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# REEXAMINATION OF THE GHOST SHRIMP *LEPIDOPHTHALMUS LOUISIANENSIS* (SCHMITT, 1935) FROM THE NORTHERN GULF OF MEXICO AND COMPARISON TO *L. SIRIBOIA,* NEW SPECIES, FROM BRAZIL (DECAPODA: THALASSINIDEA: CALLIANASSIDAE)

*Darryl L. Felder and Sérgio de Almeida Rodrigues*

ABSTRACT

A complex of western Atlantic species has been confused in previous literature under the name *Callianassa jamaicense* Schmitt, 1935, a taxon assigned recently to the genus *Lepidophthalmus* Holmes, 1904. Members of this genus from the northern Gulf of Mexico have been treated as varieties or subspecies of the typical form or have been elevated to species rank without reanalysis of characters to justify that placement. Specimens from Brazil were formerly treated as typical representatives of *C. "jamaicensis"* (spelling as by Rodrigues, 1971) but with notation of some variations in morphology. Reexamination of both the northern Gulf of Mexico populations and those from Brazil establishes that populations in each of these localities are, while closely related to one another, distinguishable as separate species from *Lepidophthalmus jamaicense* (Schmitt, 1935). Unique and consistent morphological characters of the eyestalks, maxillipeds, chelipeds, gonopods, uropods, carapace, and abdominal armature justify previous elevation of the varietal taxon for northern Gulf of Mexico populations to specific rank as *L. louisianensis* (Schmitt, 1935), and justify the recognition of a new species, *L. siriboia,* from the coast of Brazil.

Identification of callianassid crustaceans in the western Atlantic, including those now assigned to the genus *Lepidophthalmus* (see Manning and Felder, 1991), has puzzled specialists for more than half a century. The problem has stemmed largely from the limited material available to earlier taxonomists who were justifiably reluctant to assign species rank on the basis of small or fragmentary collections. The difficulty of extracting these abundant but fossorial animals from intertidal habitats has been for the most part overcome by collecting with yabby pumps (see Hailstone and Stephenson, 1961), and this has provided a much greater access to material for contemporary genetic (J. L. Staton and D. L. Felder, in progress) and morphological comparisons. Recent understanding of restricted dispersal in larval stages of *Lepidophthalmus* (Felder *et al.,* 1986; Manning and Felder, 1991) has also led us to expect that isolation of populations and speciation within the genus may be greater than is reflected in current taxonomy.

Present confusion over the identity of western Atlantic species of *Lepidophthalmus* dates to Schmitt's (1935) description of *Callianassa jamaicense* on the basis of two specimens from the shores of Montego Bay, Jamaica, and description of *C. jamaicense* var. *louisianensis* on the basis of a single specimen collected from near Grand Isle, Louisiana. Limited to a single specimen which was believed to show some evidence of injury, the varietal designation was deemed by Schmitt (1935: 15) to be appropriate "until such time as additional material may call for a change of opinion." Additional materials from the type locality of "*C. jamaicense louisianensis*" were examined by Willis (1942), who detailed characters of the chelae to further affirm uniqueness of the variety from the typical form. Over the next 30 years most subsequent workers also retained the varietal designation. However, in attempting to apply the accepted diagnostic characters to materials from the northern and northeastern coasts of Brazil, Rodrigues (1966, 1971) noted that those materials appeared to be variable or intermediate in character (Rodrigues, 1971: 203, table 2), and he therefore proposed that the variety *C. j. louisianensis* be abandoned (while also modifying the species name to *jamaicensis* in accord with an editor's in-

terpretation of Article 32 of the International Code of Zoological Nomenclature). Although Biffar (1971) reexamined the types of *C. jamaicense* from Montego Bay and noted previously unreported characteristics of those materials, he nevertheless accepted Rodrigues' proposal, since he suspected that unusual characteristics of the Jamaican materials were due to parasitism. Use of the varietal or subspecies designation was thereafter also abandoned in a number of other works concerning the biology of populations from the northern Gulf of Mexico (Felder, 1973, 1978, 1979; Rabalais *et al.*, 1981).

In the course of studying new specimens from the mouth of the Amazon River, Tiefenbacher (1976) undertook a brief reexamination of Rodrigues' specimens from Brazil, Schmitt's types from Jamaica and Louisiana, additional northern Gulf of Mexico material from Florida and Mississippi, and a single specimen from Cuba that had been reported by Holthuis (1974). While Tiefenbacher regarded this set of materials to represent intermediate character states in at least some features, he recognized unique features of the chelipeds that supported recognition of the variety *louisianensis* as a subspecies. He also concluded that Brazilian specimens and Caribbean specimens, both of which he treated under *C. jamaicensis,* were closely related to one another even though he could not assign them to that species with certainty.

In recent papers concerning northern Gulf of Mexico populations, the varietal name has either been retained (Felder *et al.*, 1986), or these populations have been recognized (without further discussion or justification), as the species *Callianassa louisianensis* (as in Manning, 1987; Manning and Felder, 1989; Lovett and Felder, 1989; Felder and Lovett, 1989; Dworschak, 1992), a name which has with recent reassignment become *Lepidophthalmus louisianensis* (Schmitt, 1935) as in Manning and Felder (1991, 1992). Among the few recent citations of Brazilian materials, Coelho and Ramos (1972) continued to follow Rodrigues (1971) in assignment of materials to *Callianassa jamaicensis* Schmitt, 1935, while Coelho and Ramos-Porto (1987) followed Saint Laurent and LeLoeuff (1979) in referring to the species under *Callichirus jamaicensis* (Schmitt, 1935), prior to restriction of *Callichirus* by Manning and Felder (1986).

The present paper reports simultaneous morphological studies of materials of *Lepidophthalmus* from both the northern Gulf of Mexico and the coasts of Brazil. Populations from the two areas are compared morphologically, distinguished from one another, and distinguished from *L. jamaicense* (Schmitt, 1935) and other known representatives of the genus. Species rank is confirmed for the northern Gulf of Mexico population under the name *L. louisianensis* (Schmitt, 1935) and is accorded to the Brazilian population under the name *L. siriboia,* new species.

## Materials and Methods

Most materials from the northern Gulf of Mexico that were used in this study were selected from a large collection accumulated by DLF and colleagues in the course of physiological, developmental, allometric, genetic, and ecological studies between 1971 and 1991. Collections were made either by jetting specimens from intertidal substrate with a gasoline-powered water pump (see Felder, 1978) or by extraction of specimens from these habitats with hand-operated yabby pumps (see Hailstone and Stephenson, 1961; Manning, 1975). Most materials from Brazilian coasts that were examined in this study were collected by SAR and colleagues in the course of studies on systematics and ecology of Brazilian callianassid populations from the mid-1960s through 1984. All those materials were taken in intertidal habitats, either by extraction with a shovel or by use of hand-operated yabby pumps (see Rodrigues, 1966).

Material examined is listed by location followed by date, collector, number of specimens by sex and condition (imm = immature, mutl = mutilated, ov = ovigerous), and, if applicable, museum number (MZUSP = Museu de Zoologia, Universidade de São Paulo, USLZ = University of Southwestern Louisiana Zoological Collections, USNM = National Museum of Natural History). The holotype and some paratypes of *Lepidophthalmus siriboia,* along with topotypic materials of *L. louisianensis,* have been deposited in the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil. Paratypes of *L. siriboia* and topotypic materials of *L. louisianensis* have also been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and the University of Southwestern Louisiana Zoological Collections, Lafayette, Louisiana. Size is expressed as postorbital carapace length (CL) measured in millimeters (mm).

## *Lepidophthalmus* Holmes, 1904
(see also Manning and Felder, 1991)

### *Lepidophthalmus louisianensis*
(Schmitt, 1935)
Figs. 1 a–i, 2 a–d, 3 a–i

(see also fig. 4 of second appended color plate in Williams *et al.*, 1989)

*Callianassa jamaicense* var. *louisianensis.*—Schmitt, 1935: 1, 12–15, pl 1, fig. 2, pl. 2, figs. 4, 7, pl. 4, fig. 4.—Hedgpeth, 1950: 113–114.—Dawson, 1967b: 190.—Biffar, 1971: 641–642, 650; 1972: 71.—Phillips, 1971: 165–195, figs. 1–3a, c, e, 6, 7b, c, d, 8b, c, d, tables 1–3, 5–7.—Felder *et al.*, 1986: 91.—Manning and Felder, 1989: 9.

*Callianassa stimpsoni.*—Reed, 1941: 42, 47 (part, those near "streams or in marshes").

*Callianassa jamaicense louisianense.*—Anonymous, 1941:5.

*Callianassa jamaicense louisianense.*—Willis, 1942: 1, 2, 4, 5.—Behre, 1950: 21.—Hedgpeth, 1950: 114, table 1.—Darnell, 1958: 369, 400.—Pounds, 1961: 26, pl. 1, fig. 1.—Leary, 1964 (reissued 1967): 26–27.—Dawson, 1967a: 224.—Felder, 1973: 3, 24.—Fotheringham and Brunenmeister, 1975: 114–116, 166, fig. 6.12.—Fotheringham, 1980 (reissued 1985, 1988): 63, 106, fig. 7.12.—Fotheringham and Brunenmeister, 1989: 62, 118, fig. 7.12.

*Callianassa jamaicense.*—Hedgpeth, 1950: 114.—Rodrigues, 1966: 11, 14, 34–44, 76, 160 (part, North American only).—Biffar, 1971: 650, 654 (part, North American only); 1972: 71 (part, only materials "originally described as the variety").—Menzel, 1971: 78.—Phillips, 1971: 166.—Felder, 1973: 3, 24, pl. 2, figs. 6–8; 1978: 409–427, figs. 2, 3, 5–10, tables I, II; 1979: 125–136, figs. 1–6.—Rabalais *et al.*, 1981: 96, 105, 112.—Heard, 1982: 47.—Felder *et al.*, 1984: 67A.—Lovett and Felder, 1984: 74A.—Abele and Kim, 1986: 27, 295 (part, North American only, *not* 302, 303, figs. j, k, l).—Felder *et al.*, 1986: 91–104, figs. 1–8.

*Callianassa jamaicense louisianensis.*—Wass, 1955: 46, 148.—Menzel, 1956: 43.

*Callianassa* (*Calichirus*) *jamaicense.*—Rodrigues, 1966: ii, 34 (part, North American only).

*Callianassa* (*Callichirus*) *jamaicense.*—Rodrigues, 1971: 198 (part, North American only).

*Callianassa jamaicensis.*—Rodrigues, 1971: 191, 202–204, table 2 (part, North American only).—Coelho and Ramos, 1972: 162 (part, Florida, Gulf of Mexico only).—Manning and Felder, 1986: 439.—Williams *et al.*, 1989: 28.—Britton and Morton, 1989: table 1-1.

*Callichirus jamaicense.*—Felder, 1975: i–x, (Part I) 1–63, table 1, figs. 1, 4, 6, 8, 10–15, (Part II) 74–110, tables 1, 2, figs. 1–6; 1979: 125.—Abele and Kim, 1986: 296.

*Callianassa jamaicensis* var. *louisianensis.*—Tiefenbacher, 1976: 314–316.

*Callianassa jamaicensis louisianensis.*—Humm, 1953: 6.—Tiefenbacher, 1976: 314–316, fig. 1a, b.

*Callianassa jamaicense*?.—Shipp, 1977: 48–60, figs. 32–37.

*Callichirus jamaicensis.*—Saint Laurent and Le-Loeuff, 1979: 67, 96 (part, North American only).—Coelho and Ramos-Porto, 1987: 30 (part, Florida, Gulf of Mexico only).

*Callianassa jamaicense* var.—Felgenhauer and Felder, 1986: 34A.

*Callianassa louisianensis.*—Manning, 1987: 397.—Staton *et al.*, 1988: 125A.—Britton and Morton, 1989: 6, 121, 193, 195, 209, figs. 6, 7e, j, 7–9 T.—Felder and Lovett, 1989: 540–552, figs. 1–6, tables 1–3.—Lovett and Felder, 1989: 530, figs. 1, 2, tables 1, 2.—Manning and Felder, 1989: 9.—Rabalais *et al.*, 1989: 32–34, table 3.—Williams *et al.*, 1989: 28, fig. 4 of color plate.—Griffis and Suchanek, 1991: table 2.—Dworschak, 1992: 198, fig. 7.

*Lepidopthalmus louisianensis.*—Felder and Staton, 1990: 137A.

*Lepidophthalmus louisianensis.*—Felder *et al.*, 1991: 101A.—Lemaitre and Rodrigues, 1991: 629.—Manning and Felder, 1991: 778; 1992: 560.

*Callianassa latispina.*—Kalke and Montagna, 1991: table 1.

*Material Examined.*—HOLOTYPE.—Chenière Ronquille, just east of Grand Isle, Louisiana, 18 July 1928, coll: E. H. Behre, 1 male holotype (CL 14.1 mm), USNM 69364. TOPOTYPES.—margins of oligohaline tidal pond, 11 ppt salinity, Grand Terre island, Jefferson Parish, just east of Grand Isle, Louisiana, 9 January 1973, coll: D. L. Felder, 11 ♂♂, 14 ♀♀, USLZ 1424 (illustrated individuals numbered 1424–1 through 1424–8), 5 ♂♂, 5 ♀♀, MZUSP 11104, 5 ♂♂, 5 ♀♀, USNM 243576.—same locality, 15 ppt salinity, 11 June 1974; coll: D. L. Felder, 17 ♂♂, 18 ♀♀, vouchers for physiological and growth studies, USLZ 3506, 2 ♂♂, 2 ♀♀, USNM 243577.—same locality, July 1983, coll: J. M. Howell and S. C. Hand, 1 ♀ (ov), voucher for larvae used in physiological study, USLZ 3530.—same locality, 17 ppt salinity, 6 March 1985, coll: D. L. Felder and J. M. Felder, 1 ♂, 2 ♀♀, vouchers for color photographs, USLZ 3505.—same locality, 25 May 1988, coll: D. L. Felder, J. L. Staton, and N. A. Bayakly, 3 ♂♂, 1 ♀ (ov), parts of 17 mutl unsexed dissected for tissue samples, vouchers for genetics study, USLZ 3503. OTHER SPECIMENS.—FLORIDA: subtidal sand beach, Pine Island, northwest of Weekiwachee Spring, "with *Pinnixa,*" 12 May 1990, coll: M. Schotte and R. Higgins, 2 ♂♂, 1 ♀, USNM 256947.—stomach of sturgeon, *Acipenser oxyrhynchus desotoi,* East Pass, Suwannee River, 26 April 1982, coll: S. Carr, 3 ♀♀, 1 mutl unsexed, USNM 251648.—in sand, Hog Island, Suwannee River, 23 February 1986, coll: S. Carr, 1 ♂, USNM 251647.—intertidal, Wakulla Beach, Apalachee Bay, 13 January 1951, coll: S. Sevin, 1 ♂, 1 ♀, USNM 92830.—mouth of tidal creek, FSU Marine Laboratory, St. Teresa, 6 April 1985, coll: D. L. Felder, 4 ♂♂, 1 ♀, USLZ 3516.—same locality, 28 June 1992, coll: R. B. Griffis, 3 ♂♂, 7 ♀♀ (1 ov), USLZ 3537.—shore of Choctawhatchee Bay, 8 ppt salinity, near Villa Tasso, 24 April 1990, coll: D. L. Felder, 9 ♂♂, 15 ♀♀ (1 ov), parts of 31 mutl unsexed dissected for tissue samples, vouchers for genetic studies, USLZ 3521.—shore of East Bay, 12 miles (19.3 km) east of Pensacola, 24 August 1960, coll: P. A. Butler, 3 ♂♂, 6 ♀♀, USNM 106169. ALABAMA: sandy flat near outflow from small fresh-water pond, 1–30 ppt across flat, west end of Little Lagoon, Bon Secour National Wildlife Refuge, west of Gulf Shores, 9 August 1990, coll: D. L. Felder and R. D. Felder, 3 ♂♂, 4 ♀♀ (3 ov), vouchers for genetic studies, USLZ 3522.—upper Mobile Bay, October 1960, coll: J. R. Thompson, 4 ♂♂, 1 ♀, USNM 106426.—same locality, 19 November 1981, coll: T. S. Hopkins, 3 imm unsexed, USLZ 3536.—intertidal mudflat near *Phragmites* stand, 5 ppt salinity, upper Mobile Bay,

Meaher State Park, 8 August 1990, coll: D. L. Felder, 2 ♂♂, USLZ 3523.—sandy intertidal mudflat just west of ramp to causeway, lower Mobile Bay, north shore of Dauphin Island, 12 November 1989, coll: D. L. Felder and J. M. Felder, 4 ♂♂, 4 ♀♀, 2 mutl unsexed, vouchers for genetic studies, USLZ 3524. MISSISSIPPI: muddy intertidal sand along beachfront seawall, Pascagoula, 19 February 1989, coll: D. L. Felder and R. D. Felder, 2 ♂♂, USLZ 3528.—sand beach, Ocean Springs, summer 1950, coll: J. F. Walker, 3 ♂♂, 1 ♀, USNM 91254.—east end of Mississippi Sound, 1 September 1947, coll: J. W. Ward, 1 ♀, USNM 85539.—dug from sand, Deer Island, February 1931, coll: unknown, 2 ♂♂, USNM 77466.—Deer Island, 22 August 1947, coll: J. W. Ward *et al.*, 1 ♀, USNM 85538.—sand flats, Biloxi, 15 December 1943, coll: M. W. Williams, 1 ♂, 1 ♀, USNM 122444.—muddy intertidal beachfront sand bars, Long Beach, 11 November 1989, coll: D. L. Felder and J. M. Felder, 6 ♂♂, 1 ♀, USLZ 3527.—stomach of *Menticirrhus,* Pass Christian, coll: unknown, September, 1928, USNM 123365.—muddy sand flat, seaward side of jetty, 15 ppt salinity, west shore of lower Bay St. Louis, 3 October 1989, coll: D. L. Felder and J. L. Staton, 40 ♂♂, 2 ♀♀, vouchers for genetic studies, USLZ 3525.—muddy exposed sand bars, landward side of jetty, 15 ppt salinity, west shore of lower Bay St. Louis, 3 October 1989, coll: D. L. Felder and J. L. Staton, 82 ♂♂, 25 ♀♀, 2 mutl unsexed, vouchers for genetic studies, USLZ 3526. LOUISIANA: 3 miles (4.8 km) northwest of Irish Bayou, 11 feet (3.4 m) deep, 4.3 ppt salinity, Lake Pontchartrain, 6 May 1955, coll: unknown, 2 ♀♀, USNM 98141.—east end of Grand Isle, 27 July 1939, coll: A. G. Humes and E. R. Willis, 2 ♂♂, 1 ♀, USNM 79176.—west end of Grand Isle, 27 July 1938, coll: C. L. Jones, 5 ♀♀ (2 ov), USLZ 3529.—muddy sand margins of roadside tidal pond in marsh, 24 ppt salinity, 3 miles (4.8 km) west of bridge to Grand Isle, 9 December 1986, coll: D. L. Felder and J. L. Staton, 2 ♂♂, 8 ♀♀, vouchers for genetic studies, USLZ 3534.—same locality, 16 December 1987, coll: D. L. Felder, J. L. Staton, and N. A. Bayakly, 8 ♂♂, 3 ♀♀, vouchers for genetic studies, USLZ 3535.—muddy beach, Lighthouse Point, Southwest Pass of Vermilion Bay, 29 June 1976, coll: D. L. Felder *et al.*, 3 ♂♂, USLZ 610.—dug from mud overlain by oyster shells, Porpoise Point, Southwest Pass of Vermilion Bay, 2 July 1976, coll: D. L. Felder and G. Eldridge, 1 ♂, 1 ♀, USLZ 611.—sandy mud margins of tidal creek leading to beach, 2.5 ppt salinity, about 10 miles (16 km) west of Holly Beach, 20 January 1988, coll: D. L. Felder, J. L. Staton, and N. A. Bayakly, 5 ♂♂, 1 ♀, vouchers for genetic and gut morphology studies, USLZ 3533.—deeply burrowed in margins of shallow warm brackish pond on backbeach, 12 miles (19.3 km) east of Sabine Pass, 15 October 1972, coll: D. L. Felder, 3 ♂♂, 2 ♀♀, USLZ 3532. TEXAS: muddy intertidal bank of Sabine Pass, 2 November 1989, coll: D. L. Felder, 2 ♂♂, USLZ 3517.—shore of Lavaca Bay, Port O'Connor, 3 August 1990, coll: D. L. Felder and J. L. Staton, 1 ♂, 1 ♀, USLZ 3514.—Aransas National Wildlife Refuge, 26 March 1946, coll: J. W. Hedgpeth, 1 ♀, USNM 84354.—core sample, Aransas National Wildlife Refuge, Texas, 22 July 1976, coll: D. L. Felder, R. Guidry, and G. Eldridge, 2 ♂♂, USLZ 614.—mud flat near marsh, Copano Bay, Bayside, 3 August 1990, coll: D. L. Felder and J. L. Staton, 10 ♂♂, 14 ♀♀ (9 ov), 1 mutl unsexed, vouchers for genetics study, USLZ 3513.—stomach of catfish, Rockport, May 1942, coll: G. Gunter, 2 mutl ♂♂, 1 mutl unsexed (sample includes notation of additional 2 ♂♂, 1 ♀♀, sent on exchange to British Museum), USNM 81904.—mud flat near marsh grass, Nueces Bay Causeway, Portland, 2 August 1990, coll: D. L. Felder and J. L. Staton, 1 ♂, 5 ♀♀ (3 ov), USLZ 3520.—mud flat on shoreline of bay fronting Corpus Christi Coliseum, Ocean Drive, Corpus Christi, 2 August 1990, coll: D. L. Felder and J. L. Staton, 9 ♂♂, 23 ♀♀ (9 ov), vouchers for genetics study, USLZ 3504.—mud flat at South Padre Island end of causeway from Port Isabel, 26 June 1991, coll: D. L. Felder, 1 ♂ (gonopods atypical), USLZ 3519.—muddy shoreline near marsh grass, north bank of Rio Grande River, 17 ppt salinity, about 1 mile (1.6 km) upstream from mouth of river at Boca Chica, 26 June 1991, coll: D. L. Felder and J. L. Staton, 4 ♂♂, 1 ♀, parts of 19 mutl unsexed dissected for tissue samples, vouchers for genetic studies, USLZ 3518. TAMAULIPAS, MEXICO: mangrove shoreline 1 mile (1.6 km) west of La Pesca, 27 ppt salinity, 22 March 1979, coll: J. W. Tunnel, Jr., *et al.*, 1 imm ♂, 1 imm ♀, USLZ 3512.—mud flat on tidal channel, 33 ppt salinity, Rio Soto la Marina estuary, La Pesca, 31 March 1991, coll: D. L. Felder, J. L. Staton, *et al.*, 1 ♂, parts and eggs of 4 mutl others dissected for tissue sample, vouchers for genetic studies, USLZ 3508.—shallow subtidal muddy sand inshore of bed of *Halodule,* south shoreline of Rio Carrizal estuary, Barra del Tordo, 25 May 1982, coll: D. L. Felder and R. Tinnin, 2 ♂♂, 2 ♀♀ (1 ov), USLZ 3510.—same locality, 14 August 1987, S. C. Rabalais, 3 ♂♂, 3 ♀♀ (1 ov), USLZ 3511.—same locality, 32 ppt salinity, 31 March 1991, coll: D. L. Felder, J. L. Staton, *et al.*, 2 mutl ♂♂, 4 mutl ♀♀, abdomens removed for tissue samples, vouchers for genetic studies, USLZ 3509. VERACRUZ, MEXICO: clayey mud shore of tidal channel, 36 ppt salinity, southern end of Laguna Tamiahua, village of Tamiahua, 30 March 1991, D. L. Felder, J. L. Staton, *et al.*, 1 mutl ♂, 1 ♀, USLZ 3507.

*Description* (based on male holotype, USNM 69364, and topotypic males and females USLZ 1424).—Frontal margin of carapace with acute, narrow rostral spine flanked laterally by low, weakly produced shoulders (Fig. 1a), apices of which overlying lateral margins of eyestalks; rostral spine often directed slightly upward and extending about two-thirds to four-fifths length of eyestalks in dorsal view, basoventral end of spine with tuft of setae, longest of which extending between eyestalks beyond cornea. Carapace anterior to dorsal oval usually with several pairs of setose punctae on either side of midline and scattered fields of smaller punctae laterally; dorsal oval well defined, smooth, usually with single pair of widely separated, small, setose punctae near midlength, length of oval about six-tenths of postrostral carapace length; marginal suture of oval diminished at anterior midline, stronger and with low cornified articulation to cardiac region at posterior midline.

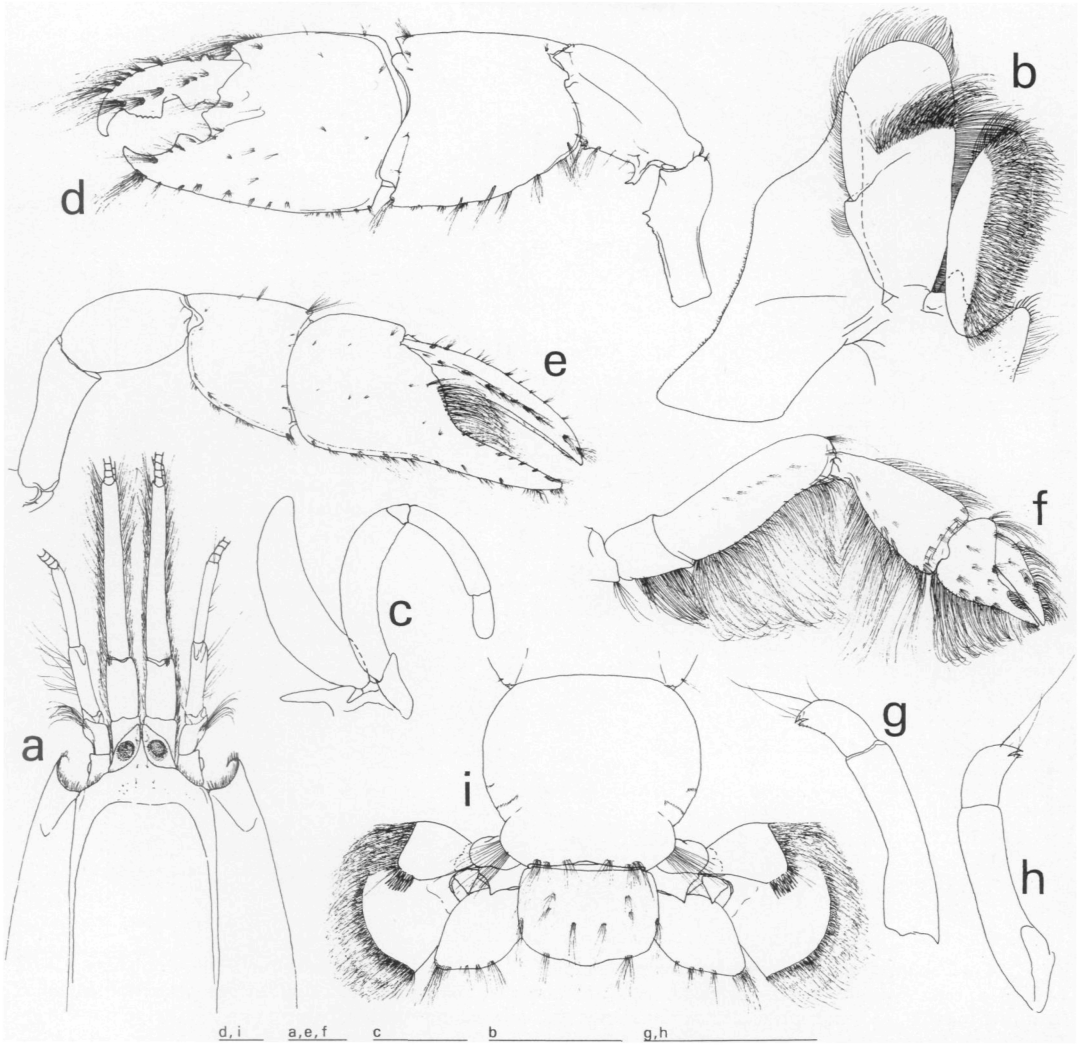


Fig. 1. *Lepidophthalmus louisianensis,* topotypic male (CL 13.8 mm) from near Grand Isle, Louisiana, USLZ 1424–7. a, anterior carapace, eyestalks, and antennae, dorsal view; b, right first maxilliped, external surface; c, right second maxilliped, external surface, setae not shown; d, major cheliped, external surface; e, minor cheliped, external surface; f, right second pereiopod, external surface; g, male first pleopod, external surface; h, male first pleopod, internal surface; i, sixth abdominal somite, telson, and uropods, dorsal surface. Scale lines indicate 2 mm.

Eyestalks subtriangular in dorsal view, reaching to about three-fourths length of basal antennal article; anterolateral margins tapered to thin, arcuate edge, dorsomesial margin with distinct small pit lateral to proximal one-fourth, distinct marginal tubercle arising at about two-thirds length and tapering into weak marginal lip and blunt terminal protuberance of eyestalk (Fig. 2a); mesial face of eyestalk deep basally, tapering distally to tip; distinct, pigmented cornea centered on dorsal surface, area of pigmentation often broader than faceted surface. Antennular peduncle heavier, longer than antennal peduncle; basal article dorsally invaginated to form open statocyst, opening occluded by closely set fan of anteromesially directed setae and overlain by eyestalk; second article slightly longer than basal article, third article about 2.8 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

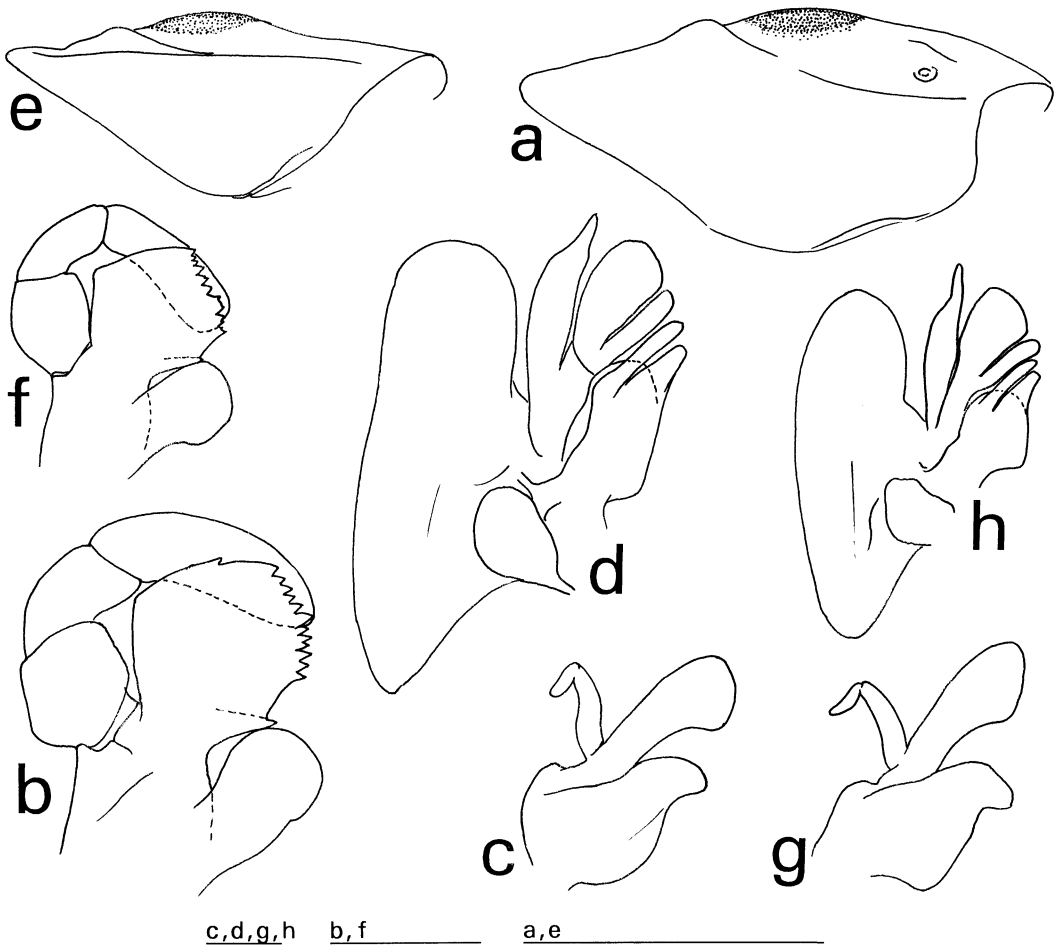


Fig. 2. *Lepidophthalmus louisianensis,* topotypic male (CL 14.1 mm) from near Grand Isle, Louisiana, USLZ 1424–3. a, right eyestalk, mesial surface; b, right mandible and paragnath, external surface, setae not shown; c, right first maxilla, external surface, setae not shown; d, right second maxilla, external surface, setae not shown. *Lepidophthalmus siriboia,* new species, male holotype (CL 10.2 mm) from near São Luís, Maranhão, Brazil, MZUSP 11083. e, right eyestalk, mesial surface; f, right mandible and paragnath, external surface, setae not shown; g, right first maxilla, external surface, setae not shown; h, right second maxilla, external surface, setae not shown. Scale lines indicate 1 mm.

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 about midlength of third article of antennular peduncle; basal article with dorsolateral carina proximally forming angular lip above lateral excretory pore, ventrally with setose ventrodistal protuberance; second article with complex ventrolateral and mesial longitudinal sutures, distally with fields of long setae on either side of ventrolateral suture; third article elongate, subequal to combined lengths of first 2, almost equal to length of fourth, laterally with row of long setae; fourth article narrower and less setose than third; flagellum sparsely setose and about 3 times length of antennular flagellum.

Mandible (Fig. 2b) with large, heavily setose (setae omitted in figure), 3-segmented palp, elongated third article of palp slightly narrowed distally, terminally rounded; incisor process with well-defined teeth on cutting margin, occasionally with isolated tooth on distal margin, concave internal surface with lip giving rise to molar process proximal to incisor teeth; thin, rounded paragnath set against proximal convex surface of

molar process. First maxilla (Fig. 2c) with endopodal palp long, narrow, terminal article deflected at poorly defined articulation; proximal endite with setose margin sinuous, distal endite elongate and terminally broadened; exopod low, rounded. Second maxilla (Fig. 2d) with endopod narrowed terminally, first and second endites each longitudinally subdivided, exopod forming large, broad scaphognathite. First maxilliped (Fig. 1b) with endopod limited to rudimentary, low lobe, overlain by distal endite; proximal endite triangular, marginal setation including stronger, curved setae at distal corner; distal endite elongate, ovoid, mesial half heavily setose; exopod incompletely divided by oblique suture, lateral margin near midlength interrupted by slightly produced corner 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, its anterior end tapered, angular. Second maxilliped (Fig. 1c) with long, narrow endopod; endopodal merus arcuate, slightly broader distally than proximally, flexor margin with comb of close-set, long setae; carpus short; propodus arcuate, straplike, length about 4 times width, about three-fourths length of merus; dactylus at least twice as long as broad, terminally rounded; exopod longer than endopodal merus, arcuate, terminally rounded; epipod small, with short proximal lobe and narrow distal lobe. Third maxilliped with small, naked, rudimentary exopod and large endopod with long marginal setation; endopodal ischium subquadrate, about twice as long as broad, internal surface with low medial, longitudinally oriented elevation marked by broken rows of very small spiniform granules and proximally with few small tubercles; merus subtriangular, slightly broader than long; carpus subtriangular, slightly longer than broad; propodus large, ovoid, about as broad as long, terminally truncate with curve of inferior margin distally angled toward articulation with dactylus; dactylus narrow, arcuate, with stiff terminal setae.

Branchial formula as reported by Lemaitre and Rodrigues (1991: 625) for *L. sinuensis*; 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; sexual dimorphism of relative chela size strongly allometric as previously reported (Felder and Lovett, 1989). Major cheliped of mature male (Fig. 1d) massive and strongly armed; ischium slender, superior margin sinuous, row of small, sometimes hooked, denticles on proximal two-thirds of inferior (flexor) margin, row usually terminated distally with 1–4 stronger, sometimes compound, teeth; merus with depression in proximal one-fourth of superior margin, inferior (flexor) margin with strong, sinuous proximal hook at base of keel, hook variously bifid, usually with sharp tip and weak subterminal lobe, distal half of inferior margin with several (usually 3–7) strong denticles; carpus broad, increasing in breadth distally though increase slight in distal half, inferior margin arcuate and weakly sinuous, superior and inferior margins keeled, terminated distally in acute corners; propodus broad, heavy, length about 1.5 times height, swollen inner surface of palm produced to form distinct proximal boss just above midline, weak unarmed furrow extending posteriorly from gape of fingers on outer face of palm; distinct keel of superior propodal margin restricted to proximal one-half, keel of inferior margin usually distinct and lined by series of large setose punctae in proximal one-third, ill defined and overlain by setose punctae at midlength, and absent on fixed finger; fixed finger with unarmed (inner) and armed (outer) prehensile margins facing gape and joining at acute upturned tip, base of armed margin with broad triangular tooth separated by U-shaped gap from second massive triangular tooth near two-fifths length; dactylus with sharp, strongly hooked tip and distinct, erect tubercle at proximal end of superior margin, outer inferior (prehensile) margin with 2 massive teeth, proximal tooth centered near one-third length and sometimes weakly bilobed or knobbed, separated by a U-shaped gap from broadly triangular, bladelike distal tooth, its distal shoulder usually ornamented by several small denticles. Major cheliped of female also massive (Fig. 3a–c) but less so (Felder and Lovett, 1989) and less heavily armed than that

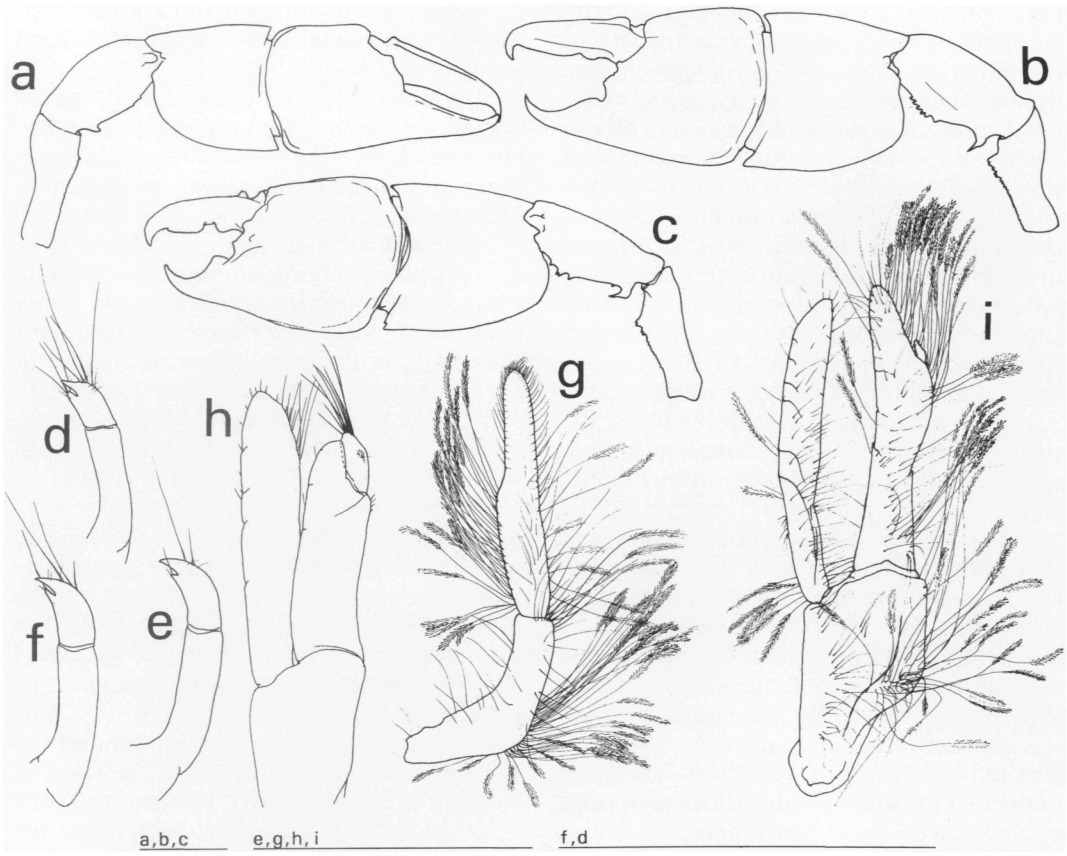


Fig. 3. *Lepidophthalmus louisianensis,* topotypic specimens from near Grand Isle, Louisiana. a, major cheliped, external surface, female (CL 15.0 mm), USLZ 1424–4; b, major cheliped, external surface, female (CL 14.6 mm), USLZ 1424–5; c, major cheliped, external surface, female (CL 13.8 mm) USLZ 1424–8; d, right first pleopod (gonopod), external surface, male (CL 10.4 mm) USLZ 1424–1; e, right first pleopod (gonopod), external surface, male (CL 12.9 mm) USLZ 1424–2; f, right first pleopod (gonopod) external surface, male (CL 14.1 mm) USLZ 1424–3; g, right first pleopod, external surface, female (CL 13.8 mm), USLZ 1424–8; h, right second pleopod, posterior surface, male (CL 13.8 mm), USLZ 1424–7; i, right second pleopod, posterior surface, female USLZ 1424–8. Scale lines indicate 5 mm.

of mature males (as also the case in juvenile males and males regenerating major chela); teeth of fixed finger and dactylus usually of lower profile, less massive than males, except in largest of females; superior margin of dactylus with proximal tubercle usually lower, sometimes forming proximal corner of superior keel on proximal half of dactylus.

Minor cheliped (Fig. 1e) sparsely armed, ischium with row of small denticles on proximal four-fifths of flexor margin; merus unarmed; propodus with acuminate distal corners; fixed finger with dense brush of setae on proximal two-fifths of inner and outer superior margins, setae largely filling gape between fingers; gape and setation less developed in females and juvenile males than in mature males; dactylus with dentition of inferior (prehensile) surface limited to low, rounded denticles or granules, especially along subterminal reaches of outer margin.

Second pereiopod (Fig. 1f) 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 of both fingers corneous; superior margin of dactylus with stiff, arched bristles reduced in length, close-set, and

more arched distally. Third pereiopod merus length about 2.5 times width; propodus with inferodistal margin below articulation of dactylus bilobate, lobes demarcated by furrows on internal surface, distal margins of both lobes (especially lower) sinuous with stiff bristles concentrated on prominences and absent from depressions, long bristles on inferior margin of lower lobe, patterned tufts of lighter setae on outer face of article; dactylus tear-shaped, length about 1.4 times width, terminated in low blunt corneous tubercle, inferior margin lined by short, stiff setae, outer face with lower field of fine setae and upper pattern of setal tufts. Fourth pereiopod 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 1 or more short, articulated corneous spines obscured by dense brush of stiff setae. Fifth pereiopod 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.

Abdominal somites dorsally smooth, glabrous, typically with 1 or 2 isolated pairs of setose punctae on each segment; second–fifth tergites each encompassing lateral membranous suboval area, that of second tergite posterolateral and with anterior line and posterior tuft of inconspicuous setae, those of third and fourth tergites posterolateral and densely setose, that of fifth tergite midlateral and densely setose; sixth tergite (Fig. 1i) with 2 posterolateral lines of short setae anterior to posterolateral groove, tufts of stiff setae on posterolateral corners, and usually 4–6 short lines or tufts of stiff setae on posterior margin. Ventral surfaces of abdominal somites largely membranous; 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, but with no complex pattern of multiple plates and tubercles arming most of thin ventral cuticle on first and second somites. First pleopod of male and female uniramous, composed of 2 articles; in male (Figs. 1g, h; 3d–f), total length about one-half that of second pleopod, proximal article at least 2 times length of terminal article, terminal article subspatulate with anteriorly directed, bifurcate tip bearing few long terminal and subterminal setae; in female (Fig. 3g), total length subequal to that of second pleopod, proximal article slightly shorter than terminal article, terminal article narrowed beyond midlength, both articles setose. Second pleopod of male and female biramous, with appendix interna on endopod; in male (Fig. 3h), dense setation restricted to distal extreme of exopod and terminus of appendix interna, large appendix interna slightly crossing and usually overreaching tip of endopod, with small field of rudimentary, hooked setae on its posterior or posteromesial surface; in female (Fig. 3i), both rami setose, appendix interna minute. 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) broad, subrectangular, about as wide at anterolateral corners as at posterolateral corners, width about 1.4 times length, posterior margin weakly trilobate; dorsal surface usually with 3 pairs of setal tufts, of which 2 pairs (sometimes fused into 1 pair or nearly so) are set well lateral of midline in anterior half, another pair set close to midline just posterior to midlength; lateral margins with pair of setal tufts near two-thirds length, posterior margin with tuft on each of weak lateral lobes. Uropod with short, posteriorly directed spine on protopod overreaching anterior margin of endopod, and short, posterior spine on proximal article of exopod abutting anterior margin of endopod; endopod broad, subrhomboidal, less than twice as long as broad, tapered to angular terminus bearing tuft of long setae, several smaller tufts of setae distributed along posterior margin; exopod with anterodorsal plate falling well short of distal endopod margin, distal edge of plate lined with short, thick spiniform setae grading to thinner longer 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 and densest posteriorly.

*Size.*—Among the materials examined, the largest male is from Grand Terre, Louisiana

(CL 18.6 mm) and the largest female is from Corpus Christi, Texas (CL 17.6 mm). Egg size (maximum diameter) on an ovigerous specimen from Bay St. Louis, Mississippi, is 1.0–1.2 mm, on another from Corpus Christi, 1.1–1.2 mm, and on another from Tamiahua, Mexico, 0.9–1.0.

*Color.*—Except for opaque white of third maxillipeds, chelipeds, and remaining pereiopods, and brown to yellow brown of setal tufts, integument largely translucent; major chela sometimes with diffuse pale yellow (or faint rose) near articulations or on prominences; rose or rose violet chromatophores anterolateral to dorsal oval just posterior to front of carapace; distinct pattern of same always evident dorsally on abdominal somites 3–6 and telson, patterned as represented in Williams *et al.* (1989: fig. 4 of second color plate); abdominal somites 3–5 with varying intensity of faint yellow ground color primarily on anterolateral quarters of each tergite; pale yellow ground color also on much of pleopods 3–5 proximally on exopods, on uropods, and laterally and posteriorly on telson.

*Known Range and Habitat.*—Endemic to northern and western coastlines of the Gulf of Mexico, from western Florida (Pine Island, Hernando County) through Alabama, Mississippi, Louisiana, and Texas at least to Laguna de Tamiahua in northern reaches of the state of Veracruz, Mexico; constructs burrows (occasionally to depths >2 m) in intertidal and shallow, subtidal estuarine substrates ranging from sandy mud to muddy sand; adapted to oligohaline habitats of coastal marshes, tidal channels, and embayments, in salinities from <1 ppt to >35 ppt. In Alabama estuaries, swarms of small individuals have been taken on occasion in midwater plankton samples (T. Matthews, Dauphin Island Sea Lab, Alabama, personal communication). This may represent a postlarval dispersal phenomenon not unlike that reported to occur in other callianassids with reduced larval life histories (see Felder and Lovett, 1989: 550).

*Remarks.*—Comparison of *L. louisianensis* to *L. siriboia* and to other congeners is treated under the Remarks section following the description of *L. siriboia* below. As noted by Willis (1942), the correct type locality for *L. louisianensis* is Chenière Ronquille near Grand Isle, Louisiana, and the collector of the type specimen was Ellinor H. Behre; in the original description, Schmitt (1935) erroneously reported that the specimen was "taken by Chenier Ronaville" and noted the locality only as Grand Isle, Louisiana. The male holotype (USNM 69364) is an unusually large specimen and exhibits several characteristics that have been found developed to various degrees only in some other large male specimens. As in some other large males, the ischium of the major chela has a weakly developed secondary carina just outside and roughly parallel to the denticulate inferior margin, and the denticulate margin itself bears denticles that are more elongate and lobiform than those in smaller specimens. In addition, the holotype is anomalous in that the endopod of the second pleopod has a very reduced (rudimentary) distal lobe that is conspicuously overreached by a very large appendix masculina.

The commensal caridean shrimp *Leptalpheus forceps* Williams, 1965, has been reported as a probable inhabitant of burrows of *Lepidophthalmus louisianensis* in Mississippi (Dawson, 1967a). Our findings support this observation in that specimens of *Leptalpheus forceps* have been taken from burrows of *Lepidophthalmus louisianensis* in northwestern Florida, Bay St. Louis, Mississippi, and Tamaulipas, Mexico. However, the report that "a small form of *P.* [*Pinnixa*] *lunzi*" occurs with the species (Britton and Morton, 1989: 193) is doubted as is the notation by Fotheringham and Brunenmeister (1975: 116; 1989: 62) and Fotheringham (1980: 63) that this animal sometimes shares its burrow with *Pinnixa chaetopterana.* Given the usual symbiotic affinities of these pinnotherids and our failure to find these crabs in burrows of *L. louisianensis* over the course of collecting thousands of specimens of this thalassinoid shrimp from throughout its range, we suggest that the previously reported associations most likely involve symbioses with some other thalassinoid shrimp, such as *Callichirus,* or occurrence of these pinnotherids in worm burrows adjacent to those of *Lepidophthalmus.* It remains to be firmly established whether any species of *Pinnixa* actually occurs as a symbiont of *L. louisianensis.* Fotheringham and Brunenmeister

also reported that this animal sometimes builds its burrow in mud which has accumulated in a shell of *Mercenaria.* Given our observations that *L. louisianensis* is an obligate burrower and that its burrows commonly extend to depths of 1–2 m, the report of containment in a clam shell could perhaps represent a rare case of a recently settled juvenile becoming entrapped in such a shell or could be based upon misidentification of the local species of *Upogebia* which does occasionally tend to exhibit such shallow burrowing behavior.

One of us (DLF) has, in the course of collecting from several sites in Florida, Louisiana, and Tamaulipas, Mexico, taken a number of specimens of the normally nocturnal pink wormfish (*Microdesmus* sp.) from burrows of *Lepidophthalmus louisianensis.* It appears that this association may represent either some form of symbiotic burrow use, or perhaps predation by the wormfish on ghost shrimp or their eggs. A dense infestation of pink wormfish in shrimp burrows within a semiconfined tidal pond on Grand Terre island, Louisiana, in May 1988 preceded a dramatic decline in the ghost shrimp population at this site during the following year. In at least one case at Grand Terre, Louisiana (DLF observation), and others at Ocean Springs, Mississippi (R. W. Heard, Gulf Coast Research Laboratory, Ocean Springs, personal communication) captured wormfish appeared to be engorged with small eggs, apparently grazed from the egg-laden pleopods of ovigerous *L. louisianensis.*

In the course of making field collections on mudflats in both Texas and Louisiana, predation on *L. louisianensis* by wading birds was observed on several occasions, especially during low tides. Willets were observed feeding upon small, shallow-burrowed animals, while herons and egrets were observed on several occasions to take mature-sized ghost shrimp. Hedgpeth (1950) previously reported that the species was probably included in the diet of the whooping crane on the Aransas Refuge, Texas. Identification of *L. louisianensis* in stomach contents has documented predation on the species by sturgeon, catfish, and sciaenid fishes (see above, Materials Examined; also Darnell, 1958: 369, 400), while nocturnal observations (by DLF) on shallow flats of Bay St. Louis, Mississippi, suggest that stingrays also prey actively on the species.

In a recently published checklist for decapods of the United States and Canada (Williams *et al.,* 1989), the common name "estuarine ghost shrimp" was assigned to "*Callianassa jamaicensis*." This assignment was made prior to recognition that all populations of the continental United States instead belong to *Lepidophthalmus louisianensis,* the species to which this common name most correctly applies, but which appeared in the checklist (as *C. louisianensis*) without indication of the common name. The range of *L. jamaicense* may be restricted to Jamaica or may include Cuba (see Holthuis, 1974; Tiefenbacher, 1976). Studies are underway to address distributions and relationships of these and other Caribbean populations.

Larval development in this species is very abbreviated and consists of only two zoeal stages which have been collected in wild-caught plankton (Shipp, 1977) and have been reared in the laboratory. In the laboratory studies (Felder *et al.,* 1986), larval development from hatching to settlement of postlarvae required only two days. Physiological adaptation to low-salinity habitats, previously reported for adults (Felder, 1978), was also found to be evident in the two zoeal stages, both of which regulated blood osmotic concentrations at reduced salinities.

### ***Lepidophthalmus siriboia***, new species

Figs. 2 e–h, 4 a–f, 5 a–g, 6 a–l
(see also Rodrigues, 1971: figs. 21–40)

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

*Callianassa jamaicense.*—Rodrigues, 1966: 11, 14, 34–44, 93, 160, figs. 21–40, table 2 (part, Brazilian only).—Biffar, 1971: 650, 654 (part, Rodrigues' specimens only).—Abele and Kim, 1986: 27 (part, Brazilian only).

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

*Callianassa jamaicensis.*—Rodrigues, 1971: 202–204, figs. 21–40, table 2 (part, Brazilian only).—Coelho and Ramos, 1972: 162 (part, Brazilian only).

*Callichirus jamaicensis.*—Saint Laurent and Leloeuff, 1979: 67, 96 (part, South American "ouest-atlantique" only).—Coelho and Ramos-Porto, 1987: 30 (part, Brazilian only).

*Callianassa jamaicense.*—Griffis and Suchanek, 1991: table 2.—Dworschak, 1992: 196 (part Brazilian only).

*Material Examined.*—TYPES.—mouth of Rio Anil, São Luís, Maranhão, Brazil, 18 February 1984, coll: S. de A. Rodrigues, 1 ♂ (CL 10.2 mm), holotype, MZUSP 11083, 11 ♂♂ (CL 5.9–8.4 mm), 8 ♀♀ (CL 4.2–9.6 mm), paratypes, MZUSP 11084, 2 ♂♂ (CL 8.6 and 9.6 mm), 2 ♀♀ (CL 8.5 and 8.8 mm; 1 ov), paratypes, USNM 243575, 3 ♂♂ (CL 5.7–9.2 mm), 2 ♀♀ (CL 9.2 and 9.3 mm; 1 ov), paratypes, USLZ 3502 (illustrated individuals numbered 3502-1 through 3502-4). OTHER SPECIMENS.—Marapanin, Pará, Brazil, September 1965, coll: P. E. Vanzolini, 2 ♂♂, MZUSP 3898.—mouth of Rio Mumbaba, Conde, Paraiba, Brazil, 29 February 1984, coll: S. de A. Rodrigues *et al.*, 1 ov female, MZUSP 11101.—mouth of Rio Gramame, João Pessoa, Paraiba, Brazil, 28 February 1984, coll: S. de A. Rodrigues *et al.*, 1 ♂, MZUSP 11103.—mouth of Rio Caravelas, Bahia, Brazil, 23 September 1965, coll: S. de A. Rodrigues, 2 ♂♂, 6 ♀♀ (2 ov), MZUSP 11102.

*Description* (based upon holotype male, MZUSP 11083, and male and female paratypes, MZUSP 11084, USNM 243575, USLZ 3502.—Frontal margin of carapace with acute, narrow rostral spine flanked laterally by slightly produced, angular shoulders (Fig. 4b), apices of which being lateral to lateral margins of eyestalks; rostral spine usually directed slightly upward (Fig. 4a) and extending about two-thirds to four-fifths length of eyestalks in dorsal view, basoventral end of spine with tuft of setae, longer setae extending between eyestalks beyond cornea. Carapace anterior to dorsal oval usually with several pairs of setose punctae either side of midline and scattered lines or fields of smaller punctae laterally; dorsal oval well defined, smooth, usually with at least 1 pair of widely separated small setose punctae in anterior half, length of oval about six-tenths of postrostral carapace length; marginal suture of oval diminished at anterior midline, stronger and with slightly cornified articulation to cardiac region at posterior midline.

Eyestalks subtriangular in dorsal view, produced terminally, reaching to about three-fourths length of basal antennal article; anterolateral margins tapered to thin, sinuous edge, distinct tubercle arising adjacent to dorsomesial margin at about three-fourths length and tapering into low ridge terminating short of anterior protuberance of eyestalk (Fig. 2e); mesial face of eyestalk deep basally, triangular, tapering distally to tip; distinct, pigmented cornea centered on dorsal surface. Antennular peduncle heavier, longer than antennal peduncle; basal article dorsally invaginated to form open statocyst, opening occluded by closely set fan of anteromesially directed setae and overlain by eyestalk; second article slightly longer than basal article, third article about 2.5 times length of second; second and third articles with 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 longer setation than dorsal ramus, subterminal articles of dorsal ramus heavier than those of ventral ramus, and endowed with short, stiff ventral setae. Antennal peduncle reaching to about midlength of third article of antennular peduncle; basal article with strong dorsolateral carina produced proximally to form rounded lip above lateral excretory pore, ventrally with setose distomesial protuberance; second article with complex ventrolateral and mesial longitudinal sutures, distally with fields of long setae on either side of ventrolateral suture; third article elongate, subequal to combined lengths of first two, almost equal to length of fourth, laterally with few long setae; fourth article narrower than third, with at most few long subterminal setae; flagellum sparsely setose and about 3 times length of antennular flagellum.

Mandible (Fig. 2f) with large, heavily setose, 3-segmented palp ending in long, truncate terminal article; incisor process with teeth on cutting margin, often with some teeth compound or bracketed by smaller teeth, concave internal surface with lip giving rise to weak molar process proximal to incisor teeth; thin, rounded paragnath set against proximal convex surface of molar process. First maxilla (Fig. 2g) with endopodal palp long, narrow, terminal article deflected at poorly defined articulation; proximal endite with setose margin sinuous, distal endite elongate and terminally broadened; exopod low, rounded. Second maxilla (Fig. 2h) with endopod narrowed terminally, first and second endites each longitudinally subdivided, exopod forming large, broad, scaphognathite. First maxilliped (Fig. 5a) with endopod limited to vestigial, low lobe, overlain by distal endite; proximal endite triangular, marginal setation including conspicuous strong, curved setae at distal corner; distal endite elongate, ovoid, mesial half heavily setose; exopod slightly marked by oblique suture extending from small incision on lateral margin near

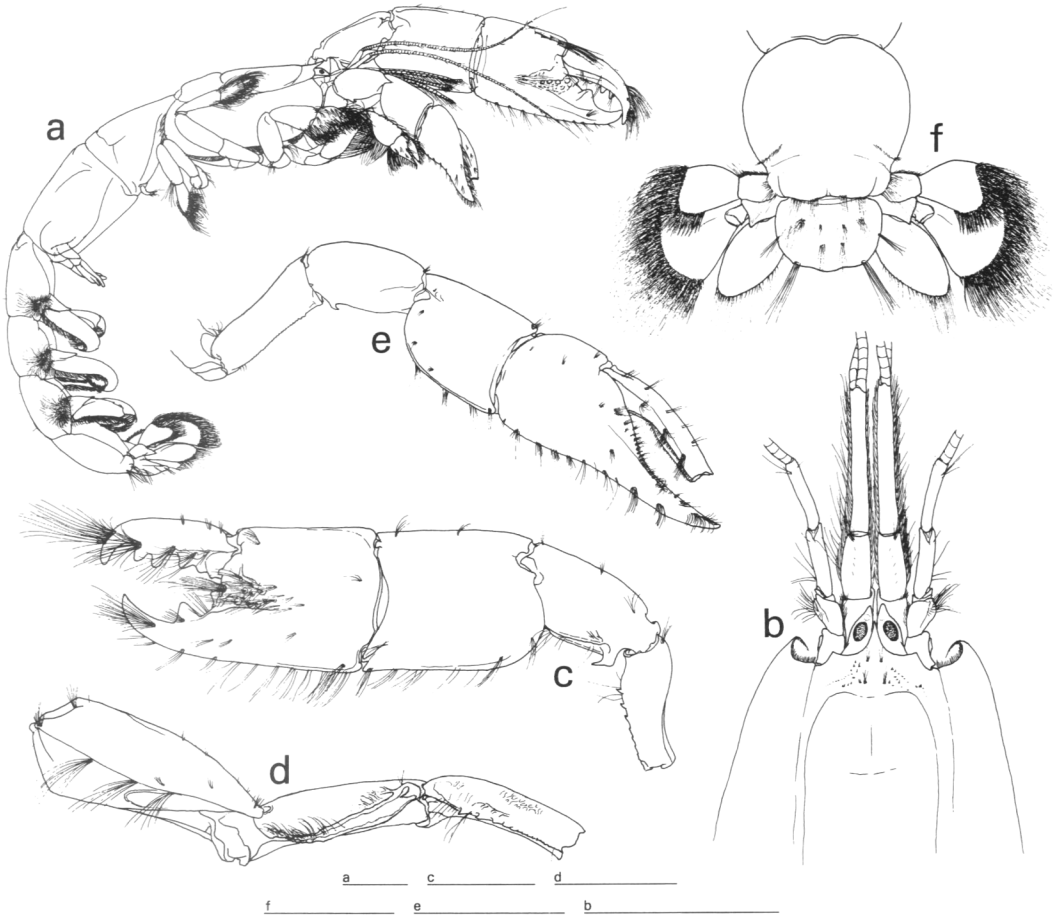


Fig. 4. *Lepidophthalmus siriboia,* new species, holotype male (CL 10.2 mm), from near São Luís, Maranhão, Brazil, MZUSP 11083. a, lateral view of whole animal; b, anterior carapace, eyestalks, and antennae, dorsal view; c, major cheliped, external surface; d, ischium, merus, and carpus of major cheliped, inferior surfaces; e, minor cheliped, external surface; f, sixth abdominal somite, telson, and uropods, dorsal surface. Scale lines indicate 5 mm.

midlength, 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, its anterior end tapered, angular. Second maxilliped (Fig. 5b) with elongate endopod; endopodal merus weakly arcuate, flexor margin with comb of close-set, regularly spaced, long setae; carpus short; propodus weakly arcuate, widening terminally, length about 3 times width, about three-fourths length of merus; dactylus about twice as long as broad, terminally rounded; exopod longer than endopodal merus, arcuate, terminally rounded; epipod with short proximal lobe and narrow distal lobe. Third maxilliped with small, naked, rudimentary exopod and large endopod with long marginal setation; endopodal ischium subquadrate, about twice as long as broad, internal surface with very low longitudinal elevation marked proximally with few minute spines or spiniform granules; merus subtriangular, slightly broader than long; carpus subtriangular, slightly longer than broad; propodus large, ovoid, about as broad as long, narrowing terminally with inferior margin curving broadly to articulation with dactylus; dactylus narrow, arcuate, with strong, stiff setae terminally and on superior margin.

Branchial formula as reported for *L. sinuensis* by Lemaitre and Rodrigues (1991: 625); endopods and epipods as described above; branchiae limited to single rudimen-

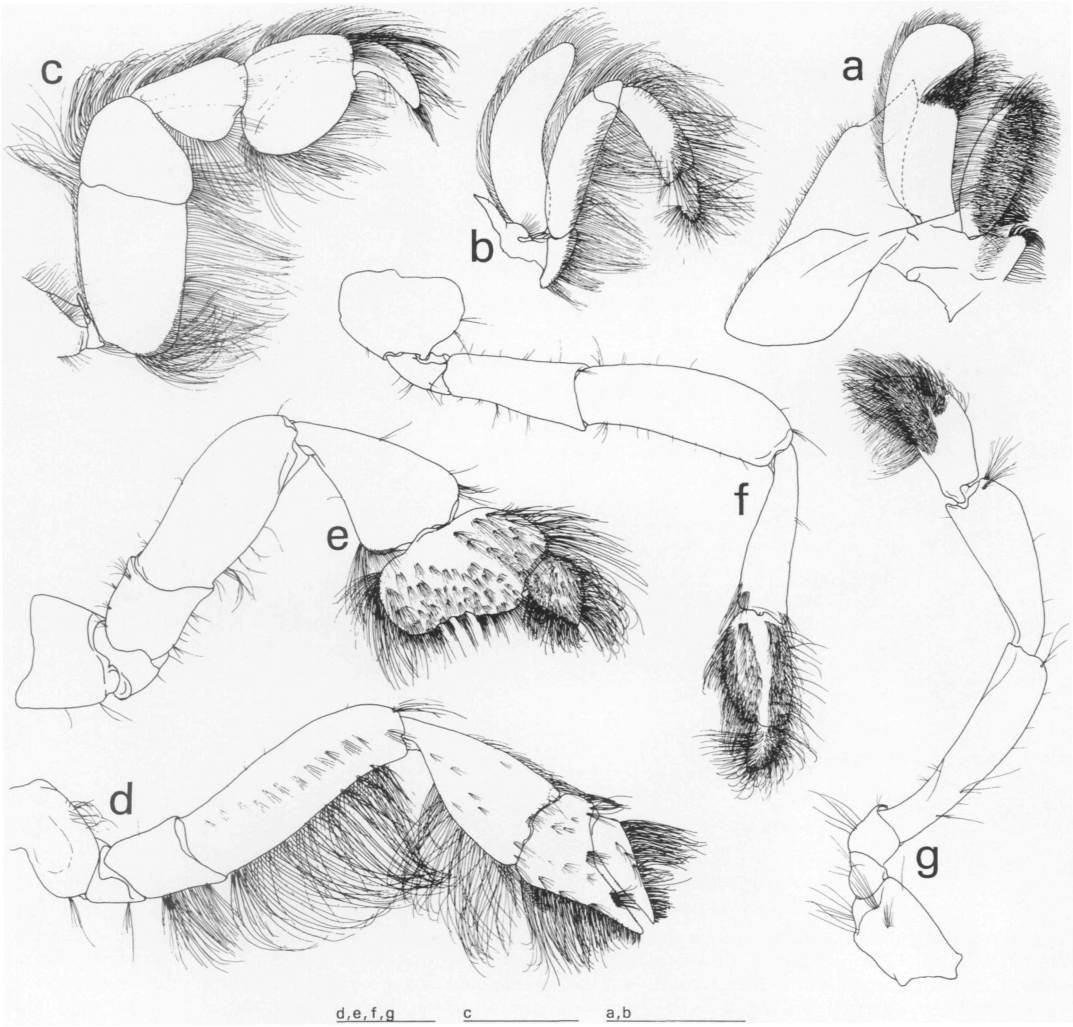


Fig. 5. *Lepidophthalmus siriboia,* new species, holotype male (CL 10.2 mm), from near São Luís, Maranhão, Brazil, MZUSP 11083. a, right first maxilliped, external surface; b, right second maxilliped, external surface; c, right third maxilliped, external surface; d, right second pereiopod, external surface; e, right third pereiopod, external surface; f, right fourth pereiopod, external surface; g, right fifth pereiopod, external surface. Scale lines indicate 2 mm.

tary 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, sexually dimorphic. Major cheliped of mature male (Fig. 4a, c) massive, strongly armed; ischium slender, superior margin sinuous, row of hooked denticles on proximal two-thirds of inferior (flexor) margin, row usually terminated distally with 1–4 stronger, well-separated, hooked teeth; merus with distinct, abrupt notch in proximal one-fifth of superior margin, inferior (flexor) margin with strong, sinuous proximal hook at base of shallow furrow formed by parallel carinae (Fig. 4d), hook with sharp tip and weak subterminal lobe, distal half of internal carina on inferior margin with several (usually 4–8) teeth or angular lobes; carpus broad, subrectangular, inferior and superior margins keeled, parallel over distal half of article length, terminated distally in acutely angled, but bluntly tipped corners; propodus heavy, elongate, length distinctly more than 1.5

times height; inner face of palm swollen, most so near midline but without formation of distinct boss, outer and inner surfaces both with distinct broad furrow extending posteriorly from gape of fingers, furrow ornamented with punctate setose tubercles, lower margin of furrow formed by carina extended posteriorly from fixed finger; distinct keel of superior protopodal margin restricted to proximal three-fifths, keel of inferior margin lined by series of large, setose punctae and distinct only in proximal two-fifths, obsolescent distally; fixed finger with unarmed (inner) and armed (outer) prehensile margins facing gape and joining at acute upturned tip, base of armed margin with triangular tooth at proximal end of gape separated by broad, U-shaped notch from second massive triangular tooth near one-third to two-fifths length; dactylus with sharp, strongly hooked tip, superior margin without distinct proximal tubercle, outer inferior (prehensile) margin usually with 4 strong teeth arranged as proximal pair and distal pair separated by deep, U-shaped notch, distal pair usually longer, distalmost tooth variable, either narrow or distally shouldered and bladelike. Major cheliped of female also massive but less so and less heavily armed than that of mature males (as also in juvenile males, Fig. 6a); teeth of fixed finger and dactylus of much lower profile than in males, most prehensile teeth rudimentary or obsolescent (Fig. 6b).

Minor cheliped (Fig. 4e) sparsely armed, ischium with row of small denticles on proximal four-fifths of flexor margin; merus armed with proximal hook on inferior margin; propodus with blunt distal corners; fixed finger with dense tufts of setae on and between proximal two-fifths of inner and outer superior (prehensile) margins, setae not thickly occluding gape between fingers, distal one-fourth of outer margin usually with row of very low corneous denticles, row often rudimentary in males, strongest in females; gape and setation less developed in females and juvenile males than in mature males; dactylus with most of inferior (prehensile) surface without teeth, outer margin low rounded ridge over most of length, weakly excavate in distal one-fourth and lined by row of low, close-set, corneous denticles; distal excavation and row of denticles often rudimentary in males, strongest in females.

Second pereiopod (Fig. 5d) chelate, flexor margins of ischium, merus, and carpus lined with evenly spaced long setae, inferior margin of propodus with setae long proximally, progressively reduced in length and stiffened distally, subterminally becoming row of close-set, short stiff bristles; dense patch of short stiff bristles centered near three-fifths length of fixed finger just outside prehensile margin; tips of both fingers corneous; superior margin of dactylus with stiff bristles reduced in length distally, subterminally becoming dense row of stiff bristles. Third pereiopod (Fig. 5e) merus length about 2.2 times width; propodus with inferodistal margin below articulation of dactylus bilobate, lobes demarcated by shallow furrows on internal surface, distal margins of both lobes (especially lower) sinuous with stiff bristles concentrated on prominences and absent from depressions, long bristles on inferior margin of lower lobe, patterned tufts of lighter setae on outer face of article; dactylus tear-shaped, with superior margin strongly arched, length about 1.1 times width, terminated in small, laterally directed corneous tooth, inferior margin lined by short stiff setae, outer face with lower field of fine setae and upper pattern of setal tufts. Fourth pereiopod (Fig. 5f) very weakly subchelate, inferodistal process of propodus (=fixed finger) short angular lobe less than one-third length of dactylus, lower margin of lobe with short, articulated corneous spine obscured by dense brush of stiff setae. Fifth pereiopod (Fig. 5g) 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.

Abdominal somites (Fig. 4a) dorsally smooth, glabrous, typically with 1 or 2 small, isolated pairs of setose punctae on each segment; second–fifth tergites each encompassing lateral membranous suboval area, that of second tergite posterolateral and with anterior line and posterior tuft of inconspicuous setae, those of third–fourth tergites posterolateral and densely setose, that of fifth tergite midlateral and densely setose; sixth tergite (Fig. 4f) with posterolateral line of short setae anterior to posterolateral groove,

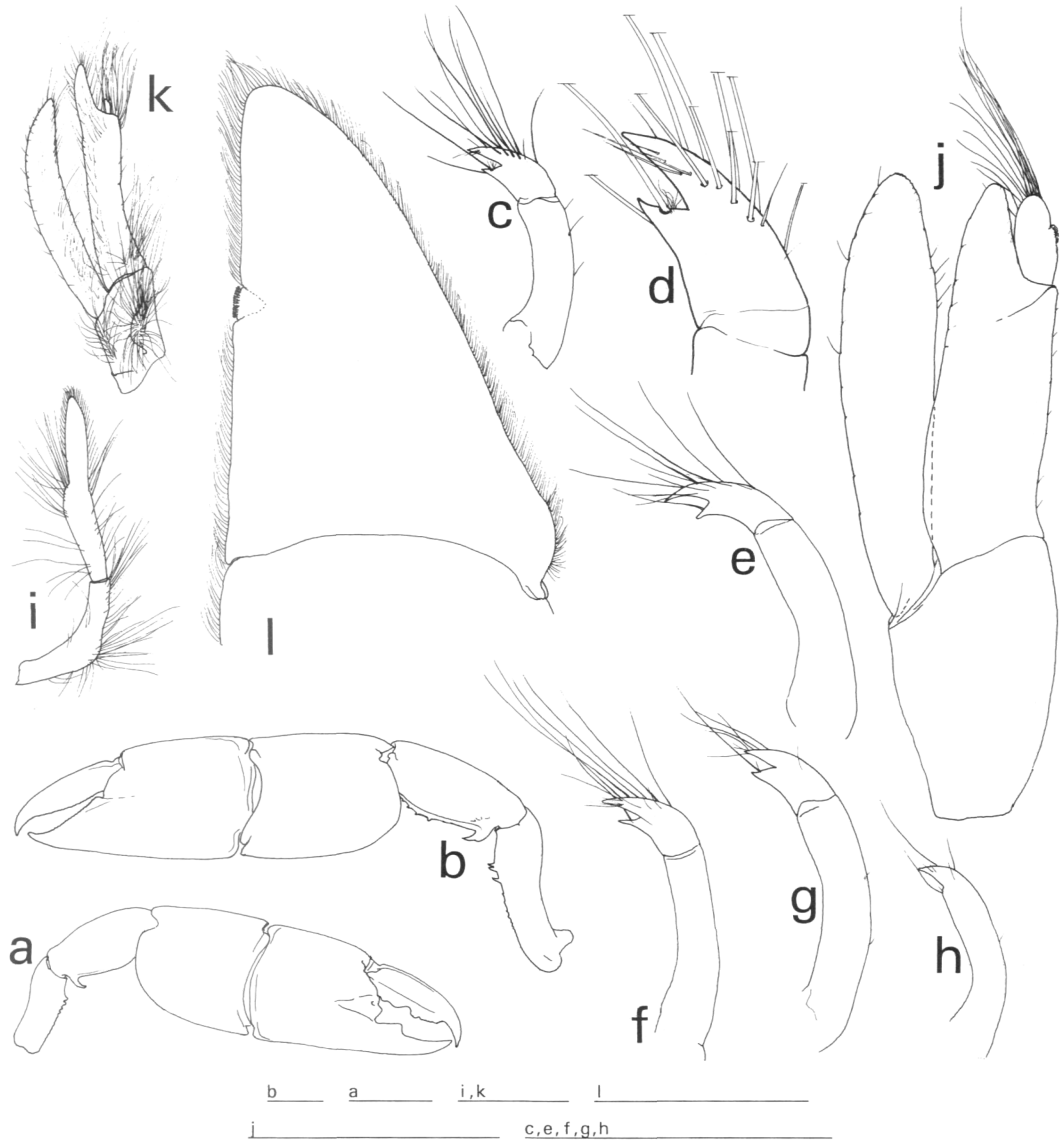


Fig. 6. *Lepidophthalmus siriboia,* new species, type materials from near São Luís, Maranhão, Brazil. a, major cheliped, external surface, paratype small male (CL 5.7 mm), USLZ 3502–2; b, major cheliped, external surface, paratype female (CL 9.2 mm), USLZ 3502–1; c, d, right first pleopod (gonopod), external surface, holotype male (CL 10.2 mm), MZUSP 11083; e, right first pleopod (gonopod), external surface, paratype male (CL 9.2 mm), USLZ 3502–4; f, right first pleopod (gonopod), external surface, paratype male (CL 8.9 mm), USLZ 3502–3; g, right first pleopod (gonopod), external surface, paratype male (CL 9.6 mm), USNM 243575; h, right first pleopod (gonopod), external surface, paratype small male (CL 5.7 mm), USLZ 3502–2; i, right first pleopod, posterior surface, paratype female, USLZ 3502–1; j, right second pleopod, posterior surface, holotype male, MZUSP 11083; k, right second pleopod, paratype female, USLZ 3502–1; l, endopod of right third pleopod, anterior surface, holotype male, MZUSP 11083. Scale lines indicate 2 mm.

tufts of stiff setae on posterolateral corners, and usually 4 short lines or tufts of stiff setae on posterior margin. Ventral surfaces of abdominal somites largely membranous; ventral sclerotization limited primarily to pair of broad, thin plates in anterior one-third of first somite, cornified ridges at base of, alongside, and anterior to first pleopods in flexed position, pair of broad, thin, translucent plates posterior to origins of first and

second pleopods; no complex pattern of multiple plates and tubercles arming most of thin ventral cuticle on first and second somites. First pleopod of male and female uniramous, composed of 2 articles; in male (Fig. 6c–h), total length about one-half that of second pleopod, proximal article at least 2 times length of terminal article, terminal article subspatulate with anteriorly directed, strongly bifurcate tip usually bearing number of long terminal and subterminal setae; in female (Fig. 6i), total length subequal to that of second pleopod, proximal article shorter than terminal article, terminal article narrowed beyond lobe at midlength, both articles setose. Second pleopod of male and female biramous, with appendix interna on endopod; in male (Fig. 6j), dense setation restricted to distal extreme terminus of appendix interna, appendix interna not crossing or exceeding tip of endopod and with small field of rudimentary, hooked setae on its mesial margin; in female (Fig. 6k), both rami setose, appendix interna minute. 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. 6l), articulation of stubby appendix interna embedded in mesial margin. Telson (Fig. 4f) broad but narrowing posteriorly, width about 1.4 times length, posterior margin weakly trilobate; dorsal surface usually with 4 pairs of setal tufts of which anteriormost 2 pairs (sometimes fused into 1 pair or nearly so) set well lateral of midline in anterior half, third pair set nearer to midline in anterior half, and fourth pair set near midline in posterior half; lateral margins typically with pair of setal tufts near two-thirds length, posterior margin with tuft on each of weak lateral lobes. Uropod (Fig. 4f) with short, posteriorly directed spine on protopod overreaching anterior margin of endopod and short, posterior spine or lobe (often weakly bifid) on proximal article of exopod abutting anterior margin of endopod; endopod elongate, ovoid, near 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 endopod margin, distal edge of plate lined with short, thick, spiniform setae grading to thinner, longer 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 and densest posteriorly.

*Size.*—Among the material examined, the largest male is the holotype from São Luís (CL 10.2 mm) and the largest female is an ovigerous specimen from Caravelas (CL 10.1 mm). Egg size (maximum diameter) on the ovigerous female from Caravelas is 0.9–1.0 mm, on an ovigerous female from Conde 0.9–1.2 mm, on an ovigerous female from São Luís 1.15–1.35 mm.

*Color.*—The body is yellowish in males and females, with telson yellower than the rest of the body; the major cheliped is slightly pinkish (from Rodrigues, 1971).

*Known Range and Habitat.*—Atlantic coast of Brazil, from the mouth of the Amazon River, southeast and south to Caravelas, Bahia, Most common in oligohaline waters at mouths of rivers, usually burrowing in intertidal and shallow subtidal sandy mud and muddy sand. At the mouth of the Rio Caravelas, the species is confined to a strip of sand about 3 m wide that is exposed at only extremely low tides. Tiefenbacher (1976: 314) reported specimens collected by H. Sioli from Salinas, Pará, in the intertidal between stones, but these were almost certainly also burrowed into sands beneath this beach rubble.

*Remarks.*—While the description and figures provided previously by Rodrigues (1971) for "*Callianassa* (*Calichirus*) *jamaicensis*" were based upon some of the same materials described in the present paper, the earlier analysis was undertaken without access to comparative materials from the Jamaican type locality and the Gulf of Mexico. Our reevaluation and comparative study of the Brazilian material has led us to conclude that it represents a new species which is herein named, described, and illustrated.

*Lepidophthalmus siriboia* and *L. louisianensis* both lack characteristic dense plates and tubercles on the membranous ventral surfaces of the first and second abdominal somites, which will readily distinguish these species from *L. jamaicense, L. bocourti, L. eiseni,* and several related but undescribed (currently under study) eastern Pacific and western Atlantic congeners. Both species can

be distinguished from the western Caribbean species *L. sinuensis* by their lack of produced lobes on the front of the carapace lateral to the rostrum.

A wide variety of characters will serve to readily distinguish *L. siriboia* from *L. louisianensis,* though some apply to only one sex, fully mature specimens of either sex, or specimens with the major chela intact. In mature males and females, almost every article of the major cheliped differs between the two species. In comparison to that of *L. louisianensis,* the major cheliped in *L. siriboia* has: (i) teeth on the inferior margin of the ischium more strongly hooked; (ii) the superior margin of the merus with a much stronger proximal notch; (iii) the inferior margin of the merus distinctly bicarinate rather than single; (iv) the carpus with the superior and inferior margins parallel rather than weakly divergent in the distal half; (v) the propodus longer than, rather than subequal to, 1.5 times its height; (vi) the propodus with much stronger depressions (forming distinct tuberculate furrows) extending posteriorly from the gape on the inner and outer surfaces; and (vii) the dactylus with 4 (2 pairs) of strong teeth, rather than 2 large teeth, on the prehensile margin.

In mature males of *L. louisianensis,* the propodus of the cheliped also bears a strong proximal boss on the internal surface, but this feature is lacking in *L. siriboia.* Mature males of the species also differ in the strength of the bifurcation in the gonopods; in *L. louisianensis* the incision between the terminal and subterminal blades is narrow, and the subterminal blade is small, while in *L. siriboia* the blades are more widely separated and the subterminal blade is more conspicuous.

In both males and females (mature and juvenile), apices of the shoulders on the frontal margins in *L. louisianensis* overlie lateral margins of the eyestalks, while in *L. siriboia* the apices lie outside these margins. Also, in both sexes, articles of the pereiopods tend to be shorter, relative to width, in *L. siriboia* than they are in *L. louisianensis.* For example, in the third pereiopod of *L. siriboia* the length of the merus is about 2.2 times its width and the length of the dactylus is about 1.1 times its width, while in *L. louisianensis* the length of the merus is about 2.5 times its width and that of the dactylus is about 1.4 times its width. Specimens of either sex of these species can also be distinguished by the setation of the telson, which bears 2 or 3 pairs of dorsal setal tufts in *L. louisianensis* and 4 pairs of dorsal setal tufts in *L. siriboia,* or by the shape of the uropodal endopod, which is subrhomboidal in *L. louisianensis* but elongate-ovoid in *L. siriboia.* Finally, specimens of either sex in the two species can be distinguished by more subtle features such as the tuberculation of the eyestalks, the shape of the mandibular palp, and characters of the first and second maxillipeds.

The number of characters distinguishing these species from each other is rather surprising, given the history of confusion in their taxonomy. It suggests that many of these characters, which have not been compared previously between various populations of *Lepidophthalmus* from the western Atlantic or eastern Pacific, may have considerable utility in future systematic studies of the genus. Varied morphological features that have been previously assumed to be the product of parasitism, or have been assumed to be highly labile in this genus, may instead reflect the isolation and divergence of populations on a much more complex scale than previously assumed.

*Etymology.*—The species is named for the term applied to it by Tupi Amerindian fishermen in the Amazon region who believe, apparently without validity, that this animal is extremely poisonous. They refer to the animal as "siriboia" (Rodrigues, 1966: 93) or "sirimboia" (Tiefenbacher, 1976: 314), derived from the local term "siri" for crab and "mboia" for snake.

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Addresses: (DLF) Department of Biology and Center for Crustacean Research, University of Southwestern Louisiana, Lafayette, Louisiana 70504, U.S.A.; (SAR) Departamento de Ecologia Geral Instituto de Biociências, Centro de Biologia Marinha, Universidade de São Paulo, C. Postal 11461, 05499 São Paulo, S. P., Brazil.