yellow brown on setal tufts; and dark pigmentation of eyestalks and as small crescent under articular membrane near midlength of antennal peduncle (appearing to be in proximal extreme of fourth peduncular segment of most preserved specimens). Major chela often with faint rose or less commonly diffuse yellow near articulations or on dorsal surfaces of articles; rose chromatophores and general pale rose cast evident on more opaque regions of cuticle anterior and anterolateral to dorsal oval just posterior to front of carapace; rose sometimes extended onto opaque cuticle of rostral base. Distinct, complex pattern of small rose to rust chromatophores always evident dorsally on abdominal somites 3–6 and telson, patterned somewhat as previously described in *L. louisianensis* (see Williams *et al.,* 1989:fig. 4 of second color plate), forming a poorly defined longitudinal band to either side of abdominal midline on abdominal somite 6; abdominal somites 3–5 with varying intensity of translucent pale brown to yellow ground color as patch on setose dorsolateral lobes of each tergite; similar translucent ground color on anterior of dorsal membranous areas of first abdominal tergite, thicker parts of pleopods 3–5, much of both uropods and posteriorly on telson. Translucence of abdomen revealing large yellow lobes of hepatopancreas filling anterior somites of abdomen.

Known Range and Habitat.—Lepidophthalmus jamaicense is known from only northwestern Jamaica and the adjacent coastline of southeastern Cuba in the northern Caribbean Sea, and from Tobago and eastern Venezuela in the extreme southeastern Caribbean Sea. This species constructs burrows to unknown depths in margins and shallow benthic sediments of brackish to nearly fresh coastal pools and rivers, or in intertidal to shallow subtidal substrates of estuarine beaches near the mouths of rivers; typical substrates include mixtures of stones and gravel overlying clayey to muddy sands, sandy river mouth bars and margins, or sand-dominated estuarine beaches mixed with coralline rubble. It is adapted to oligohaline habitats, some of which may be isolated ephemerally from the sea and exposed to only occasional tidal effects; salinities of overlying waters were measured at 1 ppt in the Mosquito Cove River of Jamaica, and overlying waters were noted to be nearly fresh where animals were taken in Tobago. While most of these habitats appear subject to periodic flooding by riverine fresh-water runoff, deep burrows of the animals may access higher salinity pore waters retained in sediments.

Remarks.—Definitive comparison of *L. jamaicense* to *L. richardi,* new species, and further comment on its relation to other congeners is undertaken in the Remarks section following the description of *L. richardi* below. From our study of the two type specimens and the recently obtained topotypic series, it is apparent that *L. jamaicense* is a western Atlantic representative of the ventrally armored component of the genus. It shares that general character not only with *L. richardi,* herein described as a new species, but also with *L. sinuensis* from Colombia (Fig. 7c–e) and most materials of the genus from the eastern Pacific which we currently have under review, including *L. eiseni* and *L. bocourti* (A. Milne-Edwards). However, of the three western Atlantic plated species, only *L. jamaicense* has the median plate of the second abdominal somite flattened, without a median longitudinal furrow. All such ventral armor is lacking in *L. louisianensis,* the northernmost ranging of the western Atlantic species, *L. siriboia,* the southernmost ranging of the western Atlantic species, and a newly discovered species which constitutes the southernmost known population in the eastern Pacific (Felder and Manning, in preparation). These species also appear to lack a complete posterior suture to demarcate the posterolateral lobe of the sixth abdominal tergite, a feature which is well developed in all three of the ventrally plated western Atlantic species. However, *L. jamaicense* resembles the unplated western Atlantic species in the development of a relatively large appendix interna on the male second pleopod, a feature which also distinguishes it from the other two ventrally plated western Atlantic species. Further comparison of its characters, including those which link or separate Atlantic and Pacific populations, will be deferred until the latter have been adequately redescribed.

A peculiar small crescent of dark pigmentation at the articulation between the third and fourth articles of the antennal peduncle was first observed in live specimens of *L. jamaicense* from Jamaica (by DLF) and thought to be unique to that species. However, this feature was subsequently discerned in preserved materials of *L. richardi,* new species (see below), *L. sinuensis,* and *L. louisianensis,* and may occur to some extent in all or most species of the genus. While it may represent nothing more than a recurrent chromatophoric pattern, its consistent placement and configuration suggest that it could be a functional, accessory light-sensitive ocellus, though we are unaware that any such organ has been reported previously among the thalassinids. We can postulate some utility for such a receptor, perhaps in predator avoidance when the shrimp occasionally approaches and inserts its antennae up the narrowed surface chimney of its burrow, while briefly expelling a dense stream of sedimentary ejecta that blocks light to the eyes. Such behavior has been observed occasionally for *L. louisianensis, L. sinuensis,* and other thalassinids (DLF, unpublished), both in the field and in laboratory fossoria.

The presumed broad distribution of *L. jamaicense,* herewith documented on the basis of records from opposed coastlines of Cuba and Jamaica in the northwestern Caribbean and from proximate areas of Venezuela and Tobago in the extreme southeastern Caribbean, is not readily predictable on the basis of known larval histories in the genus. Whereas ovigerous females have yet to be found for *L. jamaicense,* and the life history remains unknown, both *L. louisianensis* and *L. sinuensis* have very abbreviated larval life histories which appear to favor retention of recruits within estuarine habitats and thus limit larval dispersal (Felder *et al.,* 1986, 1995; Nates *et al.,* in press). The relatively large egg size in ovigerous females of *L. siriboia* from Brazil (Felder and Rodrigues, 1993) and in selected eastern Pacific congeners (DLF, unpublished) is comparable to that in the aforementioned species, and suggests that all these may share such abbreviated development. Estuarine retention and limited dispersal may account for the very restricted distribution of *L. sinuensis,* known to date from only a few proximate estuaries on the Colombian coast. The wider distribution of the northern Gulf of Mexico endemic, *L. louisianensis,* a species with similar limitations to larval dispersal and adult habitats, may be accounted for by the relative lack of isolation between estuaries which define the range there. However, the distribution of *L. jamaicense* suggests a greater than expected capacity for interinsular dispersal in this species, which may be linked to unique attributes of life history or to less estuarine restriction in adult habitat than suggested by presently available records. In that case, the species should be expected to occur in appropriate substrates throughout the northern and eastern Antilles, and perhaps elsewhere along the Mesoamerican mainland. Alternatively, a long history of intra-Caribbean maritime trade, much conducted through shipping ports based in river mouths, might have at some point facilitated introductions. However, any abbreviation of larval history in this species, as well as the restriction of its postlarvae to a fossorial existence, would limit ballast water transport as a possible pathway.

In the course of using yabby pumps to collect materials of *L. jamaicense* from near the mouth of the Mosquito Cove River, Jamaica, single specimens of a caridean shrimp, *Micratya* sp., and a laomediid thalassinid shrimp, *Axianassa jamaicensis* Kensley and Heard (the first female specimen of this species), were also aspirated from associated sediments. This caridean, possibly a specimen of *M. poeyi* (Guérin-Méneville), occurs typically in lower reaches of streams on West Indian islands, often associated with pebbles and rocks (Chace and Hobbs, 1969), such as occurred in the lower Mosquito Cove River. The laomediid was previously known only from the holotype male which was, as for the types of *L. jamaicense,* collected at Montego Bay, Jamaica, by C. B. Wilson in 1910 (Kensley and Heard, 1990). Other than being collected in the same locality, there is no evidence that either of these species represents a commensal association with *L. jamaicense.*

Lepidophthalmus richardi, new species
Figs. 4a–j, 5a–f, 6a–i, 7a

Lepidophthalmus jamaicense complex.—Felder *et al.*, 1991: 101A (part of Caribbean group assigned to "complex").

Callianassa jamaicense.—Dworschak, 1992: 196–198, fig. 4a–d (part, Belizian only).

Material Examined.—HOLOTYPE.—shelly, muddy, quartzite riverine sand of intertidal shoreline at Pelican Beach Hotel, near Dangriga (Stann Creek Town), Belize, 18 April 1983, collected by R. B. Manning and D. L. Felder, 1 ♂ (CL 14.5 mm), photographic voucher, USNM 277777. PARATYPES.—same locality, date, and collectors as holotype, 10 ♂♂ (2 imm), 8 ♀♀ (1 illustrated), USNM 277779, 2 ♂♂, 2 ♀♀, USLZ 3577.—muddy bank near mouth of Monkey River estuary, Belize, 3 May 1983, collected by R. B. Manning and D. L. Felder, 2 ♂♂ (1 illustrated), 2 ♀♀, USNM 277778.

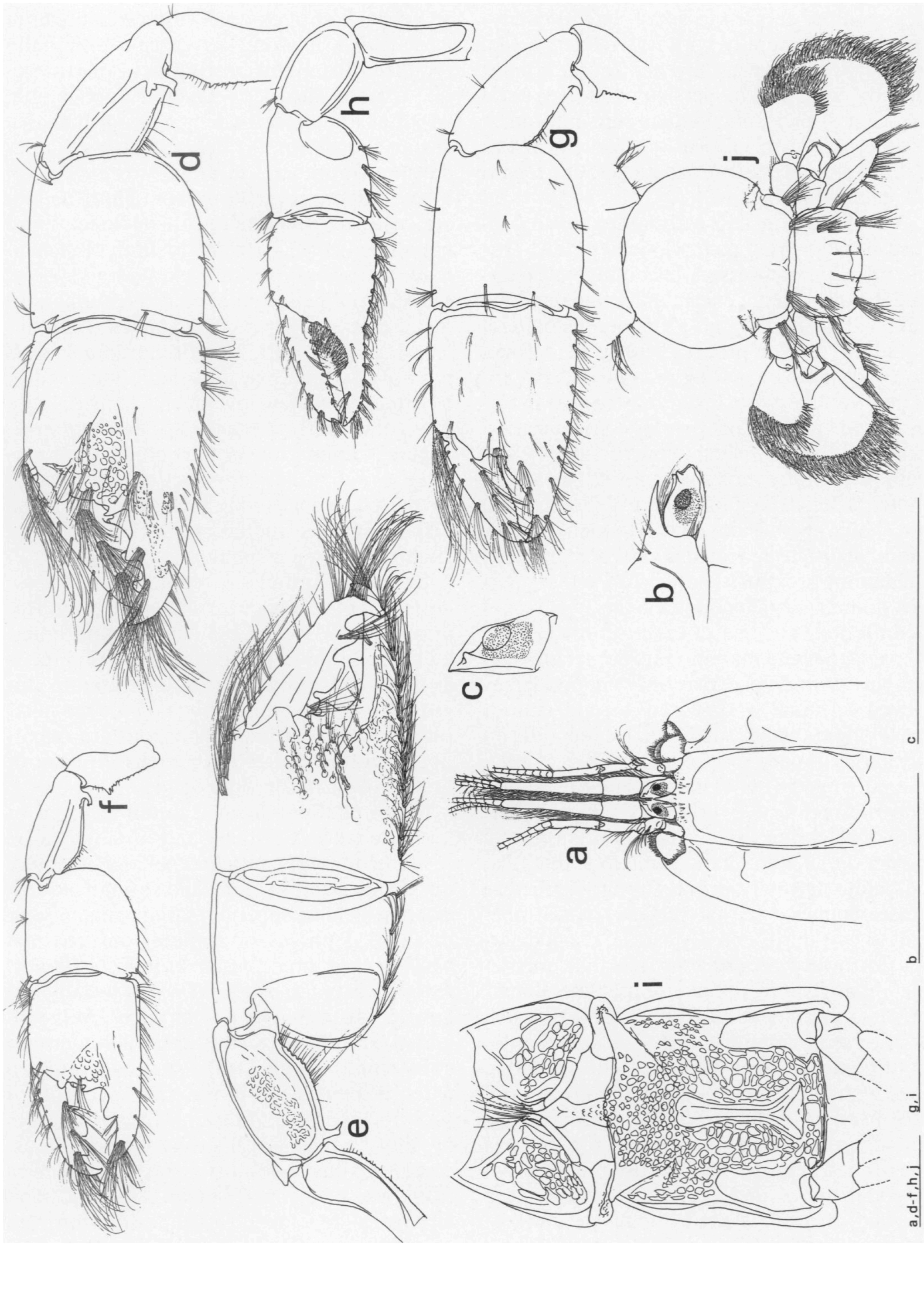
Description (based upon holotype male, USNM 277777, and male and female paratypes, USNM 277778, 277779, USLZ 3577).—Frontal margin of carapace with acute, narrow rostral spine flanked laterally by low, slightly produced rounded shoulders (Fig. 4a), their apices immediately lateral to eyestalks; rostral spine usually directed forward or arched slightly upward in mature specimens (Fig. 4b), less so in juveniles, extending about one-half to three-fourths length of eyestalks in dorsal view, ventral base of spine with tuft of setae, longest of which extending anteriorly between eyestalks to or just beyond cornea. Carapace anterior to dorsal oval with pairs of short setose punctae on either side of midline and scattered smaller punctae laterally; dorsal oval well defined, smooth, usually with single pair of widely separated, small, setose punctae near or just anterior to midlength and short transverse lateral lines of smaller punctae in posterior third, length of oval about seven-tenths of postrostral carapace length; marginal suture of oval diminished at anterior midline, stronger and with cornified tubercular articulation to cardiac region at posterior midline.

Eyestalks subtriangular in dorsal view, reaching to or nearly to distal end of basal antennal article; anterolateral margins tapered to thin, arcuate edge, dorsomesial margin with strong marginal tooth arising at about three-fourths length, inclined or arched toward subacute terminal end of eyestalk (Fig. 4b, c); distinct, pigmented cornea centered on dorsal surface, area of subcuticular pigmentation often much broader than faceted surface. Antennular peduncle heavier, longer than antennal peduncle (Fig. 4a); 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, ventrally directed setae; rami of flagellum slightly longer than third article of peduncle, ventral ramus slightly longer and with much denser, longer setation than dorsal ramus, subterminal articles of dorsal ramus heavier than those of ventral ramus and with short ventral setae. Antennal peduncle reaching just to or almost to midlength of third article of antennular peduncle; basal article with dorsolateral carina strongest proximally, forming lip above excretory pore, lip abutted to ridge on anterior margin of carapace, ventrally with setose distomesial protuberance; second article ventrally with large longitudinal suture, distally with field of long setae on angular boss lateral to ventral suture; third article elongate, subequal to combined lengths of first 2, slightly shorter than fourth, proximally forming shoulder sutured to small, lateral condylar element, laterally with row of long setae; articulation between third and fourth articles usually with small, persistent, dorsolateral crescent of dark subcuticular pigment; fourth article narrower, less setose than third; flagellum sparsely setose, about 3 times length of antennular flagella.

Mandible (Fig. 5a) with large, heavily setose, 3-segmented palp, elongated third article of palp compressed, becoming subspatulate distally, truncate terminally; gnathal lobe subquadrate, with bluntly angular distolateral shoulder, incisor process with well-defined corneous teeth on cutting margin, concave internal surface with lip giving rise to molar process bearing 2 or 3 small corneous teeth proximal to incisor teeth; thin, rounded paragnath set against proximal convex surface of molar process. First maxilla (Fig. 5b, setation not shown) with endopodal palp long, narrow, terminal article deflected at poorly defined articulation; proximal endite with setose margin sinuous, distal endite elongate, terminally broadened and setose; exopodite low, rounded. Second maxilla (Fig. 5c, setation not shown) with setose margins, endopod narrowed terminally, first and second endites each longitudinally subdivided, exopod forming large, broad, scaphognathite. First maxilliped (Fig. 5d) with setose margins, endopod rudimentary, overlain by distal endite; proximal endite thick, angular, distomesial corner directed to internal side of endite; distal endite narrowly ovoid, strongly arched to create convex external surface, mesial one-half to two-thirds densely setose; exopod narrowed toward proximal articulation, incompletely divided by oblique suture, lateral margin near midlength marked by shallow notch at intersection with suture, mesial margin with comb of close-set 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. 5e) with setose margins, endopodal merus and propodus arcuate, both slightly broader distally than proximally, flexor margin of merus with comb of closely set, long setae, internal surface distally produced to form rounded lobe extending over internal surface of short carpus; length of merus less than 4 times width; length of propodus near three-fourths length of merus, longest setae originating on extensor margin and distal half of external surface; dactylus at least twice as long as broad, terminally rounded, distal half bearing field of stiff setae; exopod distinctly tapered over length, width at three-fourths length about half that at one-fourth length, overreaching endopodal merus, arcuate, terminally rounded; bilobed epipod originating from short peduncle, with narrow tapered distal lobe. Third maxilliped (Fig. 5f) with small, thick, terminally setose rudimentary exopod and large, setose endopod; endopodal ischium subrectangular, length about 1.5 times width, internal surface with low, longitudinal crest proximally, fading at midlength, unarmed or bearing at most few low tubercles; merus subtriangular, broader than long; carpus subtriangular, slightly longer than broad; propodus large, ovoid, usually broader than long; dactylus narrow, arcuate, long setae of extensor and distal margins including stiff bristles at slightly truncate terminus.

Branchial formula as reported for *L. sinuensis* and other 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 first through fourth pereiopods.

Major cheliped located on either right or left side of body, shape and ornamentation sexually dimorphic. Major cheliped of mature male (Fig. 4d–f) massive and strongly armed; ischium slender, superior margin sinuous, row of small denticles or spinules on proximal two-thirds to three-fourths of inferior (flexor) margin, teeth largest distally, row usually terminated distally with 1–4 stronger, well-separated spiniform teeth, largest sometimes compound; merus with shallow rounded notch or depression in proximal one-fifth of superior margin, inferior (flexor) margin broadly rounded, with strong, angular or arcuate proximal hook offset on outer surface from base of distinctly bicarinate keel, hook terminally developed to single spiniform tip or with terminal spine and weak subterminal lobe, distal two-fifths of inferior meral margin with row of several (usually 3–5) subtriangular denticles derived from inner carina, obscured by parallel row of intracarinal setae set immediately to inner side of outer carina; carpus broad, subquadrate, end superior



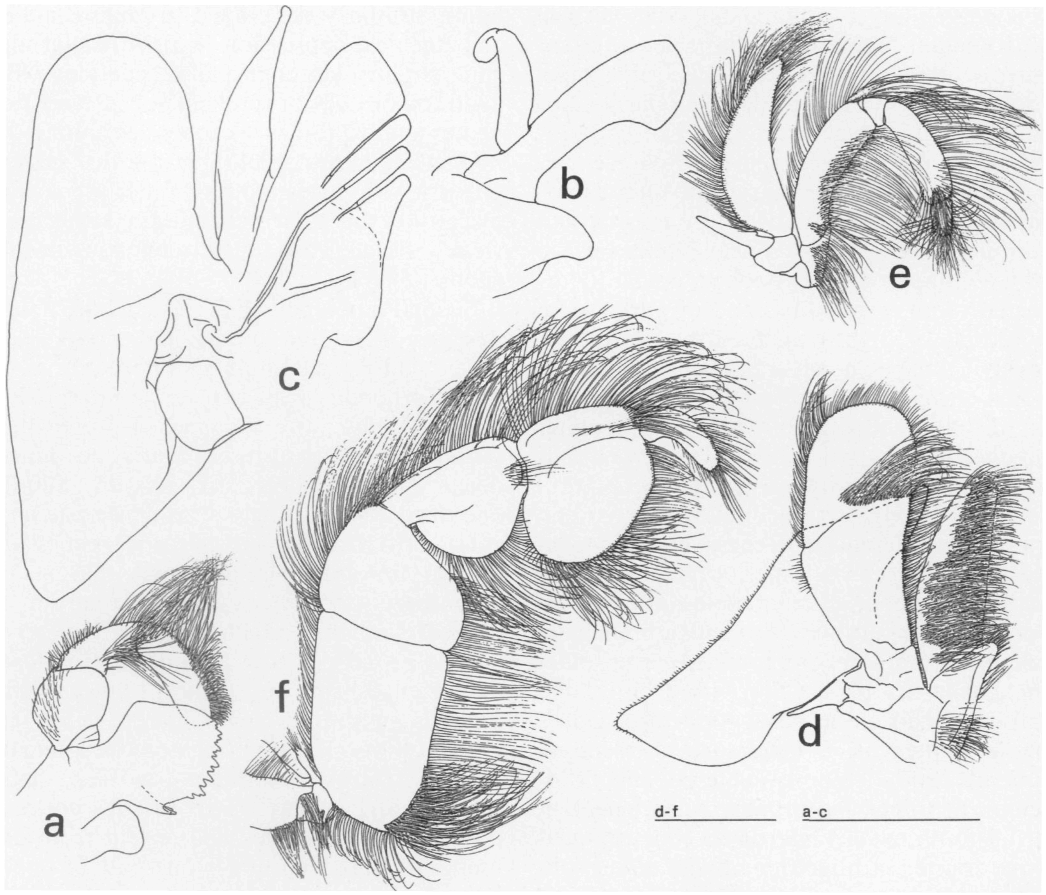


Fig. 5. *Lepidophthalmus richardi,* new species, male holotype from near Dangriga (Stann Creek Town), Belize, USNM 277777 (CL 14.5 mm): a, right mandible and paragnath, external surface; b, right first maxilla, external surface, setae not shown; c, right second maxilla, external surface, setae not shown; d, right first maxilliped, external surface; e, right second maxilliped, external surface; f, right third maxilliped, external surface. Scale lines indicate 2 mm.

and inferior margins keeled, nearly parallel in distal half, terminating distally in angular corners, keel along proximal lobe of arcuate inferior margin smoothly rounded; propodus broad, heavy, length of fixed finger distinctly exceeding one-half length of palm; inner surface of palm swollen proximally, producing smooth proximal boss centered at or slightly below midline, rounded carina and shallow adjacent furrow extending slightly proximal from fixed finger below subtriangular field of rounded tubercles proximal to gape of fingers and above irregularly punctate and eroded lower surfaces of palm and finger (most con-

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Fig. 4. *Lepidophthalmus richardi,* new species, male holotype (CL 14.5 mm) from near Dangriga (Stann Creek Town), Belize, USNM 277777 (CL 14.5 mm): a, anterior carapace, eyestalks, and antennae, dorsal surface; b, right eyestalk and rostrum, lateral view; c, right eyestalk, dorsomesial surface; d, major cheliped, external surface; e, major cheliped, internal surface; h, minor cheliped, internal surface; i, anterior abdominal segments, ventral surface, microsetation of sclerites not shown; j, sixth abdominal somite, telson, and uropods, dorsal surface. *L. richardi,* new species, male paratype from near mouth of Monkey River, Belize, USNM 277778 (CL 9.0 mm): f, major cheliped, external surface. *L. richardi,* new species, female paratype from Dangriga (Stann Creek Town), Belize, USNM 277779 (CL 10.9 mm): g, major cheliped, external surface. Scale lines indicate 5 mm.

spicuous in larger individuals); outer surface with sinuous longitudinal carina and adjacent furrow extending proximally from gape, forming inferior border for triangular field of rounded tubercles; distinct keel of superior propodal margin restricted to proximal one-half, keel of inferior margin distinct proximally, distally overlain by setose punctae and forming inferior lip for concave inner surface of fixed finger; weakly hooked, upwardly directed tooth at proximal end of gape, tooth bordering or slightly undercut by broad, variously U-shaped notch at base of fixed finger, notch terminated distally by strong, triangular, distally inclined tooth derived from outer prehensile margin near two-fifths to one-half length of finger; inner prehensile margin forming strong, rounded carina extending onto palm; dactylus with sharp, hooked or angularly deflected tip, superior margin weakly carinate, without erect tubercles, at proximal end, inferior surface with inner prehensile margin forming smooth, rounded carina, outer prehensile margin usually with 3 large, distally inclined teeth, basal tooth broad, low molar abutted on its inner surface by strong tubercle, middle tooth centered near midlength of finger and broadly subrectangular, distal tooth usually narrower, centered near three-fourths of finger length and either subtriangular or tapered to truncate terminus. Major cheliped of female less massive (Fig. 4g), less strongly armed and furrowed than that of mature males (as in juvenile males); outer prehensile margins of fixed finger and dactylus weakly serrate, dactyl relatively less massive and fixed finger basally broader than in males, base of fixed finger with open U-shaped or V-shaped notch proximal to angular prehensile tooth; superior and inferior margins of propodus slightly convergent distally, inferior margin broadly arcuate; when fingers closed, tips crossing conspicuously and dactyl filling gape, except for basal notch in fixed finger.

Minor cheliped (Fig. 4h) sparsely armed, ischium with at most row of minute denticles on most of flexor margin; merus usually unarmed; carpus usually with bluntly angular distal corners; proximal one-half of fixed finger with dense brush of setae set in broad excavation of prehensile margins, densest setation distally terminating at broad swelling or tooth centered near midlength of finger, setae largely filling gape between fingers; setation similarly developed in mature males and females, depression in fixed finger and gape slightly larger in males; dactylus with dentition of inferior (prehensile) surface limited to at most few weak tubercles among setal punctae in proximal three-fourths, subterminally with broad tooth on outer prehensile margin, distal to which margin sometimes weakly serrate; each finger terminating in corneous tubercle.

Second pereiopod (Fig. 6a) chelate, flexor margins of ischium, merus, and carpus lined with evenly spaced long setae, inferior margin of propodus with long setae proximally, progressively more reduced in length and stiffened distally, subterminally becoming dense patch of short, stiff bristles; middle one-third of fixed finger with dense patch of short, stiff bristles just outside prehensile margin; tips and distal prehensile margins of both fingers corneous; superior margin of dactylus with stiff, arched bristles reduced in length distally. Third pereiopod (Fig. 6b) merus length barely exceeding 2 times width; propodus with inferodistal margin below articulation of dactylus bilobate, lobes demarcated by furrows on internal surface, distal margins of lobes with stiff bristles concentrated on prominences and absent from depressions, those on upper one-half of upper lobe partially concealing blunt, corneous, distally directed tooth arising from margin; longest setae on inferior margin of lower lobe, patterned tufts of lighter setae on outer face of article; dactylus tear-shaped, distal half of upper margin weakly sinuous, narrowed distally to short neck giving rise to laterally directed corneous tooth of same diameter, outer surface with lower field of fine stiff setae grading to pattern of setal tufts in upper half. Fourth pereiopod (Fig. 6c) weakly subchelate, inferodistal process of propodus (=fixed finger) distinct angular lobe extended distally at least one-fourth length of dactylus, lower margin of lobe with usually 2–4 articulated corneous spines, obscured by dense brush of stiff setae, dactylus tear-shaped, without weak sinuations on superior margin, article narrowed distally to short narrow neck giving rise to laterally directed corneous tooth. Fifth pereiopod (Fig. 6d) minutely chelate, opposable surfaces of fixed finger and minute dactylus spooned, terminally rounded, forming beaklike chela obscured by dense fields of setation on distal two-thirds of propodus

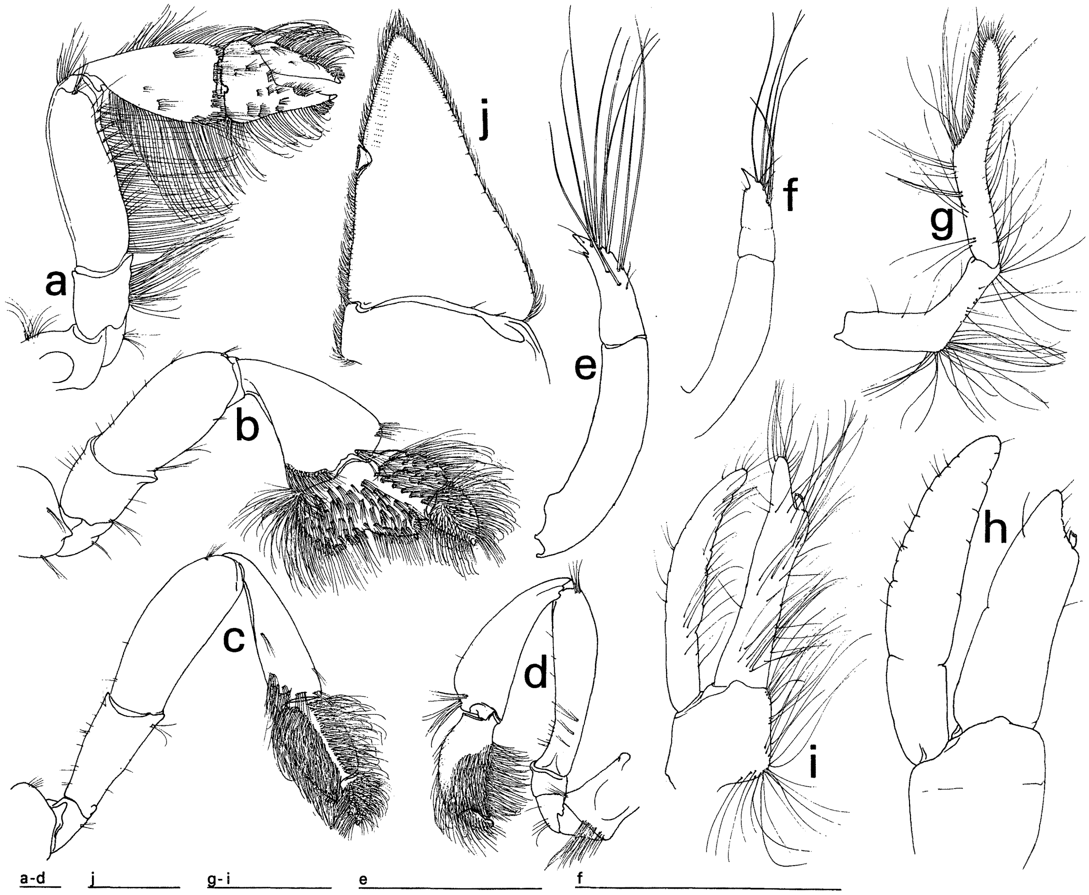

Fig. 6. *Lepidophthalmus richardi,* new species, male holotype from near Dangriga (Stann Creek Town), Belize, USNM 277777 (CL 14.5 mm): a, right second pereiopod, external surface; b, right third pereiopod, external surface; c, right fourth pereiopod, external surface; d, right fifth pereiopod, external surface; e, right first pleopod (gonopod), lateral surface; h, right second pleopod, posterior surface. *L. richardi,* new species, male paratype from mouth of Monkey River, Belize, USNM 277778 (CL 9.0 mm): f, right first pleopod (gonopod), lateral surface. *L. richardi,* new species, female paratype from near Dangriga (Stann Creek Town), Belize, USNM 277779 (CL 10.9 mm): g, right first pleopod, lateral surface; i, right second pleopod, posterior surface. Scale lines indicate 2 mm.

and superior surface of dactylus, deflected tip of dactylus broad, broader than spooned terminus of fixed finger.

Abdominal somites mostly smooth dorsally, glabrous; first abdominal tergite (Fig. 7a) with thickened, translucent, bell-shaped middorsal sclerite, flanked to either side by narrow membranous areas sometimes bearing few scattered small, minutely setose plates, membranous areas enclosed laterally by arms of anterolateral sclerite diverging to posterior of somite; second tergite with posterolateral lobe below suture sclerotized much as remainder of tergite, lobe with sparse, well-defined anterior and short, ill-defined posterior transverse lines of inconspicuous setae, except for elongate tuft in posterolateral extreme; third to fifth tergites each encompassing finely setose, lateral, membranous subcircular or suboval area, that of third tergite larger, and more posteriorly positioned than in fourth and fifth tergites, that of fifth tergite smallest and most circular; sixth tergite (Fig. 4j) with 2 posterolateral, transverse lines of short setae anterior to posterolateral groove from which transverse and posterior sutures originating, longest line medially divergent from adjacent tranverse suture, transverse suture terminally with at least one bifurcation, posterior suture bent distinctly to posterior at origin from posterolateral groove, continued posteriorly in smooth arch toward poste-

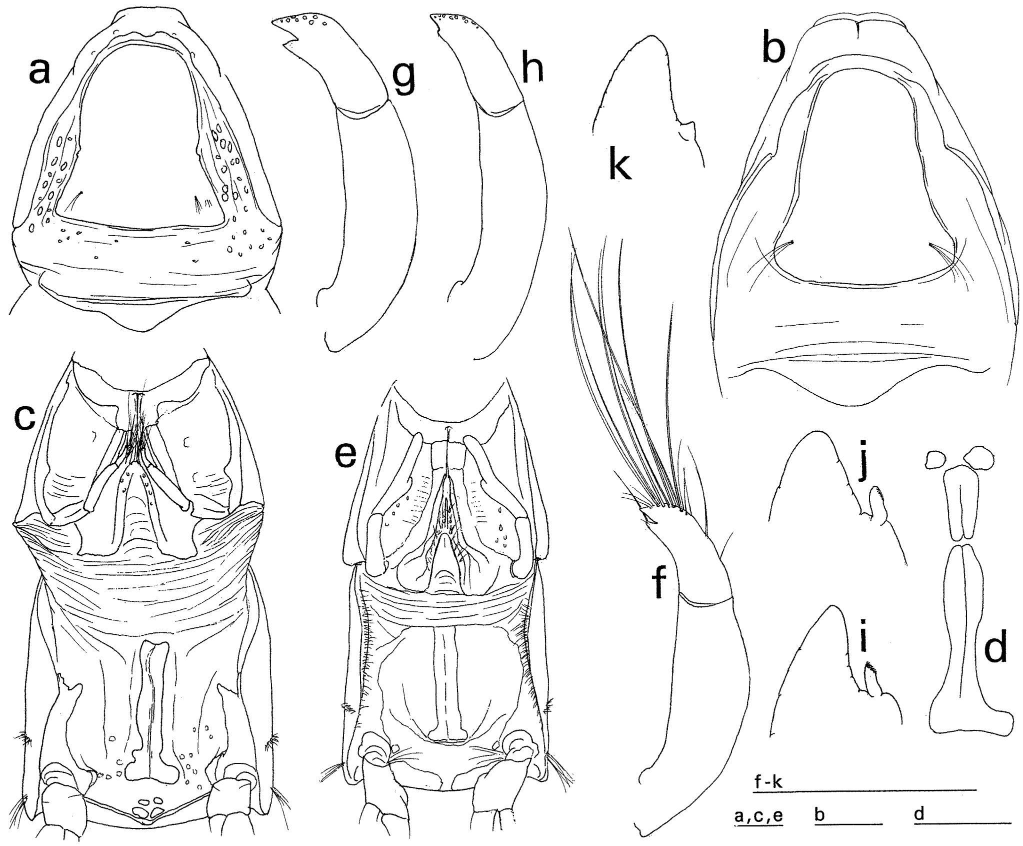

Fig. 7. *Lepidophthalmus richardi,* new species, male holotype from near Dangriga (Stann Creek Town), Belize, USNM 277777 (CL 14.5 mm): a, first abdominal somite, dorsal surface. *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, 1991, southern Caribbean topotypic specimens from Agrosoledad S. A. shrimp farm, Departamento de Cordoba, Colombia, USLZ 3578: b, first abdominal somite of male, dorsal surface (CL 13.5 mm); c, anterior abdominal somites of male, ventral surface (CL 13.5 mm); d, median ventral abdominal sclerites of second abdominal somite in atypical male (CL 14.5 mm); e, anterior abdominal somites of female, ventral surface (CL 12.7 mm); f, right first male pleopod (gonopod), external surface (CL 13.5 mm); g, right first male pleopod (gonopod), external surface, setae not shown (CL 15.2 mm); h, right first male pleopod (gonopod), external surface, setae not shown (CL 14.5 mm); i, appendix interna of right second male pleopod, posterior surface (CL 14.5 mm); j, appendix interna of right second male pleopod, posterior surface (CL 15.2 mm); k, appendix interna of right second male pleopod, posterior surface (CL 13.5 mm). Scale lines indicate 2 mm.

rior margin, primary tufts of stiff setae medial to 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. 4i) armored extensively with plates and tubercles; heavy ridges at base of, alongside, and anterior to first pleopods in flexed position, pair of broad corneous plates posterior to origins of first and second pleopods; complex pattern of multiple plates and tubercles arming most of ventral cuticle on second somite, this somite bearing large, elongate, narrow, longitudinally furrowed median plate; sclerites anterior and anterolateral to median plate usually most erect, dentiform, surrounding sclerites tuberculiform or flat, sometimes ornamented with microtuberculate prominences but lacking distinct sets of bristles.

First pleopod of male and female uniramous, composed of 2 articles; in male (Fig. 4i, 6e, f), originating just anterior to lateral third of broad corneous plate, total length slightly less than one-half that of second pleopod, proximal article less than or subequal to 2 times length of terminal article, terminal article tapering distally, weakly bifurcate and compressed, anteriorly directed tip usually bearing strong subterminal setae; in female (Fig. 6g), total extended length subequal to that of second pleopod, proximal article slightly shorter than terminal article, terminal article narrowed to spatulate blade beyond midlength, both articles bearing long setae. Second pleopod of male and female biramous, with appendix interna on endopod; appendix interna of male (Fig. 6h) minute, markedly overreached by terminus of endopod, without long terminal setation, small field of rudimentary hooked setae on posteromesial shoulder; in female (Fig. 6i), both rami setose, appendix interna small, slightly elongate. 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 pleopod pair subtriangular (Fig. 6j), articulation of stubby appendix interna embedded into mesial margin.

Telson (Fig. 4j) broad, subrectangular, width about 1.6 times length, broadest at, or posterior to midlength, posterior margin distinctly trilobate, median lobe forming slightly upturned lip; dorsal surface usually with 3 primary pairs of setal tufts, of which 2 anteriormost set well lateral of midline in anterior half, with usually more medial pair positioned near midlength; lateral margins typically with pair of setal tufts near midlength (sometimes second tuft in posterior half), posterior margin with erect tuft on each of produced posterolateral lobes. Uropod (Fig. 4j) usually with strong posterodorsally directed tooth on protopod overreaching proximal margin of extended endopod and small tubercle on proximal article of exopod abutting anterior margin of extended endopod; endopod elongate, sinuous, ovoid to subrhomboidal, more than twice as long as broad, tapered to rounded terminus bearing terminal fringe of long setae, posteromesial margin with broken fringe of setae; exopod with anterodorsal plate falling well short of distal endopodal margin, distal edge of plate with short, thick, spiniform setae grading to thinner, dense, elongate setae like those of exopod margin, posterodistal corner of plate bearing dense field of long, stiff, spiniform setae; distal margin of exopod with dense fringe of long and short setation, longest of which predominating posteriorly.

Size.—On basis of postorbital lengths, largest known male being holotype from Dangriga (Stann Creek Town), Belize (CL 14.5 mm, TL 68.0 mm); largest female from same locality (CL 11.5 mm, TL 56.0 mm). Egg size unknown, since no ovigerous specimens collected to date.

Color (based primarily upon 35-mm color slides of live holotype male USNM 277777, from site near Dangriga, Belize, photographed 19 April 1983; supplementary notes made from preserved specimens taken from same site).—Integument largely translucent except for varied opaque white over much of third maxillipeds, chelipeds, remaining pereiopods, anterior of carapace, anterior and posterior of dorsal oval, and dorsal extreme of cervical groove; translucent white or yellow-white on bell-shaped dorsal sclerite of first abdominal tergite, thicker portions of abdominal tergites 2–6, and sclerites arming ventral membranes of abdomen. Setal tufts pale brown to yellow brown. Dark pigmentation beneath cornea and often extensively occupying most of eyestalk, and as small crescent under articular membrane near midlength of antennal peduncle (appearing to be in proximal extreme of fourth peduncular segment of most preserved specimens). Major chela sometimes with diffuse yellow near articulations of articles; small area of yellow to yellow-orange chromatophores on opaque cuticle of rostral base, immediately anterior to dorsal oval. Distinct, complex pattern of small yellow green to brownish or pale orange chromatophores always evident dorsally on abdominal somites 3–6 and telson, patterned somewhat as previously described in *L. louisianensis* (see Williams *et al.*, 1989: fig. 4 of second color plate), arranged in 5 primary areas (one large anteromedial, 4 smaller lateral) on each of abdominal somites 3–5, forming poorly defined longitudinal band immediately to either side of abdominal midline on abdominal somite 6, with darker broad band near each lateral margin; yellowish color also proximally on pleopods 3–5, and darker yellow to yellow brown on uropods and posteriorly on telson. Translucence of abdomen revealing large yellow lobes of hepatopancreas filling anterior somites of abdomen.

Known Range and Habitat.—This species is known from only two localities on the western coastal margins of the Gulf of Honduras, mainland shoreline of Belize, both of which are oligohaline. It is found in tidally influenced river mouths, brackish estuaries, and beaches near sources of low salinity waters. It constructs burrows in intertidal and shallow subtidal mud or muddy sand to unknown depths. Specimens from near Dangriga (Stann Creek Town) occurred in muddy quartzite sands, which are known to be of local riverine and creek origin (K. Rützler, Smithsonian Institution, personal communication). Those from the mouth of the Monkey River in southern Belize were extracted from a tidally exposed muddy bar on a small unvegetated area of a shoreline that was elsewhere lined by mangroves. Several kilometers upstream from this site, beneath 2–3 m of clear water, we observed large, mounded burrow openings on the sandy river bottom which may be attributable to *L. richardi.* While we were unsuccessful in extracting animals here with yabby pumps, ejecta surrounding these burrows included fecal pellets typical of callianassids, and active pumping of sediments could be seen at some burrow apertures. The remarkable characteristic of this site was a strikingly inverse thermal stratification of the water column, which suggests that the animals living there must tolerate at least some substantial period of exposure to high temperatures. The saltier monimolimnion of the deepest pool here encompassed water within about 1 m of the bottom, with a sharp pycnocline separating it from the less salty and much cooler overlying water. While the temperature of the monimolimnion was not measured, it was so warm as to prohibit lengthy exposure of an unprotected diver, thus limiting our attempts to extract animals. Since both runoff floods and tidal effects could potentially disrupt stratification in this tributary of the Monkey River, it is likely that the extreme conditions we observed there are ephemeral and not likely to represent optima for *L. richardi.*

Remarks.—Among western Atlantic species of the genus, *L. richardi,* new species, can be readily separated from the Gulf of Mexico endemic, *L. louisianensis,* and the Brazilian species, *L. siriboia,* both of which lack elaborate cuticular armor or plating on ventral surfaces of the abdomen. While the distribution of sclerites in the ventrally plated species may extend across much of the ventral cuticle of the abdomen, and diagnoses of species could include the presence or shape of sclerites on various abdominal somites, the presence and unique patterning of sclerites is usually most obvious on the ventral surface of the second abdominal somite. Our examination of this surface in known species of the genus revealed that, in addition to *L. jamaicense,* the recently described *L. sinuensis* from the Caribbean coast of Colombia also has ventral armor comparable with that of *L. richardi.* Despite the sharing of this general feature, *L. richardi* can be readily separated from both *L. jamaicense* and *L. sinuensis* on the basis of a surprising number of detailed but consistent morphological characters, many of which may ultimately be of value in establishing lineages within the genus.

In the course of comparing our illustrations for the present paper to materials of the genus in the Museum of Natural History, Vienna, P. C. Dworschak (personal communication) has informed us that archived lots from Brazil (NHMW 6897) and Belize (NHMW 6815) treated under *L. jamaicense* sensu lato in his earlier report (Dworschak, 1992) are instead assignable to *L. siriboia* and *L. richardi,* new species, respectively. In revision of his remarks in the aforementioned paper, he has also communicated that only the two specimens from Belize have the median cuticular structure on the ventral surface of the second abdominal somite.

Compared to *L. jamaicense,* both males and females of *L. richardi* may be readily distinguished on the basis of their strikingly furrowed median, ventral, cuticular plate on the second abdominal somite, a plate that is consistently flat and unfurrowed in all populations of *L. jamaicense.* However, our iterative comparison of morphological characters in these two species, as featured in the above descriptions, revealed over 20 other diagnostic characters that distinguish between them. Among the more easily observed features of *L. richardi* in this pairing are its larger and more produced dorsomesial tubercle on the eyestalk, shallower superior notch on the merus of the major chelipeds, bicarinate inferior margin of the cheliped merus, much stronger tuberculation and armor on the major cheliped propodus, stronger dentition of the dactylus and fixed finger of the major cheliped, less sinuous superior margins on dactyli of the third and fourth pereiopods, multiple corneous spines on the inferior margin of the fixed finger of the fourth pereiopod, bell-shaped rather than subrectangular median dorsal sclerite on the first abdominal somite, relative absence of microsetation or spinules on accessory sclerites surrounding the median ventral plate of the second abdominal somite, relatively longer terminal article in the male first pleopod, much smaller appendix interna on the male second pleopod, broader and terminally more trilobate telson, and absence of dorsal spines on basal articles of the uropods. However, under detailed examination there are also subtle differences in the terminus of the mandibular palp, shapes of the distal endite and exopod of the first maxilliped, relative length of the antennal peduncle, shape of the exopod of the second maxilliped, shape and setation of the rudimentary exopod of the third maxilliped, breadth and dentition of the merus of the major cheliped, shape of the proximo-inferior margin in the carpus of the major cheliped, location of the boss on the inner surface of the palm of the major cheliped, depth of the setose depression and position of prehensile teeth on fingers of the minor cheliped, strength and position of corneous teeth on the terminal articles of the third and fourth pereiopods, breadth of the dactylar spoon on the fifth pereiopod, relative width of a corneous cuticular plate immediately posterior to the male first pleopod, shape of the transverse and posterior sutures on posterolateral areas of the sixth abdominal tergite, position of setation adjacent to the aforementioned transverse suture, and relative development of an upturned terminal lip on the median lobe of the telson.

While somewhat variable in development and less sclerotized than in most specimens of other plated species, armor of the anterior abdominal somites in *L. sinuensis* (Fig. 7b–d) resembles particularly that of *L. richardi,* new species, in both the general shape of the median dorsal sclerite on the first abdominal somite and in the development of a longitudinal furrow within the median ventral plate of the second abdominal somite. However, there are conspicuously fewer accessory sclerites surrounding the median ventral plate in *L. sinuensis,* and the furrow of the median plate is for the most part closed, limited to little more than a median suture in some specimens. In one specimen of those available, the median plate of *L. sinuensis* was subdivided transversely into anterior and posterior components (Fig. 7d), somewhat resembling a condition also seen in one specimen of *L. jamaicense.* While the pattern of ventral abdominal armor in this species will distinguish it from *L. richardi* as well as from *L. jamaicense, L. sinuensis* can also be readily distinguished from *L. richardi* and all other known species of the genus by the unique frontal lobes on the carapace which flank the rostrum, a diagnostic feature pointed out in the original description (Lemaitre and Rodrigues, 1991). We find notable similarities between *L. sinuensis* and *L. richardi* in at least the strength of the eyestalk tubercle, dentition and tuberculation of the major chela, relative length of the terminal article in the somewhat variable male first pleopod (Fig. 7f–h), relative size of the strikingly variable appendix interna on the male second pleopod (Fig. 7i–k), and shape of the telson.

A single specimen of an alpheid shrimp, *Leptalpheus* sp., a genus found commonly in commensal association with thalassinid shrimp, was obtained with a yabby pump while we were extracting specimens of *L. richardi,* new species, from the lower beach at Dangriga, Belize. This species of *Leptalpheus* appears to be conspecific with undescribed forms that we have recently discovered in southeastern Florida, where they occur in probable association with thalassinid genera other than *Lepidophthalmus.* Their description and our analysis of their associations will be treated in a forthcoming paper.

Etymology.—This species is named for our friend and colleague, Dr. Richard W. Heard, Gulf Coast Research Laboratory, Ocean Springs, Mississippi, in recognition of the many occasions upon which he has collected and made available materials essential to our studies. His remarkable firsthand knowledge of marine organismal biology, authorship of numerous scientific publications, thorough recall of relevant literature, and unselfish assistance to all who call upon his talents have made a lasting impression on numerous students and research collaborators who share his interests in evolution and ecology of the western Atlantic biota.

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