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Ventrally sclerotized members of *Lepidophthalmus* (Crustacea: Decapoda: Callianassidae) from the Eastern Pacific

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Abstract

Reports from the eastern Pacific have long suggested that only one or two wide-ranging species of the genus *Lepidophthalmus* occurred there, depending upon whether the names *L. bocourti* and *L. eiseni* were treated as separate species or synonyms. A new species, *L. rafai*, was recently described from a single locality in southern Colombia. Re-examination of museum materials and studies of new collections from Colombia, Panama, Costa Rica, and Nicaragua, reveal a total of no less than six separate eastern Pacific species, three of which remain undescribed. Only two of the known eastern Pacific congeners, *L. bocourti* and *L. eiseni*, bear conspicuous ventral abdominal sclerites, a little-known feature of these populations that is shared with some western Atlantic forms. Despite confusion of these two ventrally plated species in literature, they are distinct forms and differ in coloration and a number of diagnostic morphological characters herewith illustrated. Both of these plated species range widely among coastal estuaries from western Panama northward to Mexico, and have in some instances invaded commercial penaeid shrimp culture ponds where they are considered as pests to be targeted in eradication programs. The duration of larval development in at least *L. eiseni* markedly exceeds that in previously studied Atlantic species, and could account for the broad distribution range and potential for colonization of widely disjunct estuaries. *Lepidophthalmus rafai* and up to three other species from the eastern Pacific, currently under study, lack strong development of ventral abdominal sclerites and are to date known from only restricted distributions in Nicaragua, Panama and Colombia.

Keywords: Pacific, thalassinideans, callianassids, ghost shrimp, systematics

Zusammenfassung

Es wurde lange Zeit angenommen, dass im Ostpazifik nur eine oder zwei Arten der Gattung *Lepidophthalmus* vorkommen, je nachdem ob *L. bocourti* und *L. eiseni* als unterschiedliche Arten oder als Synonym betrachtet wurden. Kürzlich wurde mit *L. rafai* eine neue Art von einer einzelnen Lokalität in Kolumbien beschrieben. Nachuntersuchungen von Museumsmaterial und von Material aus neueren Aufsammlungen in Kolumbien, Panama, Costa Rica und Nicaragua zeigten, dass insgesamt nicht weniger als sechs verschiedene Arten dort vorkommen; drei davon sind noch nicht beschrieben. Nur zwei der bisher beschriebenen Arten, *L. bocourti* und *L. eiseni*, zeigen auffällige Kutikularstrukturen auf der Ventralseite der Abdominalsegmente. Dieses kaum bekannte Merkmal ist auch bei einigen Westatlantischen Formen zu finden. Trotz der Widersprüche, die zu den beiden Ostpazifischen Arten in der Literatur bestehen, handelt es sich um getrennte Arten. Sie weisen Unterschiede in der Färbung und in zahlreichen morphologischen Merkmalen auf, die in dieser Arbeit beschrieben und teilweise abgebildet werden. Beide Arten sind weit verbreitet in Ästuaren von West-Panama nordwärts bis Mexiko und haben in einigen Fällen kommerzielle Garnelenzuchtbecken besiedelt. Hier werden sie als "Pest" betrachtet und sind Anlass zu Bekämpfungsmaßnahmen. Die Dauer der Larvenentwicklung von zumindest *L. eiseni* übersteigt die der bisher von Atlantischen Arten bekannte. Dies könnte für die große Verbreitung und die Möglichkeit der Besiedlung weit auseinanderliegender Ästuare verantwortlich sein. *Lepidophthalmus rafai* und bis zu drei andere Arten aus dem Ostpazifik (die derzeit in Bearbeitung sind) fehlen die ventralen Kutikularstrukturen; sie sind bisher nur von begrenzten Vorkommen aus Nicaragua, Panama und Kolumbien bekannt.

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Introduction

Members of the fossorial ghost shrimp genus *Lepidophthalmus* HOLMES, 1904, characteristically populate coastal river mouths, estuaries and lagoons (MANNING & FELDER 1991, FELDER & RODRIGUES 1993, FELDER & GRIFFIS 1994, FELDER & MANNING 1997, 1998, FELDER & STATON 2000). They are also known to invade and densely colonize commercial penaeid shrimp culture ponds located in these settings (LEMAITRE & RODRIGUES 1991, NATES & al. 1997, NATES & FELDER 1999). Members of the genus tolerate prolonged hypoxia and high concentrations of reduced nutrients that may accumulate in the richly organic, decompositional sediments that they typically exploit (FELDER 1979, FELDER & MANNING 1998, NATES & FELDER 1998). Osmoregulatory ability of both the adults and larvae accommodates oligohaline conditions in these habitats (FELDER 1978, FELDER & al. 1986). Endemism in the genus is in at least some cases favored by a highly abbreviated life cycle that limits dispersal and maintains relative isolation of populations wherever estuaries are widely separated (NATES & al. 1997, STATON & al. 2000). Recognition of this high potential for endemism among western Atlantic populations has prompted careful re-examination of specimens formerly assignable to *L. jamaicense* (SCHMITT, 1935) and led to subsequent recent recognition of at least eight western Atlantic congeners, two of which are currently in description (D. L. Felder in prep.). Similar studies have been initiated with eastern Pacific congeners (FELDER & MANNING 1998) but to date have not dealt with forms bearing conspicuous ventral abdominal sclerotization which includes a median plate on the second abdominal somite.

Among western Atlantic species, the presence of ventral abdominal plates or armor was originally thought to represent some form of parasitization (BIFFAR 1971: 650). Later interpretation of these plates as typical morphology greatly facilitated species separations among Atlantic forms, especially once these plate arrangements and shapes were found to be of diagnostic value (FELDER & RODRIGUES 1993, FELDER & MANNING 1997, FELDER & STATON 2000). In the course of reporting on these varied Atlantic materials and describing an unplated form from the Pacific coast of Colombia (FELDER & MANNING 1998), comparisons were made to materials of Pacific congeners which were noted to bear ventral abdominal sclerites. These plated Pacific specimens included the single large type specimen of *L. bocourti* (A. MILNE-EDWARDS, 1870) and the possible type series of *L. eiseni* HOLMES, 1904, both from the Pacific coast of Mexico. Ventral plating of these materials was not mentioned in text accounts or figured in the very limited original descriptions of either species. Brief mention of abdominal sclerites was made in a subsequent description of *L. eiseni* from El Salvador (HOLTHUIS 1954), but no comparative analysis of such structures was made by BIFFAR (1972), who concluded that *L. eiseni* should be regarded as a junior synonym of *L. bocourti.*

The present paper reexamines type and other materials assignable to *L. bocourti* and *L. eiseni* from throughout Central America and northern South America, including new collections and museum holdings. Diagnostic characters and known distributions are reported for each species, as well as preliminary observations on the duration of larval life history in *L. eiseni*.

Material and Methods

Material examined is listed by location followed by date, collector, number of specimens by sex and condition (ovigerous = ov; mutilated = mutl), museum catalog number

and size (in parenthesis). Notations also indicate those specimens that were used as subjects for line illustrations in the text figures and those archived as voucher specimens for 35-mm color photographic slides (used herein as source materials for color descriptions) prior to preservation. Size is expressed as postorbital carapace length (CL) measured in millimeters (mm) and thus excludes the rostrum. Materials have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); the Colección Nacional de Crustáceos, Instituto de Biología, CNCR-IB, Universidad Nacional Autonoma de México (UNAM); Naturhistorisches Museum in Wien, Austria (NHMW), and zoological collections of the University of Louisiana at Lafayette (ULLZ). Holdings of the USNM, ULLZ, Nationaal Natuurhistorisch Museum, Leiden, Netherlands (RMNH-D), Universidad Autonoma de Baja California (UABC) and Alan Hancock Foundation (AHF) collection, the latter housed by the Natural History Museum of Los Angeles County, were the source for comparative materials for varied populations of the genus. The male holotype of *L. bocourti* (A. MILNE-EDWARDS, 1870) was examined while on loan from the Muséum National d'Histoire Naturelle, Paris (MNHN-Th 64) to the late Dr. Raymond B. Manning, Smithsonian Institution. The possible eastern Pacific type specimens of *L. eiseni* HOLMES, 1904, or what at very least appear to represent topotypic materials, were obtained for examination from the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ 4370). As previously noted by BIFFAR (1972), accession records at the MCZ indicate that these materials, collected by Dr. Gustav Eisen, were received from the California Academy of Sciences in 1893, well prior to destruction of the latter collection and its records in the San Francisco earthquake. Preliminary observations of larval life history in *L. eiseni* were based upon the larval hatch of an ovigerous female collected from Estero Ciego on the Pacific coast of Nicaragua in September 2000.

Results

Lepidophthalmus bocourti (A. MILNE-EDWARDS, 1870) (Figs. 1 - 19)

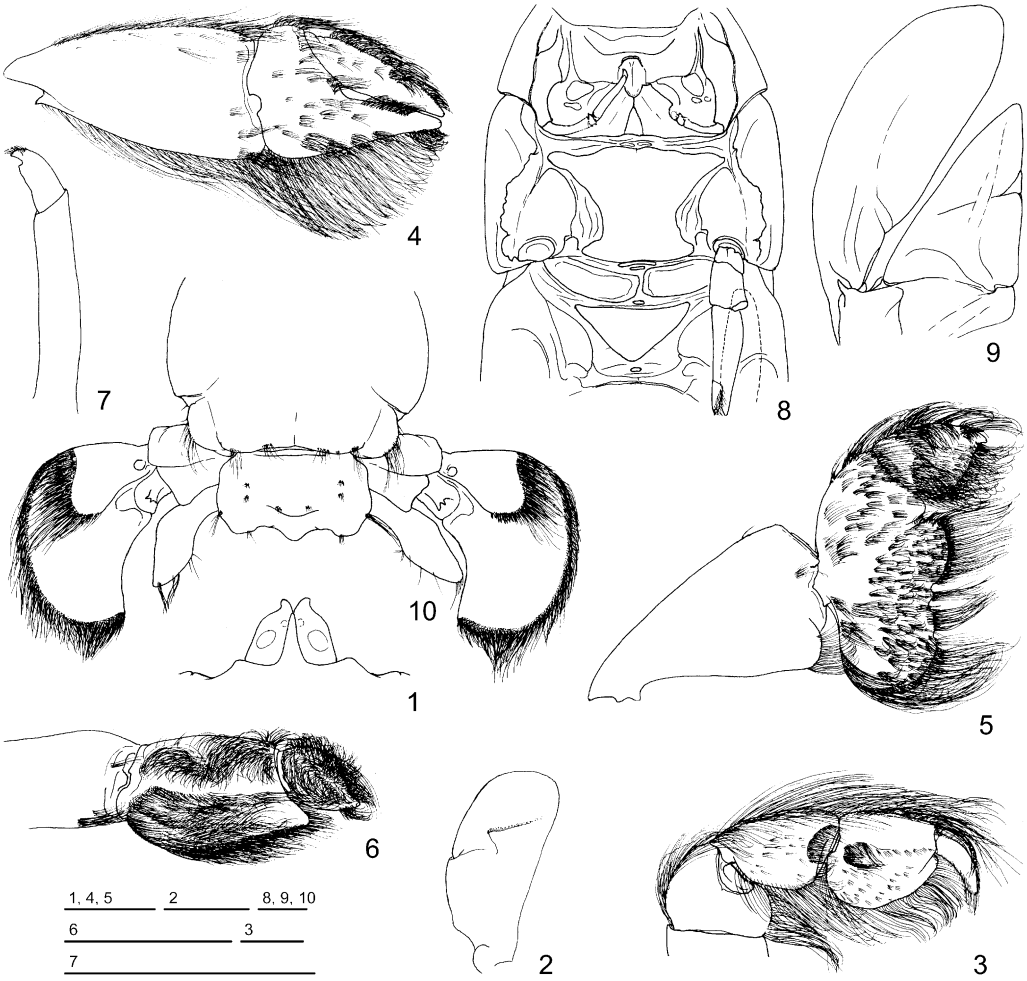
Callianassa bocourti A. MILNE-EDWARDS, 1870: 95.
Callianassa (*Callichirus*) *bocourti*. – BORRADAILE, 1903: 547. – DE MAN, 1928: 28, 94, 115
Callianassa bocourti. – BIFFAR, 1972: 65-72 (part, excluding "TYPES of *C. eiseni*" therein re-examined, records originally reported as *L. eiseni* HOLMES, and Panamanian materials described in text and featured in figs. 17 and 18. – DE SAINT LAURENT & LELOEUFF, 1979: 96 (part, excluding that indicated as "= *Callianassa eiseni* HOLMES").
Lepidophthalmus bocourti. – MANNING & FELDER, 1991: 778 (part, excluding treatment of *L. eiseni* as junior subjective synonym). – FELDER & RODRIGUES, 1993: 373. – FELDER & MANNING, 1997: 319. – FELDER & MANNING, 1998:398, 406. – NATES & FELDER, 1998: 188, 190, 194-196, 204 (part, Costa Rica only, excluding Colombia report) – STATON & al., 2000: 158, 167. – FELDER & STATON, 2000:171, 179. – FELDER, 2001:442. – FELDER & al., 2002: fig. 3C,D.
[Not *L. bocourti* from Malaga Bay and Isla Gorgona, Colombia, of LEMAITRE & RAMOS, 1992, LEMAITRE & ALVAREZ-LEÓN, 1992, and TUDGE & al., 2000.]

Holotype: Present label reads "Ocean Pacifique" (type locality reported as "sur les côtes de l'océan Pacifique, à la Union", in possible reference to La Unión, state of Guerrero, Mexico, or La Union in southeastern El Salvador on Golfo de Fonseca), coll. M. Bocourt, 1 mutl male (CL 24.5) MNHN-Th 64.

Other material examined: MEXICO: N Branch of Estero de Barra, Cauhuacan, W side, S of Puerta Madero, Chiapas, Pacific Ocean, 2 August 1972, coll. C. A. Child, Dawson-Child Central American Expedition, Sta. 1562, 7 male, 13 female (CL 3.5 to 16.0 mm) USNM 142366 excluding 2 on exchange to

Museum of Victoria and 3 on loan to British Museum. EL SALVADOR: estuarine mud, Estero El Zepote, Barra de Santiago, Depto. Ahuachapan, 23 November 1978, coll. K. DeRiemer, 1 male, dry (CL 12.0 mm), AHF 1668-01. – estuarine mud at low tide, El Cabón, Barra de Santiago, Depto. Ahuachapan, 23 November 1978, coll. D. Moran, 1 female (CL 12.1 mm) USNM 1002605 (= Acc no. 337563). NICARAGUA: mangrove-lined flat and channels, 12°39.467'N, 87°22.508-534'W, Estero Ciego, Pacific, 15 April 2000, coll. D. Felder & S. Nates, 9 male including 4 mutl and 1 illustration voucher, 3 female (CL 11.2 to 19.9 mm) ULLZ 4557. – same site, 29 September 2000, coll. D. Felder & R. Robles, 1 female photo voucher (CL 18.7 mm) ULLZ 4313. – same site, 29 September 2000, coll. D. Felder & R. Robles, 1 male photo voucher, 10 female including 7 ov, 9 dissected for analyses and 1 illustration voucher (CL 15.0 to 23.4 mm) ULLZ 4555. – back beach tidal ponds, 12°31.556'N, 87°12.507'W, Paso Caballos, Pacific, 11 April 2000, coll. D. Felder & S. Nates, 12 male including 1 mutl, 7 female (CL 8.1 to 14.9 mm) USNM 1002607. – same site, 11-12 April 2000, coll. D. Felder & S. Nates, 3 male, 1 female, photo and illustration vouchers (CL 14.2 to 17.5 mm) ULLZ 4556. – same site and mangrove flat on lagoon behind beach, 12 April 2000, coll. D. Felder & S. Nates, 4 male, 3 female (CL 5.7 to 13.8 mm), UNAM CNCR-20961. – same site, 30 September 2000, coll. D. Felder & R. Robles, 40 male including 2 mutl, 28 female including 7 ov and 3 mutl, ULLZ 4558, 1 male, 1 female, NHMW 19789 (CL 6.5 to 20.4 mm). – same site, back beach ponds and tidal streams, 15 August 2001, coll. D. Felder & R. Robles, 1 male with commensal alpheid, ULLZ 4639 (CL 25 mm). – sandy beach pond, rain-diluted, salinity 11 ‰, 12°23.03'N, 87°02.89'W, Bocana de Poneloya, Pacific, 27 September 2000, coll. D. Felder & R. Robles, 2 male, 2 female, (CL 11.6-15.9 mm), ULLZ 4623. – behind sand spit, estuary side, 12°45.903'N, 87°28.452'W, Lagoon Los Zorros, Estero Padre Ramos, Pacific, 14 April 2000, coll. D. Felder, S. Nates, & A. Diaz, 1 male, 4 female (CL 10.6-15.3 mm) ULLZ 4624. – near shrimp hatchery along shore of estuary mouth and flooded salt flat with mangroves, 12°21.66'N, 87°01.25'W, Las Peñitas, Pacific, SW of Leon, 27 September 2000, coll. D. Felder & R. Robles, 2 female, photo vouchers (CL 17.3-17.6 mm), ULLZ 4510. – same site and coll., 14 August 2001, 1 male with commensal alpheid (CL 11.9 mm), ULLZ 4637. COSTA RICA: commercial shrimp ponds, Pacific, 1991, coll. Velardo, 6 male, 3 female including 1 mutl, 1 unsexed juvenile, USNM 256542 (CL 3.3-11.5 mm). – Chomes, Puntarenas, January 1991, 5 male including 1 mutl, 5 female, USNM 1002606 (CL 5.2-12.2 mm). – nursery ponds, shrimp farm, Criadero de Camarones de Chomes, 9 September 1991, coll. S. Nates, 13 male, 9 female, ULLZ 4689 (CL 6.9-10.7 mm). – shrimp pond, Criadero de Camarones de Chomes, 18 August 1992, coll by S. Nates, 16 male including 1 mutl, 7 female including 1 ov, ULLZ 4688 (CL 8.5-17.0 mm). PANAMA: Aquachame S. A. shrimp farm, Pta. Chame, Pacific, 20 September 1994, coll. N. Begarano, forwarded by J. Vicente Mogollon, 3 male, 3 female, ULLZ 4628 (CL 5.0-11.5 mm).

Diagnosis: Eyestalk tips slightly divergent, slightly hooked anterolaterally. Rostrum distinctly angled upward in anterodorsal direction, weakly hooked, broad base originating from slightly less inclined narrow front of carapace anterior to dorsal oval, angle of incline in narrow front near that of rostrum, sloping up from origin at anterior end of dorsal oval, creating distinct median depression in lateral view. Major chela with external surface of propodus in males bearing small, tuberculate, weakly punctate and sparsely setose depression extending posteriorly from gape, lacking suture connecting depression to dactylar condyle, bordered ventrally with at most a short carina extending from gape proximally to point below dactylar condyle; depression very weak to absent in females. Minor chela with dorsal and ventral distal corners of carpus bearing short, acute spines or teeth, chela narrowing distally, maximum gape, when fingers closed, less than maximum width of movable finger in both sexes. First abdominal somite well sclerotized over most of dorsal and lateral surface except for narrow membranous tract on each posterolateral slope, tract originating at posterolateral margin and extending anterodorsally about half the length of somite; sclerotized lateral extreme of somite forming a broad, weakly sinuous channel generally parallel to membranous area, posteroventral margin forming a sharp, sinuous, crest extending anterodorsally, becoming bifurcated anteriorly to produce a second short channel between pair of crests; adjacent articulation of first pleopod bordered laterally by distinct sharp spine or bladelike tooth in both sexes. Second abdominal somite with thin ventrolateral margin of pleuron produced ventrally



Figs. 1 - 10: *Lepidophthalmus bocourti* (A. MILNE-EDWARDS, 1870), holotype male (CL 24.5 mm) from "sur les côtes de l'océan Pacifique, à la Union", probably Mexico or El Salvador , MNHN-Th 64: 1. eyes and carapace front, dorsal surface, setae not shown; 2. exopod of right first maxilliped, external surface, setae not shown; 3. left third maxilliped, terminal articles, internal surface; 4. right second pereiopod, terminal articles, external surface; 5. right third pereiopod, terminal articles, external surface; 6. right fourth pereiopod, terminal articles, external surface; 7. right first pleopod, lateral surface; 8. abdominal somites 1-3, ventral surface, with right first and left second pleopods; 9. left third pleopod, anterior surface, setae not shown; 10. sixth abdominal somite, telson and uropods, dorsal surface. Scale lines indicate 3.0 mm.

to form obtuse angle in anterior half of somite length, crest curved laterally in posterior half, forming sharp, laterally canaliculate, rough-edged crest; median ventral sclerite with broad anterior flange, distinctly constricted from midlength to posterior 1/4, flanged again at posterior end, overall chalice or somewhat hourglass in shape. First pleopod of male with subterminal tooth small, much narrower than terminal tooth. Third through fifth pleopods bearing distinct ventrolaterally directed spine on the anterior

condylar lobe of the basis near articulation of exopod (in both sexes). Telson broadest near or just posterior to midlength, strongly trilobate posteriorly, posterolateral lobes forming acute angles in posterodorsal view.

Coloration (live animals from Nicaragua): Chelipeds and anterior of carapace varying in ground color from white to yellow-white, sometimes shaded with very faint pink on dorsal-most areas, especially near joints of cheliped articles and immediately posterior to rostrum. Most of carapace and abdomen translucent whitish. Faint pale yellow-green or light brown and white producing patterning on posterior four abdominal pleura and telson. Uropods translucent yellow-green or light brown over much of surface.

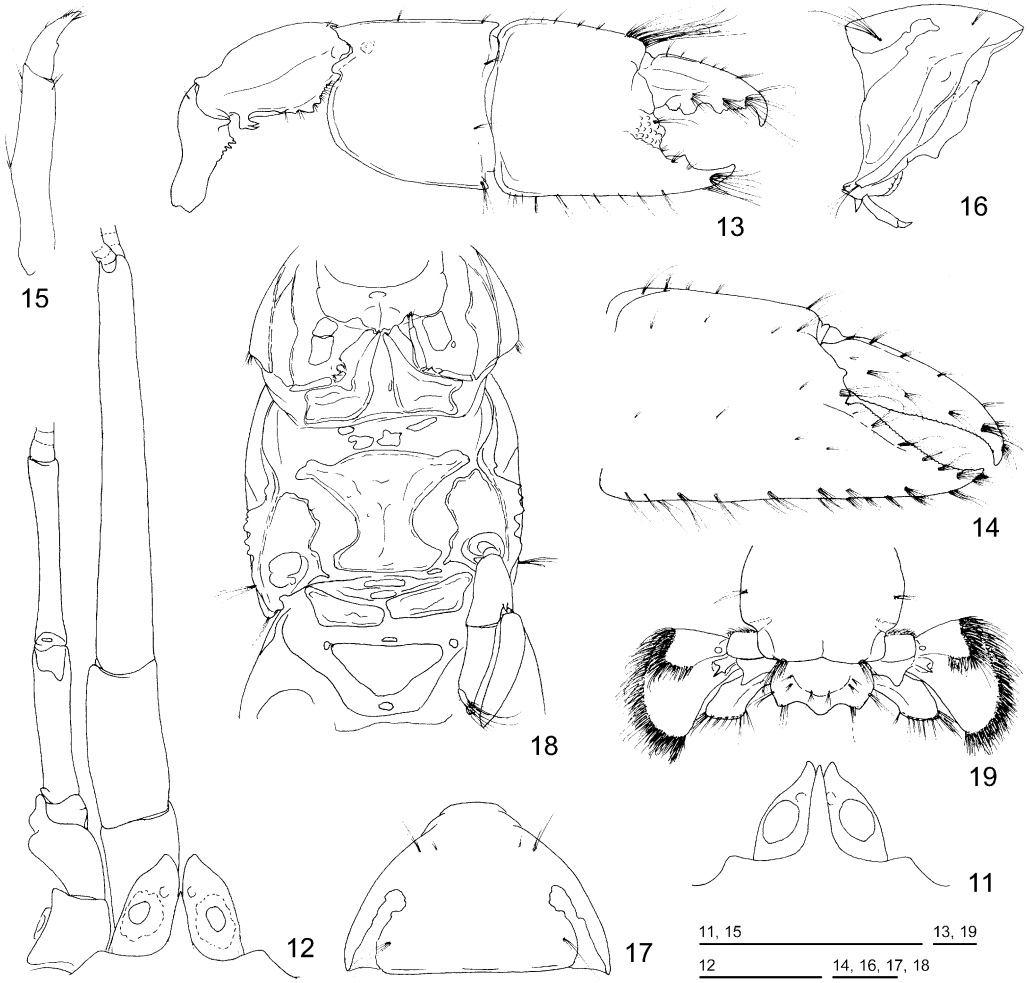
Remarks: As the original description of *L. bocourti* was not accompanied by illustrations, both the presently used diagnostic characters (Figs 1, 7-10) and features of other intact major appendages (Figs 2-6), were illustrated when the somewhat mutilated holotype male specimen (MNHN-Th 64) was examined. While the holotype appears to represent an atypically large specimen, lacking the chelipeds, smaller specimens closely resemble it in diagnostic features (Figs 11-19), as well as in the general form of the other cephalothoracic appendages that can be compared.

Examination of specimens reported as *L. bocourti* from the Pacific coast of Colombia by LEMAITRE & RAMOS (1992: 349, fig. 4a-h) indicates that neither of these specimens (USNM 251735, 251736) is in fact assignable to that species. While both are small, immature specimens, they lack ventral plating, carinae and spination diagnostic of *L. bocourti* at a comparable size. Both are, however, clearly assignable to *Lepidophthalmus*, and represent one of several undescribed eastern Pacific species.

Materials from the Pacific coast of Panama treated as "*L.* nr. *bocourti*" by STATON & al. (2000) (ULLZ 4821, 4822) are also not assignable to *L. bocourti*. While those specimens reportedly share "to varied degrees" the ventral armor typical of *L. bocourti*, *L. eiseni* and Caribbean plated species (STATON & al. 2000: 167), re-examination of these vouchers revealed no evidence of a median ventral plate on the second abdominal somite comparable to that in either *L. bocourti* or *L. eiseni.* Where thickenings do occur, they appear to be ill-defined and leathery, as opposed to the more calcified armor seen in plated forms. These specimens also represent an undescribed form and are possibly conspecific with the aforementioned immature specimens from Colombia. Both will be treated in a forthcoming paper.

Populations of *L. bocourti* occur sympatrically with those of *L. eiseni*, in intertidal and shallow subtidal mangrove-lined oligohaline estuaries and lagoons of Nicaragua, with no readily apparent differences in habitat preferences. Habitats for such mixed populations were there found to range in surface water salinity from < 1 to > 45 ‰. Burrows of the two species were at some sites mixed in near equal proportions, while at others one or the other markedly dominated or both were mixed with yet a third species that lacks ventral plating and remains undescribed (FELDER & al. 2002).

Ovigerous females of *L. bocourti* were common in Nicaragua during September and were found among collections taken from a Costa Rican shrimp farm in August. In general, the August to September period is regarded as the wet season, with high coastal rainfall. No ovigerous specimens were found in Nicaragua during April, late in the dry season, despite concerted efforts to collect them.



Figs. 11 - 19: *Lepidophthalmus bocourti* (A. MILNE-EDWARDS, 1870). – Male (CL 11.2 mm) from Estero Ciego, Nicaragua, ULLZ 4557 (11); female (CL 22.5 mm) from Estero Ciego, Nicaragua, ULLZ 4555 (12, 14); male (CL 17.5 mm) from Paso Caballos, Nicaragua, ULLZ 4556 (13, 15-19): 11. eyes and carapace front, dorsal surface, setae not shown; 12. eyes, carapace front and left antennae, dorsal surface, setae not shown; 13. major male cheliped, external surface; 14. major female chela, external surface; 15. right first male pleopod, internal surface; 16. first abdominal somite, right surface; 17. first abdominal somite, dorsal surface; 18. abdominal somites 1-3, ventral surface, with left first and second pleopods; 19. sixth abdominal somite, telson and uropods, dorsal surface. Scale lines indicate 3.0 mm.

As evident among the "Other material examined" above, populations of *L. bocourti* have invaded penaeid shrimp aquaculture farms in at least Costa Rica and Panama. Apparent detrimental impacts on penaeid shrimp production are similar to those reported for Caribbean populations of *L. sinuensis* LEMAITRE & RODRIGUES, 1991, in Colombia (NATES & FELDER 1998). As in the Caribbean, control of these Pacific populations has been attempted by applications of carbaryl pesticide (S. F. Nates, personal communication).

Lepidophthalmus eiseni HOLMES, 1904 (Figs. 20 - 29)

Lepidophthalmus eiseni HOLMES, 1904: 311, pl. 35, figs 6-13. – DE MAN, 1928: 110. – FELDER & RODRIGUES, 1993: 373. – FELDER & MANNING, 1997: 311, 319. – FELDER & MANNING, 1998: 398, 406. – STATON & al., 2000: 158, 167. – FELDER & STATON, 2000: 171, 179. – TUDGE & al, 2000: 144. – FELDER, 2001: 442. – FELDER & al., 2002: fig. 3E,F.

Callianassa (*Callichirus*) *eiseni.* – DE MAN, 1928: 28.–SCHMITT, 1935:9.

Callianassa eiseni. – HOLTHUIS, 1954: 12-15, fig 3a-k.–BOTT, 1955: 47, Abb. 6a-g.

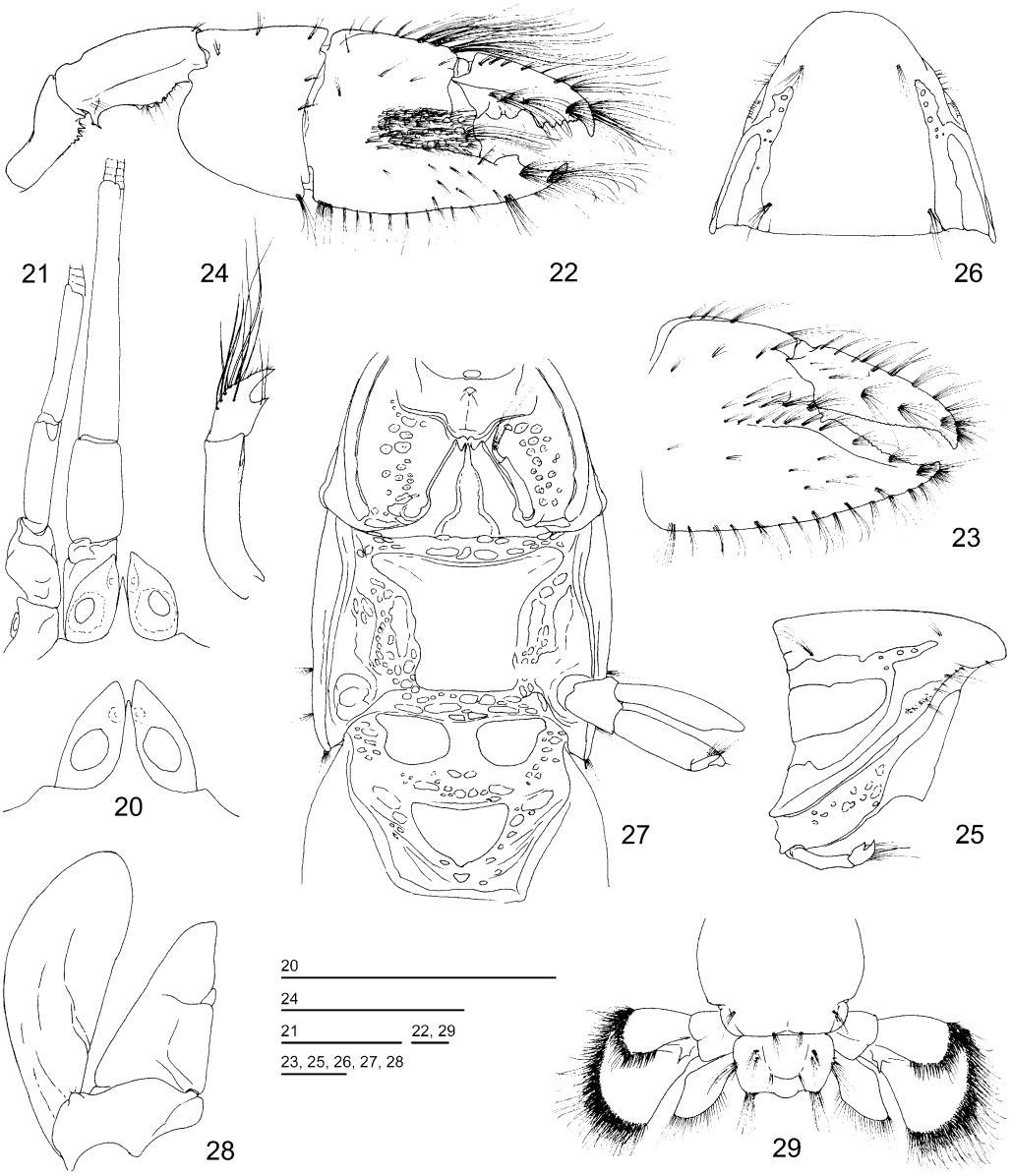
Callianassa bocourti. – BIFFAR, 1972: 65-72 (part, including "TYPES of *C. eiseni*" therein re-examined, excluding Panamanian materials. – DE SAINT LAURENT & LEOUFF, 1979: 96 (part indicated as "= *Callianassa eiseni* Holmes").

Lepidophthalmus bocourti. – MANNING & FELDER, 1991: 778 (part treating *L. eiseni* as junior subjective synonym).

Possible types: Fresh water, San Jose del Cabo, Lower California, Pacific, 1893, coll. by G. Eisen, 1 male, 4 female, MCZ 4370 (CL 24.5-26.5 mm).

Other material examined: MEXICO: Amadrigado en Fondo Blando-Esturarino, Lo De Marcos KM18 Carr. Tepic- P. Vallarta, Estado Nayarit, Municipio Lo De Marcos, Nayarit, Pacific, 14 July 1985, coll. C. Parra, 1 female mutl, UABC-RM70 (CL 23.5 mm). – rain-flooded estuary behind sandy beach berm, surface water salinity < 1 ‰, Lo de Marcos, Nayarit, Pacific, 30 June 2000, coll. D. Felder & S. Nates: 4 male, 4 female, 1 juvenile, ULLZ 4636; 1 male, 2 female, NHMW 19790; 1 male, 3 female, UNAM CNCR-20962; (CL 4.6-20.3 mm). GUATEMALA: Iztapa, 5 April 1950, coll. T. Burch, 3 male including 1 mutl, 8 female including 1 mult and 1 illustration voucher, USNM 91736 (CL 13.0-18.6 mm). EL SALVADOR: estuary near Playa de los Flores, la Libertad, Pacific, 18 August 1952, coll. G. Kruseman, 2 male, 1 female, RMNH-D 9841 (CL 6.8 to 12.1 mm). – near 2nd bridge south of town, Estero de San Diego, la Libertad, Pacific, 7 August 1972, coll. Dawson-Child Central American Expedition, Sta. 1563, 1 female, USNM 142367 (12.3 mm). NICARAGUA: tidal stream, 12°39.468'N, 87°22.521'W, Estero Ciego, Pacific, 29 September 2000, coll. D. Felder & R. Robles, 6 male, 24 female, including 20 ov, parental voucher for hatched larvae, 2 photo vouchers, 10 dissected for analyses, ULLZ 4312 (CL 11.9-20.9). – same site, date, and coll., 1 male photo voucher, ULLZ 4508 (CL 20.4). – same site, 15 April 2000, coll. D. Felder & S. Nates, 5 male including 2 mutl and 1 photo voucher, 1 female (CL 11.3-18.9 mm) ULLZ 4625. – playa ponds, Paso Caballos, Pacific, 30 September 2000, coll. D. Felder & R. Robles, 1 male ULLZ 4626 (CL 14.8 mm). COSTA RICA: small creek, high tide, Playa Carrillo, Pacific, 20 Dec 1995, coll. S. Nates, 1 male, 2 female ULLZ 4627 (CL 6.6-17.1 mm).

Diagnosis: Eyestalk with closely opposed narrow tips, little if any deflection anterolaterally. Rostrum weakly angled in anterodorsal direction, primarily directed to anterior, weakly hooked, base originating from less inclined narrow front of carapace anterior to dorsal oval, median depression at anterior of dorsal oval not greater than that at base of rostrum in lateral view. Major chela with external surface of propodus in males bearing tuberculate, punctate, setose depression extending posterior from gape, connected by faint suture to dactylar condyle, bordered ventrally by distinct carina extended from gape to point well proximal of dactylar condyle; similar but shallower depression in female, enclosing few or no tubercules, bearing concentration of setal punctae. Minor chela with dorsal and ventral distal corners of carpus blunt, lacking acute teeth or spines, gape maximal proximally when fingers closed, there exceeding maximum width of movable finger in males. First abdominal somite well sclerotized over most of dorsal surface, laterally with pair of membranous tracts joining anteriorly on each posterolateral slope, enclosing isolated sclerite, tracts originating at posterolateral margin and joining anterodorsally at about half the length of somite, then extended as single tract to anterior third of somite; sclerotized lateral extreme of somite forming a narrow channel generally parallel to the lower membranous tract, posteroventral margin forming a distinct but rounded carina extending anterodorsally, terminated at a low boss bearing short line of



Figs 20-29. *Lepidophthalmus eiseni* HOLMES, 1904. – Male (CL 11.8 mm) from Estero Ciego, Nicaragua, ULLZ 4312 (20); female (CL 18.9 mm) from Estero Ciego, Nicaragua, ULLZ 4312 (21, 23); male (CL 18.7 mm) from Estero Ciego, Nicaragua, ULLZ 4625 (22, 24-29): 20. eyes and carapace front, dorsal surface, setae not shown; 21. eyes, carapace front and left antennae, dorsal surface, setae not shown; 22. major male cheliped, external surface; 23. major female chela, external surface; 24. right first male pleopod, internal surface; 25. first abdominal somite, right surface; 26. first abdominal somite, dorsal surface; 27. abdominal somites 1-3, ventral surface, with left first and second pleopods; 28. third left pleopod, anterior surface, setae not shown; 29. sixth abdominal somite, telson and uropods, dorsal surface. Scale lines indicate 3.0 mm.

small setal punctae, ventrolateral plate of somite forming narrow channel parallel to marginal carina, adjacent articulation of first pleopod bordered laterally by short, obtuse tooth in both sexes. Second abdominal somite with ventrolateral margin of pleuron forming broadly rounded ventral lobe in anterior half of somite length, forming simple rounded carina in posterior half; median ventral sclerite with broad flange at anterior end, otherwise subquadrate without distinct constriction along length, lacking flange at posterior end. First pleopod of male with subterminal tooth very strong, near equal in breadth to terminal tooth. Third through fifth pleopods with anterior condylar lobe of basis rounded, lacking ventrolaterally directed spine at articulation of exopod (in both sexes). Telson broadest near or just anterior to midlength, trilobate posteriorly, posterolateral lobes rounded in posterodorsal view.

Coloration (live animals from Nicaragua): Chelipeds and anterior of carapace variable, either pinkish white, pale scarlet or yellow-white, when present, deeper reddish shading is on dorsal-most areas, especially near joints of cheliped articles and external surfaces of major chela. Carapace and abdominal somites varying from pale scarlet to yellow-white, often with slash of deeper orange or scarlet evident through translucent, membranous, setose patch on lateral areas of third to fifth abdominal somites. Pale orange, scarlet, or pink giving rise to pattern on posterior four abdominal pleura and telson. Uropods pinkish, pale orange or light scarlet over most of surface.

Remarks: Distinction of this species from *L. bocourti*, the only other presently known eastern Pacific species with well developed ventral abdominal plating, is readily based upon the more quadrate shape of the ventral median sclerite or plate on the second abdominal somite, a structure that is distinctly chalice or hourglass-shaped in *L. bocourti*. However, in comparison to *L. bocourti*, *L. eiseni* also has much stronger development of a setose external depression proximal to the gape on the major chela and a more extensive and complex arrangement of unsclerotized membranous tracts on posterolateral surfaces of the first abdominal somite. *Lepidophthalmus eiseni* lacks anything resembling the sharp, canaliculate posteroventral crest found on the second abdominal somite in *L. bocourti* and also lacks distolateral spines found on the basis of the third through fifth pleopods in the latter species. While both *L. eiseni* and *L. bocourti* appear to reach larger sizes than do other known American congeners, *L. eiseni* also usually appears to be somewhat narrower or less massive in general body form.

Some of the characters here included in the rediagnoses for these two species are subtle and require careful posing of specimens or may not be obvious in specimens damaged during collection. The eyes may take on a slightly hooked appearance in *L. eiseni*, but are not as strongly hooked to the side as they are in similar-sized specimens of *L. bocourti*. The subterminal tooth of the male first pleopod (gonopod) may sometimes be slightly damaged in either species (as appears to be the case in the holotype of *L. bocourti*), but overall shape of the terminal article of this appendage can nonetheless separate the species. The small spine just lateral to the articulation of the first pleopod in *L. bocourti* may be broken or largely worn away (again the case in the holotype of this species), making structure there look similar to that of *L. eiseni*. Also, the posterolateral lobes of the telson, rounded in *L. eiseni* and angular in *L. bocourti*, are not always evident in dorsal view if the telson is not fully extended, and are best inspected from a posterodorsal perspective.

As for *L. bocourti*, ovigerous specimens of *L. eiseni* were found in Nicaragua during September, the wet season, when they were collected from sediments of a rain swollen tidal stream carrying surface water of < 1 ‰ salinity. Larvae of *L. eiseni* were hatched in the lab from a parental female (ULLZ 4312) and culture was attempted at 25 °C, but the complete larval life history was not obtained. Larvae did not appear to feed on furnished nauplii of *Artemia* in either the first or second zoeal stage, though second stage zoeae did ingest small amounts of algal cultures when furnished. Survival rates were very low, though larvae did molt to a third zoeal stage prior to expiring between 9 and 12 days after hatching. While the full larval history was not obtained, both the duration of larval life and the number of stages do appear to markedly exceed what has been observed in other species of the genus (see NATES & al. 1997). Assuming these preliminary observations represent typical larval history for this species, they suggest a markedly longer planktonic life and thus a much greater potential for dispersal than evident in western Atlantic congeners. This is not unexpected, given the comparatively wide geographic range of *L. eiseni* along coastlines of the eastern Pacific. Comparative treatment of morphology for the known stages of *L. eiseni* will be reserved for future treatment.

Discussion

The original description of *Callianassa bocourti* A. MILNE-EDWARDS, 1870, was brief and did not include illustrations. A somewhat more detailed account, with line illustrations, accompanied the description *L. eiseni* HOLMES, 1904, at the same time the genus *Lepidophthalmus* was established to accommodate this species. However, the latter work made no comparison of this new genus and species to *C. bocourti*, and the line illustrations featured few characters of diagnostic value. A subsequent report of Holmes' species from El Salvador by HOLTHUIS (1954) included both additional descriptive text and well prepared line illustrations, and leaves little doubt that these materials were correctly assigned. While this treatment referred to Holmes' species as *C. eiseni* in accord with taxonomic reassignments by other workers (DE MAN 1928, SCHMITT 1935), it included no comparisons to *C. bocourti*. A slightly later report of *C. eiseni* by BOTT (1955), again from El Salvador, included a very short diagnosis and a few highly schematic figures of limited comparative utility, though the figured cheliped does most resemble that of *L. eiseni*; but again, no comparison was made to *C. bocourti*.

Comparison of these two species was attempted by BIFFAR (1972), but without first-hand access to the type material of *C. bocourti*. Rather, specimens thought to be *C. eiseni* from Panama were furnished to M. de Saint Laurent for comparison at the Muséum National d'Histoire Naturelle, Paris. While differences were reported in what may have been diagnostic features of the telson and pleopods, these were discounted given the extreme size difference of the specimens being compared. This conclusion seemed to be validated by differences of the same nature observed in comparing other "large specimens from Mexico with other Panamanian specimens" (BIFFAR 1972: 71), and led to the synonymizing of the two species names under the senior synonym *C. bocourti*. This synonymy was also indicated by DE SAINT LAURENT & LELOEUFF 1979. In the course of resurrecting the genus *Lepidophthalmus*, *L. bocourti* was thus noted to be the only known eastern Pacific representative of the genus (MANNING & FELDER 1991).

However, from recent reexamination of the "Panamanian specimens" that Biffar had access to at the time of his study, it is now clear that those materials represent neither *L. eiseni* nor *L. bocourti*, but rather are assignable to one of three other undescribed eastern Pacific congeners lacking development of ventral abdominal sclerites. Contributing to the confusion, that particular Panamanian species (presently in description), even when fully mature, does not approach the maximum size of mature *L. eiseni* or *L. bocourti*. It could be mistaken for a juvenile of either of those species were identification constrained by previously published diagnoses. Thus, what were interpreted by previous workers to be size-dependent characters were likely diagnostic differences between species. Both *L. eiseni* and *L. bocourti* exhibit ventral abdominal plating and all other diagnostic features in even the smallest examples herein reported, well prior to sexual maturity. These characters will at all sizes readily distinguish either of these species from the known but undescribed eastern Pacific congeners that lack development of ventral abdominal sclerotization.

The function of this ventral plating remains in question, and it does not occur in all species of the genus. Its occurrence among the known species of the genus does not appear to reflect restriction to any particular clade, at least in those phylograms recently based on heuristic analysis of morphology (TUDGE & al. 2000). However, all species of the Callianassidae thus far found to have ventral abdominal plating of this pattern are readily assignable to the genus *Lepidophthalmus*. It is also for the first time here noted that this characteristic plating occurs in examined specimens (ULLZ 4737) of the west African species, *L. turneranus* (WHITE, 1861) a species noted for its resemblance to *L. jamaicense* and *L. bocourti* by previous workers (DE SAINT LAURENT & LE LOEUFF 1979), and treated under *Lepidophthalmus* by SAKAI (1999) and TUDGE & al. (2000).

Conspicuous ventral plating of the abdominal somites was noted to be lacking in *L. rafai* by FELDER & MANNING (1998), but is also lacking or very poorly developed in specimens from several other eastern Pacific populations of *Lepidophthalmus* that were examined in the course of the present study. For all of those populations, which appear to represent three undescribed species, it is readily evident that no well-defined, sclerotized median plate is evident on the ventral side of the second abdominal somite.

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