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A WESTERN ATLANTIC PEPPERMINT SHRIMP COMPLEX: REDESCRIPTION OF *LYSMATA WURDEMANNI*, DESCRIPTION OF FOUR NEW SPECIES, AND REMARKS ON *LYSMATA RATHBUNAE* (CRUSTACEA: DECAPODA: HIPPOLYTIDAE)

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ABSTRACT

The present study is the first revision of the western Atlantic peppermint shrimp complex *Lysmata wurdemanni* (Gibbes). *Lysmata wurdemanni*, originally described from Florida and South Carolina, is redescribed. Gibbes' types of *L. wurdemanni* are considered as lost, therefore, a neotype is selected from specimens collected near Key West, Florida. *Lysmata rathbunae* Chace is rediagnosed; the locality of this species is restricted to Florida and Yucatán; Chace's "variety" of *L. rathbunae* is separated from *L. rathbunae* and assigned to a new species. In total, four new species are recognized: *Lysmata ankeri* n. sp., *Lysmata boggessi* n. sp., *Lysmata pederseni*, n. sp. (corresponding to Chace's "variety" of *L. rathbunae*), and *Lysmata bahia* n. sp.; all four previously were mistaken for *L. wurdemanni* and/or *L. rathbunae*. Classical morphological and morphometrical analyses (Discriminant Function Analysis), in conjunction with examination of life color patterns and interbreeding experiments, were used to corroborate the separation of these cryptic species. Each species may be most easily recognized by the unique color pattern. *Lysmata pederseni*, n. sp. also differs ecologically in being associated with tube sponges. *Lysmata rathbunae* appears to be a deep-water species, while the other five species are found mostly in shallow waters.

Members of the decapod family Hippolytidae Dana, a presumably polyphyletic group (Christoffersen, 1990), are mostly small, benthic shrimps of hard substrates, often associated with algae, sea grass, and various sessile invertebrates (Bauer, 2004). Within this family, the shrimps of the genus *Lysmata* Risso, 1816 appear to be unique both morphologically and biologically (Bauer, 2004). Christoffersen (1990) placed *Lysmata* with the closely related *Lysmatella* Borradaile, 1915 and *Exhippolysmata* Stebbing, 1916 in its own family, Lysmatidae Dana, 1852. *Lysmata* includes 31 species (Chace, 1997; Wicksten, 2000a,b; Burukovsky, 2000), 10 of which occur in the Atlantic Ocean (Chace, 1972; d'Udekem d'Acoz, 1999). From these ten species, six are known from the western Atlantic: *Lysmata grabhami* (Gordon, 1935), *Lysmata intermedia* (Kingsley, 1878), *Lysmata moorei* (Rathbun, 1902), *Lysmata anchisteus* Chace, 1972, *Lysmata rathbunae* Chace, 1970, and *Lysmata wurdemanni* (Gibbes, 1850) (Chace, 1970, 1972, 1997).

The shrimps of the genus *Lysmata* have been studied rather extensively (e.g., Bauer and Holt, 1998; Fiedler, 1998; Bauer, 2000, 2004; Lin and Zhang, 2001b,c; Calado et al., 2003a,b, Rhyne and Lin, 2004; Zhang and Lin, 2005). Long kept for their beauty, these shrimps are among the most intensively traded decapods in the marine aquarium industry. Currently *Lysmata* species are roughly divided into two informal, nontaxonomic ecological groupings (Bauer, 2000): (1) low density, pair living, "cleaner shrimps," with bright and contrasting coloration, including yellow and red colors and long white antenna, and famous for their ability to actively "clean" fish (e.g., *Lysmata amboinensis* De Man, 1888, *L. grabhami*, *Lysmata debelius* Bruce, 1983, and *Lys-*

mata splendida Burukovsky, 2000); (2) high density, aggregate living, "peppermint shrimps," with color patterns consisting of semi-translucent bodies with longitudinal and lateral red bands (e.g., *L. wurdemanni*, *Lysmata californica* (Stimpson, 1866) and *Lysmata seticaudata* (Risso,1816)). Some of the peppermint shrimps (e.g., *L. seticaudata* and *L. californica*) are also known to clean fish (e.g., moray eels); however, they appear to clean passively (Bauer, 2004). The discovery of a rare reproductive mode in decapods, protandric simultaneous hermaphrodism, first demonstrated in an unpublished Masters thesis by Bundy (1983), and later anecdotally observed by aquarists (Wilkerson, 1994), aquaculturists (Riley, 1994; Fletcher et al., 1995) and marine biologists (Wirtz, 1997), prompted publications of several landmark studies documenting this novel reproductive system in the order Decapoda (Bauer and Holt, 1998; Fiedler, 1998; Bauer, 2000; Lin and Zhang, 2001b).

The western Atlantic peppermint shrimps, mostly traded as "*L. wurdemanni*," have been used for many years to control pest anemones (*Aiptasia* spp.), which may partially explain the popularity of these shrimps on the aquarium market (Rhyne et al., 2004). Concerns due to potential over-harvesting and increased market demand of decapods and other marine ornamental species have induced extensive research in developing aquaculture protocols for the most demanded species. For instance, several studies deal with the feasibility of culturing the peppermint shrimps known as "*L. wurdemanni*" (Crompton, 1992, 1994; Zhang et al., 1998a,b). However, unexplained differences in length of larval period between research groups prompted questions about the true identity of *L. wurdemanni*, compelling Lin (2000) to publish a correction of previous studies (Zhang et al., 1998a,b), in which, according to Lin (2000), *L. rathbunae* was mistaken for *L. wurdemanni*. As laboratory-rearing work progressed, we began to doubt Lin's (2000) identification of *L. rathbunae*, and whether this species was common at all in the aquarium trade (Rhyne, 2002).

Lysmata wurdemanni was originally described by Gibbes (1850) as *"Hippolyte Wurdemanni"* on the basis of specimens collected in Key West, Florida and Charleston, South Carolina. Gibbes' description was very brief, and unfortunately, no illustrations were provided. Gibbes (1850) deposited the type(s) in his personal collection "Charleston Cabinet," which consisted of mounted dried specimens. After Gibbes' death the collection was kept in the possession of family members until the remaining lots were deposited in the Charleston Museum, Charleston, South Carolina in the early 20th century. Unfortunately, the majority of Gibbes' collection was lost or destroyed and the current collection consists mostly of crabs (A. Sanders, Charleston Museum, pers. comm). To our knowledge no previous workers have ever examined the original types of *L. wurdemanni*.

Hay and Shore (1918) recorded this species as *Hippolysmata wurdemanni* from North Carolina, without detailed figures, but with a black and white photograph. Holthuis (1959) reported *H. wurdemanni*, without figures, from Surinam and French Guiana. Although Holthuis (1959) noted differences in morphology between specimens from different localities, he did not draw further conclusions because of insufficient sample size. However, based on these differences, he suggested restricting the type locality of *H. wurdemanni* to Key West, Florida. Williams (1965) recorded *H. wurdemanni* from Beaufort, North Carolina, providing several figures. Williams' redescription of *H. wurdemanni* was based on specimens collected in North Carolina, but he extended the North American range of this species from the Lower Chesapeake Bay, Virginia to Port Aransas, Texas and the South American range from

French Guyana to São Paulo, Brazil. The genus *Hippolysmata* Stimpson, 1860 was placed in synonymy of *Lysmata* (Chace, 1972), and all subsequent records of this species, along with other species described under *Hippolysmata* (i.e., *Hippolysmata grabhami*, *Hippolysmata amboinensis*), are under the generic name *Lysmata*.

Lysmata rathbunae was described on the basis of museum specimens identified as *Hippolysmata*, n. sp. by Mary J. Rathbun, collected in waters of Florida and Yucatán, Mexico (Chace, 1970, 1972). Chace (1970) provided a series of detailed figures and reproduced precise notes on the color pattern made by Waldo L. Schmitt. Furthermore, Chace (1970) recognized a typical form of *L. rathbunae* from deeper water and an unnamed "variety" of *L. rathbunae* from shallow waters, which were associated with tube sponges. *Lysmata rathbunae* is a valid species, however, the morphological characters of Chace's "varieties" of *L. rathbunae* are obviously not consistent with those of the type specimens of *L. rathbunae*.

Chace (1972, 1997) provided keys for *Lysmata* species, but did not provide any new descriptions or illustrations for *L. rathbunae* and *L. wurdemanni*. In the first key Chace (1972) used the length of the rostrum, the number of carpal segments of the second pereiopod and the shape of the antennal scale as characters separating the two species. Williams (1984) reported *L. wurdemanni* and *L. rathbunae* in detail, with figures, and extended the northern range of *L. wurdemanni* to Great Egg Harbor, New Jersey.

Popular field guides (e.g., Debelius, 2001; Humann and Deloach, 2002) and various aquarium magazines commonly publish color photographs of peppermint shrimp under the names *L. wurdemanni* or *L. rathbunae*. However, when specimens matching the respective color patterns are examined, they do not fit any species in the species key provided by Chace (1997). Obviously none of these identifications are based on taxonomic examination of actual specimens. For example, specimens with a characteristic color pattern identified as "*L. rathbunae*" in Debelius (2001) and Humann and Deloach (2002), do not conform to Chace's (1970) description of *L. rathbunae*. Likewise, specimens associated with tube sponges and having a very diagnostic color pattern, referred to "*L. wurdemanni*" in Debelius (2001) and Humann and Deloach (2002), do not correspond to the descriptions of *L. wurdemanni*, but appear to match the shallow water sponge dwelling "variety" of *L. rathbunae* (Chace, 1970). All this adds to the uncertainty and confusion around *L. wurdemanni*, *L. rathbunae*, and closely related cryptic species.

The present study is the first revision of the western Atlantic *L. wurdemanni* species complex. Four species are recognized as new and are described herewith on the basis of both museum and freshly collected specimens. One of these new species was previously confused with *L. rathbunae*, while three others were previously misidentified and reported either as *L. wurdemanni* and/or *L. rathbunae* (e.g., Bauer and Holt, 1998; Lin and Zhang, 2001b,c). The four new species and *L. wurdemanni* are described or redescribed, respectively, compared to each other and illustrated (including their diagnostic color patterns). Key diagnostic features for *L. rathbunae*, described in detail by Chace (1970), are also provided. A revised key to the six species of the peppermint shrimps, including *L. wurdemanni s. str.* (sensu Gibbes, 1850), *L. rathbunae*, and four new species, is presented.

MATERIALS AND METHODS

The senior author examined all available western Atlantic specimens identified under generic names *Lysmata* or *Hippolysmata*. These include specimens deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Florida Fish and Wildlife Research Institute, St. Petersburg, Florida (FSBC-I). Also examined were three lots loaned from the Grice Marine Laboratory, Southeastern Regional Taxonomic Center, South Carolina Department of Natural Resources, Charleston, South Carolina (SERTC), and one lot from each of the following institutions: the Nationaal Natuurhistorisch Museum Leiden (RMNH-D), Oxford University Museum of Natural History (OUMNH ZOO COLL), the Muséum National d'Histoire Naturelle, Paris, France (MNHN-Na), and Texas Cooperative Wildlife Collection (TCWC) (Texas A & M University at College Station). Of the 131 specimen lots examined, approximately half were misidentified as *H. wurdemanni*, *L. wurdemanni*, or *L. rathbunae*. Two lots were correctly listed as new species and will be described at a later date. Specimens incorrectly labeled as *L. wurdemanni* are hereafter marked with "†," *H. wurdemanni* with "‡," and *L. rathbunae* with "*" after the catalog number in the material listed under the new species. Types are deposited in the USNM, MNHN-Na, RMNH-D, FSBC-I, OUMNH ZOO COLL, Florida Museum of Natural History, University of Florida, Gainesville, Florida (UF), the Natural History Museum of Los Angeles County, Los Angeles, California (LACM-CR), and the Museu de Zoologia da Universidade de São Paulo (MZUSP). Material listed as "non-type" material was examined to confirm the identity of the specimen(s) and are not designated as paratypes.

Other material was obtained through extensive field collections that were carried out from October 2001 to August 2005, primarily in Florida, but also in Texas, North and South Carolina, New York, Salvador and Rio de Janeiro, Brazil. Specimens from Haiti were directly imported through local marine life wholesalers. Freshly collected specimens were either immediately preserved in 70% ethanol or transported alive to the laboratory for observations and photographing.

Detailed morphological and morphometric analyses were performed on specimens of each species from both wild populations and museum collections. When enough material was available, only field-collected specimens were used for analysis. Major morphological features, such as the number of carpal segments on the second pereiopod, the rostral formula (number of teeth on dorsal and ventral margins of the rostrum), the number of spines on the dactyli of the third to fifth pereiopods, and ratios (e.g., relative length or width of various parts of the appendages or the carapace) were analyzed for each species. Length measurements were determined with a stereo or compound microscope fitted with a calibrated ocular micrometer. Morphometric data from 35 variables was graphically analyzed via box plot graphs with standard deviation and 95% confidence levels. For each feature, data was plotted for every species, thus enabling a direct comparison between species. From this graphical analysis, the most important morphological features in box plots determined by percent overlap, in box plots, were analyzed by Discriminant Function Analysis (DFA).

Lysmata wurdemanni was fully dissected and illustrated. Due to the cryptic nature of the new species, illustrations showing the most important morphological differences between the species are given. *Lysmata rathbunae* is well illustrated by Chace (1970), therefore only characters omitted by Chace (1970) were drawn from USNM specimens that agreed well with the Holotype. All illustrations were drawn by Mr. Denis Poddoubtchenko using a camera lucida.

To determine reproductive compatibility, breeding experiments were carried out. All shrimps used for reproductive compatibility trials were collected from wild populations (directly or imported). For species with wide geographic ranges (e.g., *L. wurdemanni*), the specimens were restricted to a single locality. Only mature, reproductively active shrimps in the euhermaphrodite phase (Lin and Zhang, 2001b,c) were used for breeding experiments. Groups ranging from 5 to 12 shrimps of each species (except for *L. rathbunae*, which is known only from museum specimens) were held in 20 L aquaria. For Brazilian specimens reproductive compatibility was determined at Universidade Santa Úrusla by Mr. Helio Laubenheimer. These groups were allowed to adjust to experimental conditions for several weeks until all or most of the shrimps were gravid and mated successfully. To test the assumption that no hybridization would occur, gravid euhermaphrodites of two different putative species were placed in a 20 L aquarium. Pairs were observed until both shrimps molted and successful or unsuccessful fertilization of eggs or hatching of viable larvae could be determined. Unsuccessful fertilization was characterized by the extrusion of eggs to the abdomen of the shrimp and a total loss of those eggs within 5 d (normally less than 24 hrs) (Fiedler, 1998). A successful fertilization event was determined by the presence of eggs for more than 5 d and confirmed by microscopic examination of the embryos, or hatching of viable larvae at the completion of brooding.

For new species determined to be simultaneous hermaphrodites, the holotype sex is considered "euhermaphrodite" (Lin and Zhang, 2001b,c) due to the ability of the shrimp to mate as both male and female without a phase shift. The term "female phase" proposed by Bauer (2000) is not used here. The carapace length (CL) was measured to the nearest mm along the medio-dorsal line from the post-orbital margin to the posterior margin of the carapace.

Systematics

Order Decapoda Latreille

Infraorder Caridea Dana

Family Hippolytidae Dana

Genus *Lysmata* Risso, 1816

Lysmata wurdemanni (Gibbes, 1850)

(Figures 1–4, Plates 1A, 2)

Hippolyte wurdemanni Gibbes, 1850: 197, (type localities: Key West, Florida and Charleston, South Carolina).

Hippolysmata wurdemanni – Hay and Shore, 1918: 392, pl. 26, (Beaufort, North Carolina); – Holthuis, 1959: 111, in part, (material from St. Augustine, Florida); – Williams, 1965: 84, fig. 68, in part, (not Surinam, French Guyana, Brazil, and west Florida).

Not *H. wurdemanni* – Wass, 1955: 132 (key), 144, (Alligator Harbor, west Florida); – Holthuis, 1959: 111, in part, (material from Florida Keys, Surinam, French Guyana); – van Arm and Smith, 1970: 133, fig. 1A, (Biscayne Bay, Florida).

Lysmata wurdemanni – Williams, 1984: 127, fig. 90, in part, (not Surinam, French Guyana, Brazil, W Florida); – Abele and Kim, 1986: 22, (checklist and key) (same as Williams, 1984); – Crompton, 1992: 1, (Port Aransas, Texas); – Crompton, 1994: 202, (Port Aransas, Texas); – Riley, 1994: 1 (Port Aransas, Texas); – Chace, 1997: 87, (checklist and key); – Bauer and Holt, 1998: 223; – Bauer, 2000: 742; – Bauer, 2001: 434; - Giri and Wicksten, 2001: 1305, (Galveston, Texas); – Bauer, 2002a: 347; – Bauer, 2002b: 742; – Baldwin and Bauer, 2003: 157; – Baeza and Bauer, 2004: 544, (all Bauer or Bauer et al., material from Port Aransas, Texas); – Zhang and Lin, 2004: 470 (Port Aransas, Texas). Zhang and Lin 2005: 11, (Port Aransas, Texas). Zhang and Lin 2006.

Type Material.—Neotype, euhermaphrodite, CL 12.4 mm, USNM 1082798, Key West Lakes, West of Key West, Florida; under ledge, depth: 1 m, coll. A.L. Rhyne, 16 June 2003.

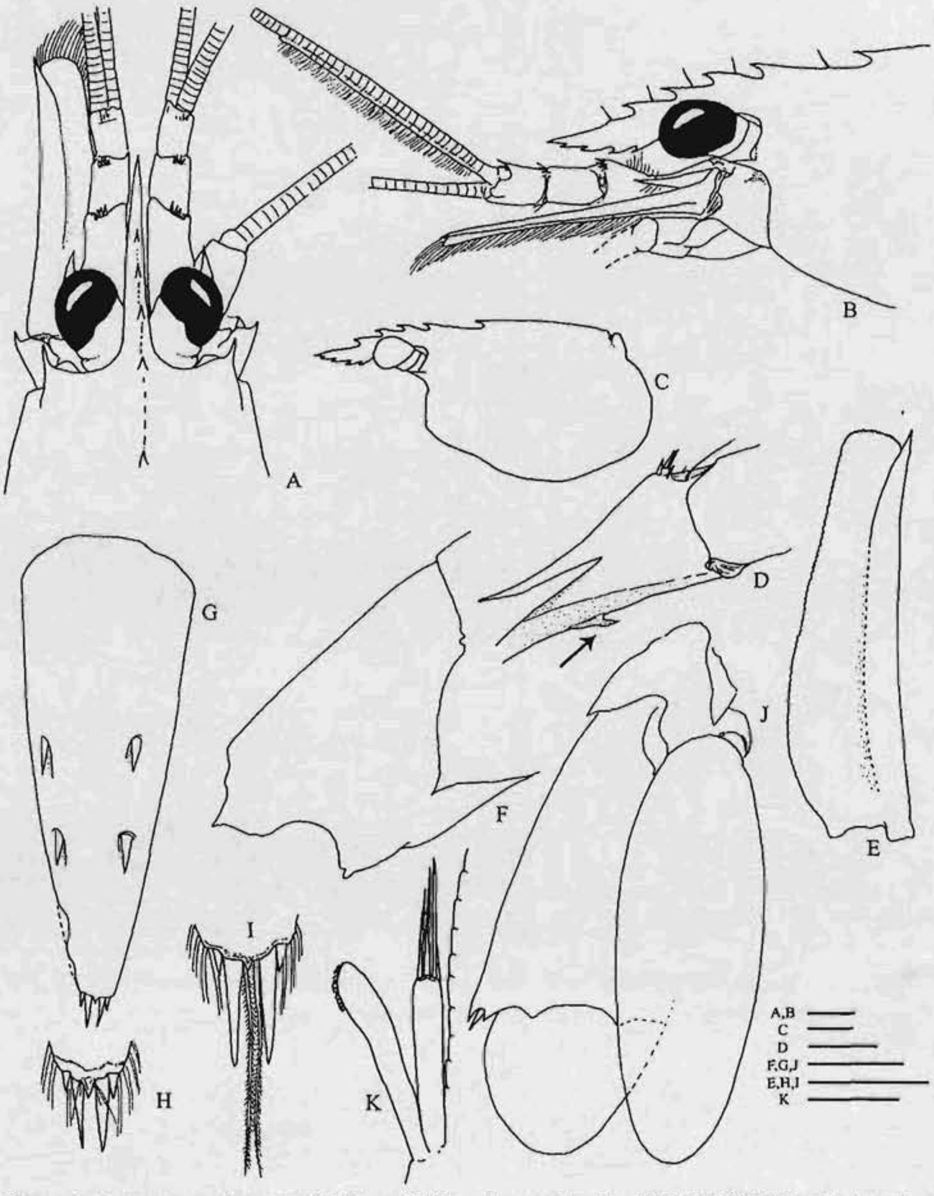

Figure 1. *Lysmata wurdemanni* (Gibbes, 1850), euhermaphrodite, USNM 1802796. (A) Anterior region, dorsal view. (B) Anterior region, lateral view. (C) Carapace, lateral view. (D) First segment of antennular peduncle, arrow indicates ventral mesial carnate tooth. (E) Right antennal scale. (F) Lateral view fifth and sixth abdominal pleura segments. (G) Telson, dorsal view. (H) Tip of telson (abnormal, missing long setae). (I) Tip of telson (USNM 1082794, normal). (J) Left uropods. (K) Appendix masculina and appendix interna of second pleopod of male specimen (USMN 1082797). Scales A,B,D–G, J,K 1 mm; C 2 mm; H,I 0.5 mm.

Non-type Material Examined.—Specimens Collected from the Field.—Two specimens, USNM 1082794, Georgetown, South Carolina; shell bottom, inside North inlet, depth: 3 m, coll. Paul Kenny October 2003; one specimen, USNM 1082793, Long Island Sound, New York; depth: 2 m, coll. Todd Gardner, September 2004; – two specimens each, USNM 1082795, OUMNH ZOO COLL 2005-08-04, LACM-CR 2003-014.1, MZUSP 16881, RMNH-D 51599, MNHN-Na 16068, UF 8345, FSBC-I 066739, Port Aransas, Texas, on jetties under stones, coll. Matt Palmtag, 15 June 2003; – one specimen, USNM 1082797, Port Aransas, Texas, on jetties under stones, coll. Matt Palmtag, 15 June 2003; – one specimen USNM 1082796 Florida Bay, approx. 75 km northwest of Marathon, Florida, sponge and gorgonian bottom, caught in stone crab traps, depth: 15 m, coll. R. Boggess, November 2003; – one specimen, USNM 1082799, Key West Lakes, Key West Florida in ledge 1 m, coll. A. L. Rhyne, June 2003.

Specimens Identified as Hippolysmata wurdemanni.—Two specimens, USNM 23579, Key West, Florida, along shore and among rocks, coll. Henry Hemphill, 1883; – two specimens, USNM 00255130, South of Marineland, Florida, coll. H. B. Herrick, 20 June 1964; – six specimens, USNM 31396, South End of May River, Calibogue Sound, South Carolina; Sta. 1651, January 1891; – one specimen, USNM 31430, South End of May River, Calibogue Sound, South Carolina; Sta. 1651; – one specimen, USNM 31431, Charleston Harbor, Charleston, South Carolina, Sta. 1659, 13 March 1891; – six specimens, USNM 31432, Mouth of Bull's Creek, South Carolina, 15 January 1891; – one specimen, USNM 31433, Position 3, Kiawah River, South Carolina, 6 March 1891; – one specimen, USNM 31434, Kiawah River, South Carolina, 6 March 1891; – seven specimens, USNM 42155, Beaufort, North Carolina, Union College Collection, 1756; – 15 specimens USNM 77754, St. Augustine, Florida; on sea buoy, coll. G. R. Lunz, Jr., 25 Jan 1935; – two specimens, USNM 81759, Beaufort, North Carolina, on pilings, coll. A. S. Pearse, 7 August 1941; – two specimens, USNM 87946, Port Aransas, Texas, on jetties under stones, coll. J. W. Hedgpeth, 18 November 1948; – two specimens, USNM 89049, North Edisto River, South Carolina, coll. G. R. Lunz, 27 March 1949; – two specimens, USNM 91213, South Jetty, Port Aransas, Texas, coll. M. D. Burkenroad, June 1950; – one specimen, USNM 101122, Center of Chandeleur Sound, Louisiana, Sta. AI-503, depth: 6 m, coll. R. M. Darnell, 10 June 1957; – one specimen, USNM 104171, St. Simon Island Georgia, beach, coll. L. Hubright, 11 October 1959; – five specimens, USNM 180992, southeast of Little Egg inlet, seaward of ridge, coll. G. J. Miller, 26 August 1974; – five specimens, USNM 180993, southeast of Little Egg inlet, seaward of ridge, coll. G. J. Miller, 26 August 1974; – 14 specimens SERTC S2303; two specimens SERTC S2304; – one specimen SERTC S2305, Charleston Harbor, Charleston, South Carolina.

Specimens Identified as Lysmata wurdemanni.—16 specimens, USNM 181877, Sapelo Sound, Georgia, depth: 12 m, coll. M. Grey, 18 January 1962; – eight specimens, USNM 181879, Walburg Creek, Georgia, depth: 20–30 m, coll. M. Grey, 20 February 1962; – three specimens, USNM 220753, Georgia, 31°23′06″N-80°53′06″W, depth: 18 m, 9 August 1980; – five specimens, USNM 222999, Charleston Harbor, Breach Inlet, Charleston, South Carolina, depth: 5 m, coll. D. R. Wiseman, 14 July 1979; – one specimen, USNM 224982, Georgia, 31°41′18″N-80°21′06″W, depth: 27 m, 24 October 1981; – one specimen, USNM 224984, Georgia, 31°41′24″N-80°20′54″W, depth: 27 m, 24 October 1981; – one specimen, USNM 253076, Park Jetty, South Padre Island, Texas, coll. unknown, 4 July 1993.

Description.—Rostrum varying from slightly curved ventrally to straight, 0.4–0.7 times as long as carapace, usually reaching at least to middle of intermediate segment of antennular peduncle, rarely past the distal margin of the intermediate (Fig. 1A,B); dorsal margin with 4–6 teeth, most posterior tooth situated on dorsal carina of cara-

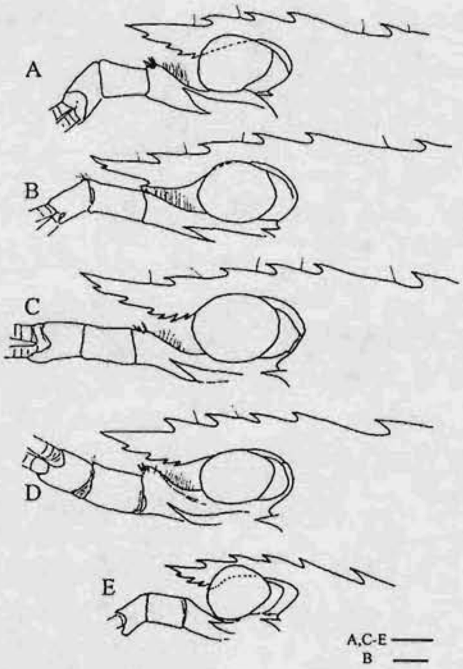

Figure 2. Rostral variation within *Lysmata wurdemanni* (Gibbes 1850). (A) USNM 1082794. (B) USNM 1082798 Neotype. (C) USNM 1082793. (D) USNM 77754. (E) USNM 1082794. Scales A–E 1 mm.

pace well beyond the post-orbital margin, second tooth above post-orbital margin, remaining teeth anterior to post-orbital margin; ventral margin of rostrum usually with four teeth, occasionally with two, three, five, or six; most proximal ventral tooth situated at level of or slightly beyond stylocerite (Figs. 1B, 2A–E). Carapace smooth, robust, ventro-posterior margin rounded, eyes large, not reaching dorsal margin of rostrum (Fig. 1C). Antennule with stylocerite reaching to or just past anterior margin of eye, not reaching distal margin of proximal segment of antennular peduncle (Fig. 1B); tooth of ventral mesial carnate of first segment of antennular peduncle acute, anteriorly directed (Fig. 1D); intermediate segment of < 1.7 (1.2–1.7) times long as high (Fig. 1B); lateral antennular flagellum with rudimentary secondary ramus (Fig. 1B). Antennal scale with disto-lateral tooth approximately 3.8 (3.2–4.4) times as long as wide, slightly overreaching blade (Fig. 1E).

Abdominal somites of the fifth segment with sharp posterolateral tooth and sixth with posteroventral tooth (Fig. 1F). Telson tapering posteriorly, dorsal surface with two pairs of spines (Fig. 1G); posterior margin acute mesially with a pair of long slender spines each flanked (on the outside margin) by a short spine (Fig. 1H,I). Spines separated by two long setae originating from the terminal of the telson (Fig. 1I).

Gill formula is presented in Table 1. Mouth parts as illustrated (Figs. 3A–F, 4A). Exopod of third maxilliped reaching 2/3 length of antepenultimate segment, ultimate segment two times longer than penultimate, terminating in 3–4 spines (Fig. 4A). First pereiopod with simple chela (Fig. 4B,C), palm less than three times as long as dactylus (Fig. 4C). Second pereiopods slender, subequal in length, with small chelae (Fig. 4D); carpus nearly twice the length of merus, carpus with 27–30 (rarely up

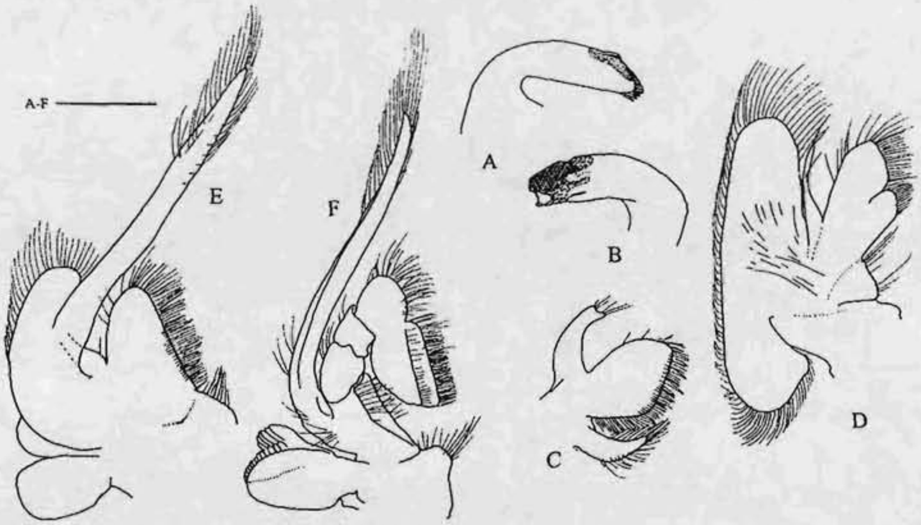

Figure 3. *Lysmata wurdemanni* (Gibbes, 1850), euhermaphrodite, USNM 1082796, (A) Left mandible. (B) Right mandible. (C) Right first maxilla. (D) Second maxilla. (E) Right first maxilliped. (F) Right second maxilliped. Scale A–F 1 mm.

to 32) segments, merus with about 15 segments (Fig. 4D). Third–fifth pereiopods similar, decreasing in length from third–fifth; dactyli usually armed with five spines (rarely four or six); dactylus biunguiculate, dorsal unguis longer than ventral, flexor margin with three (rarely two or four) spines, decreasing in size from proximally, most proximal spine minute (Fig. 4E–G). Fifth pereiopod with merus armed with 1–4 spines, propodus with 3–4 rows of dense setae on distal end of flexor margin. All ratios for pereiopods 1, 2 and 5 given in Table 2. Sternum between pereiopods without acute projections.

Color in Life.—Body semi-translucent with red longitudinal, transverse, and oblique bands (Plate 1A); carapace with broad transverse and oblique v-shaped bands; abdominal pleura with short, narrow longitudinal stripes, third pleuron with a broad transverse band (appearing more intense than bands of other pleura in dorsal view, cf. Plate 1A); telson and uropods with broad, intense longitudinal bands; specimens from northern-most range occasionally with slight blue tinge on tail; eggs bright green. Embryos of stage I–III bright green, last stage silver.

Distribution.—Eastern and southeastern U.S.: Long Island, New York (seasonal population) to southeast Florida; Key West, Florida; Florida Bay (in depths below 12 m); uncommon along west coast of Florida to Panhandle; common in Galveston and Port Aransas, Texas; possibly also in northern Caribbean (needs confirmation) (Plate 2).

Ecology.—Common on rocky hard bottoms, shell bottoms inside inlets, jetties; also on buoys, pilings, and docks, in depth ranging from < 1 m to about 25 m. Protandrous simultaneous hermaphrodite (Bundy, 1983; Bauer and Holt, 1998; Bauer, 2000)

Remarks.—Gibbes (1850) very briefly described *L. wurdemanni* from two localities: Key West, Florida and Charleston, South Carolina. Because Gibbes' types of *L. wurdemanni* were lost (A. Sanders, Charleston Museum, pers. comm.; A. Rhyne, Florida Institute of Technology, pers. obs.). It is impossible to determine whether the type specimens that F. Wurdemann collected for Gibbes in 1845 are identical with

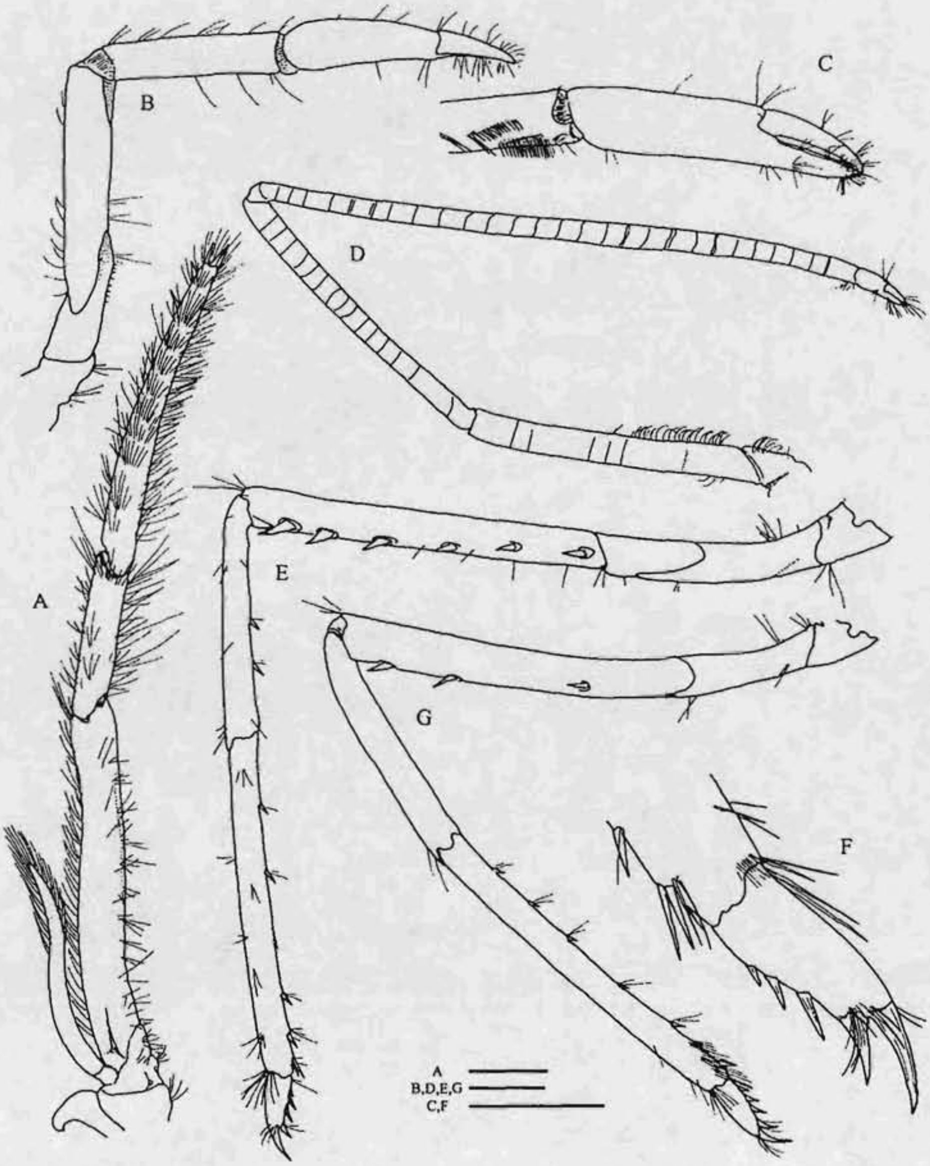

Figure 4. *Lysmata wurdemanni* (Gibbes, 1850), euhermaphrodite, USNM 1082796. (A) Right third maxilliped. (B) Right first pereiopod. (C) Chela of right first pereiopod. (D) Right second pereiopod. (E) Left third pereiopod. (F) Dactylus of left third pereiopod. (G) Left fourth pereiopod. Scale A–E, G 1 mm; F 0.5.

those from Charleston. Holthuis (1959) restricted the type locality of *L. wurdemanni* to Key West. However, we found that three different species occur syntopically in the same type of habitat in the Florida Keys. In one case two species were collected under the same ledge (USNM 1082799, USNM 1082803). Therefore, based solely on the Key West material, it is impossible to ascertain which of the three species corresponds to *L. wurdemanni* (sensu Gibbes, 1850).

To determine the correct identity of *L. wurdemanni,* we examined *Lysmata* specimens collected from Charleston and Georgetown, South Carolina, and found them to be the same species as one of the three species found in the Florida Keys. Based on these findings, a neotype from Key West, Florida, consistent with the South Carolina specimens, was designated to stabilize the taxonomic identity of *L. wurdemanni* sensu (Gibbes, 1850). The material from French Guyana, Surinam, Brazil and west coast of Florida, including Alligator Harbor (Wass, 1955) and Cedar Key (USNM 6456), belongs to several closely related species described below as new. The most reliable features to discriminate *L. wurdemanni* from the other species are the rostral formula, the number of the carpal segments on the second pereiopod (normally 27–29, sometimes up to 32), the shape, size, and number of spines on the flexor margin of the dactylus of the third–fifth pereiopods (two large spines, three small spines, rarely two or four), the ratio of length and height of the second antennular peduncle segment, the green eggs or gonad, and the broad transverse band on the third abdominal pleuron, which appears to be more intense than the transverse bands on the other abdominal pleura (cf. Plate 1).

Lysmata rathbunae Chace, 1970

(Figures 5–6 Plates 1B, 2)

Lysmata rathbunae Chace, 1970: 59, figs. 1–3, in part, (not *L. rathbunae* "variety," fig. 4); – Chace, 1972: 3, 125 (key), 12; – Williams, 1984: 126, fig. 89 (material should be restricted to deep water specimens; Florida to Yucatán); Abele and Kim 1986: 22 (checklist and key) (same as Williams, 1984).

Not *Lysmata rathbunae* – Chace, 1970: 64, fig. 4, (*L. rathbunae* "variety"); – Debelius, 2001: 17, color photograph; – Humann and Deloach, 2002: 171, color photograph = *L. pederseni,* n. sp. (see below); – Lin, 2000; Zhang and Lin, 2005.

Type Material.—Holotype: male, CL 6.25 mm, USNM 99446, off Boynton Beach, Florida, 26°31'N–80°01'W; depth: 55–64 m, PELICAN sta. 15, 25 March 1956; – Paratypes: – one specimen, USNM 101292, northeast of Cape Canaveral, Florida; 28°52'N–80°05'W, depth: 119 m, COMBAT sta. 90, 3 September 1956; – one specimen, USNM 127815, Fort Jefferson, Dry Tortugas, Florida, coll. W. H. Longley, July 1924; – two specimens, USNM 127816, along east side of White Shoals, Dry Tortugas, Florida, depth: 28–30 m, sta. 49–30, coll. W. L. Schmitt, 9 August 1930; – two specimens, USNM 127817, near upper end, west side of lower section of White Shoal, Dry Tortugas, Florida, sta. 41–31, coll. W. L. Schmitt, 24 July 1931; – two specimens, USNM 25640, west of Marco, Florida, 25°50'15"N–82°41'45"W, depth: 38 m, FISH HAWK sta. 7124, 2 April 1901; – one specimen, USNM 9841, Cape Romano, Florida, 26°00'00"N–82°57'30"W, depth: 44 m, ALBATROSS sta. 2413, 19 March 1885; – two specimens, USNM 25641, west of Charlotte Harbor, Florida, 26°33'N–83°11'W, depth: 51 m, FISH HAWK sta. 7123, 2 April 1901; – two specimens, USNM 101293, west of Tarpon Springs, Florida, 28°09'N–83°50'W, depth: 37 m, Silver Bay sta. 54, 16 July 1957; – one specimen, USNM 23585, south of Apalachicola, Florida, 28°46'00"N–84°49'00"W, depth: 48 m, ALBATROSS sta. 2406, 15 March 1885; – one specimen, USNM 23584, northeast of Cabo Catoche, Yucatán, Mexico, 22°08'30"N–86°53'30"W, depth: 46 m, ALBATROSS sta. 2362, 30 January 1885.

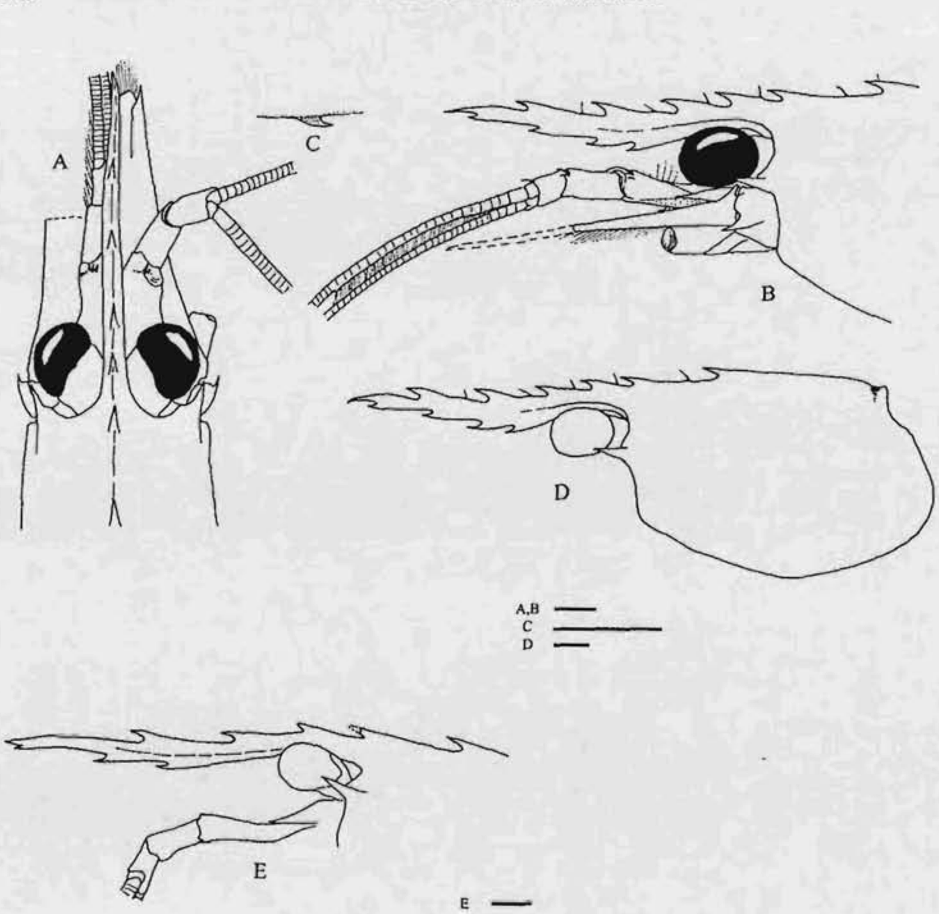

Figure 5. *Lysmata rathbunae* Chace 1970, USNM 242943. (A) Anterior region, dorsal view. (B) Anterior region, lateral view. (C) Antennular carina tooth (D) Carapace, lateral view. (E) USNM 242944. Scales A–E 1 mm.

Non-Type Material.—One specimen, USNM 242943, Gulf of Mexico, Florida, 25°45′53″N–082°31′37″W, depth: 31 m, Sta. 15, 9 November 1980; – one specimen, USNM 242944, Gulf of Mexico, Florida, 25°17′16″N–82°52′10″W, depth: 44 m, Sta. 21, 26 April 1981; – one specimen, USNM 273164, Gulf of Mexico, Florida, 25°45′35″N–83°20′14″W, depth: 58 m, Sta. 17, 15 November 1980; – one specimen, FSBC-I 6982, Hillsborough County, Florida, 38 mi west of Egmont Key, coll. R. Presley, R/V Hernan Cortez, depth 37 m., September 1967. – Three specimens, FSBC-I 7579, Hillsborough County, Florida, 50 mi west of Egmont Key, R. Topp and W. Lyons, R/V Hernan Cortez, depth: 37 m, December 1970; – one specimen, FSBC-I 7602, Hillsborough County, Florida, 38 mi west of Egmont Key, coll. R. Presley, R/V Hernan Cortez, depth: 37 m, September 1967.

Diagnostic Features.—Rostrum long, thin, mostly straight, slightly descending or ascending, reaching beyond distal margin of third segment of antennular peduncle, often overreaching antennal scale (Fig. 5A); dorsal margin with 5–6 teeth, most posterior tooth situated on carapace well beyond postorbital margin, second tooth above post-orbital margin, remaining teeth anterior to post-orbital margin; ventral margin of rostrum usually with 3–5 teeth (Fig. 5B, D–F), most proximal ventral tooth situ-

Figure 6. Color pattern of *Lysmata rathbunae* Chace 1970, dorsal view, redrawn from line drawing in the NMNH Dry Tortugas station data 49-30 of W. Schmitt. Scale 1 mm.

ated at level of posterior margin of first segment of antennular peduncle (Fig. 5B, D–F). Antennal scale five times as long as wide, disto-lateral tooth distinctly overreaching blade. Second pereiopods with small chela, long, subequal, slender, carpus with 30–35 segments. Third–fifth pereiopods long and slender, dactyli biunguiculate dorsal ungues larger than ventral, flexor margin with 3–4 (usually three) spines; decreasing in size from tip to proximal portion, most proximal spine occasionally minute and inconspicuous. For more detailed description and illustrations see Chace (1970). Chace's "variety" of *L. rathbunae* (Chace, 1970: 64, fig. 4) based on material collected from tube sponges represents a new species described below (see below under *L. pederseni* n. sp.).

Color in Life.—"Body beautifully multihued. Carapace marked with bright carmine stripes outlining sub-trapezoidal area on anterior two-thirds of dorsal surface: stripes forming irregular transverse bands posteriorly and longitudinal or diagonal rows on branchial region with a red splotch behind each orbit. Abdominal somites similarly striped with bright carmine, most predominantly in dorsal midline; lateral stripes finer, except on three anterior somites, where third lateral stripe strong, converging along posterior margin of third somite to form median point in midline. Telson with broad median stripe. Eyes with cornea black; eyestalk with deep red dorsal stripe seeming to join red splotch on orbital margin. Antennular peduncle and flagellum solid red. Antennal peduncle with longitudinal red stripe; flagellum solid red. Striking opaque China white Y seen in ventral view embracing antennular peduncle and terminating posteriorly in white spot anterior to mouth. Pereiopods bright red; dactyls of three posterior pairs white in distal half. Lateral branch of uropods with wide red stripe near mesial margin and narrow stripe near lateral margin; mesial branch of uropods with wide red stripe near lateral margin; wide stripes on two branches resembling scissors when uropods open and close" (Chace 1970, based on field notes by W. Schmitt, 1930). A reproduction of the diagrammatic drawing indicating the color pattern of *L. rathbunae* by W. Schmitt in the USNM station report 49–30 is presented in Figure 6, which agrees well with an undocumented color photo taken in 1970 of *L. rathbunae* (FSBC-I 7579) from the HOURGLASS Cruise (Plate 1B).

Distribution.—Southeastern and southern U.S. (Florida and Gulf of Mexico off Florida) and Yucatán, Mexico (Chace 1972; present study, Plate 2).

Ecology.—Largely unknown; found in relatively deep water (depth range: 28–119 m).

Remarks.—The possibility that Chace's (1970) "variety" of *L. rathbunae* could represent a new species was first suggested by Williams (1984). All records of *L. rathbunae* other than those of Chace (1970, 1972, excluding "variety") and Williams (1984) are likely erroneous, especially the "identifications" and color photographs in various aquarium magazines and popular field guides (e.g., Debelius, 2001; Humann and Deloach, 2002). The detailed description of the color pattern (Chace, 1970; see page 64) indicates that *L. rathbunae* has a distinct transverse band on the third pleuron (Fig. 6; Plate 1B). This band is absent in the two new species most frequently mistaken for *L. rathbunae*: *Lysmata boggessi* n. sp., and *Lysmata pederseni* n. sp., the latter corresponding to Chace's (1970) sponge dwelling "variety" of *L. rathbunae* (see below). However, the length of the rostrum, the width of the antennal scale, the number of carpal segments on the second pereiopod, and the number of spines on the dactyli of third–fifth pereiopods are all very different in *L. boggessi* n. sp. and *L. pederseni* n. sp. Furthermore, *L. rathbunae* is a species found in relatively deep water (usually well below 30 m) and therefore is not collected for the aquarium trade. The specimens identified as *L. rathbunae* collected in shallow water (< 15 m) are, in all probability, misidentified and should be reexamined. *Lysmata rathbunae* is similar to *Lysmata gracilirostris* Wicksten, 2000, having elongated legs and rostrum and occupying depths below 30 m. However, this species can be easily distinguished from *L. rathbunae* by the position of second dorsal rostrum tooth, small spines on the dactylus, and the presence of a pterygostomian spine.

Lysmata ankeri new species

(Figures 7–9; Plates 1C, 2)

Lysmata wurdemanni (not Gibbes, 1850) – Holthuis 1959: 111, in part, (Surinam; French Guyana); – Williams 1965: 85, in part, (Surinam; French Guyana); – Chace 1972: 129, in part, (Surinam; French Guyana); – William, 1984: 127, in part, (Surinam; French Guyana); – Lin et al. 1999: 52; – Lin and Zhang, 2001a: 351; – Lin and Zhang, 2001b: 919; – Lin and Zhang, 2001c: 1155; – Calado et al., 2003a: 329; Calado et al., 2003b: 221, fig. 15.1, (all Lin et al. and Calado et al. material was imported from Haiti).

Lysmata wurdemanni (not Gibbes, 1850); – Rodriguez, 1980: 168, fig. 48, (Venezuela); – Abele and Kim, 1989: 19, in part, (Panama).

Lysmata wurdemanni (Haiti "variety") (not Gibbes, 1850) – Rhyne, 2002: 2, Table 1, fig. 2, (Haiti).

Lysmata sp. (Haiti "variety") – Rhyne et al. 2004: 227, (Haiti).

Type Material.—Holotype: euhermaphrodite, 8.2 mm, USNM 1082801, Pompano Beach, Florida, southeast of inlet, under a rock ledge, depth: 4 m, coll. M. Park, 24 July 2004; – Paratypes: one specimen USNM 1082800 same data as holotype. One specimen, USNM 1082802, imported from Haiti by AllSeas Inc., Miami, Florida, June 2003. – Two specimens, OUMNH ZOO COLL 2005-08-03; LACM-CR 2003-015.1; MZUSP 16882; RMNH-D 51600; MNHN-Na 16069; UF 8346; FSBC-I 066740, imported from Haiti by AllSeas Inc., Miami, Florida, June 2003.

Non-Type Material Examined.—One specimen, MNHN-Na 16070, Isla Cubagua, Venezuela, from and around *Millepora* corals, coll. students of Universidad de Oriente, Boca del Río, Margarita, 2001-2002; – One specimen, USNM 134765[†], Lameshur Bay, St. John Island, U.S. Virgin Islands, end of sewer, depth: 21 m, coll. C. Mahnken, 5 April 1969; – two specimens, USNM 143352[†], Discovery Bay, Jamaica, coll. unknown, 1970; – one specimen, USNM 134764[†], Lameshur Bay, St. John Island, U.S. Virgin Islands, end of sewer, depth: 19 m, coll. C. Mahnken, 5 April 1969; – one specimen, USNM 103062[‡], Surinam, 6°24′N–54°59.5′W, shell bottom, depth: 8 m, COQUETEE sta. 23, 12 May 1957; – One specimen, USNM 103063[‡], Surinam, 6°24′N–54°59.5′W, mud and shell bottom, depth: 8 m, COQUETEE sta. 24, 12 May 1957, [specimens in poor condition]; – two specimens, RMNH-D 12643, Isle de Salut, French Guiana, 5°49.5′N–53°09′ W, mud, coral and shell bottom, depth: 27 m, COQUETEE sta. 86, 22 May 1957.

Description.—Rostrum mostly straight, 0.6–0.8 times as long as carapace, reaching usually to middle, rarely past the end of third segment of antennular peduncle (Fig. 7A–C); dorsal margin with 6–8 teeth (predominantly six, commonly seven, rarely eight), most posterior tooth situated on carapace well beyond postorbital margin, second tooth above post-orbital margin, remaining teeth anterior to post-orbital margin; ventral margin of rostrum usually with 4–6, rarely three or seven teeth, most proximal ventral tooth situated at level of or slightly beyond stylocerite (Fig. 8). Carapace robust, three-fourths as high as long, forming obtuse angle at most ventral margin, ventro-posterior margin of carapace not well rounded, flattened posteriorly, eyes large, covering to the dorsal of rostrum (Fig. 7C). Antennule with stylocerite reaching just beyond distal margin of eye, falling well short of end of first segment of antennular peduncle, in large specimens reaching to the mid point of the first segment; intermediate segment 1.8 (1.4–2.3) times long as high. Antennal scale with

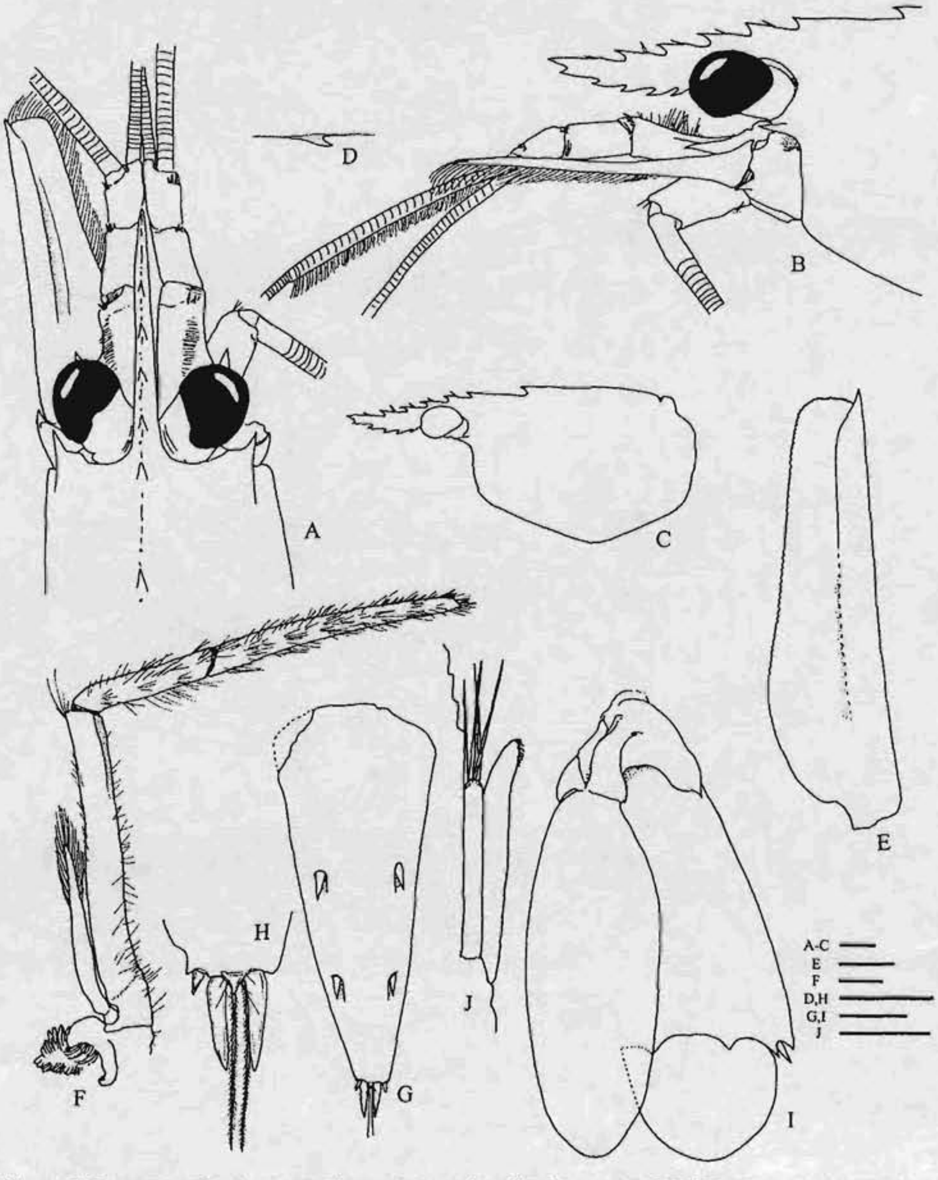

Figure 7. *Lysmata ankeri* new species, euhermaphrodite, Paratype 1082802. (A) Anterior region, dorsal view. (B) Anterior region, lateral view. (C) Carapace, lateral view. (D) Antennular carina tooth. (E) Right antennal scale. (F) Right third maxilliped. (G) Telson, dorsal view. (H) Tip of telson. (I) Right uropods. (J) Appendix masculina and appendix interna of second pleopod of male specimen. (MNHN-Na 16070). Scales. A,B,D–G, I ,J 1 mm; C 2 mm; H 0.5 mm.

disto-lateral tooth overreaching blade, approximately 3.9 (3.4–4.5) times as long as wide (Fig. 7D). First and second pereiopods as illustrated (Fig. 9A,B); carpus of second pereiopod with 33–41 (usually 35–37) segments (Fig. 9B), very rarely with < 33 segments (possibly due to autonomy). Third–fifth pereiopods with dactyli biunguiculate, dorsal ungues larger than ventral, flexor margin with three (rarely four) spines, decreas-

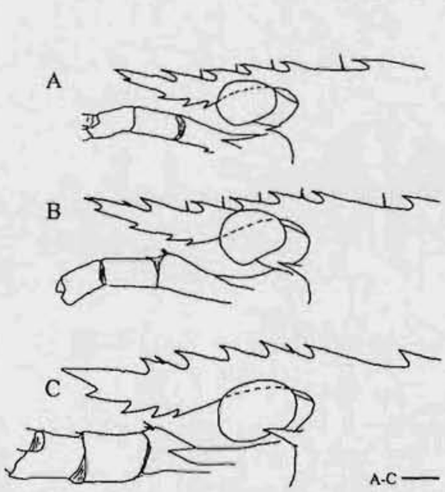

Figure 8. Rostral variation within *Lysmata ankeri* new species. (A) USNM 1082800. (B) USNM 1082801. (C) RMNH-D 12643 Scale 1 mm.

ing in size from tip, most proximal spine minute (Fig. 9C, D). Fifth pereiopod with merus armed with 0–6 spines. Ratios for pereiopods 1, 2, and 5 are given in Table 1.

Color in Life.—Body semi-translucent with red longitudinal, transverse, and oblique bands and stripes (Plate 1C); carapace with broad and narrow oblique and transverse bands, some forming shallow U or V; abdominal pleura with narrow longitudinal stripes, third pleuron with a broad, more intensely colored, transverse, broadly u-shaped band; telson and uropods with relatively narrow longitudinal stripes (narrower and less bright than in *L. wurdemanni*); eggs and gonad pink. Stages I–III of embryos pink, last stage silver.

Distribution.—Southeastern U.S.; Florida: north to Pompano Beach, rare in Florida Bay; Caribbean: Haiti, Venezuela, Panama, Surinam, and French Guyana; northeastern Brazil: Buzios, Rio de Janeiro to Bahia (Plate 2).

Ecology.—Coral reefs, rocky shores; depth possibly ranges from very shallow water (intertidal) to about 25 m. Protandrous simultaneous hermaphrodite (Lin and Zhang, 2001b,c).

Etymology.—Named after the caridean shrimp taxonomist Dr. Arthur Anker (University of Alberta, Edmonton, Canada), who helped with preparation of the manuscript.

Remarks.—This species was previously confused with *L. wurdemanni*. Holthuis (1959) noted that there were differences between "northern" and "southern" populations of *L. wurdemanni*; his southern populations correspond to *L. ankeri* n. sp. In life *L. ankeri* n. sp. is easily distinguished from *L. wurdemanni* by the pink gonad/eggs (vs green gonad/eggs in *L. wurdemanni*). The conspicuous, transverse, shallowly u-shaped band (becoming more v-shaped in large adults) on the third pleuron of the abdomen is another feature distinguishing the new species from *L. wurdemanni*. Preserved specimens can be distinguished by the number of carpal segments on the second pereiopod: 33–41 in *L. ankeri* n. sp. vs 27–30 in *L. wurdemanni* (important remark: both right and left second pereiopods should be examined as reduction of carpal segments may occur after autonomy of the appendage), and the number of dorsal teeth on the rostrum (6–8 in *L. ankeri* n. sp. vs 4–6 in *L. wurdemanni*). Furthermore, in *L. ankeri* n. sp., the rostrum appears to be longer as it usually reaches

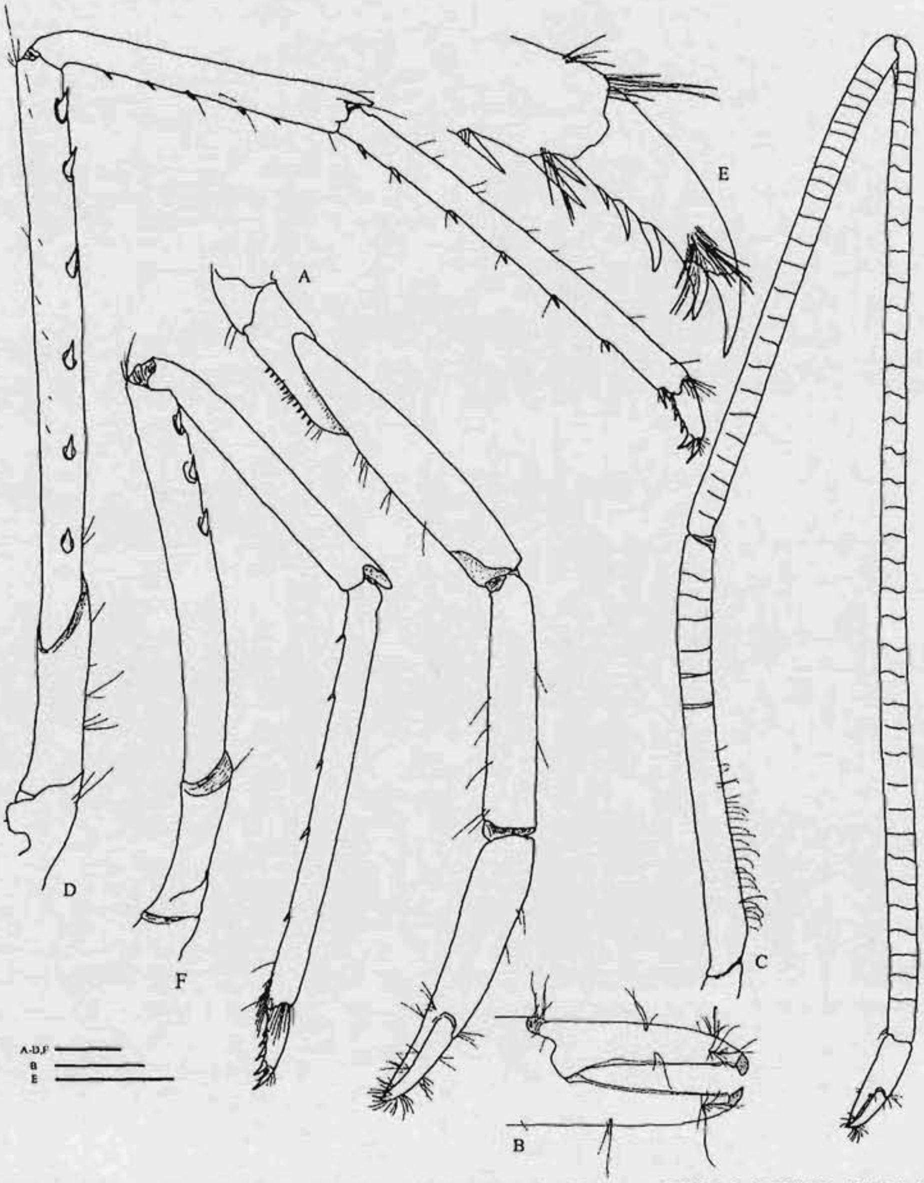

Figure 9. *Lysmata ankeri* new species, euhermaphrodite, Paratype USNM 1082802. (A) Right first pereiopod. (B) Chela of right first pereiopod. (C) Right second pereiopod. (D) Right third pereiopod. (E) Dactylus of right third pereiopod. (F) Right fifth pereiopod. Scales A, C, D 1 mm; B 0.25 mm; E 0.5 mm.

level of the middle of the distal segment of the antennular peduncle, while in *L. wurdemanni* it usually falls short of the distal segment (normally reaching only to the middle of the intermediate), or only slightly exceeds the distal margin of the intermediate segment. The specimens from Venezuela reported as *L. wurdemanni* by Rodriguez (1980) mostly correspond to *L. ankeri* n. sp.

Lysmata boggessi new species

(Figures 10–12, Plates 1D, 2)

Hippolysmata wurdemanni (not Gibbes, 1850) – Wass, 1955: 144, 133 (key), (Alligator Harbor, Florida); – Williams, 1965: 85, in part, (material of Wass 1955 from Alligator Harbor); – Holthuis, 1959: 111, in part, (material from Pine Key, Florida Keys).

Lysmata wurdemanni (not Gibbes, 1850) – Williams, 1984: 128, in part, (material of Wass 1955 from Alligator Harbor); – Markham, 1985: 73, in part; – Zhang et al., 1998a: 97; – Zhang et al., 1998b: 471; – (Zhang et al.'s material from west Florida or Florida Bay).

Lysmata rathbunae (not Chace 1970); – Lin 2000: (same as Zhang et al., 1998a,b); – Debelius, 2001: 17, color photograph; – Humann and Deloach, 2002: 171, color photograph; – Calado et al., 2003c: 964, Table 1;– Zhang and Lin, 2005.

Lysmata sp. (Florida Gulf coast "variety") – Rhyne, 2002: 9, Table 1, fig. 2; – Rhyne et al. 2004: 227 (Florida Bay); – Rhyne and Lin, 2004: 1179 (Rhyne and Lin's material from northwest of Hernando Beach, west Florida).

Type Material.—Holotype: euhermaphrodite, CL 10.0 mm, USNM 1082808, northwest of Hernando Beach, Florida, in seagrass bed, caught by roller trawl, depth: 4 m, coll. A. L. Rhyne, June 2003. Paratypes: – 25 specimens, USNM 1082805, same data as for holotype; – seven specimens, LACM-CR 2003-016.1, same data as for holotype; – 10 specimens, OUMNH ZOO COLL 2005-08-02, same data as for holotype; – 10 specimens, MNHN-Na 16071, same data as for holotype; – five specimens RMNH-D 51601, FSBC-I 066741, MZUSP 16883, same data as holotype; – one specimen, USMN 1082804, 1082806, same data as holotype;– one specimen USNM 1082803, Key West Lakes, Key West, Florida in ledge 1 m of water, coll. A. L. Rhyne, June 2003 – four specimens UF 8347, Florida Bay, 50 km northwest of Marathon, Florida, sponge and gorgonian bottom, caught in stone crab traps, depth: 7–10 m, coll. R. Boggess, November 2003. – One specimen USNM 1082807, UF8347, Florida Bay, 50 km northwest of Marathon, Florida, sponge and gorgonian bottom, caught in stone crab traps, depth: 7–10 m, coll. R. Boggess, November 2003. – Two specimens USMN 1082809, Florida Bay, 30–50 km northwest of Marathon, Florida, sponge and gorgonian bottom, caught in stone crab traps, depth: 7–10 m, coll. R. Boggess, January 2005.

Non-Type Material Examined.—One specimen, USNM 127860†, Lemon Bay, Florida, coll. C. Hartmann, 25 January 1938; – two specimens, USNM 127862†, mouth of Whitaker Bayou, Sarasota Bay, Florida, among tube worms, infested with bopyrids, coll. M. W. Williams, 13 March 1944; – 20 specimens, USNM 6456†, Cedar Key, Florida, coll. H. Hemphill, December 1883; – 40 specimens, USNM 6464†, inner shore of Pine Key, Boca Ceiga Bay, Florida, coll. H. Hemphill, January 1884; – four specimens, USNM 23580†, Marco, Florida, among sponges, depth: 2–6 m, coll. H. Hemphill, date unknown; – five specimens, USNM 23581†, W Florida, coll. Henderson and Simpson, date unknown; – 10 specimens, USNM 78701†, Sarasota Bay, Florida, coll. J. S. Kingsley, date unknown; – one specimen, USNM 84369†, Key West, Florida, sta. 462, coll. J. S. Kingsley, date unknown; – two specimens, USNM 92749†, Alligator Harbor, Florida, coll. J. A. Smith, 3 November 1951; – one specimen, USNM 00354571†, Fakahatchee Pass, Florida, haul 2, Sta. 14, 15 December 1982; – three specimens, USNM 231720*, Rocky Channel, Florida Bay, Florida, coll. J. Holmquist, 26 December 1985. – Two specimens, FSBC-I 16620†, Hillsborough County, Florida, east of Skyway Bridge main span, coll. W. G. Lyons and D. K. Camp, depth: 7 m., Oc-

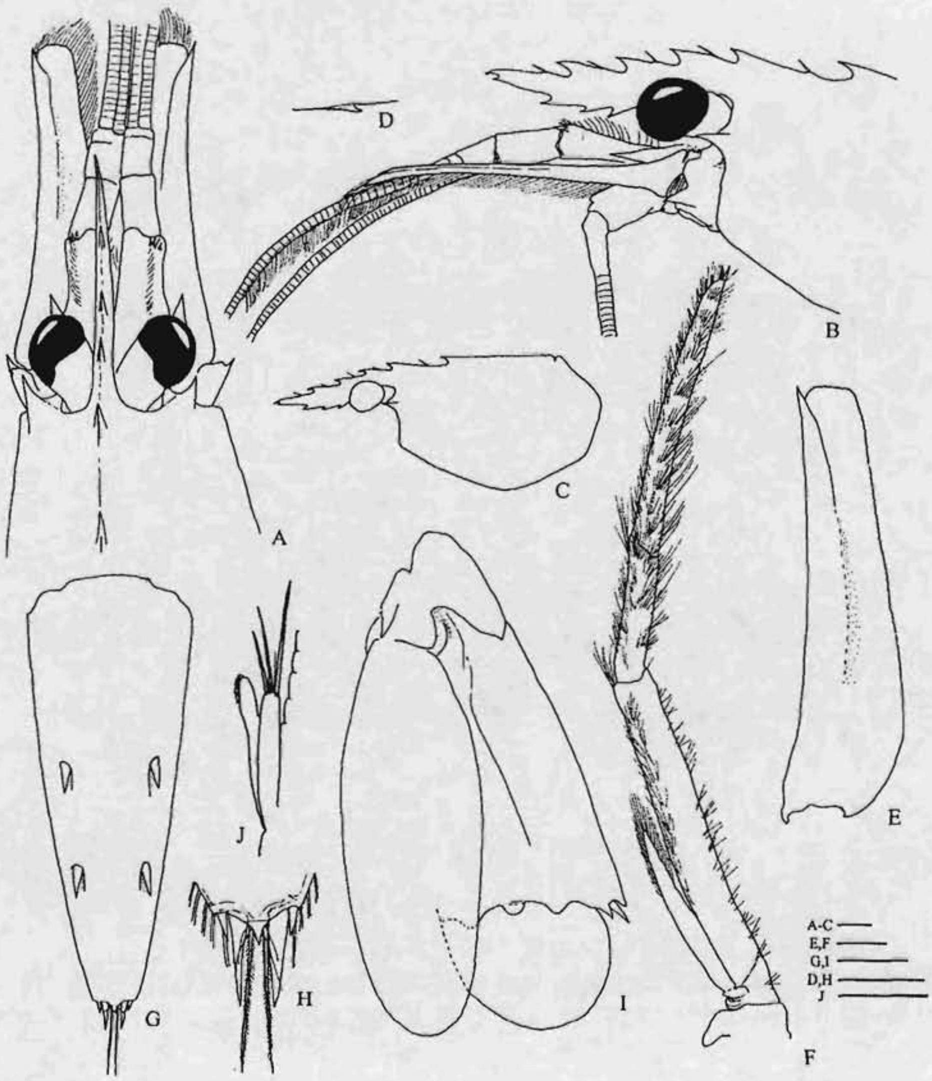

Figure 10. *Lysmata boggessi* new species, euhermaphrodite, Paratype USNM 1082807. (A) Anterior region, dorsal view. (B) Anterior region, lateral view. (C) Carapace, lateral view. (D) Antennular carina tooth. (E) Let antennal scale. (F) Right third maxilliped. (G) Telson, dorsal view. (H) Tip of telson. (I) Right uropods. (J) Appendix masculina and appendix interna of second pleopod of male specimen (USMN 1082809). Scales A,B,D-G, I, J 1 mm; C 2 mm; H 0.5 mm.

tober 1976; – five specimens, FSBC-I 16605', Collier County, Florida, Marco Island, stone crab trap, inshore, coll. J. R. Sullivan and A. H. Huff, depth: 5 m, July 1976. – Two specimens, FSBC-I 7631', Pinellas County, Florida, Gulf of Mexico, off Sawyer and Sister Keys, coll. R. F. Presley, depth: 0.6 m, March 1971. – Five specimens, FSBC-I 4313', Pinellas County, Florida, Gulf of Mexico, Mullet Key near boat ramp area at northeast end, coll. R. F. Presley, depth: 0.3 m, November 1966. – One specimen, FSBC-I 3082', Pinellas County, Tampa Bay, Florida, Bayboro Harbor, dock at Marine Research Laboratory, coll. M. R. McMahon, August 1966.

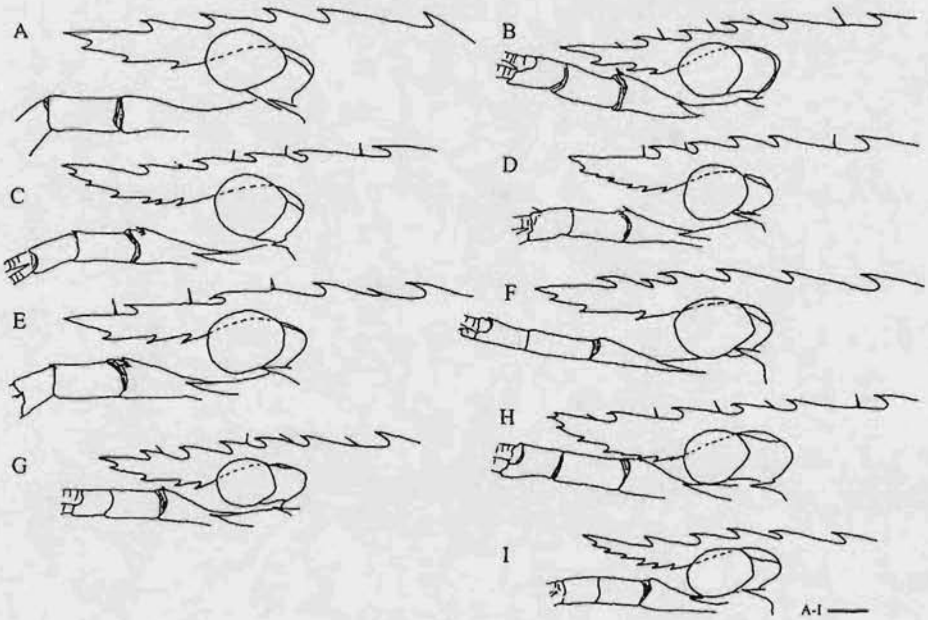

Figure 11. Rostral variation within *Lysmata boggessi* new species. (A) USNM 1082807. (B) USNM 1082806. (C-I) USNM 1082805.Scale 1 mm.

Description.—Rostrum extremely variable in shape and length (Figs. 10A; 11A–I) mostly straight, 0.6–1.0 (rarely > 0.8) times as long as carapace, reaching at least to middle, or to distal margin of intermediate segment of antennular peduncle (Fig. 10A); dorsal margin with 3–6 teeth (predominantly five, commonly four, very rarely three or six), most posterior tooth situated on carapace well beyond post-orbital margin, second tooth above post-orbital margin, remaining teeth anterior to post-orbital margin; ventral margin of rostrum usually with 3–5, rarely with two, six, or seven teeth, most proximal ventral tooth usually situated well beyond stylocerite (Fig. 10B). Carapace smooth, robust, ventro-posterior margin rounded, eyes large, dorsally almost reaching rostral carina (Fig. 10C). Antennule with stylocerite reaching to or slightly beyond level of eye, but well short of end of proximal segment of antennular peduncle (Fig. 10B); intermediate segment 2.1 (1.9–2.4) times as long as wide (Fig. 10B). Antennal scale with disto-lateral tooth overreaching blade, approximately 4.5 (3.8–5.0) times as long as wide (Fig. 10E). First and second pereiopods as illustrated (Fig. 12A,B). Carpus of second pereiopod with 25–32 segments (most often 26–28) (Fig. 12B). Third–fifth pereiopods with dactyli biunguiculate, dorsal ungues larger than ventral, flexor margin with four or five (rarely three or six) spines, decreasing in size from tip to proximal portion, most proximal spine minute (Fig. 12C,D). Fifth pereiopod with merus armed with 3–6 spines. All ratios for pereiopods 1, 2, and 5 are given in Table 1.

Color in Life.—Body semi-translucent reddish or brownish (clearer in individuals living in captivity in light colored background containers), with narrow, longitudinal, transverse and oblique pale red stripes (Plate 1D); carapace with v- and u-shaped oblique and transverse stripes; abdominal pleura with very narrow longitudinal stripes situated between broader and more intense longitudinal stripes, third pleu-

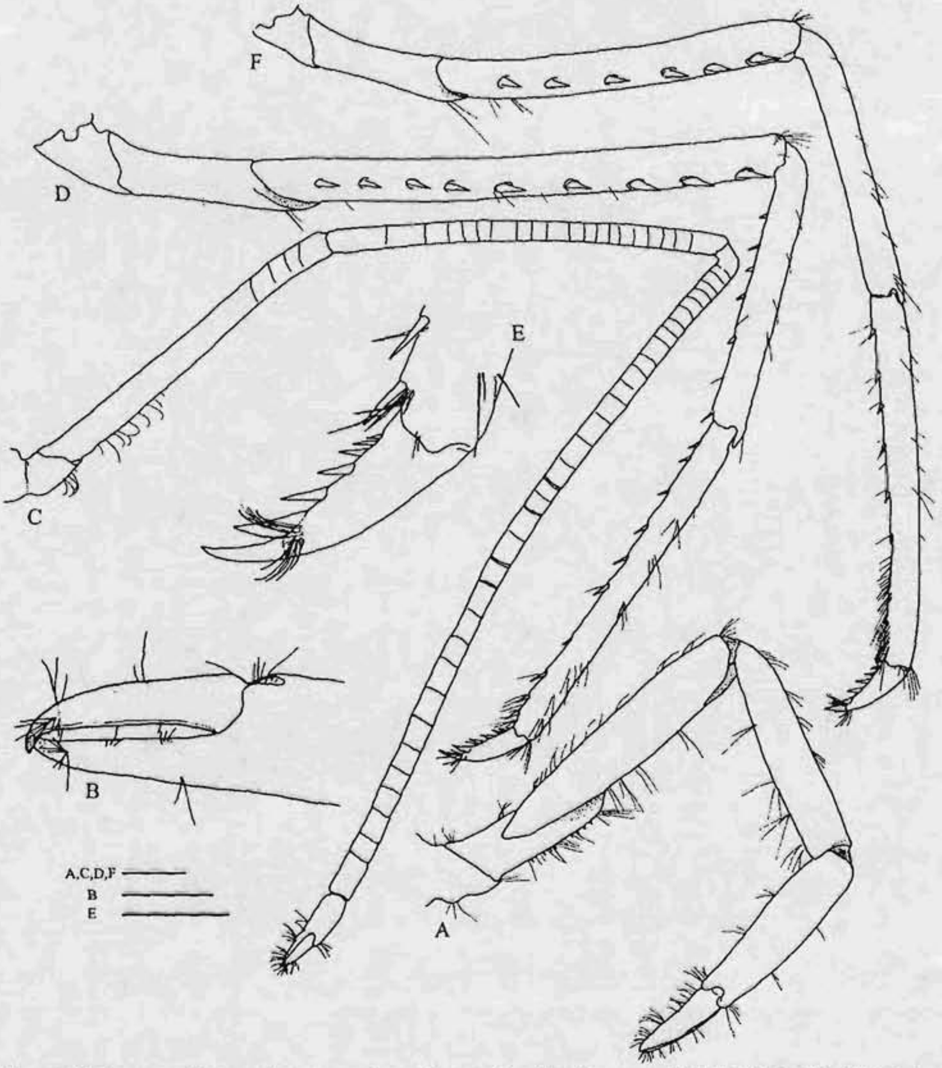

Figure 12. *Lysmata boggessi* new species, euhermaphrodite, Paratype USNM 1082807. (A) Right first pereiopod. (B) Chela of right first pereiopod. (C) Right second pereiopod. (D) Right third pereiopod. (E) Dactylus of right third pereiopod. (F) Right fifth pereiopod. Scales. A, C, D, F 1 mm; B 0.25 mm; E 0.5 mm.

ron lacking red transverse band; telson and uropods dark blue to blackish; eggs olive green. Embryos in stage I–III are olive green, last stage silver.

Distribution.—Southeastern U.S.: southern Florida (Florida Bay–Key West) and western Florida from Naples to Panhandle; may extend to Caribbean (Plate 2).

Ecology.—In shallow seagrass beds (west Florida) and sponge and gorgonian covered hard bottoms (Florida Bay), under ledges (Key West Lakes); depth range: 1–15 m. Protandrous simultaneous hermaphrodite (A. L. Rhyne per. obs.). Frequently infested with the bopyrid isopod, *Parabopyrella mortenseni* (Markham, 1985).

Etymology.—Named after Ronnie Gene Boggess, a commercial fisherman in Marathon, Florida Keys, that collected the species for the aquarium trade.

Remarks.—Lysmata boggessi, n. sp. was previously confused with *L. wurdemanni* (e.g., Wass, 1955; Markham, 1985; Zhang et al., 1998a,b) or *L. rathbunae* (e.g., Lin, 2000; Debelius, 2001; Humann and Deloach, 2002; Zhang and Lin, 2005). Many specimens in the USMN and FSBC-I collection were also misidentified either as *L. wurdemanni* or as *L. rathbunae*. In life *L. boggessi* n. sp. is easily distinguished from *L. wurdemanni* by the very dark tail fan and by lacking the transverse band on the abdominal pleura (Plate 1D). The most consistent diagnostic morphological features of *L. boggessi*, n. sp. are the number of spines on the dactyli of the third–fifth pereiopods and the relative length and height of the second segment of the antennular peduncle (Table 1). *Lysmata boggessi* is similar morphologically to the Pacific Ocean species *L. californica*, the two can be distinguished by the number of spines on the palm of the dactyli and the absence of any armature of the pterygostomial margin.

Lysmata pederseni new species

(Figures 13–15, Plates 1E, 2)

Lysmata rathbunae sponge dwelling "variety" (not *rathbunae s. str.* Chace, 1970) – Chace 1970: 64, fig. 4, (Bermuda; S Florida; Venezuela) – Markham 1985: 73, in part, (all references to *L. rathbunae*).

Lysmata wurdemanni (not Gibbes, 1850) – Debelius 2001: 17, color photograph, (Bahamas); – Humann and Deloach, 2002: 171, color photograph.

Type Material.—Holotype: euhermaphrodite, CL 10.9 mm, USNM 1082810, 500 m southeast of Sombrero Reef, Marathon, Florida, in tube sponge, depth: 15 m, coll. A. L. Rhyne, January 2004. Paratypes: – One specimen, USNM 1082811, 500 m southeast of Sombrero Reef, Marathon, Florida, in tube sponges, depth: 12–18 m, coll. A. L. Rhyne, June 2003; – three specimens, USNM 1082816, 500 m southeast of Sombrero Reef, Marathon, Florida, in tube sponges, depth: 12–18 m, coll. A. L. Rhyne, August 2004; – One specimen, USNM 1082812, Duck Key Reef, Grassy Key, Florida, in tube sponges, depth: 18–24 m, coll. A. L. Rhyne and G. Penha-Lopes, October 2004; – One specimen, USNM 1082813, Duck Key Reef, Grassy Key, Florida, in tube sponges, depth: 24–28 m, coll. A. L. Rhyne, August 2005; – One specimen, USNM 1082814, Duck Key Reef, Grassy Key, Florida, in tube sponges, depth: 15–18 m, coll. A. L. Rhyne, August 2005; – One specimen, USNM 1082812, Duck Key Reef, Grassy Key, Florida, in tube sponges, depth: 20–24 m, coll. A. L. Rhyne and G. Penha-Lopes, October 2004; – three specimens, FSBC I 066742, Duck Key Reef, Grassy Key, Florida, in tube sponges, depth: 18–24 m, coll. A. L. Rhyne 2005; – three specimens, UF8348, 500 m southeast of Sombrero Reef, Marathon, Florida, in tube sponges, depth: 12–18 m, coll. A. L. Rhyne, June 2003; – three specimens, RMNH-D 51602, 500 m southeast of Sombrero Reef, Marathon, Florida, in tube sponges, depth: 12–18 m, coll. A. L. Rhyne, August 2005; – three specimens, LACM-CR 2003-017.1, Duck Key Reef, Grassy Key, Florida, in tube sponges, depth: 18–24 m, coll. A. L. Rhyne October 2003; – three specimens, MNHN-Na 16072, 500 m southeast of Sombrero Reef, Marathon, Florida, in tube sponges, depth: 12–18 m, coll. A. L. Rhyne, June 2003; – three specimens, MZUSP 16884, Duck Key Reef, Grassy Key, Florida, in tube sponges, depth: 18–24 m, coll. A. L. Rhyne, August 2005; – three specimens, OUMNH ZOO COLL

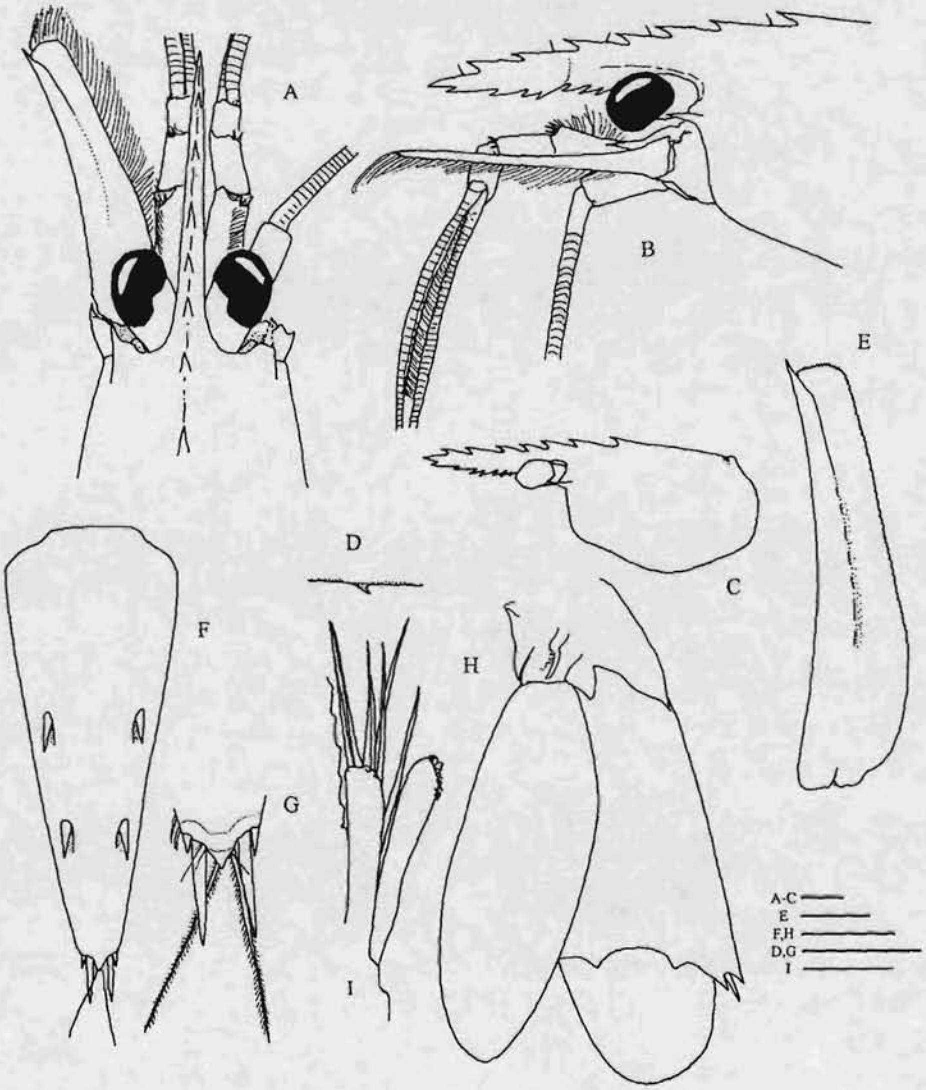

Figure 13. *Lysmata pederseni* new species, euhermaphrodite, Paratype USNM 1082811. (A) Anterior region, dorsal view. (B) Anterior region, lateral view. (C) Carapace, lateral view. (D) Antennular carina tooth. (E) Left antennal scale. (F) Telson, dorsal view. (G) Tip of telson. (H) Right uropods. (I) Appendix masculina and appendix interna of second pleopod of male specimen (USMN 1082812). Scales. A,B,D–F, H, I 1 mm; C 2 mm; G 0.5 mm.

2005-08-01, Duck Key Reef, Grassy Key, Florida, in tube sponges, depth: 18–24 m, coll. A. L. Rhyne and G. Penha-Lopes, October 2003.

Non-type Material Examined.—One specimen, USNM 107086*, Castle Harbor, Bermuda, in sponge, sta. 3-B-60, coll. Winn and Hazlett, 9 August 1960; – One specimen, USNM 169666*, Harbor, Bonaire, Dutch Antilles, coll. R. V. HARRISON, 25 December 1976; – one specimen, USNM 136403*, Aragua, Venezuela, 10°28'N–067°51'W, from sponge, depth: 9 m, Sta. OS06, coll. P. Morales, date unknown; – two specimens, USNM 120093*, South of Alligator Light, Florida Keys, infested

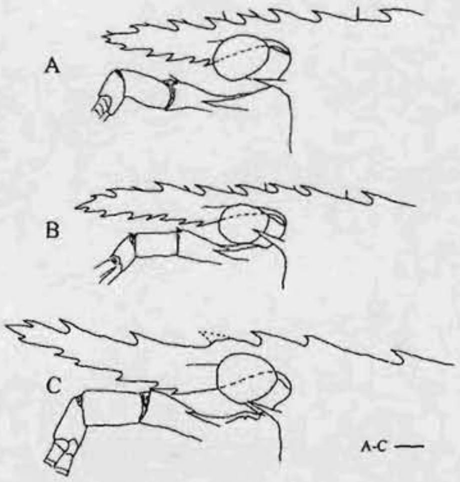

Figure 14. Rostral variation within *Lysmata pederseni* new species. (A) USNM 1082815. (B) USNM 1082814. (C) USNM 1082813. Scale 1 mm.

with bopyrid isopods, depth: 10 m, coll. E. Maynard, 4 August 1965; – one specimen, OUMNH ZOO COLL 2004-19-01. Tobago, Man-O-War Bay, western side of Booby Island, 11°19.344'N, 60°33.484'W; depth: 10 m, in *Callyspongia vaginalis*, coll. S. De Grave, 19 September 2003.

Description.—Rostrum straight, broad and long, 0.7–1.1 times as long as carapace, reaching at least level of end of distal segment of antennular peduncle (Figs. 13A, 14A–C), often overreaching third segment; dorsal margin usually with 7–8 teeth, rarely six or 9–11, most posterior tooth situated on carapace well beyond post-orbital margin, second tooth posterior to post-orbital margin, rarely at the same level as post-orbital margin, remaining teeth anterior to post-orbital margin; ventral margin of rostrum usually bearing 5–7 teeth, occasionally eight or nine; most proximal ventral tooth situated slightly beyond level of stylocerite (Fig. 14). Carapace not robust, longer than high, ventro-posterior margin slightly rounded (Fig. 13D). Eyes large, almost reaching medio-dorsal carina of rostrum (Fig. 13B). Antennule with stylocerite reaching to or slightly beyond eye, falling short of distal margin of proximal segment of antennular peduncle (Fig. 13B); intermediate segment 1.9 (1.7–2.2) times as long as high. Antennal scale with disto-lateral tooth overreaching blade, approximately 4.6 (3.8–5.3) times as long as wide (Fig. 13E). Third maxilliped, and first and second pereiopods as illustrated (Fig. 15A–C). Carpus of second pereiopod with 33–41 segments (usually 34–37; Fig. 15C). Third–fifth pereiopods dactyli extremely shortened; dactyli biunguiculate, dorsal ungues larger than ventral, flexor margin with three, rarely two spines, decreasing in size from tip to proximal portion, most proximal spine minute (Fig. 15F). Fifth pereiopod with merus bearing 3–6 spines. All ratios for pereiopods 1, 2, and 5 are given in Table 1.

Color in Life.—Body almost translucent, with narrow but well marked, contrasting, longitudinal, transverse and oblique, vine-red stripes or bands (Plate 1E); carapace with oblique and transverse broadly v- or u-shaped bands; abdominal pleura with very narrow longitudinal stripes situated between slightly broader and more intensely colored longitudinal stripes, third pleuron without or slight remnant of a

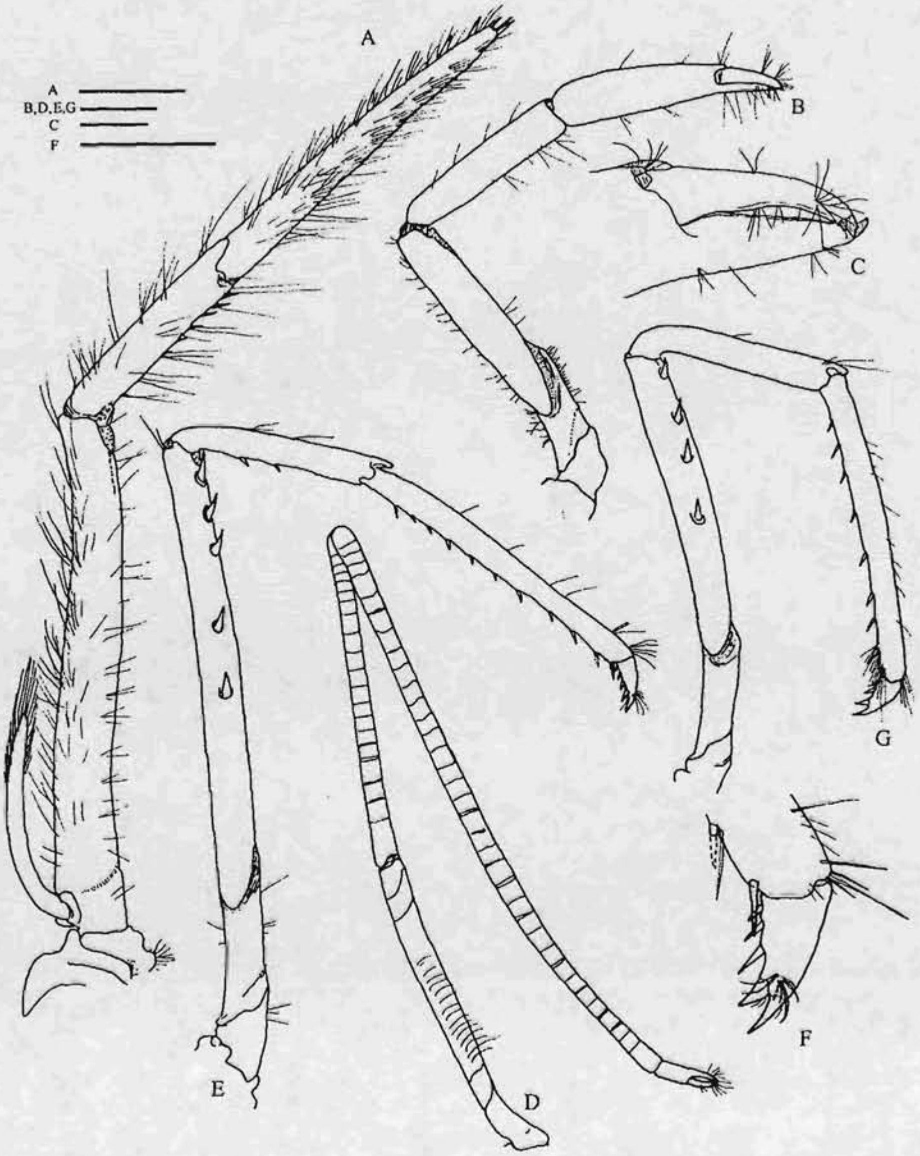

Figure 15. *Lysmata pederseni* new species, euhermaphrodite, Paratype USNM 1082811. (A) Right third maxilliped. (B) Right first pereiopod. (C) Chela of right first pereiopod. (D) Right second pereiopod. (E) Right third pereiopod. (F) Dactylus of right third pereiopod. (G) Right fifth pereiopod. Scales A, B, D, E 1 mm; C 0.25 mm; F 0.5 mm.

red transverse band; uropods with two broad, bright, longitudinal bands; walking legs, antennae, antennules and chelipeds bright red; eggs green. Embryos at stage I–III green, late stage silver.

Distribution.—Extreme southeastern U.S.: Florida Keys; Bermuda; Bahamas; Caribbean: U.S. Virgin Islands, Jamaica, Bonaire, Venezuela (Plate 2E).

Ecology.—Coral reefs, depth range: 3–25 m, commonly associated with tube sponges in the genera *Callyspongia*, *Niphates*; occasionally found in *Aplysina*. Protandrous simultaneous hermaphrodite (A. L. Rhyne, pers. obs.). Commonly infested with the bopyrid isopod, *P. mortenseni*.

Etymology.—Named after Eric Pedersen Sr., a tropical fish collector in Marathon, Florida, who first suggested to collect and examine this species.

Remarks.—*Lysmata pederseni*, n. sp. was previously misidentified as *L. rathbunae* in taxonomic literature (Chace, 1970) or as *L. wurdemanni* in popular field guides (e.g., Debelius, 2001; Humann and Deloach, 2002). Chace (1970) initially reported this species as a "variety" of *L. rathbunae*. However, a comparative analysis of preserved specimens provides numerous morphological differences between *L. pederseni* n. sp. and *L. rathbunae*. For instance, in *L. pederseni* n. sp. the dactylus of the third–fifth pereiopod is shorter compared to that of *L. rathbunae*. Also, the rostrum is long and broad in the new species, whereas in *L. rathbunae* it is long but slender (cf. Fig. 5A). Furthermore, the color patterns of *L. pederseni* n. sp. are clearly different from those of *L. rathbunae*, as described by Schmitt (*in* Chace, 1970) along with the photograph taken from FSBC-I 7579: *L. rathbunae* has a transverse band on the third abdominal pleuron, while such a band is lacking in the new species. *Lysmata pederseni* n. sp. may be distinguished from all other species of the *L. wurdemanni* complex by the characteristic color pattern (Plate 1E), and morphologically by the length and shape of the rostrum; the shape and number of spines on the dactyli on the third–fifth pereiopod; and the number of segments in the carpus of the second pereiopod. Finally, *L. pederseni* n. sp. appears to be uniquely different from other peppermint shrimps. Most peppermint shrimps are considered to be group living and gregarious; while cleaner shrimps are pair bonded (see Bauer, 2000, 2004). Initial population surveys have revealed that this species lives isolated or in very small groups without close contact, quite unlike *L. wurdemanni* and other peppermint shrimps. Individuals occur, perhaps, several meters apart or are found in very small groups (2–3) within the same sponge colony, but almost never in the same sponge branch (A. L. Rhyne, unpubl. obs.). This low population density is very unusual in peppermint shrimp; furthermore, *L. pederseni* is the only member of the genus known to be permanently associated with tube sponges. Sponge association in the hippolytids is rare, other species known to associate with sponges include: *Gerastocaris paronae* (Nobili, 1905), *Paralebbeus zotheculatus* Bruce and Chace, 1986, *Paralebbeus zygius* Chace, 1997, and *Lebbeus spongiaris* Komai, 2001.

Lysmata bahia new species

(Figures 16–18, Plate 1F, 2)

Hippolysmata wurdemanni (not Gibbes, 1850) – Coelho and Ramos, 1972: 153, (Brazil).
Lysmata wurdemanni (not Gibbes, 1850) – Chace, 1972: 129, in part, (material from Brazil) – Williams, 1984: 127, in part, (material from Brazil); – Christoffersen, 1998: 351, in part, (part of material from Brazil).

Type Material.—Holotype euhermaphrodite CL 8.9 mm MZUSP 16885, Bahia, Salvador, Brazil, collected from seawall at harbor, purchased from a pet store by A. L. Rhyne, 18 May 2003. Paratypes: – two specimens, USNM 92842', Santos Harbor, São Paulo, Brazil, sta. CD 100, coll. Dr. Carvalho, 2 June 1950. – Two specimens,

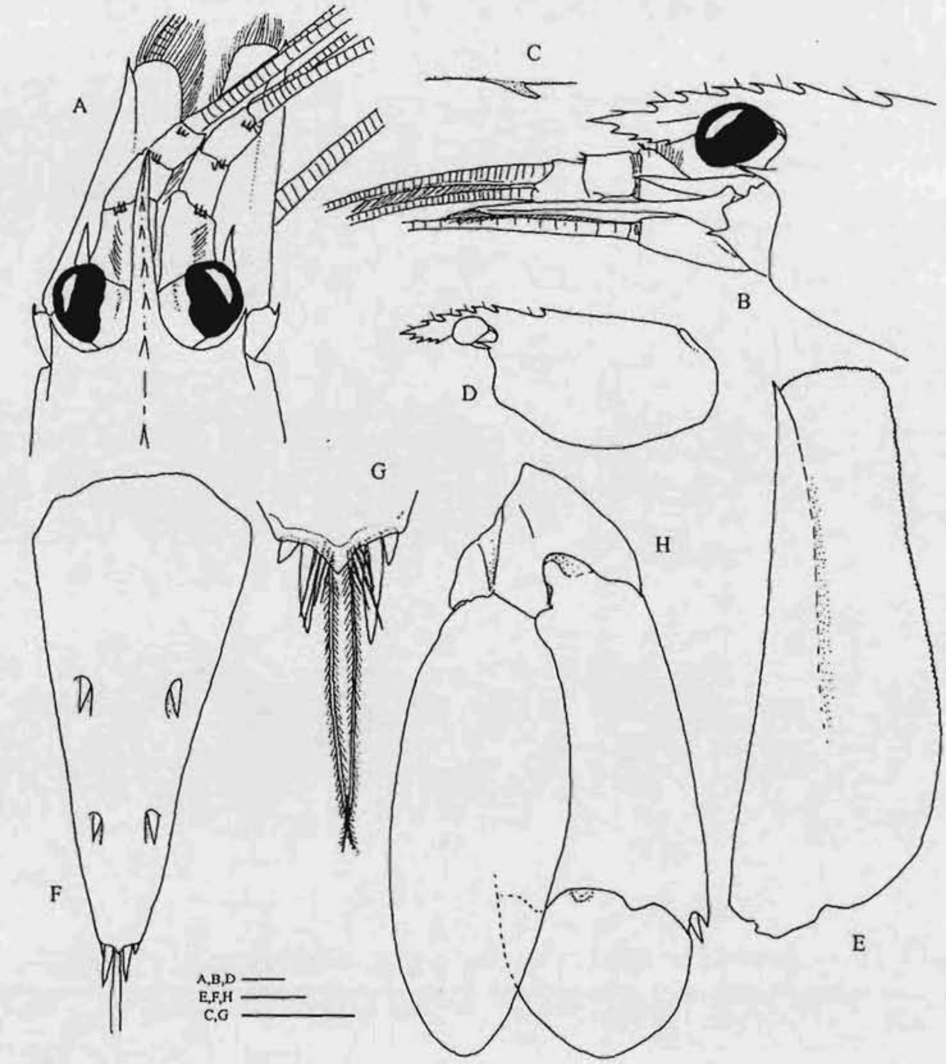

Figure 16. *Lysmata bahia* new species, euhermaphrodite, Holotype MZUSP 16885 (A,B, D) Paratype USNM 92842 (C,E-H). (A) Anterior region, dorsal view. (B) Anterior region, lateral view. (C) Antennular carina tooth. (D) Carapace, lateral view. (E) Left antennal scale. (F) Telson, dorsal view. (G) Tip of telson. (H) Right uropods. Scales. A-C, E, F, H 1 mm; D 2mm; G 0.5 mm.

USNM 222027†, Rio de Janeiro, Marica, Praia do Jacone, Brazil, in tide pools, coll. M. L. Christofferson, 25 January 1978.

Description.—Rostrum straight or slightly descendant, about 0.5 times as long as carapace, reaching level of middle of intermediate segment of antennular peduncle (Figs. 16A,B,D, 17A–C), dorsal margin with 6–7 teeth, most posterior tooth situated on carapace well beyond post-orbital margin, second tooth above post-orbital margin, remaining teeth anterior to post-anterior margin; ventral margin with 3–4 teeth; second most proximal ventral tooth situated at level of or slightly beyond stylocerite. Carapace stout, ventro-posterior margin rounded (Fig. 16D). Eyes large, reaching only halfway to the medio-dorsal margin of rostrum (Fig. 16B). Antennule with stylocer-

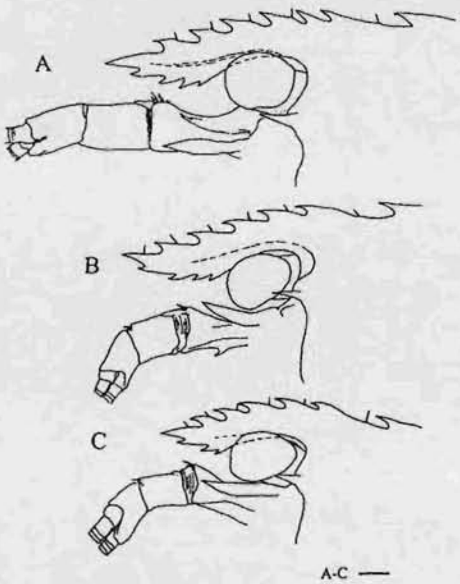

Figure 17. Rostral variation within *Lysmata bahia*, new species. (A) USNM 92842. (B,C) USNM 222027. Scale 1 mm.

ite reaching well beyond level of eye, falling just short of distal margin of proximal segment of antennular peduncle (Fig. 16B); intermediate segment 1.2 (1.1–1.4) times long as high. Antennal scale with disto-lateral tooth not or only slightly overreaching blade, approximately 3.0 (2.8–3.3) times as long as wide (Fig. 16E). First pereiopod stout (Fig. 18A). Second pereiopod robust, with small chela (Fig. 18C) carpus with 29–31 segments (Fig. 18C). Third–fifth pereiopod with dactyli biunguiculate, dorsal ungues larger than ventral, flexor margin with two, rarely three spines, decreasing in size from tip (Fig. 18D–F). Fifth pereiopod with merus unarmed or bearing 1–6 spines. All ratios for pereiopods 1, 2, and 5 are given in Table 1.

Color in Life.—Body semi-translucent with broad, longitudinal, transverse and oblique bright red bands or stripes (Plate 1F); carapace with broad, oblique and sub-longitudinal bands; abdominal pleura with broad sub-longitudinal bands and irregular patches, third pleuron without distinct transverse band; telson and uropods semi-translucent or pinkish, with reddish markings; eggs greenish.

Distribution.—Brazil: states of Rio de Janeiro and São Paulo; Salvador, Bahia (Plate 2).

Ecology.—Rocky bottom areas and tide pools; intertidal and shallow subtidal, possibly ranging down to about 25 m. Protandrous simultaneous hermaphrodite (H. Laubenheimer, Universidade Santa Úrsula, pers. comm.).

Etymology.—Named after the Brazilian state of Bahia, where this species appears to be very common (A. L. Rhyne, pers. obs.). In this case, "bahia" is used as a noun in opposition.

Remarks.—The living or freshly collected specimens of *L. bahia* n. sp. may be distinguished from *L. wurdemanni* and *L. ankeri* n. sp. by the absence of conspicuous transverse band on the third pleuron of the abdomen. Morphological differences include the number of carpal segments on the second pereiopod; the number and po-

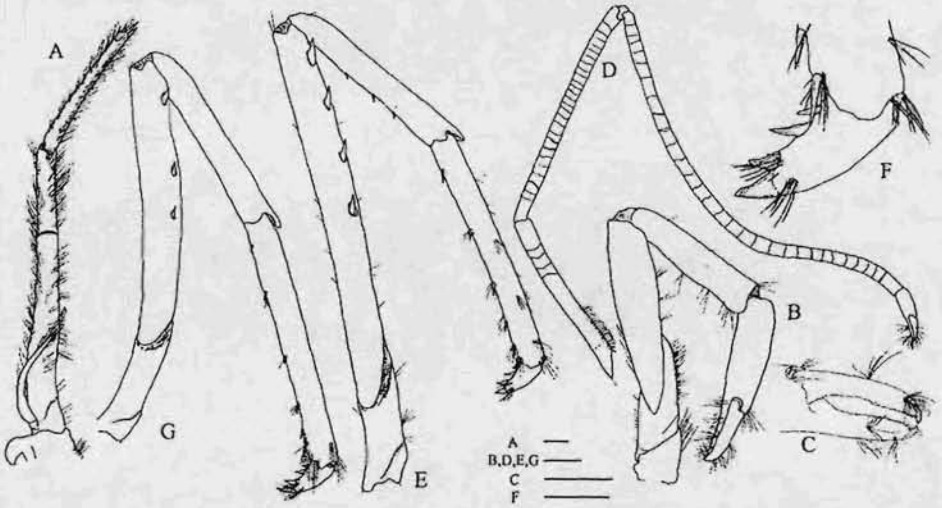

Figure 18. *Lysmata bahia* new species, euhermaphrodite, Paratype USNM 92842. (A) Right third maxilliped. (B) Right first pereiopod. (C) Chela of right first pereiopod. (D) Right second pereiopod. (E) Right third pereiopod. (F) Dactylus of right third pereiopod. (G) Right fourth pereiopod. Scales A, B, D, E 1 mm; C 0.25 mm; F 0.5 mm.

sition of teeth on the rostrum; the armature of dactyli on the third–fifth pereiopods; the length of the stylocerite; and the width of the antennal scale (cf. Table 1).

RESULTS

MORPHOLOGICAL ANALYSIS.—The morphological data for each species are presented in Table 3 and used in the Discriminant Function Analysis (DFA). The results (Fig. 19) display a clear discrimination of all six species of *Lysmata*. The Axis 1 separates species based mainly on differences in the relative length of the rostrum and the length of the dactylus of the fifth pereiopods (Table 3). The Axis 2 separates the species based mainly on the number of spines on the dactyli of the third–fifth pereiopods and the relative length of the intermediate segment of the antennular peduncle (Table 3). The probability of misclassification in the DFA is zero (Table 4). Although the sample size for *L. bahia* and *L. rathbunae* are very small (four specimens), several key features (number of spines on the dactyli of third–fifth pereiopods, number of carpal segments on second pereiopod, and length, shape and armature of the rostrum) are consistent among all the examined specimens.

BREEDING EXPERIMENTS.—Shrimp of different species living in the same test aquarium may respond to the sex pheromone of the nonspecific congenerics and attempt to mate (A. L. Rhyne, pers. obs.). This was observed on one occasion when a *L. ankeri* n. sp. individual attempted to copulate with a freshly molted *L. wurdemanni* individual. However, results of the breeding trials (Table 5) demonstrate that hybridization is not possible between any of the species tested (*L. bahia* was not crossed with all species in the breeding trials) although fertilization and early embryonic development may occur in certain crossings (Zhang and Lin, unpubl. data).

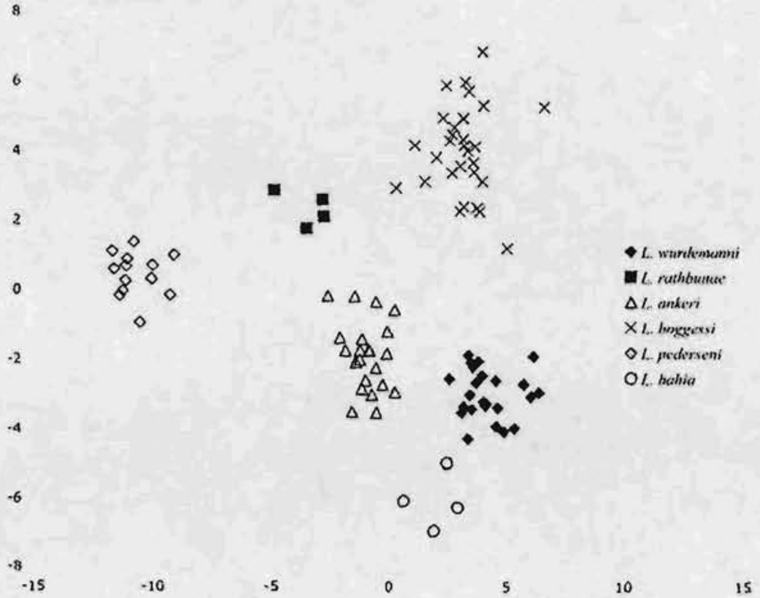

Figure 19. Discriminant Function Analysis (DFA), based on six selected morphological characters of five species in the *Lysmata wurdemanni* complex and *Lysmata rathbunae*.

DISCUSSION

Species misidentifications are generally commonplace within the genus *Lysmata* (see also Wicksten, 2000b; d'Udekem d'Acoz, 2001). The identity of the peppermint shrimp, *L. wurdemanni* has created many problems in the past. Museum specimens are often challenging for taxonomists because preserved specimens are colorless, often incomplete, or in poor condition (especially from earlier collections), and the sample size is often very limited. The ability to correctly identify closely related species is critical for studies of phylogeny, behavior, reproduction, and ecology. Incorrect identifications may create taxonomic confusion and erroneous conclusions in ecology or phylogeny.

The present study clearly shows the necessity for thorough taxonomic revisions of western Atlantic caridean shrimps, and underlines the importance of combining classical morphological analyses with examination of live color patterns and laboratory investigations of reproductive compatibility. The *L. wurdemanni* species complex, previously containing only two species, is clarified for the first time and now includes five species: *L. wurdemanni*, *L. ankeri* n. sp., *L. bahia* n. sp., *L. boggessi* n. sp., and *L. pederseni* n. sp. *Lysmata rathbunae* appears to be a relatively deep-water species, found mostly in depths below 30 m (to 119 m, cf. Chace, 1972), and is morphologically distinct from the *L. wurdemanni* complex by having a long narrow rostrum and extended thin legs. These two morphological characters appear to be part of a distinct complex. Wicksten (2000a) remarks in the description of *L. gracilirostris*, a deep-water eastern Pacific species, that the species appears to be closely related to *L. rathbunae*. Two other undescribed species from the western Atlantic and Gulf of Mexico also share similar features with this complex and require further investigation (A. L. Rhyne; unpubl. data).

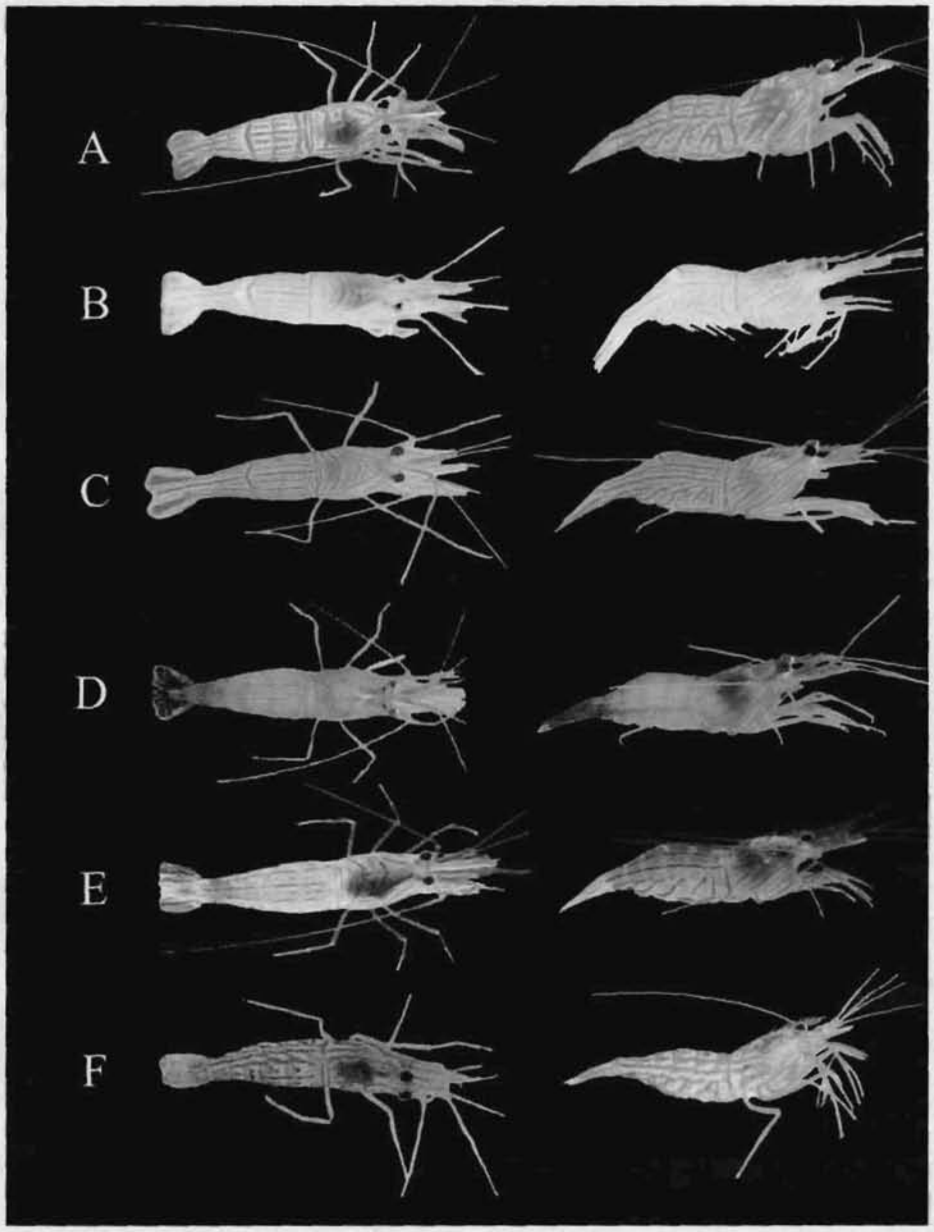

Plate 1. Live specimens of five species of peppermint shrimp (*Lysmata wurdemanni* complex). (A) *Lysmata wurdemanni* (Gibbes). (B) *Lysmata rathbunae* Chace. (C) *Lysmata ankeri* new species. (D) *Lysmata boggessi* new species. (E) *Lysmata pederseni* new species. (F) *Lysmata bahia* new species.

The *L. wurdemanni* complex is found in mostly shallow waters (intertidal/upper subtidal down to 25 m). Among these, *L. wurdemanni* should be considered as a temperate-subtropical species, not tropical as suggested by Baldwin and Bauer (2003), distributed along the southern and southeastern coasts of the U.S. and reaching to New York in the northern-most limit of its distribution range. The other four species

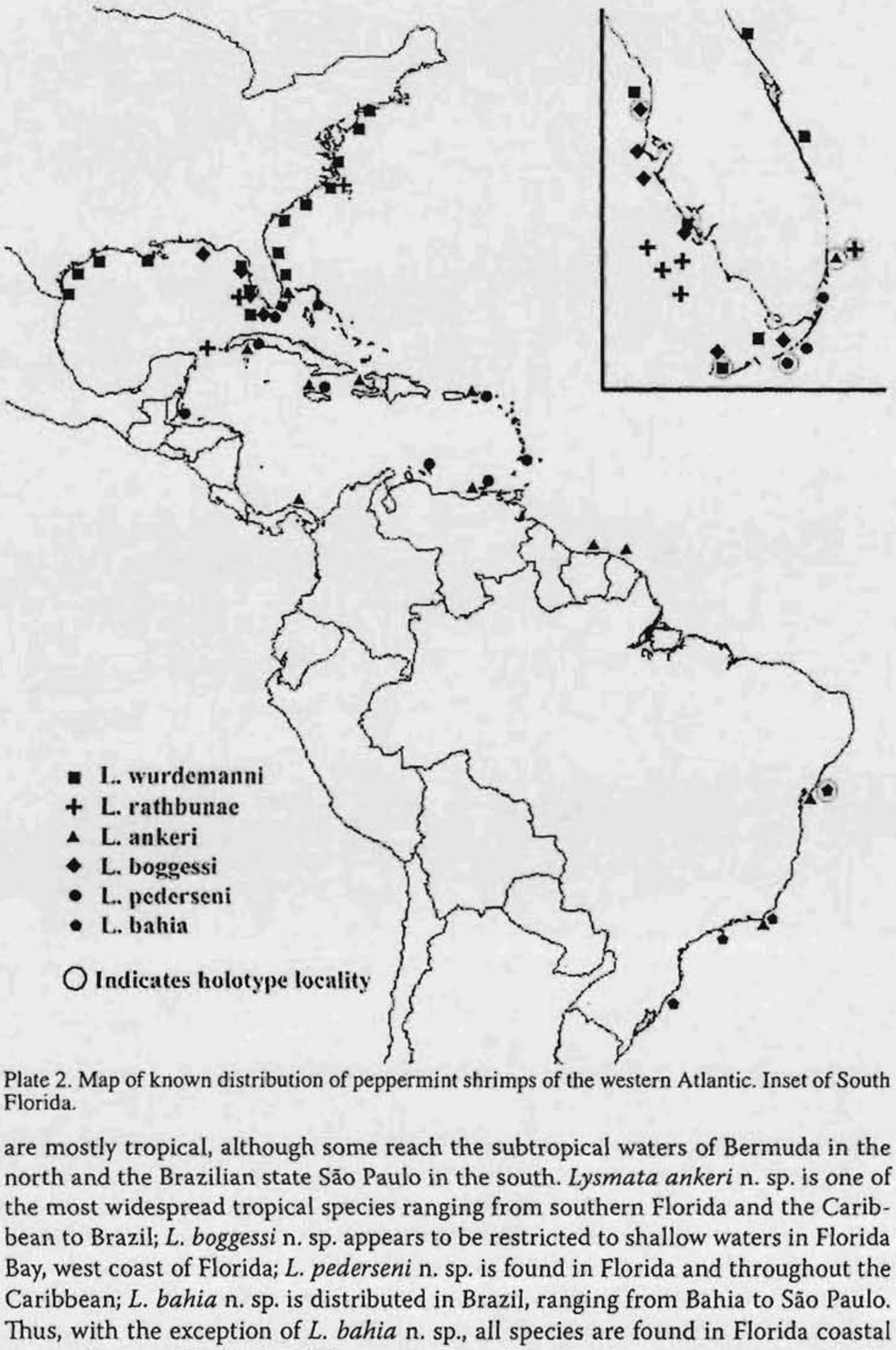

Plate 2. Map of known distribution of peppermint shrimps of the western Atlantic. Inset of South Florida.

are mostly tropical, although some reach the subtropical waters of Bermuda in the north and the Brazilian state São Paulo in the south. *Lysmata ankeri* n. sp. is one of the most widespread tropical species ranging from southern Florida and the Caribbean to Brazil; *L. boggessi* n. sp. appears to be restricted to shallow waters in Florida Bay, west coast of Florida; *L. pederseni* n. sp. is found in Florida and throughout the Caribbean; *L. bahia* n. sp. is distributed in Brazil, ranging from Bahia to São Paulo. Thus, with the exception of *L. bahia* n. sp., all species are found in Florida coastal waters. In some Florida localities, two or even three species may occur syntopically. *Lysmata pederseni*, n. sp., differs ecologically from the other species, being associated with tube sponges (see photographs in Debelius, 2000; Humann and Deloach, 2002) and occurring at low densities. Protandrous simultaneous hermaphrodism has been demonstrated in *L. ankeri* (Lin and Zhang, 2001b), and noted in *L. bahia*, *L. boggessi*, and *L. pederseni*.

The taxonomic importance of color patterns, and therefore of freshly collected specimens, must be emphasized. The importance of color for taxonomy of shrimps was first recognized in the alpheid shrimp genus *Alpheus* by Knowlton and Keller (1983, 1985), who resolved the western Atlantic *Alpheus armatus* Rathbun, 1900 complex, and has more recently been demonstrated by Knowlton and Mills (1992) in the Panamanian trans-isthmian species pairs, and by Bruce (1987, 1999) and Anker (2001) in several Indo-West Pacific species. Although cryptic species appear to be particularly numerous in the family Alpheidae (A. Anker, University of Alberta, pers. comm.), they are not rare in other families, including the palaemonid genus *Periclimenes* (*Periclimenes holthuisi* Bruce 1969; *Periclimenes speciosus* Okuno, 2004; *Periclimenes venustus* Bruce, 1990; and *Periclimenes sarasvati* Okuno, 2002), rhynchocinetid genus *Cinetorhynchus* (*Cinetorhynchus reticulates* Okuno, 1997 and *Cinetorhynchus hawaiiensis* Okuno and Hoover, 1998), and the hippolytid genera *Saron* and *Tozeuma* (A. Anker, pers. comm.). Cryptic species may also exist among other species of *Lysmata* (A. L. Rhyne, pers. obs.; A. Anker, pers. comm.). Burukovsky (2000) described *L. splendida*, a cryptic species from the Maldives that was previously confused with *L. debelius*. The *L. debelius* complex comprises three species easily distinguishable by color patterns: *L. debelius* (with white legs and white spots on the carapace only), *L. splendida* (white legs and white spots on the carapace and the abdomen), and *Lysmata* sp., an undescribed species (with red legs and white spots on the carapace, A. Anker, pers. comm.).

Within the genus *Lysmata*, three groups appear to differentiate morphologically and/or by color patterns: (1) historic *Lysmata*, having an accessory branch; (2) historic *Hippolysmata* (prior to Chace, 1972), lacking a developed accessory branch and displaying typical peppermint color patterns; and (3) cleaner shrimps, within *Hippolysmata*, lacking accessory branch and displaying bright coloration with white antenna.

The most important morphological characters for assessing the identity of specimens are: (1) presence or absences of an accessory branch; (2) rostrum length, shape, and dentition; (3) number of carpal segments on the second pereiopod; (4) overall shape and number of spines on the dactylus of the third–fifth pereiopod; and (5) presence or absence of armature on the pterygostomial margin. Features of the appendix masculina as suggested by Chace (1970) should be avoided due to the variations within a species as results of the transition between the male and euhermaphrodite phases (Zhang and Lin, 2005). Western Atlantic peppermint shrimps of the *L. wurdemanni* complex are most closely related morphologically to *L. californica*, *L. vittata*, and *L. rathbunae*. In regard to color pattern, *L. wurdemanni* and *L. ankeri* n. sp. appear very similar to *L. multiscissa; L. bahia* n. sp. resembles *L. californica*, lacking thin longitudinal lines, having wider oblique markings on the carapace and abdomen, while *L. pederseni* n. sp. and *L. boggessi* n. sp. have fine longitudinal lines and lack the transverse band on the third segment of the abdomen. *Lysmata pederseni* appears to have the remnants of the transverse band on the third segment of the abdomen. It is unclear if the reduction in this character is derived or primitive. Based on accessory branch morphology, the presented species are more distantly related to *L. seticaudata*, *L. intermedia*, *L. moorei*, and other species with accessory branch, than the cleaner shrimps (*L. amboinensis*, *L. grabhami*, *L. debelius*, and *L. splendida*).

The use of the accessory branch morphology as an identifier of a division in the genus is further supported by observations of larval development (A. L. Rhyne, unpubl. data) and of the molecular phylogeny of the genus (G. Curt Fiedler; University of Maryland, Tokyo campus; unpubl. data).

Due to the economic value of the western Atlantic *Lysmata* species, living or fresh specimens are easily accessible through the aquarium trade (except for the deep-water *L. rathbunae*). Proper identification now allows research to be conducted on a wide range of species from different localities. Genetic analyses are now desirable to examine the relationships between putative cryptic *Lysmata* species. A phylogeny of the *L. wurdemanni* complex (and generally the genus *Lysmata*) would be particularly interesting in view of the unique reproductive mode of these shrimps.

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APPENDIX

Morphological Key to the Western Atlantic Peppermint Shrimp Complex (*Lysmata wurdemanni* Complex) and *Lysmata rathbunae*

1a. Rostrum overreaching distal margin of third segment of antennular peduncle..................... 2
1b. Rostrum not reaching the distal margin of third segment of antennular peduncle............... 3

2a. Rostrum broad, 0.9 times as long as carapace, rostrum with 6–9 dorsal teeth (usually seven, eight); and 5–7, (rarely eight, nine) ventral teeth. Propodus of the third–fifth pereiopods 10 times the length of dactyli, dactyli noticeably shortened.................. *Lysmata pederseni* n. sp.
2b. Rostrum narrow 1.3 times as long as carapace, rostrum with 5–6 dorsal and 3–4 ventral teeth. Propodus of the third–fifth pereiopods eight times the length of dactyli .... *Lysmata rathbunae* Chace, 1970

3a. Carpus of second pereiopod with less than 32 segments.. 4
3b. Carpus of second pereiopod with more than 32 segments. Rostrum 0.7 times as long as carapace, usually reaching the middle of the third segment of the antennular peduncle; dorsal margin with 6–8 teeth, ventral margin with 4–6 teeth .... *Lysmata ankeri* n. sp.

4a. Dactylus of third–fifth pereiopods with five or less spines on flexor margin, rarely one or two legs with six. Second segment of antennular peduncle < 2 times long as high............... 5
4b. Dactylus of third–fifth pereiopods with six or more spines on flexor margin. Occasionally one or two legs will have five. Second segment of antennular peduncle > 2 times long as high.. *Lysmata boggessi* n. sp.

5a. Rostrum more broad with 6–7 dorsal teeth, antennal scale 3.0 times long as wide. Stylocerite greatly overreaching eye, nearly to the end of first segment of the antennular peduncle. Second segment of antenllauar peduncle 1.3 times longer than high .... *Lysmata bahia* n. sp.
5b. Rostrum more narrow with 4–6 dorsal teeth, antennular scale 3.8 times as long as wide. Stylocerite reach just to or slight beyond the eye, reaching less than half way to the end of the first segment of the antennular peduncle .... *Lysmata wurdemanni* (Gibbes 1850)