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Two new species of the genus *Lepidophthalmus* (Decapoda, Axiidea, Callianassidae) from coastal Pacific waters of Central America

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Abstract

Two new species of intertidal ghost shrimp are described from coastal Central American habitats of the eastern Pacific Ocean, bringing the total known membership of the genus to 18 species. *Lepidophthalmus natesi* **sp. nov.** from Colombia and Nicaragua shares with *Lepidophthalmus panamensis* **sp. nov.** from Colombia and Panama the lack of extensive ventral pleomere armor, especially in lacking a median ventral sclerite on the second pleomere. The absence of this plate is also a character of the eastern Pacific species *L. rafai* Felder & Manning, 1998, but the two new species differ from it in telson shape. Ventral armor including this plate is present in *Lepidophthalmus bocourti* (A. Milne-Edwards, 1870) and *L. eiseni* Holmes, 1904 which occur sympatrically with *L. natesi* **sp. nov.** in eastern Pacific tropical estuaries. As also known for at least *L. bocourti*, *L. natesi* **sp. nov.** invades and densely colonizes penaeid shrimp aquaculture ponds in regional estuarine settings. Individuals of *L. panamensis* **sp. nov.** are of smaller body size but also may be densely concentrated, especially in clayey substrates including those adjacent to intertidal rocks. Despite their similarities in the pleon and shape of the telson, the species can be readily separated by dentition of the cheliped fingers, relative length of the minor chela fingers, the second pleopod appendix of mature males, and egg size. The large eggs of *L. panamensis* **sp. nov.** suggest extremely abbreviated development. Characteristic coloration is described for both new species.

Key words: *Lepidophthalmus*, Callianassidae, ghost shrimp, eastern Pacific, Central America

Introduction

Following the landfall of Hurricane Mitch in October, 1998, impacts of heavy rain and mudslides included major damage to penaeid shrimp aquaculture developments on the Pacific coast of Nicaragua. Studies of those impacts included our surveys of burrowing decapods associated with culture ponds and surrounding habitats in coastal estuaries, which led to the discovery of several taxa new to science. One of those species, treated by Felder *et al.* (2003) as "*Lepidophthalmus* nov. sp." but not formerly named, is herewith described and assigned a species name. While the aforementioned paper included molecular phylogenetic analyses based on 16S mtDNA, which clearly separated this particular new species from its then-known sympatric eastern Pacific congeners and a few others of the genus (Felder *et al.* 2003: fig. 7), it did not encompass a complete and comparative study of congeneric species. Of the three species collected in Nicaraguan estuaries, only the previously described *Lepidophthalmus bocourti* (A. Milne-Edwards, 1870) and *L. eiseni* Holmes, 1904 were shown to have the anterior pleon "ventrally plated", as opposed to the relatively unplated condition found in "*Lepidophthalmus* nov. sp." (Felder *et al.* 2003: figs. 3 A, B). However, the ventrally unplated pleon was also known to characterize eastern Pacific materials from other than Nicaragua, one species being *Lepidophthalmus rafai* Felder & Manning, 1998 from southwestern Colombia. Yet other eastern Pacific materials collected from Panama were found to lack conspicuous ventral plating, these having been included as "*Lepidophthalmus* nr. *bocourti*" in an earlier allozyme analysis of limited representatives by Staton *et al.* (2000). However, the much smaller body size of Panamanian materials in itself suggested they were unlikely conspecific with the apparently new Nicaraguan species. Conspicuous characters of its telson immediately separated it from *Lepidophthalmus rafai*, thus setting the stage for its inclusion in the present study.

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Ventral pleon sclerotization or plating is of value for species separations in the genus *Lepidophthalmus*, as noted in previous treatments (Felder & Rodrigues 1993; Felder & Manning 1997, 1998; Felder & Staton 2000; Felder 2003). The forms of median plates on the second pleomere, or their absence, can provide a character for separations between subgroups of both western Atlantic and eastern Pacific members of the genus. As noted in preceding citations, the presently treated eastern Pacific populations lacking ventrally sclerotized plates on the pleon have long been under study by the authors and colleagues. A clearer resolution of their relationships is treated in a companion paper on molecular phylogenetic analyses (Robles & Felder 2015). The present descriptions account for two of these species, laying groundwork for study of yet others suspected to occur in the same region.

Material and methods

Field collections were made with hand-operated suction extractors commonly termed yabby pumps, or by use of shovels in clayey sediments. Specimens were fixed and stored in 75% ethanol. Where recorded, salinity was estimated with a field refractometer. Line illustrations were made on a Wild M5 dissecting microscope with a camera lucida. Where required, chlorazole black staining was used to enhance contrast of morphological features. Digital color scans were made from Kodachrome 25 color slide photographs, originally taken in the field by DLF in direct and reflected natural sunlight, all on a Nikon FE camera equipped with a 55 mm Nikkor macrolens. Clove-oil or an salt/ice bath was used in the field to immobilize specimens following collection, after which they were positioned below the surface in a shallow water-filled tray with the bottom lined by black felt. Carapace length excluding the rostrum (cl) was measured in millimeters (mm) from the orbital margin to the posterior margin of the carapace (= postorbital carapace length); egg size was expressed as the greatest egg dimension. All measurements were determined ± 0.1 mm with a calibrated ocular micrometer or digital calipers. Specimens were archived in the Smithsonian Institution National Museum of Natural History (USNM), Washington, D. C., USA; Coleccción Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM/CNCIB), Mexico City, Mexico; and University of Louisiana at Lafayette Zoological collections (ULLZ), Lafayette, Louisiana, USA. Where possible, tissue samples for 16S and 12S mitochondrial sequence analyses were taken from type, topotypic, and other related materials for use in a companion molecular phylogenetic study (Robles & Felder 2015).

Taxonomy

Lepidophthalmus Holmes, 1904

(For generic diagnosis, see Manning & Felder 1991)

Lepidophthalmus natesi sp. nov.

Figures 1 a–g; 2 a–k; 3 a–j

"Lepidophthalmus nov. sp."—Felder *et al*. 2003: table 1; fig. 3 A, B; fig. 7.

Type material. Pacific coast of Colombia. Holotype: male, cl 16.7 mm (USNM 1275006), = ULLZ 6057 tissue/ sequence voucher, Tumaco, Colombia (01°46.64'N, 78°46.30'W), bottom of partially drained commercial shrimp culture ponds, clayey to silty mud, 18 November 1995, S. F. Nates. Paratypes: 2 males, cl 11.0, 5.9 mm (USNM 1275007), 1 female (ovigerous), cl 15.5 mm (USNM 1275008), 39 males, cl 3.3–16.1 mm, 44 females (6 ovigerous), cl 3.9–16.6 mm (ULLZ 6051), Tumaco, Colombia, Pacific coast (01°46.64'N, 78°46.30'W), bottom of partially drained commercial shrimp culture ponds, clayey to silty mud, 18 November 1995, S. F. Nates.

Pacific coast of Nicaragua. Paratypes: 1 male, cl 15.5 mm, 1 female, cl 12.7 mm, photographic vouchers (ULLZ 4509), 1 male, cl 12.4 mm (ULLZ 5174), 1 male, cl 13.2 mm, 1 pleon unsexed (ULLZ 11809), 4 males, cl 9.7–14.3 mm, 4 females, cl 10.1–13.6 mm (UNAM/CNCR 30003), Estero de Las Peñitas (12°21.66'N, 87°01.25'W), intertidal sand flats and clayey mudflats beside and among mangroves, 27 September 2000, D. L. Felder and R. Robles; 1 male, cl 19.2 mm (ULLZ 5772), ephemeral opening of lower Estero Ciego (12°39.47'N, 87°22.53'W), muddy intertidal sand flats, 29 September 2000, D. L. Felder and R. Robles; 1 female, cl 12.0 mm

(ULLZ 4632), 1 female, cl 13.2 mm (ULLZ4633), 1 male, cl 15.6 mm (ULLZ 4638), 1 male, cl 12.4 mm, 1 female, cl 10.0 mm (ULLZ 10872) Estero de Las Peñitas (12°21.66'N, 87°01.25'W), sand flats and clayey mudflats among mangroves, some found with alpheid symbiont, 14 August 2001, D. L. Felder and R. Robles; 1 male, cl 16.6 mm, photographic voucher (ULLZ 10838), 1 male, cl 10.6 mm, photographic voucher (ULLZ 13970), 1 female, cl 17.1 mm (ULLZ 10839), ephemeral opening of lower Estero Ciego (12°39.47'N, 87°22.53'W), muddy intertidal sand flats, 15 August 2001, D. L. Felder and R. Robles; 1 male, cl 14.9 mm, 1 female (ovigerous), cl 14.3 mm (USNM 1275009), 1 female, cl 13.8 mm, parental for larval hatch (ULLZ 11828), beach near Paso de Caballos (12°31.51'N, 87°12.63'W), muddy sand ephemeral back-beach tidal pond, 30 September 2000, D. L. Felder and R. Robles; 1 male, cl 14.2 mm (ULLZ 4634), 1 male, cl 16.4 mm (ULLZ 4635), 2 males, cl 13.8, 14.7 mm, 4 females, cl 13.2–14.2 mm (ULLZ 10884), beach near Paso de Caballos (12°31.51'N, 87°12.63'W), muddy sand ephemeral back-beach tidal pond, 16 August 2001, D. L. Felder and R. Robles; 2 females (1 ovigerous), cl 12.9, 13.3 mm (USNM 1275010), Estero Aserradores, Nicaragua, Pacific coast (12°37.35'N, 87°20.54'W) muddy sand with areas of exposed rock, 29 September 2000, D. L. Felder and R. Robles.

Diagnosis. Rostrum acute, spiniform, inclined or sloped dorsally as weak arch, flanked by rounded shoulders centered lateral to eyestalks. Flattened mesial margins of subtrapezoidal eyestalks closely opposed proximally, weakly divergent near tips, tips acute to subacute. Antennule with dorsal ramus of flagellum shorter than third article of peduncle. Antenna with third article of peduncle very sparsely setose laterally. Inferior margin of male cheliped merus dominated by strong single multidentate keel, weak evidence of parallel carina, proximal hook spatulate, terminating in multiple spines or teeth. Superior margin of merus lacking proximal notch. Propodus of male major chela with distal inferior corner forming origin of round-edged carina extending short distance vertically onto external face as subdistal margin of article. Dactyl of male major chela prehensile margin with small obliquely transverse basal molar tooth set close to weakly bilobed heavy coniform median tooth in proximal half, separated by broad deep notch from elongate narrow distal tooth, distal tooth with dentate prehensile margin declining in elevation distally. First pleonal tergite with dorsal sclerite broadening to medially centered truncate lobe posteriorly, lacking isolated posterolateral sclerotized plate in membrane to each side. Most of second pleomere ventrally leathery, lacking sclerotized medial plate. Male first pleopod terminal article slightly compressed, strongly bifurcate, deep incision between blades, subdistal blade well-developed, overreached by arching distal blade. Appendix of male second pleopod well-developed, reaching beyond narrowed distal end of endopod in mature. Second through fifth pleopods lacking acute distolateral spine on anterior of basis. Telson posterior margin distinctly trilobate. Uropodal endopod narrow, elongate subtrapezoidal, broadest distal to midlength, length more than twice breadth. GenBank accession numbers for 16S and 12S mt sequences of type materials are reported by Robles & Felder (2015: table 2).

Description. Frontal margin of carapace with acute, narrow rostral spine flanked laterally by rounded shoulders centered lateral to eyestalks (Fig. 1 a; Fig. 4 a, c, d); rostral spine variably inclined dorsally, usually somewhat arched above eyestalks in mature specimens, extending 2/3 to full length of eyestalks in dorsal view, proximal half or less of rostral spine undercut ventrally, proximal ventral surface fully covered by fine, dense elongate setae extending above and between eyestalks. Carapace postorbital region with several paired short tufts of setae, usually 2–3 aligned immediately to each side of midline; dorsal oval well-defined, smooth, pair of widely separated setal punctae bearing 1–2 setae each well anterior to midlength; marginal suture of oval diminished at postrostral midline, strong at posterior end with sclerotized suture to bulbous cardiac region on posterior midline.

Eyestalks elongate subtrapezoidal in dorsal view, reaching at least 3/4 length of basal antennular article (Fig. 1 a); anterolateral margin forming rounded corner of varied acuity and prominence, distal margin obliquely sloped mesially toward protruding distal tip; dorsomesial margin forming slightly elevated ridge in distal 1/3, ridge extending from acute or subacute tip of eyestalk to elevated, rounded tubercle positioned distal to mesial margin of cornea; well-defined, distinctly faceted cornea centered on dorsal surface.

Antennular peduncle longer and heavier than antennal peduncle (Fig. 1 a); basal article dorsally invaginated to form statocyst occluded by setae, overlain by eyestalk; second and third articles with dense ventromesial and ventrolateral rows of long, distoventrally directed setae. Antennular flagellum ventral ramus similar in length and setation to third article of peduncle, setae much longer, denser than on dorsal ramus; dorsal ramus shorter than third article of peduncle, becoming heavier distally where subterminal articles broader than those of adjacent ventral ramus, there fringed with slightly elongate, dense ventral setae.

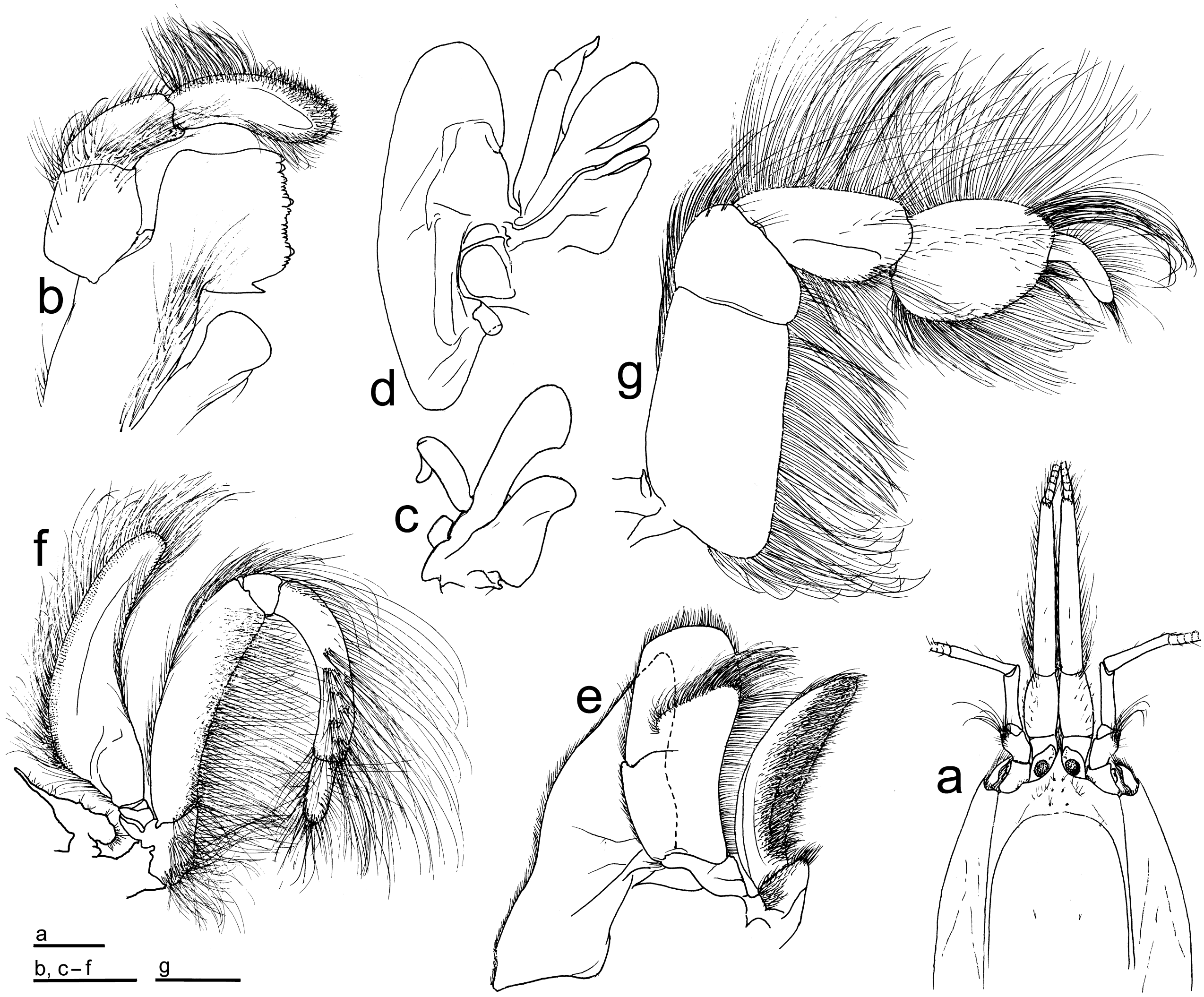

FIGURE 1. *Lepidophthalmus natesi* **sp. nov**., holotype male, cl 16.7 mm, Tumaco, Pacific coast of Colombia (USNM 1275006): a, anterior carapace, dorsal; b, right mandible, external; c, right first maxilla, without setae, external; d, right second maxilla, without setae, external; e, right first maxilliped, external; f, right second maxilliped, external; g, right third maxilliped, external. Scale bars = 2.0 mm (a, c–f), 1.0 mm (b).

Antennal peduncle reaching at least to midlength of antennular peduncle third article; basal article dorsolateral carina arched to form lip above excretory pore, ventrally with setose rounded weak distal protuberance; second article with distal field of long setae on vertically oriented lateral boss; fourth article about equal to combined lengths of first two, slightly shorter than fifth, lateral setae sparse, limited to short oblique line of 3–5 in proximal third, small tuft in distal 1/4; fifth article narrower than others, setation limited to few long subterminal setae in single punctum. Antennal flagellum about 3.5 times length of antennular flagellum, longest of sparse setae slightly exceeding 2 flagellum articles in length.

Mandibular palp (Fig. 1 b) large, setose, 3-segmented, third article robust, arched, elongate subovoid; gnathal lobe of mandible subquadrate, rounded corner forming angular distolateral shoulder, incisor process with well-defined corneous teeth on cutting margin, concave internal face with strong lip giving rise to molar process bearing weakly bilobed corneous tooth proximal and internal to incisor teeth; thin, rounded paragnath set against proximal convex face of molar process. First maxilla (Fig. 1 c) endopodal palp narrow, terminal article deflected at poorly defined articulation; proximal endite with dense, close-set setation lining sinuous mesial margin, setae spiniform distally; distal endite elongate, terminally broadened with dense long setae, some rows strongly spiniform; exopodite low, rounded. Second maxilla (Fig. 1 d) margins setose, endopod constricted to narrow terminus, first and second endites each longitudinally subdivided, exopod forming large, broad scaphognathite.

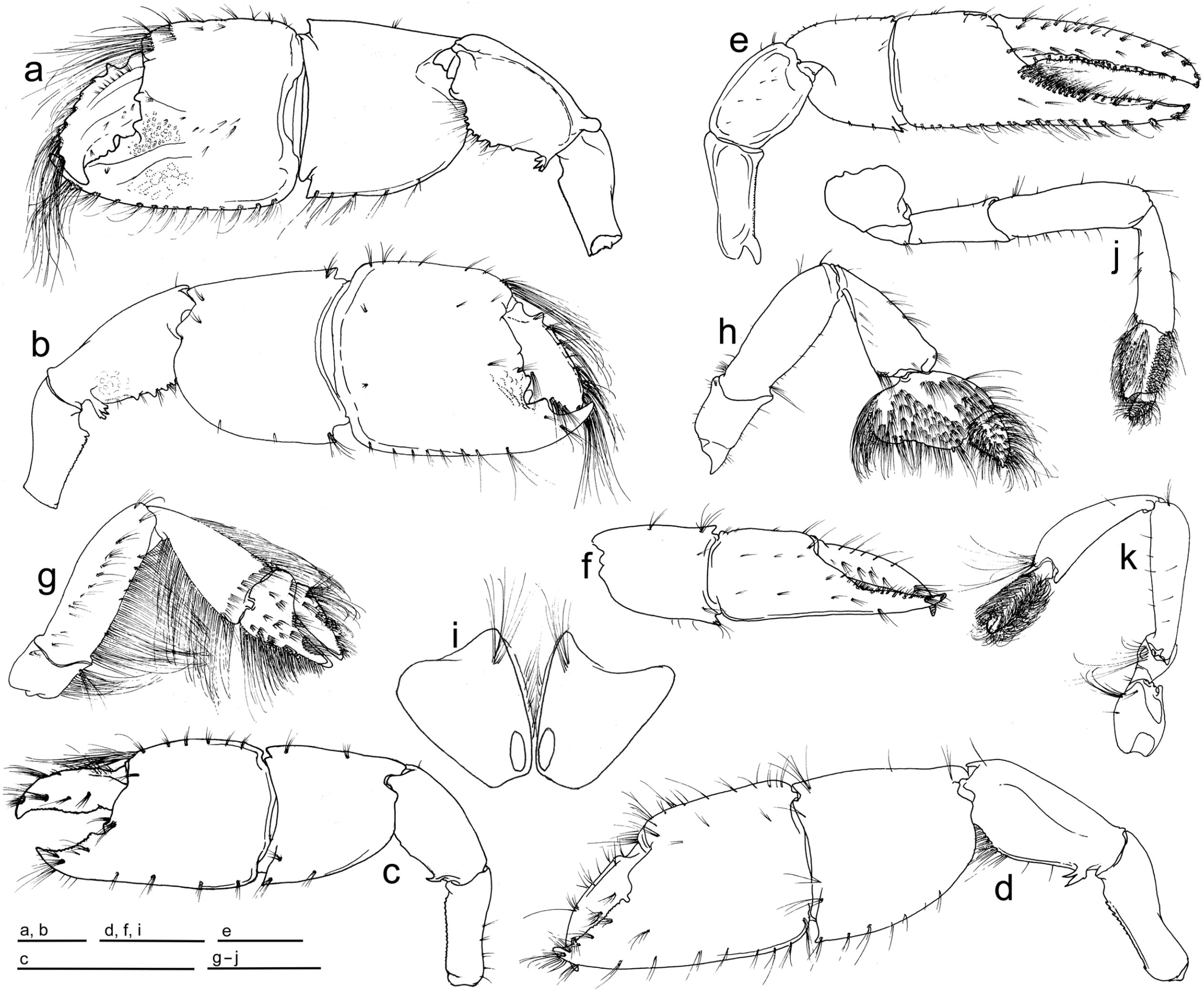

FIGURE 2. *Lepidophthalmus natesi* **sp. nov.**; a, b, e, g, h, j, k, holotype male, cl 16.7 mm, Tumaco, Pacific coast of Colombia (USNM 1275006); c, paratype male, cl 5.9 mm, Tumaco, Pacific coast of Colombia (USNM 1275007); d, f, paratype female, cl 15.5 mm, Tumaco, Pacific coast of Colombia (USNM 1275008); i, paratype ovigerous female, cl 13.8 mm, Paso de Caballos, Pacific coast of Nicaragua (ULLZ 11828): a, major (right) male cheliped, b, external; major right male cheliped, internal; c, major (left) male cheliped, external; d, major (left) female cheliped, external; e, minor (left) male cheliped, internal; f, minor (right) female cheliped, external; g, right second pereopod, external; h, right third pereopod, external; i, right third pereopod coxae and gonopores, ventral; j, right fourth pereopod, external; k, right fifth pereopod, antero-internal. Scale bars = 5.0 mm (a-h, j, k), 3.5 mm (i).

First maxilliped (Fig. 1 e) margins setose, endopod rudimentary, overlain by distal endite; blunt terminus of proximal endite setose; distal endite ovoid, narrowed distally, proximal 2/3 of external face with densely setose longitudinal elevation; exopod incompletely divided by oblique suture on external face, transverse suture obsolete on most of internal face, obvious proximolaterally near margin before intersection of lateral incision; margin lined by long setae, more arched distal than proximal to incision, rounded at distal extreme, mesial margin with comb of close-set very long setae, external face with dense field of feathery distomesially directed setae on and distal to oblique suture; epipod large, broad, anterior end strongly tapered. Second maxilliped (Fig. 1 f) margins of both rami heavily setose, endopodal merus and propodus arcuate, flexor margin of merus with parallel long internal and more feathery external combs of long setae, internal face produced distally to form rounded lobe onto which continues internal row of close-set, very long, marginal setae, lobe extending well over internal proximal margin of short carpus; merus length about 4 times width; propodus length exceeding 2/3 merus length, longest setae originating on extensor margin, patches on distal half of external face; dactylus digitiform, length more than 2 times breadth, rounded terminally, distal half bearing short stiff cornified setae; exopod broad, bladelike, narrowing distally, distinctly overreaching endopodal merus, arcuate, terminally rounded; bilobed epipod with short, broad basal lobe, elongate narrowly tapered distal lobe. Third maxilliped (Fig. 1 g) with very small, terminally subacute, rudimentary exopod; endopod large, setose; endopodal ischium subrectangular, maximum diagonal length at least twice width at midlength, internal face with rudimentary unarmed to finely tuberculate arched longitudinal carina on proximal 2/3; merus short, subrhomboidal, broader than long, mesial margin distinctly arcuate; carpus subrectangular, longer than broad, internal small fields of stiff setae becoming dense transverse field in distal third; propodus large, subovoid, longer than broad, internal dense field of stiff setae on proximal third, superior margin lined by long close-set setae, dense patch of more feathery setae at distal end, externally with low, setose, angular lobe on inferior margin immediately below articulation of dactylus, demarcated from margin by offset extending from marginal incision onto external face; dactylus narrow, arcuate proximally, long setae of extensor and distal margins including a few long stiff bristles at terminus.

Branchial formula as reported for congeners (Felder & Staton 2000); endopods and epipods as previously described (Felder & Rodrigues 1993).

Major cheliped located on either right or left side, shape and dentition sexually dimorphic. Major cheliped of male (Fig. 2 a–c; 4 c, d, e) massive, fingers heavily armed; ischium elongate, superior margin sinuous, inferior (flexor) marginal carina armed by very small denticles on proximal 2/3 to 3/4, becoming coarser distally on elevated carina, sometimes compounded or forming one or more larger teeth at distal end of elevated carina; merus superior margin weakly depressed proximally, lacking distinct notch in proximal ¼; inferior margin forming strong single keel, arcuate over distal 2/3, proximally merging into spatulate armed proximal hook at external base of keel; weak evidence (variable) of parallel secondary carina external to keel; broad distal margin of hook terminating in typically 3 (commonly 2–6) spines or teeth (most proximal of which may be lobiform or compound); external face of article distal to hook weakly tuberculate or eroded proximally (in mature); keel denticles (typically 4–8, fewer in immature) strong in distal ¾, largest on most strongly arched midsection of article (weak in immature); carpus broad, subquadrate, superior and inferior margins keeled, divergent distally, superior and inferior margins terminated distally in acutely angular comers, inferior corner origin of weak, rounded extending short distance vertically onto external face of article; propodus broad, heavy, fixed finger length exceeding 1/2 palm length (in mature); internal face of palm proximally smooth, weakly eroded (sometimes with low tubercles) in concave inferodistal region extending onto fixed finger, finely tuberculate in depression proximal to gape; broadly rounded carina extending proximally from internal prehensile margin of fixed finger below tuberculate depression behind gape and above weakly eroded inferodistal concavity of article; external face with very weak to obsolescent oblique carina or furrow defining proximal limit of slight depression extending proximally from gape, depression very weakly but densely tuberculate (or eroded); superior propodal margin distinctly keeled on proximal 3/4, inferior marginal keel distinct full length of palm, becoming broad and obscure on fixed finger where broken by large setose punctae; fixed finger originating below subtriangular, slightly upturned, heavy tooth at proximal end of gape, separated by broad U-shaped notch from strong, distally inclining, triangular tooth originating from external prehensile margin and centered at 1/3 to 2/5 length of fixed finger; fixed finger with well-defined separation of smooth internal from armed and elevated external prehensile margin, internal margin unarmed, but forming thick rounded carina extending slightly onto palm; dactylus with hooked tip, proximal end of superior marginal carina (in mature) forming erect coniform tubercle (sometimes compound) or short, strong, longitudinally oriented elevated crest, decreasing in elevation distally, carina distally broken by large setal punctae giving dentate appearance, internal dactylar face with long, strong rounded proximal carina bearing multiple smaller setal punctae, lower internal dactylus with broadly rounded carina forming unarmed internal prehensile margin of gape; dactylus external prehensile margin (in mature) typically with 3 major heavy prehensile teeth, proximal the smallest, obliquely transverse in major axis, terminally armed with rounded microtubercles, evident with dactylus fully extended, middle tooth heavy, coniform, weakly bilobed transversely, closely shouldered to proximal tooth, sparsely tuberculate on cusps, centered near 1/3 length of finger, middle tooth separated by subquadrate to U-shaped notch from narrower elongate, ridge-like distal tooth originating near midlength of dactyl, elevated proximal prominence thickest, distally sloping prehensile edge subdivided into series of strong denticles (sometimes compound) extending almost to terminal hook.

Major cheliped of female (Fig. 2 d, Fig. 4 a) less massive, less armed and sculpted, carpus and propodus relatively lower and more elongate than in male, opposed tips of fingers forming very symmetrical pincer and gape; merus inferior margin with proximal tooth typically terminated in 2 (variably 1–3) teeth or spines and a small proximal lobe, teeth of keel usually restricted to distal half of margin; prehensile margins on fixed finger and most of dactylus evenly armed by serration of low rounded denticles; dactylus narrow, relatively less massive proximally than fixed finger, prehensile margin sinuous; fixed finger basally broader than in males, notch at base of fixed finger a narrow U-shaped or V-shaped incision proximal to serration of prehensile margin, lacking distinct development of prehensile tooth, concave between internal and external prehensile margins; superior and inferior margins of propodus convergent distally, laterally compressed to ventral keel; tip of dactylus usually overreaching tip of fixed finger when fingers crossed, flexed fingers filling gape fully including incisional notch at base of fixed finger.

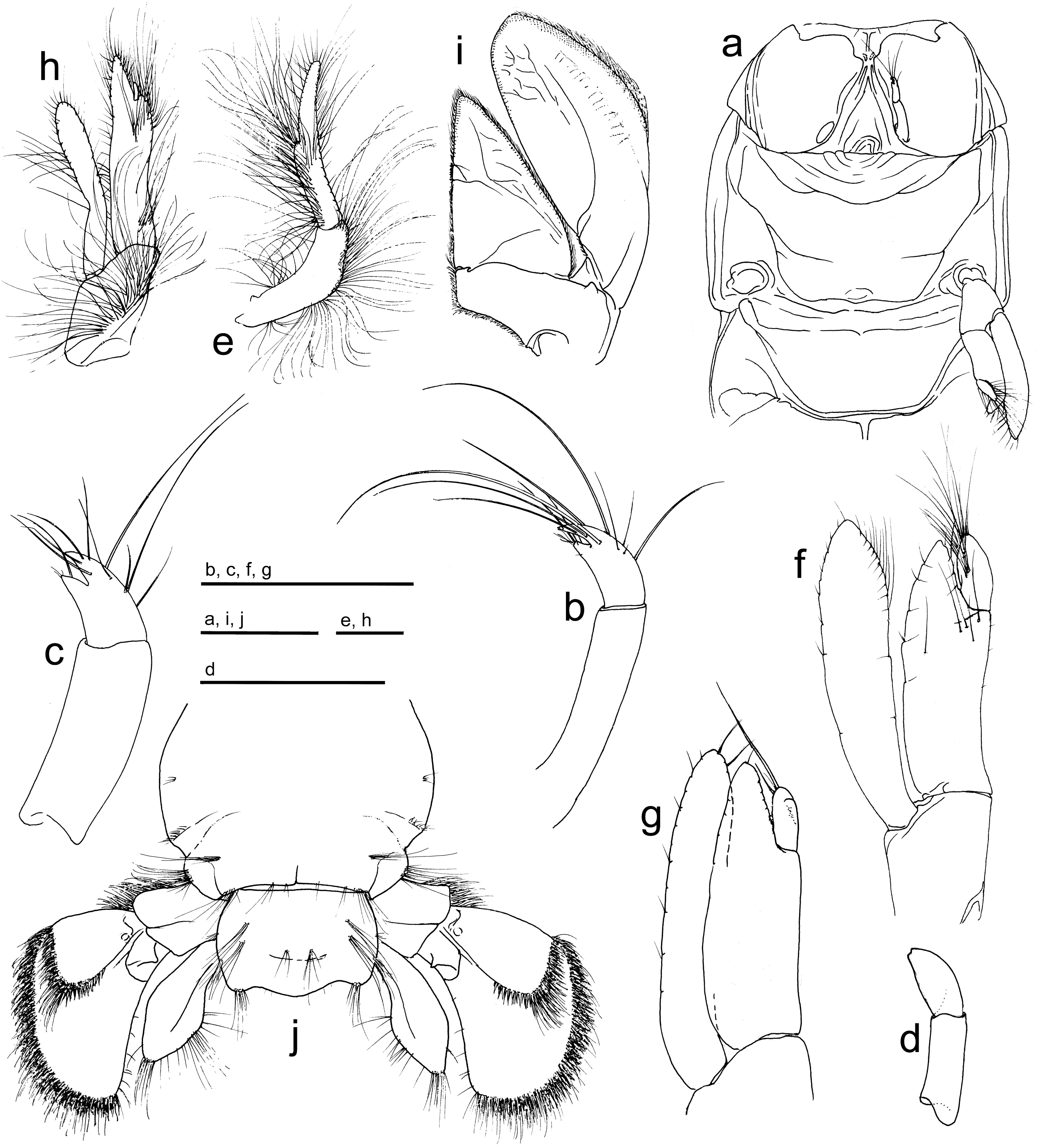

FIGURE 3. *Lepidophthalmus natesi* **sp. nov.**; a, b, f, i, holotype male, cl 16.7 mm, Tumaco, Pacific coast of Colombia (USNM 1275008); c, paratype male, cl 11.0 mm, d, g, paratype male, cl 5.9 mm, Tumaco, Pacific coast of Colombia (USNM 1275007); e, h, j, paratype female, cl 15.5 mm, Tumaco, Pacific coast of Colombia (USNM 1275008): a, anterior pleomeres of male, left pleopods removed, ventral; b, right male first pleopod, lateral; c, right male first pleopod, lateral; d, right male first pleopod, lateral; e, right female first pleopod, lateral; f, right male second pleopod, posterior; g, right male second pleopod, posterior; h, right female second pleopod, posterior; i, right third pleopod, anterior; j, telson and uropods, dorsal. Scale bars = 5.0 mm (a, i, j), 2.0 mm (b), 1.0 mm (c, g), 4.0 mm (f), 0.5 mm (d), 2.0 mm (e, h).

FIGURE 4. Color patterns and habitus of *Lepidophthalmus natesi* **sp. nov.**: a, f, female paratype, lateral habitus (a) and dorsal sclerite of first pleomere (b, contrast enhanced), cl 12.7 mm, Estero de Las Peñitas, Pacific coast of Nicaragua (ULLZ 4509); b, e, male paratype, ventral with second pleopods removed (b), and external face of cheliped (e), cl 15.5 mm, Estero de Las Peñitas, Pacific coast of Nicaragua (ULLZ 4509); c, d, male paratype, lateral habitus (c) and dorsal habitus (d), cl 16.6 mm, Estero Ciego, Pacific coast of Nicaragua (ULLZ 10838).

Minor cheliped of male (Fig. 2 e; Fig. 4 c, d) weakly armed; ischium flexor margin serrate by minute denticles becoming more widely separated distally; merus mostly unarmed, inferior margin with 1 small low tubercle proximally (in mature); carpus with acute distal comers, rounded carina extending vertically short distance from corner, forming subterminal blunt edge of lower external face; fixed finger slightly narrower than dactyl, broad prehensile surface unarmed but with dense field of setal punctae over full length, distal bearing short setae, sloping proximal 2/5 with punctae bearing elongate setae producing field filling about half of gape length, punctae and tufts extending somewhat onto internal face; dactylus prehensile surface with dense cover of setal punctae bearing short setae, weak evidence of subterminal tooth as broad swelling, each finger terminating in acute to subacute cornified tip. Minor cheliped of female (Fig. 2 f) with setation on proximal prehensile face of fixed finger shorter, less dense, less elongate than in male, external prehensile margins with fine, uniform, rounded microdentition; gape between fingers narrower than in male.

Second pereopod (Fig. 2 g) chelate, flexor margins of merus and carpus lined with evenly spaced long setae, inferior margin of propodus with long setae proximally, grading distally to dense field of shorter, variably hooked bristles; middle 1/3 of fixed finger with patch of short stiff bristles immediately external to prehensile margin; superior margin of dactylus with transverse lines and fields of proximally long setae grading to short stiff hooked bristles distally. Third pereopod (Fig. 2 h) merus length about 3 times width; propodus with inferodistal margin variably trilobate, middle lobe smallest, sometimes no more than small cusp of weakly lobate margin between major distal and proximal lobes, setal tufts giving margins of lobes weakly scalloped appearance, lobes demarcated by furrows on internal face, lobe distal margins with dense fringe of tufted setae concealing shorter corneous bristles, distal lobe with at least one heavier, weakly hooked, distally directed corneous tooth arising from margin, longest setae on and above proximo-inferior margin of proximal lobe, patterned tufts of lighter setae on external face of article; dactylus tear-shaped, superior margin concealed by short transverse rows of long dense setae on external face, becoming thick patch of short bristles on distal superior margin, margin internally evident as distinctly sinuous, article terminating in short, narrow, ventrolaterally directed corneous tooth, external face with fields of setae and shorter stiff bristles lining inferior margin, grading to fields and poorly defined rows of much finer setae above; mature female gonopore less than 1/3 coxa length (Fig. 2 i). Fourth pereopod (Fig. 2 j) weakly subchelate, inferodistal process of propodus (= fixed finger) forming subacute angular lobe, tip weakly cornified, extending distally about 1/3 length of dactylus, inferior margin of lobe with 1 or more (2 in holotype) very heavy, weakly hooked, subterminal corneous spines, margin proximally with additional lighter short bristles, obscured by dense brush of setae, setae originating from inferior margin and lower internal face strongly serrate; dactylus bearing dense cover of long setae, slightly elongate, tear-shape, superior margin arched, terminating in short ventrolaterally directed corneous tooth. Fifth pereopod (Fig. 2 k) minutely chelate, opposable faces of fingers spooned, terminally rounded with corneous, pectinate opposing margins; propodus with dense field of long, close-set setae on internal face, fixed finger slightly deflected; dactylus terminally narrower than fixed finger, hooked form of beak-like chela obscured by dense setation on distal 2/3 of propodus and superior face of dactylus.

Pleomeres dorsally smooth. First pleonal tergite (Fig. 4 a, c, d, f) with slightly thickened, translucent, mid-dorsal sclerite connected anterolaterally to narrowing, posteroventrally directed anterolateral sclerites, broadening posteriorly to truncate margin, lacking both isolated posterolateral sclerotized plate and small sclerites in membranous area to each side; second tergite posterolateral lobe below suture sclerotized like remainder of tergite, lobe crossed by well-defined anterior transverse line of very fine setae, 2 shorter less defined oblique lines in posterior half; ventrolateral lobe of tergite centered near or anterior to midlength of tergite. Third to fifth tergites each encompassing a finely setose, lateral, membranous suboval area below a weak posterolateral suture, those of third and fourth tergite more posteriorly positioned than on fifth, that of fifth tergite smallest, almost circular. Sixth tergite with 2 transverse posterolateral lines of short setae anterior to posterolateral groove from which transverse and posterior sutures originate, longest line adjacent, subparallel to transverse suture; transverse suture ill-defined across most of sixth tergite (Fig. 3 j), lacking connection to short longitudinal posterior suture; posterolateral margin of tergite marked by 3 closely parallel longitudinal lines of micropunctae bearing very fine setae; tufts of stiff setae mesial to lateral incision of transverse suture, mesial to each posterior suture, on posterolateral corners, and usually as 4 short (sometimes broken) lines or tufts of stiff setae on posterior margin.

Ventral surfaces of pleomeres generally lacking extensive armor of sclerotized plates and tubercles (Fig. 3 a; Fig. 4 b); in male, heaviest sclerites of first pleomere forming narrow furrows converging anteromesially from base of each pleopod, furrows roughly accommodating first pleopods when fully flexed against pleon; furrows on same sclerites in female forming closed suture; second pleomere in both sexes lacking evidence of neither longitudinally furrowed or flattened median plate nor thicken small sclerites forming tubercles embedded in ventral pleonal membranes.

First pleopod of male and female uniramous, composed of 2 articles; in male, first pleopod originating from outer of 2 sclerotized ridges forming trough roughly accommodating flexed pleopod, length distinctly less than 1/2 that of second pleopod, proximal article about twice length of terminal article (Fig. 3 b–d); terminal article deeply bifurcate, slightly compressed, concave anterior margin narrower than convex margin, convex subterminal margin bearing long setae on broad distal (terminal) blade, tip ending in pair of very small, short, thick corneous spines, subterminal blade well-developed, similarly shaped to distal but shorter and less broad, tip bearing several small thin setae; in female (Fig. 3 e), extended length of first pleopod subequal to that of second pleopod, proximal article bearing broad setose boss near midlength, slightly shorter than terminal article, terminal article forming narrow flattened blade beyond setose lobe at midlength. Second pleopod of male and female biramous, both rami setose, appendix on endopod; in mature male (Fig. 3 f, g), appendix (representing obscure merging of appendix interna and appendix masculina in male) large, overreaching terminal lobe of endopod, long terminal setae subequal to or exceeding appendix length, overreaching both endopod and exopod; in female (Fig. 3 h), appendix interna small, narrow, digitiform, markedly overreached by terminus of endopod. Second through fifth pleopods with, at most, a low tubercle or tooth on anterior of basis at condylar articulation with exopod. Third to fifth pleopod pairs forming large, posteriorly cupped fans when crosslinked by hooked setae of stubby appendices internae embedded in opposed margins of triangular endopods (Fig. 3 i).

Telson (Fig. 3 j) broad, subrectangular, width about 1.5 times length, broadest near midlength, posterior margin distinctly trilobate; dorsally with 3 pairs of strong setal tufts, posteriormost pair submedian in posterior half of telson, 2 anterior pairs aligned longitudinally well lateral of midline, both anterior to midlength; lateral margins with pair of strong setal tufts just posterior to midlength (slightly supramarginal), smaller lateral pair in anterior half (sometimes evident only as the small marginal punctae), posterior margin with well-developed tuft on each posterolateral lobe. Uropod (Fig. 2 o) with strong, broadly triangular, posteriorly directed flange-like tooth on protopod, positioned to overreach anterior margin of extended endopod; much smaller angular short tooth on proximal article of exopod abutting margin of extended exopod; endopod elongate, narrow, subtrapezoidal, length more than twice breadth, broadest in distal half, posteromesial margin with broken fringe of setae, tapering to rounded angular terminus bearing marginal fringe of long setae, distal end extending about as far as distal end of anterodorsal plate on flexed exopod; exopod anterodorsal plate falling well short of distal margin, posterodistal edge of plate with short, thick, spiniform setae grading to thinner, dense, elongate setae of exopod margin; distal margin of exopod with dense fringe of setation, slightly longer posteriorly.

Color. In life, color in this species (Fig. 4 a–f) is of greatly variable intensity, with the most striking individuals showing rose-pink to lavender dorsally on all sclerotized parts, including the chelipeds. When so, dorsal pigment is usually most intense on distal articles of the antennular peduncles, immediate postorbital regions of the carapace, posterior reaches of the pleomeres, basal articles of the uropods, and lateral reaches of the telson. However, some (very young and very old) individuals may totally or almost totally lack rose-pink and instead show off white sclerotized areas and chromatophores or dispersed color of brownish yellow to olive green hues, such as are commonly found on the uropodal exopods and ventral surfaces of many specimens.

Size. Maximum observed postorbital carapace length of male 19.2 mm; of female 18.7 mm. Maximum embryonated egg length on preserved ovigerous females is about 0.8 mm for immature clutches and 0.9–1.0 mm for immediate pre-hatch.

Habitat. Obligate fossorial burrowers as adults, populations of this species favor polyhaline habitats with richly organic sediments, as appears true for most species of the genus (Felder 2001). All specimens in natural settings of coastal Nicaragua were taken with hand-operated extraction “yabby” pumps from intertidal to shallow subtidal sediments on margins and mudflats of mangrove-lined estuaries or back-beach ephemeral ponds. However, exceptionally dense populations also occurred on the bottoms (< 2 m deep) and margins of clayey to silty commercial penaeid shrimp culture ponds in Tumaco, Colombia, the type locality. As in other cases where *Lepidophthalmus* invades such culture ponds (Nates & Felder 1998), these ponds were constructed on estuaries that provided optimal habitat for the members of the genus and thus populations from which larvae are recruited when ponds are filled. Burrow walls appeared to be constructed of lightly cemented clayey sand or mud, with the internal lining usually a smoother brownish surface. In all settings, sediments appeared to be richly organic, often with an identifiable detrital component. Salinities of shallow waters overlying burrows ranged from 2.0 psu in a rain-swollen tidal stream of a small estuary to 45.0 psu in a shallow pond stranded among mangroves inside an ephemeral inlet. In most Nicaraguan collecting sites, this species occurred alongside the congeners *L. eiseni* and *L. bocourti*, with no detectable microhabitat separation of the three species within the habitat. Where found on mudflats near mangroves, burrows of two burrowing axianassids, *Axianassa* spp., occurred among those of *Lepidophthalmus.* Commensal alpheid shrimp of the genus *Leptalpheus,* as reported by Anker (2011), occurred with all of these species but were in some cases unquestionably extracted from burrows of *L. natesi* **sp. nov.**

Distribution. Eastern Pacific: Extreme southern Colombia to northwestern Nicaragua (polyhaline waters along estuary margins, mudflats of inlets, ephemeral intertidal ponds, tidal streams).

Type locality. Pacific coast of Colombia, Tumaco, bottom of partially drained commercial shrimp culture pond in mangrove estuary (01°46.64'N, 78°46.30'W).

Etymology. This species is named for our colleague Dr. Sergio F. Nates, who was for several years a participating scientist in our field and lab projects concerning biology of callianassid shrimp in Nicaragua, Costa Rica, Panama, and Colombia, and who assisted in the collection of many specimens essential to this and related papers.

Remarks. *L. natesi* **sp. nov.** reaches relatively large size and has relatively small eggs compared to some species of the genus but does not appear to reach the size extremes of larger specimens among sympatric populations of the ventrally sclerotized species *L. eiseni* and *L. bocourti.* Occurring together, these two species can look superficially very similar, to the point that some earlier authors (Biffar 1972; Manning & Felder 1991; Sakai 1999, 2005), treated them as synonyms. Even after reestablishment of their well-supported separation (Felder 2003), the account of Sakai (2005) continued to confuse the characters that so clearly separate them. At first inspection, both of these ventrally plated species resemble *L. natesi* **sp. nov.**, which is in turn readily distinguished from both of them by its lacking the ventral median sclerotized plate on the second pleomere. Lifting the second pleopods to expose the ventral surface, this large plate is subrectangular in *L. eiseni* or conspicuously constricted along its length in *L. bocourti*. Of the two plated species, *L. bocourti* also differs from both *L. eiseni* and *L. natesi* **sp. nov**. in having a uniquely reflexed ventrolateral cristate margin on the second pleuron and distinct spines developed on the anterior of the basipodites of the third through fifth pleopods (Felder 2003). Yet, despite its unique features, sequence-based phylogenetic analyses (Felder *et al.* 2003, Felder & Robles, 2015) position *L. bocourti* as a closer relative to *L. natesi* **nov. sp**. than to any other congener to which it has thus far been compared by molecular methods.

Comparative molecular analyses to date have not, however, included *L. rafai* Felder & Manning, 1998, and this is the only other presently described eastern Pacific species of the genus that lacks ventral pleonal sclerites. Thus far known only from the type series of small specimens taken in western Colombia, those perhaps typifying its apparently smaller size than *L. natesi* **sp. nov**., *L. rafai* would not appear to be a close relative of the presently described species because of its lacking a trilobate posterior margin on the telson and having a broad uropodal endopod. In addition to these fundamental differences, it differs in many other likely more apomorphic characters, from shape of the third maxilliped merus, to the distinctly bicarinate keel of the male cheliped merus, shape of the proximal meral hook on this cheliped, and dimunitive appendix on the second male pleopod. In most of its characters, including its telson and uropods, *L. rafai* continues to be a candidate instead for relationship to the ventrally unsclerotized *L. louisianensis* or *L. siriboia* from the western Atlantic, as previously suggested (Felder & Manning 1998), rather than to *L. natesi* **sp. nov.**

If accepting genetic inference that relates *L. natesi* **sp. nov**. closely to *L. bocourti*, it follows that presence or absence of ventral pleonal sclerites must then vary within clades of the generic phylogeny. Such plating remains a character of utility for species identification, but perhaps not always one easily applied in slightly higher classification. Other than the trilobate posterior margin of the telson and shape of the adjacent somewhat trapezoical uropodal endopods, these two species do share other characters, notably including configuration of the almost identical dorsal sclerite and surrounding posterolateral membrane on the first pleomere. In both, there is lack of an isolated large sclerite or small dispersed sclerites within the posterolateral membrane (Fig. a, c, d, f; Felder 2003: fig. 17), despite these occurring in many congeners (Felder & Manning 1997: fig. 1 d, 7 a: Felder 2003: fig. 26; Felder & Staton 2000: 1 h). Males of these two species also share similar development of the major cheliped, from the multispinose or multidentate proximal meral hook to dentition of the fingers (Fig. 2 a, b, 4 e; Felder 2003: fig. 13) and similar development of the second pleopodal appendices.

As in most species of the genus that range from large to small sizes in collections, there is wide variation in character development among less than fully mature specimens, as well as between average-sized mature specimens and the occasional exceptionally large individual. Submature male chelipeds may have very little of the dentition and other appendage armor developed (Fig. 2 a–c), and secondary sex characters of the pleopods, including the appendix of the second, also vary with maturation (Fig. 3 c, b, d, f, g). In very large males, the rostrum is sometimes directed steeply upward over the eyes, rather than gently arched, its steep inflection reflected in some depression of the carapace front that more strongly offsets it from the dorsal oval than in typical specimens. In mature females, the rostrum is alternatively sometimes barely arched or elevated and very narrowly spiniform, extending almost as far anteriorly as the eyestalks. The eyestalks themselves can vary in acuteness of the tip and angularity of the anterolateral corner, being less acute terminally and more angular anterolaterally in large males, and more acute and less angular in females. This at times makes the male eyestalks appear shorter and broader than in females.

Lepidophthalmus panamensis sp. nov.

Figures 5 a–h, 6 a–j, 7 a–k, 8 a–c

Lepidophthalmus bocourti—Biffar 1972: 65–66, 70–72 [part, only records from Panama Canal Zone, Fort Amador Causeway]; Lemaitre & Ramos 1992:349, fig. 4.
Lepidophthalmus nr. *bocourti*—Staton *et al.* 2000: 157, 167; tables 1, 3; figs. 1–4.

Type material. Panama (Pacific coastline). Holotype: male, cl 10.2 mm (USNM 1275011), = ULLZ 5616-A tissue/sequence voucher, photographic voucher, Panama City, Isla Naos Marina (08°54.88'N, 79°31.80'W), intertidal clayey sand swash zone of small beach between waterfront buildings, 24 April 2004, D. L. Felder. Paratypes: 1 female, cl 9.6 mm (USNM 1275012), = ULLZ 5616-B tissue/sequence voucher, photographic voucher, collected with the holotype, 24 April 2004, D. L. Felder; 1 male, cl 9.2 mm, 6 females, cl 7.1, 7.1, 9.6, 9.6, 9.7, 10.3 mm, genetic vouchers (ULLZ 5756), Panama City, Isla Naos Marina (08°54.89'N, 79°31.75'W), intertidal clayey sand swash zone of between breakwater rocks, 13 August 2004, D. L. Felder.

Additional material. Panama (Pacific coastline): 3 males, 7 females, 2 ovigerous (ULLZ 4822), fragments of 8 males, 18 females, allozyme vouchers (ULLZ 4821), Panama City, Amador Causeway, Panama Bay side (08°56.27'N, 79°32.67'W), intertidal burrows in clay with sand and coarse gravel (salinity 26 psu), between and under small breakwater rocks shoring side of causeway (now covered by construction landfill), 10 September 1990, D. L. Felder, J. H. Christy, and U. Schober. 4 males, 5 females (ULLZ 5758), Panama City, Isla Naos Marina (08°54.88'N, 79°31.80'W), intertidal muddy sand swash zone of small beach between waterfront buildings, 24 April 2004, D. L. Felder. Colombia (Pacific coastline): 1 female (USNM 1275013), Isla Gorgona (approximately 02°57.9'N, 78°10.3'W), sediment near old pier, 19 February 1992, J. H. Madrid. 1 juvenile male (USNM 251736) Isla Gorgona, sediment in intertidal crevices of basaltic rocks, 01 July 1987, R. Franke. 1 female (USNM 251735), Isla Cuichiche, Bahia Malaga (approximately 03°59'N, 77°15'W), intertidal mud near freshwater stream, 24 November 1985, G. E. Ramos.

Diagnosis. Rostrum acute, narrow, inclined dorsally as variably elevated to weakly arched spine, flanked by rounded shoulders slightly advanced to anterior, centered well lateral to eyestalks, creating underlying concavity overlying antennal peduncles. Flattened mesial margins of eyestalks closely opposed, tips acute. Inferior margin of major cheliped merus forming distinct single keel, weakly bicarinate in denticulate distal half, proximal hook terminally acute, subterminal process a rounded lobe or short blunt tooth, superior margin with distinct proximal notch. Propodus of male major chela with inferior margin terminating distally in acute tooth, corner forming origin of rounded-edge carina extending short distance vertically as subdistal margin of article. Dactyl of male major chela prehensile margin with heavy subquadrate tooth in proximal half, separated by broad deep notch from shouldered series of usually 4–6 subtriangularly rounded or truncate distal teeth, largest proximal; superior margin proximally with low rounded longitudinal carina. First pleonal tergite with dorsal sclerite bell-shaped, subtruncate posteriorly. Second pleomere ventrally leathery, lacking sclerotized median plate. Male first pleopod (gonopod) terminal article slightly compressed, bifurcate, subdistal tooth short, angular, distal broadly arching, terminally narrowed to small cornified tip. Appendix of male second pleopod reaching to or exceeding terminus of endopod, directed obliquely to axis of endopod, bearing terminal long setae reaching well beyond distal end of endopod. Second through fifth pleopods lacking acute distolateral spine on anterior face of basis. Telson posterior margin distinctly trilobate. Uropodal endopod narrow, elongate subtrapezoidal, broadest near or proximal to midlength, length more than twice breadth. GenBank accession numbers for 16S and 12S mt sequences of type materials as reported by Robles & Felder (2015: table 2).

Description. Frontal margin of carapace with acute, narrow rostral spine (spine missing and front rounded in 4 paratypes) flanked laterally by anteriorly advanced rounded shoulders centered lateral to eyestalks and separated from rostrum by oblique shallow posterolaterally directed furrow defining (Fig. 5 a, b) elevated orbital margin;

orbital margin and shoulders forming concavity overlying antennal peduncles; rostrum variably inclined dorsally, terminal spine forming elevated weak arch (sometimes straight) above eyestalks (in most mature specimens) extending 2/3 to 3/5 length of eyestalks in dorsal view (Fig. 5 b), spine bearing ventral tuft of setae centered near midlength, extending above and between proximal half of eyestalks. Carapace postrostrally with 2 pairs of small setose punctae on each side of midline; dorsal oval well-defined, anteriorly intersecting shallow oblique furrow extending posterolaterally from behind eyestalks, single pair of widely separated setal punctae bearing 1 or 2 setae each near midlength, length of oval about 6/10 of postorbital carapace length; marginal suture of oval diminished at postrostral midline, stronger at posterior end with sclerotized articulation to bulbous cardiac region at posterior midline.

Eyestalks subtriangular in dorsal view, reaching at least 3/4 length of basal antennular article (Fig. 5 a); lateral margins broadly arched, distal margins weakly sinuous to nearly straight, converging to acute apices; dorsomesial margin thickened to form a slightly swollen boss in distal 1/3, (Fig. 5 b); distinctly faceted well-defined cornea centered on dorsal surface.

Antennular peduncle much longer and heavier than antennal peduncle (Fig. 5 a); basal article dorsally invaginated to form statocyst occluded by setae, mostly overlain dorsally by eyestalk; second article subequal to length of basal article, third article at least 3 times length of second; second and third articles with dense ventromesial and ventrolateral rows of long, distoventrally directed setae. Antennular flagellum ventral ramus longer than third article of peduncle, with denser setation than dorsal ramus; dorsal ramus shorter than third article of peduncle, heavier than ventral ramus in swollen distal 1/3 where subterminal articles broader than those of ventral ramus, there fringed with short, dense ventral setae.

Antennal peduncle reaching about to midlength of antennular peduncle third article; basal article dorsolateral carina arched to form strong lip above excretory pore; second article with distal field of long setae on lateral boss; fourth article slightly shorter than combined lengths of first 2, slightly shorter than fifth, ventrolaterally with three small tufts of very long setae; fifth article narrower than others, long setae limited to single, small, distal, dorsolateral tuft. Antennal flagellum with sparse short setae, about 3 times length of antennular flagella.

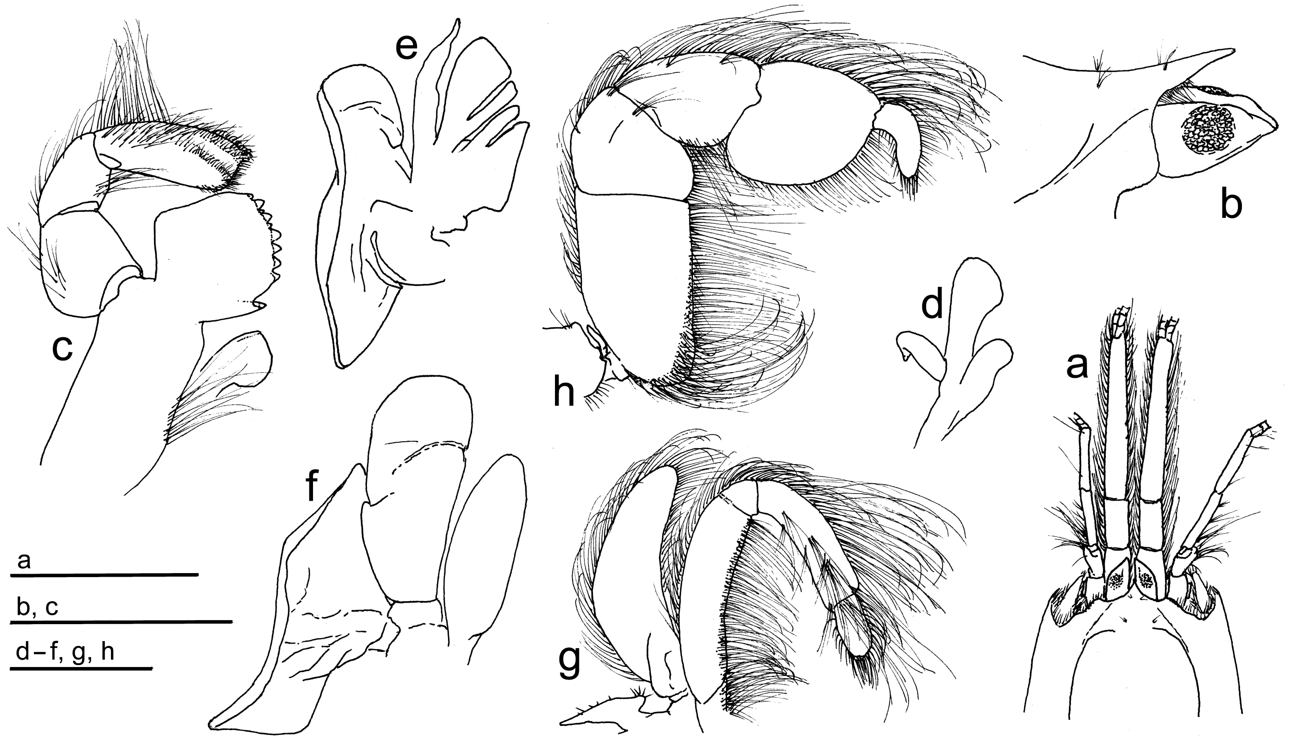

FIGURE 5. *Lepidophthalmus panamensis* **sp. nov.**, holotype male, cl 10.2 mm, Panama City, Isla Naos Marina, Pacific coast of Panama (USNM 1275011): a, anterior carapace, dorsal; b, rostrum, eyes, and frontal margin, right; c, right mandible, paragnath detached, external; d, right first maxilla, without setae, external; e, right second maxilla, without setae, external; f, right first maxilliped, without setae, external; g, right second maxilliped, external; h, right third maxilliped, external. Scale bars = 5.0 mm (a), 2.0 mm (b, d–f), 1.5 mm (c, g, h).

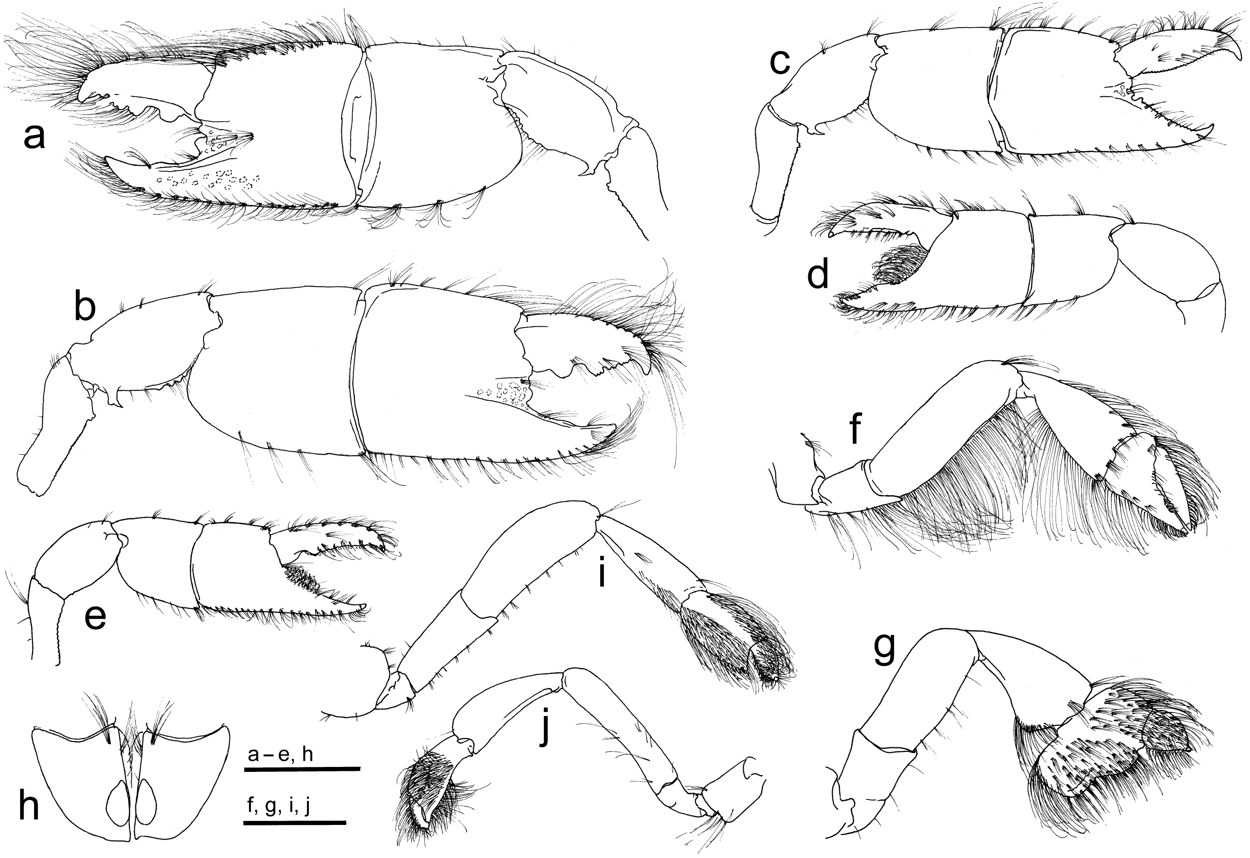

FIGURE 6. *Lepidophthalmus panamensis* **sp. nov.**; a, b, d, f, g, i, holotype male, cl 10.2 mm, Panama City, Isla Naos Marina, Pacific coast of Panama (USNM 1275011); c, e, h paratype female, cl 9.6 mm, same locality (USNM 1275012); j, paratype male, cl 9.2 mm, same locality (ULLZ 5756): a, major (left) male cheliped, external; b, major (left) male cheliped, internal; c, major (right) female cheliped, external; d, minor (right) male cheliped, external; e, minor (left) female cheliped, internal; f, right second pereopod, external; g, right third pereopod, external; h, right third pereopod coxae and gonopores, ventral; i, right fourth pereopod, external; j, right fifth pereopod, antero-internal. Scale bars = 5.0 mm (a–e, h), 3.0 mm (f, g, i, j).

Mandibular palp (Fig. 5 c) large, setose, 3-segmented, third article elongate, subrectangular, truncate to weakly concave terminally; gnathal lobe of mandible subquadrate, distolateral shoulder angular, incisor process with well-defined subacutely triangular, heavily cornified, fingernail-like teeth on cutting margin (6 major subequal, plus 3 interstitial smaller ones in holotype), concave internal face with strong lip giving rise to molar process bearing strong corneous tooth proximal and internal to incisor teeth; thin, rounded paragnath positioned against proximal convex face of molar process. First maxilla (Fig. 5 d) endopodal palp narrow, distal margin heavily setose, grading to short setae on external face, terminal article deflected at poorly defined articulation, beyond which is small weakly defined apical lobe; proximal endite with closely spaced setae lining sinuous mesial margin, becoming spiniform distally; distal endite elongate, terminally broadened and densely setose, several rows strongly spiniform; exopodite low, rounded. Second maxilla (Fig. 5 e) margins setose, endopod constricted to narrow, curved, subacute terminus, first and second endites each longitudinally subdivided, exopod forming large, broad scaphognathite. First maxilliped (Fig. 5 f) margins setose, rudimentary endopod overlain by distal endite; blunt terminus of proximal endite coarsely setose; distal endite ovoid, narrowed distally, proximal 2/3 of external face with setose elevation; exopod incompletely divided by obliquely curved suture on external face, internal face with transverse suture sinuous, complete, sinuous, full distance to lateral incision; margin lined by long setae, broadly arched proximal and distal to incision, mesial margin with comb of close-set very long setae, external face with dense field of mesially deflected setae distal to oblique suture; epipod large, broad, anterior end strongly tapered. Second maxilliped (Fig. 5 g) rami with margins heavily setose, endopodal merus and propodus arched, flexor margin of merus with comb of long setae, internal face produced distally to form rounded marginally setose lobe extending over internal proximal margin of short carpus; merus length about 4 times width; propodus length exceeding 2/3 length of merus, longest setae originating on extensor margin and distal half of external face; dactylus slightly swollen, twice as long as broad, rounded terminally, distal half bearing short stiff cornified setae; exopod broad, bladelike, narrowing distally, distinctly overreaching endopodal merus, arcuate, terminally rounded; bilobed epipod with short rounded basal lobe, elongate narrowly tapered, distal lobe. Third maxilliped (Fig. 5 h) with small, terminally subacute, rudimentary exopod; endopod large, setose; endopodal ischium subrectangular, maximum diagonal length slightly less than 2 times width at midlength, internal face with very weakly defined rudiment of obliquely oriented longitudinal carina on proximal half; merus short, subrhomboidal, broader than long, mesial margin distinctly arcuate; carpus subovoid, longer than broad, internal face with densest field of stiff setae in distal third; propodus large, subovoid to subrhomboidal, no longer than broad, internally with dense tufts of stiff setae centered on proximal half, lacking setose angular lobe on flexor margin immediately below articulation of dactylus, demarcated at most by weak carina scarely divergent from flexor margin short distance onto external face; dactylus narrow, strongly arcuate proximally, long setae of extensor and distal margins including stiff bristles at terminus.

Branchial formula as reported for congeners (Felder & Staton 2000); endopods and epipods as previously described (Felder & Rodrigues 1993), branchiae limited to single rudimentary arthrobranch on second maxilliped, pair of arthrobranchs on third maxilliped, and pair of arthrobranchs on each of the first through fourth pereopods.

Major cheliped located on either right or left side, shape and ornamentation sexually dimorphic. Major cheliped of male (Fig. 6 a, b; Fig. 8 a, b) massive, fingers heavily armed; ischium slender, superior margin sinuous, inferior (flexor) marginal carina armed by very small denticles on proximal 1/2 to 2/3, usually becoming more widely separated distally, ending in few enlarged and often compound denticles on distal elbow; merus with distinct depression or notch in proximal 1/4 of superior margin, inferior (flexor) strong marginal keel arcuate distally, single over most of length, evidence of weak parallel carina to external side in distal half, terminally bifurcate proximal hook at outer base of keel, hook terminating in spiniform or dentiform inferodistally directed tip usually paired with weak subterminal lobe, 3–6 small blunt denticles originating from keel margin; carpus broad, subquadrate, superior and inferior margins keeled, near parallel in distal half, terminated distally in subacutely angular corners, inferodistal corner forming origin of short roundly edged carina extending short distance vertically onto outer face of article; propodus broad, heavy, length of fixed finger about 1/2 length of palm; inner face of palm proximally smooth, lacking distinct rounded swollen boss centered near midline, distally with carina extending proximally from inner prehensile margin of fixed finger proximal to gape of fingers and above weak elongate roughened concavity extending almost full length of article; outer face with carina defining weak depression extending proximally from gape of fingers, depression roughened by field of low turbercles extending onto fixed finger; keel of superior propodal margin distinct in proximal half of palm, obsolete distally, keel of inferior margin distinct full length of palm, becoming obsolete on fixed finger where broken by large setose punctae; fixed finger originating below somewhat rounded short tooth at proximal end of gape, prehensile margin weakly armed by low tooth originating from outer prehensile margin, centered near 2/5 to ½ length of fixed finger; fixed finger with well-defined separation of inner and armed, elevated outer prehensile margins, inner margin unarmed but forming thick rounded carina extending onto palm; dactylus with hooked tip, superior margin with (at most) low unarmed rounded carina, lacking distinct elevation of short proximal carina or tubercle, internal face with weakly defined carina forming unarmed prehensile margin, outer face swollen above outer prehensile margin bearing (usually) 2 heavy, prehensile teeth, proximal tooth heavy, subtruncate, weakly subquadrate (sometimes roughened by microtubercles) centered near 1/3 length of finger, separated by subquadrate U-shaped notch from complex elongate bladelike distal tooth originating near midlength of dactyl and extending almost to terminal hook, elevated basal prominence of distal tooth thickest (sometimes a compound denticle), distally sloping prehensile edge armed by series of shouldered subacute denticles, truncate cutting edges usually microtuberculate.

Major cheliped of female (Fig. 6 c; Fig. 8 c) less massive, less strongly armed and sculpted than in male, dactylus narrower, less massive than fixed finger proximally, fingers forming asymmetric pincer; dactylus prehensile margin sinuous, evenly armed by serration of low rounded small denticles; fixed finger basally broader than in males, notch at base of fixed finger a narrow U-shaped incision proximal to enlarged denticle at proximal end of serration of smaller denticles on most of prehensile margin, deeply concave between inner and outer prehensile margins; superior and inferior margins of propodus convergent distally, article more compressed ventrally than dorsally; tip of dactylus overreaching tip of fixed finger when tips crossed, fully flexed fingers incompletely filling incisional notch at base of fixed finger.

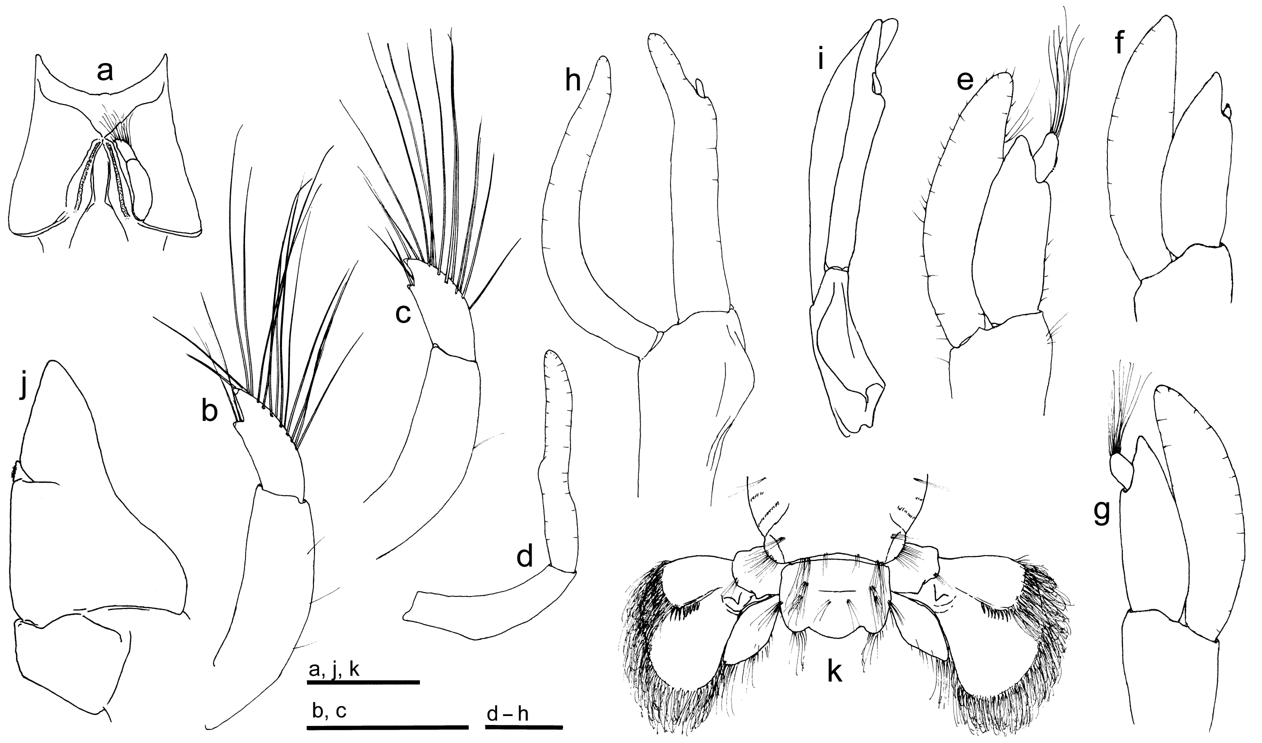

FIGURE 7. *Lepidophthalmus panamensis* **sp. nov.**; a, b, e, j, k, holotype male, cl 10.2 mm, Panama City, Isla Naos Marina, Pacific coast of Panama (USNM 1275011); c, f, g, paratype male, cl 9.2 mm, same locality (ULLZ 5756); d, h, i, paratype female, cl 9.6 mm, same locality (USNM 1275012): a, first pleomere of male, right pleopod removed, ventral; b, right male first pleopod, lateral; c, right male first pleopod, lateral; d, right female first pleopod, lateral; e, right male second pleopod, posterior; f, right male second pleopod, posterior; g, left male second pleopod, posterior; h, right female second pleopod, posterior; i, right female second pleopod, mesial; j, endopod of right third pleopod; k, telson and uropods, dorsal. Scale bars = 3 mm (a), 1 mm (b–h), 2.0 mm (j), 4.5 mm (k).

Minor cheliped of male (Fig. 6 d) sparsely armed; ischium weakly serrate by small denticles on most of flexor margin, denticles more widely separated into microtubercles distally; merus mostly unarmed, inferior margin with at most 1 weak tubercle or swelling proximally; carpus with acute distal comers, very weak rounded carina extending vertically from inferior corner; fixed finger nearly as heavy as dactyl, less hooked distally, prehensile margin lacking teeth, sloping proximal 2/5 with broad field of dense elongate setae filling about half of gape length, extending somewhat onto internal face; dactylus prehensile margin with transversely paired rounded basal tooth above setae filling gape, weak evidence of subterminal tooth as broad swelling, hook terminated in subacute cornified tip. Minor cheliped of female with proximal notch in prehensile surface distal to which is low transversely bilobate tooth proximal to dense tufts of setation on most of prehensile surface (Fig. 6 e) with dense, elongate prehensile setation of fixed finger much less developed than in males.

Second pereopod (Fig. 6 f) chelate, flexor margins of merus and carpus lined with evenly spaced long setae, inferior margin of propodus with long setae proximally, grading distally to dense field of short, hooked bristles; middle 1/3 of fixed finger with patch of short stiff bristles just outside prehensile margin; superior margin of dactylus with proximal long setae grading to short stiff hooked bristles distally. Third pereopod (Fig. 6 g) merus length less than 2.4 times width; propodus with inferodistal margin very weakly trilobate, small middle low, formed by weakly undulate margin between major distal and proximal lobes, setal tufts giving margin weakly scalloped appearance, lobes demarcated by furrows on internal face, distal margins of lobes with dense fringe of tufted setae concealing shorter corneous bristles, middle margin of distal lobe with heavier, weakly hooked, distally directed corneous tooth arising from margin, concealed by longer setae, proximal lobe bearing longest setae of article on inferior margin, patterned tufts of lighter setae densely covering upper and lower fields on external face of article; dactylus tear-shaped, superior margin concealed by long dense setae on outer face, margin internally sinuous, article terminating in short, narrow, ventrolaterally directed corneous tooth, outer face with fields of setae and shorter stiff bristles lining inferior margin, grading to fields and poorly defined rows of much finer setae above; mature female gonopore at least 4/10 coxa length (Fig. 6 h). Fourth pereopod (Fig. 6 i) weakly subchelate, inferodistal process of propodus (= fixed finger) angular, tip terminally rounded, extending distally no more than 1/3 length of dactylus, immediate inferior margin of tip with heavy, hooked, subterminal corneous spine, inferior margin proximally with additional much lighter, longer, short bristles, tip and spine obscured by dense brush of setae originating from inferior margin and lower external face, separated dense field covering upper external face and partially concealing dactylus; dactylus elongate, tear-shape, superior margin arched, prehensile margin densely covered with short hooked bristles, article terminating in short ventrolaterally directed corneous tooth. Fifth pereopod (Fig. 6 j) chelate, fingers spooned, terminally rounded, with corneous pectinate margins; propodus with dense field of long, close-set setae on internal face, fixed finger slightly deflected; dactylus terminally narrower than fixed finger, hooked form and flexure into larger spoon of fixed finger obscured by dense setation on distal 2/3 of propodus and superior surfaces of dactylus.

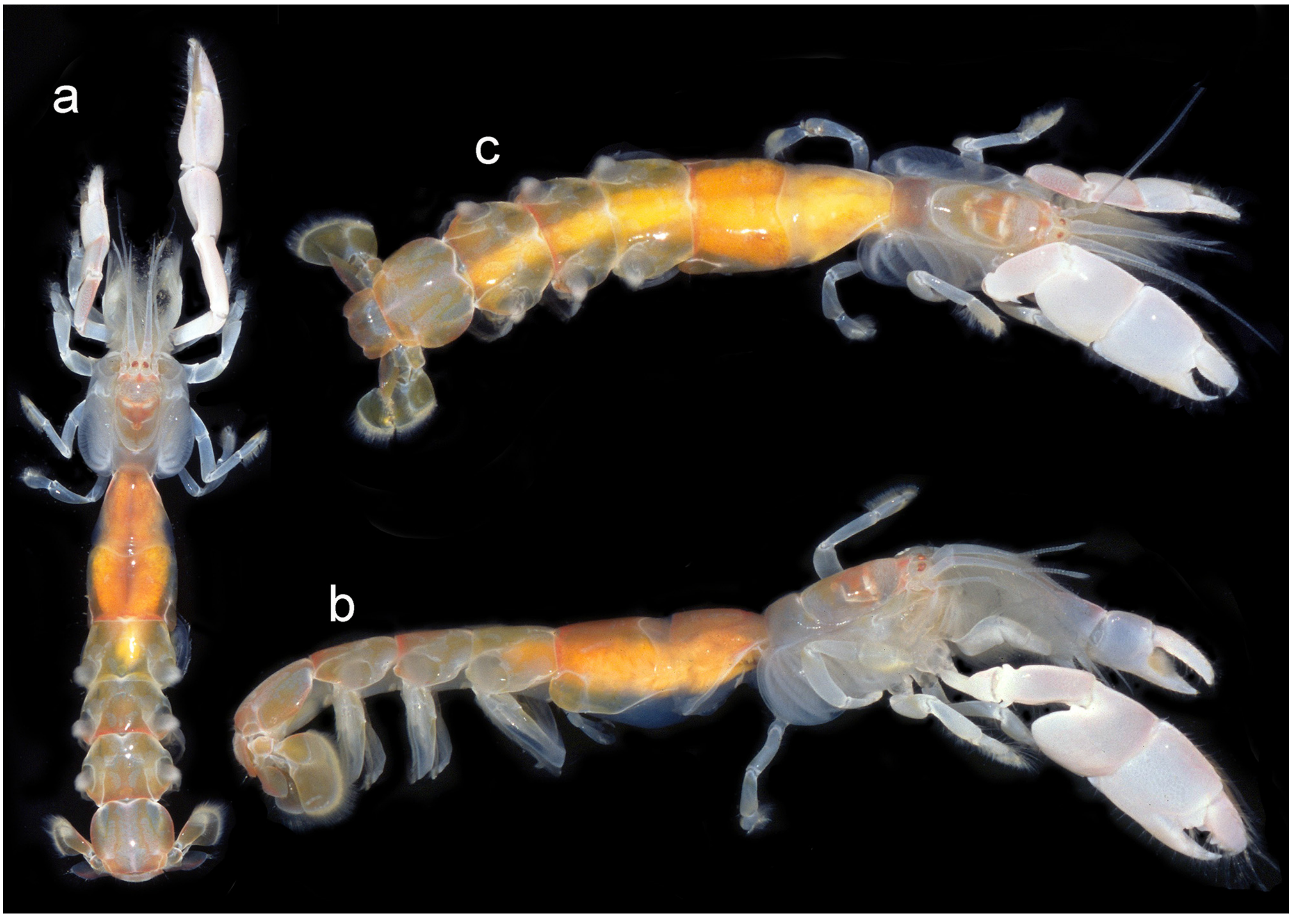

FIGURE 8. Color patterns and habitus of *Lepidophthalmus panamensis* **sp. nov.**: a, b, male holotype, dorsal (a) and right lateral (b) habitus, cl 10.2 mm, Panama City, Isla Naos, Pacific coast of Panama (USMN 1275011); c, female paratype, dorsal habitus, cl 9.6 mm, same locality (USNM 1275012).

Pleomeres mostly smooth dorsally (Fig. 8 a–c). First pleonal tergite with translucent, bell-shaped or fingernail-shaped middorsal sclerite separated anteriorly by membrane from thickened, narrow transverse anterior sclerite connected laterally to narrow thickened anterolateral sclerites, dorsal sclerite truncate to weakly rounded posteriorly, no evidence of isolated small sclerites in ill-defined posterolateral membranes to each side. Second tergite rounded posterolateral lobe below suture sclerotized at least as heavily as remainder of tergite, lobe bearing distinct tuft of fine long setae near posteroventral margin; ventrolateral prominence of tergite centered slightly anterior to midlength of tergite. Third to fifth tergites each laterally encompassing finely pubescent, membranous subcircular or suboval area below weak posterolateral suture and fringe of long setae, membraneous areas of third and fourth tergite more posteriorly positioned than on fifth, that of fifth tergite slightly smaller, more circular. Sixth tergite with 2 transverse posterolateral lines of short setae anterior to posterolateral groove from which transverse and posterior sutures originate; ventral edge of tergite posterolateral margin marked by 2 or 3 closely parallel longitudinal lines of micropunctae bearing very fine setae; transverse suture obsolete across most of sixth tergite (Fig. 7 k), laterally connecting to short longitudinal posterior suture, or very nearly so; tufts of stiff setae mesial to each posterior suture, on posterolateral corners, and as 4 short lines or tufts of stiff setae on posterior margin, lateral pair longest.

Ventral surfaces of pleomeres lacking general cover or extensive armor of sclerotized plates and tubercles; in male, heaviest sclerites of first pleomere conspicuous (Fig. 7 a), forming narrow convergent furrows or channels extending anteromesially from base of each pleopod, plates convergent, touching anteriorly, furrows roughly accommodating first pleopods when fully flexed against pleon; in female, sclerites shorter, furrow narrower, converging anteriorly and articulating or fusing to from truncate median terminus; second pleomere in both sexes ventrally lacking evidence of longitudinally furrowed or flattened median plate and of thickened small sclerites forming tubercles embedded in ventral pleonal membranes.

First pleopod of male and female uniramous, composed of 2 articles; in male, originating from atop outer of 2 sclerotized ridges forming narrow sinuous trough or channel roughly conforming to flexed pleopod (Fig. 7 a); appendage length less than 1/2 that of second pleopod, proximal article about 2 times length of terminal article (Fig. 7 b, c), terminal article weakly compressed, weakly concave anterior edge narrow, convex subterminal margin less so and bearing long setae, article bifurcate forming 2 blades, subdistal angular, short (weakest in large individuals), lightly cornified tip, distal blade much the stronger, bearing acute cornified tip; in female (Fig. 7, d), extended length slightly less than that of second pleopod, proximal article bearing low setose swelling near midlength, slightly shorter than terminal article, terminal article forming narrow compressed blade beyond setose lobe at midlength. Second pleopod of male and female biramous, with appendix on endopod; in male (Fig. 7 e–g), typical mature appendix (representing obscure merging of appendix interna and appendix masculina) large (dimunitive on one side in illustrated paratype), oriented obliquely to axis of endopod, scarely distinguishable patch of obsolescent hooks (= cincinnuli, vestige of appendix interna) roughening mesial margin (not evident in all), length subequal to or exceeding triangular tip of endopod, longest terminal setae exceeding appendix length, overreaching both endopod and exopod, both rami bearing sparse short setae; in female (Fig. 7 h, i), basis with broad lobe on mesial side, appendix interna small, narrow, markedly overreached by narrow terminus of endopod, terminally subacute, terminus and mesial subterminal shoulder with field of minute, rudimentary hooked setae, both rami bearing long setae. Second through fifth pleopods with, at most, a low tubercle or tooth on anterior face of basis at condylar articulation with exopod. Third to fifth pleopod pairs forming large, posteriorly cupped fans when crosslinked by hooked setae of stubby appendices internae embedded in opposed margins of triangular endopods (Fig. 7 j).

Telson (Fig. 7 k) broad, subrectangular, width about 1.4 times length, lateral margins weakly sinuous, broadest near midlength, posterior margin distinctly trilobate, median lobe much broader than pronounced lateral lobes; dorsally with 3 pairs of strong setal tufts, posteriormost pair nearest midline in posterior half of telson, 2 anterior pairs roughly aligned longitudinally well lateral of midline, posteriormost near midlength, lateral margins with pair of strong setal tufts just posterior to midlength, posterior margin well-developed tufts on 2 lateral lobes. Uropod (Fig. 7 k) with flattened, triangular to lobiform posterodorsally directed flange-like tooth on protopod, narrower more acute tooth on proximal article of exopod, both positioned to abut or overreach anterior margin of extended endopod; endopod elongate, subtrapezoidal, at least twice as long as broad, posteromesial margin with broken fringe of long setae, tapering to rounded angle of terminus bearing marginal fringe of long setae, distal end reaching to or almost to distal end of anterodorsal plate on flexed exopod; exopod anterodorsal plate falling well short of distal margin, posterodistal edge of plate with series of heavy spiniform setae grading to finer, dense, elongate setae of distal plate margin; distal margin of exopod with dense fringe of setation, longest posteriorly.

Color. In life, color in this species varies to some degree, even among mature individuals, but pigmented areas of the body tend to include primarily carmine red to reddish orange chromatophores patterned over translucent yellow backgrounds. Reddish orange colors are particularly apparent immediately posterior to the rostrum and frontal margin shoulders, near the middle of the dorsal oval, along the posterodorsal margins of the pleomeres, and broadly along the exposed margins of the telson. The more heavily sclerotized integument of the pereopods can be whitish with little evidence of pigment, though the chelipeds of fully mature specimens commonly have a blush of rose red to carmine over white, especially along the superior surfaces. The pleopods and uropods are commonly yellowish to olive green. These colors, based on collections from Panama, are in close agreement with coloration reported for Colombian specimens by Lemaitre & Ramos (1992), albeit at the time under the name *L. bocourti.*

Size. Maximum observed postorbital carapace length of male 10.5 mm; of female 11.9 mm. Maximum embryonated egg length on preserved ovigerous females about 1.4 mm for immature clutches and 1.6–1.7 mm for immediate pre-hatch.

Habitat. These obligate burrowers were found in 1990 by relocating a collection site on the Panama Bay side of the Fort Amador Causeway reported in the dissertation of Biffar (1972). That report described the site as moderately coarse sand occurring near the high tide line, where animals occurred in densities exceeding 140 per square meter in fragile burrows extending to about 0.5 m deep in sediments. The precise site was located but erosion control along the causeway had markedly changed the setting. Specimens were eventually found on a steep beach there, but only after turning over exposed intertidal stones, beneath which these animals had constructed channel-like burrows connected to deeper tunnels into a narrow band of clay along the shoreline (several meters wide) dominating sediments of the middle intertidal. None of these animals were burrowed deeper than 0.5 m, and the sediments in which they had constructed burrows were comprised heavily of sandy clay mixed with coarse gravel. However, fully mature animals, including ovigerous females occupied these burrows, and densities exceeding 100 per square meter were estimated. The normally applied yabby pump was of limited use in this setting, requiring excavation by shovel. This site was completely covered by construction landfill on return to it in 2004, but a search for additional specimens in the vicinity produced them on two occasions in yabby pump extractions from sparse populations on a clayey sand beach adjacent to the Naos Marina. Collections there were adjacent to and among large breakwater rocks, and subsurface layers of clay were evident in the sediments extracted. Neither site represents an unaltered natural setting, and both are subject to periodic salinity decreases, though they do not experience the extreme polyhaline conditions of upper estuaries.

It cannot be stated for certain if other specimens from the Panama Canal Zone taken by a dredge maintaining the canal channel, also reported by Biffar (1972), might also represent *L. panamensis* **sp. nov.** If so, it would indicate their ranging into deeper subtidal waters. Specific data are lacking for the single 1992 collection from Isla Gorgona, Colombia, though it can be deduced from the site alone that this is a comparatively high salinity habitat. However, original collection data for the very immature male collected there in 1987 indicated that it came from sediments in intertidal crevices of basaltic rocks. By contrast, the specimen from Bahia Malaga, Colombia, appears to have come from muddy sediments near the mouth of a freshwater stream (Lematire & Ramos 1992), suggesting adaptation to a broad range of salinity.

Distribution. Eastern Pacific: Island off southwestern Colombia and western Colombian estuarine embayments to Panama Bay and vicinity (intertidal waters along beaches and shoreline banks and tidal stream mouths of embayments).

Type locality. Pacific coast of Panama, Panama City, Isla Naos Marina (08°54.88'N, 79°31.80'W).

Etymology. This species is named for its type locality.

Remarks. The smaller size of materials here assigned to *L. panamensis* **sp. nov.** initially led Biffar (1972:70–71) to solicit the opinion of M. de Saint Laurent as to whether these materials were conspecific with the type of *L. bocourti* in collections of the Paris museum. While differences were found, these were concluded to likely represent size or ontogenetic variations, and indeed, the characters mentioned would not have been useful to separate the species. However, the presence or form of pleonal plating (Felder 2003) was not at the time a known character, while diversity and potential for regional endemism in this genus was also likely underappreciated. As for *L. rafai* and *L. natesi* **sp. nov.**, *L. panamensis* **sp. nov.** can be readily separated from both *L. bocourti* and *L. eiseni* by the lack of median ventral plating on the second pleomere, in addition to the general limitation of ventral sclerotization. It can in turn be separated from *L. rafai* by both its distinctly trilobate posterior telson margin and its elongate subtrapezoidal uropodal endopods, features that it shares with *L. natesi* **sp. nov.** In *L. rafai*, the telson lacks the strong posterior lobes and the uropodal endopods are much more broadly ovoid. Finally, *L. panamensis* **sp. nov.** differs from *L. natesi* **sp. nov.** in body size, relative mature female gonopore size, and egg size, and can be distinguished by a number of morphological features despite their similarities in the posterior margin of the telson, uropodal endopod, flange-like tooth of the uropodal protopod, and some other characters. In *L. panamensis* **sp. nov.** the rounded shoulders of the carapace frontal margin, centered immediately to each side of the eyes, project more strongly to the anterior and are more distinctly separated from the rostrum by an oblique posterolaterally directed furrow or depression. This gives the shoulders a more arched appearance, forming hoods over the antennal peduncles. Furthermore, the dorsal sclerite of the first pleomere is distinctly different, being bell-shaped and lacking a distinctly broadened membranous area to each side. Major differences are also found in dentition and shape of the major cheliped, though these can be somewhat similar in immature specimens. In mature specimens, the merus of *L. panamensis* **sp. nov.** has a clearly developed proximal notch in the superior margin and a much simpler proximal hook on the inferior margin than does *L. natesi* **sp. nov**. Also, the prehensile tooth of the fixed finger is much weaker than in *L. natesi* **sp. nov.** In both sexes, relative lengths of the minor cheliped fingers differ between the species, those of *L. panamensis* **sp. nov.** being relatively shorter compared to propodus height than in *L. natesi* **sp. nov.** Specifically for females, the dentition of the fingers in both the major and the minor chela differs between the species, with the major fixed finger having an enlarged denticle immediately distal to the proximal incision and the minor dactyl having a low but distinct proximal tooth on the prehensile margin, neither of which is seen in *L. natesi* **sp. nov.**

Characters of the male pleopods could also be cited to support the separation, both first and second, with the oblique orientation of the appendix on the male second being apparently unique to *L. panamensis* **sp. nov.** However, in comparative study of the type series for this species, it became apparent that these appendages do vary considerably with maturation and by occurrence of occasional anomalies, especially in the appendix of the male second pleopod (Fig. 7 e–g). Thus, comparative interpretations based on this structure must be made with caution.

Were a single specimen of some large series found to lack the rostrum spine, little should be made of it, but the present type series includes no less than 4 individuals in which the middle of the carapace front is represented as nothing more than a broadly rounded lobe, lacking all evidence of the rostral spine. In all other respects, these animals appear typical of the species. Whether this is some occasionally expressed labile morphological feature or a developmental malformation due to environmental effects is presently unknown, but worthy of further study.

As noted in the synonymy above, the present description applies to materials cited in Staton *et al.* (2000) as "*Lepidophthalmus* nr. *bocourti*" and "*L.* nr. *bocourti*", or referred to under the abbreviation "LBPA". Allozyme analyses in that paper were based on tissue from ULLZ 4821 collected from the Fort Amador Causeway, and fragmentary voucher materials are conclusively identifiable as *Lepiophthalmus panamensis* **sp. nov.** Being one of two undescribed eastern Pacific species alluded to by Staton *et al.* (2000: 167) as having ventral sclerites "shared to varied degrees" with other ventrally plated species, correction of that misleading statement is required. Neither the population of "*L.* nr. *bocourti*" referred to there (here described as *L. panamensis* **sp. nov.**), nor the "one additional undescribed species" (here described as *L. natesi* **sp. nov**.), have a median ventral sclerotized plate on the second pleomere. There may nonetheless be small paired anterior plates to each side or lateral plates immediately anterior to the pleopods (Fig. 4 b), but the median region is at most leathery, lacking a major centrally located sclerite and adjacent small sclerites embedded in the membrane. At most in both *L. panamensis* **sp. nov.** and *L. natesi* **sp. nov**., the leathery ventral membranes of the pleomeres in some specimens appear under high magnification to be rather uniformly peppered by very tiny whitish particles embedded in the integument. It is unknown whether or not these represent a homolog of the much larger sclerites and plates expressed in related species.

In the course of reviewing abbreviated larval development that appears to characterize most species of *Lepidophthalmus*, Nates *et al*. (1997: 512) note that some of the most extreme abbreviation may occur in one of the undescribed "Pacific congeners", a comment that in fact applied to the species herewith named *L. panamensis* **sp. nov.** Remarkably, ovigerous females collected from Panama 10 September 1990 carried large eggs until 23–24 November, while held in the lab at 26 psu in a 12:12 light:dark photoperiod. Enlarged eyespots were observed on 16 November but hatching of all 28 remaining eggs was not detected until decapodid stages (first postlarval = megalopa) were observed in the culture bowl within a maximum of 2 days after hatch. Initially docile on the bottom of the bowl, they became very active swimmers and feeders within hours, especially when exposed to light. Despite a careful search, no evidence of molted exuvia from a preceding zoeal stage was found in the culture bowl, suggesting the possibility of direct development or perhaps one that involved a brief prezoea with thin integument too fragile to remain intact. As noted by Nates *et al*. (1997), the question remains as to whether larvae in some members of this genus might undergo benthic development within the burrows of females, and at least potential for such adaptation is found in *L. panamensis*.

Finally, our inclusion of the specimens from Isla Gorgona and Bahia Malaga, Colombia, in *L. panamensis* **sp. nov.** is undertaken with some reservation. Two of these were previously treated as *L. bocourti* by Lemaitre & Ramos (1992), and all three specimens were kindly made available for study by R. Lemaitre. The only male among these three, from Isla Gorgona, is extremely immature and fragmentary, making its definitive identification very tentative. The two females, one from Isla Gorgona and the other from Bahia Malaga, both fit *L. panamensis* **sp. nov.** in terms of those features that are intact in the chelipeds (including as illustrated by Lemaitre & Ramos 1992: fig. 4), size of the mature female gonopore, pleonal sclerite development, telson shape, and configuration of the uropodal endopod (this latter feature varying from the cited illustration). However, the tooth of the uropodal protopod is somewhat atypical on both sides in both specimens in forming lateral lobes rather than broadly triangular teeth that overreach the margin of the extended exopod. Until additional materials can be secured from these habitats, preferably of gene sequence quality and including mature males, we provisionally assign these populations to *L. panamensis* **sp. nov.**

Discussion

With the two presently described species and another long-known species from the southwestern Gulf of Mexico recently described (Felder 2015), the count of known species in this genus comes to 18. All but 3 of these are represented in a companion molecular phylogenetic paper that analyses genetic relationships within the genus *Lepidophthalmus* and discusses how these relationships bear on our understanding of morphological characters, biogeography, and evolution in the group (Robles & Felder 2015). However, as noted to some extent above, genetic studies have already proven to provide valuable insights for separations between many species of the genus (Staton *et al*., 2000; Felder *et al*., 2003; Robles *et al*. 2009; Felder & Robles, 2009), with some of these works including either of the two species presently described. Thus, in addition to the morphological characters used to distinguish newly described species, there are multifold more characters vested in allozyme and sequence data to define them in papers cited in synonymies, strongly underpinning what are here treated in traditional species descriptions.

Attention is here called to the long course of these studies, in part to explain our obvious delay in naming of these taxa but also to make a point. We prefer that naming of decapod species include analytical approaches at every opportunity, genetic whenever possible or at least morphological analyses if not, even at the cost of some delay. This has nothing to do with meeting minimum requirements of the ICZN, which must liberally accommodate long-followed practices related to nomenclature *per se*, but rather has everything to do with best scientific practice in justifying what warrants a name. To work otherwise is to not only ignore modern tools and methods, but also to perhaps omit information that could potentially reverse conclusions drawn from convergent morphology, like the simple presence or absence of ventral pleonal sclerites in species of *Lepidophthalmus*. Granted, there must be exceptions for poorly preserved or difficult to collect materials and for some revisionary accounts, but to simply rush the putting of a name on a species with inquiry limited to morphological judgements (as we ourselves have done in the past)… without at least attempting to augment insights with fresh sequence-quality topotypic materials... should not pass the modern test for justification of a new name. Bearing on this, the cost of obtaining at least a single gene sequence to add to a taxonomic diagnosis is now equivalent to that for purchase of a good quality museum jar to hold the specimen, if one only makes the simple effort to contract for the services. Perhaps worse, the ignoring of pre-existing and available (published, GenBank, or otherwise archived) sequence data in the course of naming species, thus omitting the valuable step of equating of sequence vouchers to morphological descriptions, should be unacceptable, requiring deeper study of molecular systematic literature by taxonomic authors and reviewers than in the past. To dismiss this step leaves disconnected pieces of systematic data in the literature and would seem at least as unacceptable as the practice of those molecular phylogeneticists who do not bother to designate and catalog morphological vouchers for their tissues and sequences.

More extensive interpretations of phylogenetic relationships for the two presently described species has been deferred to our companion molecular genetic analysis (Robles & Felder 2015). As argued for in the preceding statement, that paper provides a full accounting of updated and augmented genetic analyses, with GenBank numbers equated to an extensive set of voucher specimens that were in turn examined in the course of preparing the present descriptions.

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