

LYSMATA HOCHI N. SP., A NEW HERMAPHRODITIC SHRIMP FROM THE SOUTHWESTERN CARIBBEAN SEA (CARIDEA: HIPPOLYTIDAE).

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A B S T R A C T

Lyсмata hochi n. sp., a new peppermint shrimp, is described from Bocas del Toro, Caribbean coast of Panama. All individuals were collected on near-shore fossil coral terraces with deep channels and caves, sparsely covered with seagrass. Besides the type locality, *L. hochi* n. sp. also occurs in Cahuita, Costa Rica, in a similar type of habitat. The new species can be distinguished from other species of *Lyсмata* by the presence of an unguis-shaped accessory branch on the lateral antennular flagellum; the rostrum with three dorsal teeth, followed by two mid-dorsal teeth on the carapace posterior to the orbital margin; the number of carpal segments of the second pereiopod ranging from 21 to 24; the presence of two to four ventrolateral spines on the merus of the third pereiopod; the dactylus of the third to fifth pereiopod bearing two spines in addition to a bifurcated unguis; and the conspicuous color pattern, especially the irregular bright red bands on the pleon. Based on morphology and (where known) color patterns, *L. hochi* n. sp. appears to be most closely related to the Indo-West Pacific *L. kuekenthali* (De Man) and the eastern Atlantic *L. uncicornis* Holthuis and Maurin. Anatomical observations, field population studies and laboratory experiments indicate that *L. hochi* n. sp. is a protandric simultaneous hermaphrodite, with a primary male phase followed by a simultaneous hermaphrodite phase.

KEY WORDS: Atlantic, biogeography, Caribbean, hermaphrodites, Hippolytidae, *Lyсмata*

INTRODUCTION

The shrimp genus *Lyсмata* Risso, 1816, currently placed in the heterogeneous family Hippolytidae Bate, 1888 (sensu Chace, 1997), includes at least 12 species in the western Atlantic Ocean (Chace, 1972; Rhyne and Lin, 2006). Among the most conspicuous and biologically best known members of this genus are the scarlet-striped cleaner shrimp *L. grabhami* (Gordon, 1935) (Humann and Deloach, 2002) and the peppermint shrimps, viz., five species of the *L. wurdemanni* Gibbes, 1850 complex (Rhyne and Lin, 2006). More cryptically living shallow water species, such as *L. moorei* (Rathbun, 1901) and *L. intermedia* (Kingsley, 1879), or the deepwater forms, such as *L. rathbunae* Chace, 1970, are less well known both taxonomically and biologically.

Recent studies have shown that several species of *Lyсмata* are protandric simultaneous hermaphrodites (Wirtz, 1996; Fiedler, 1998; Bauer and Holt, 1998; Bauer and Newman, 2004; d'Udekem d'Acoz, 2003; Rhyne and Lin, 2006; Bauer, 2006). In these shrimps, juveniles consistently mature as male individuals bearing typical caridean male characters and are only capable of reproducing as males (Bauer and Holt, 1998; Fiedler, 1998). Adolescent males acquire female sexual function and develop into functional simultaneous hermaphrodites, hereafter hermaphrodites ("euhermaphrodites" sensu Lin and Zhang, 2001 and "female phase shrimps" sensu Bauer and Holt, 1998). After maturation, hermaphrodites resemble females of caridean gonochoric species and brood embryos in a pleonal chamber. They retain testicular tissue, male ducts, and gonopores, and hence can reproduce as both male and female (Bauer and Holt, 1998). After becoming hermaphrodites, individuals do not revert to males and no self-fertilization has been ever observed (Bauer, 2002). This

sequential-simultaneous pattern of sex allocation suggests that both classical (strict protandry and protogyny, strict simultaneous hermaphroditism) and unconventional hermaphroditic sexual systems (protandric simultaneous hermaphroditism) should be explained by a single comprehensive theoretical model (Baeza, 2006). In general, studies on the sexual biology of *Lyсмata* shrimps can provide new insights on the evolution of hermaphroditism among marine invertebrates.

An intensive sampling of caridean shrimps in the Bocas del Toro region, Panama, and Cahuita, Costa Rica, yielded several species of *Lyсмata*. Among them was a brightly colored species with one-segmented accessory branch on the lateral antennular flagellum that could not be assigned to any of the described western Atlantic species. After a comparison with all described species of *Lyсмata* characterized by the absence or poor development of the accessory branch on the lateral antennular flagellum, it became obvious that this species was actually undescribed. An opportunity is herewith taken to describe it as new and to provide preliminary data on its ecology. A series of dissections, anatomical observations, field observations, as well as laboratory experiments were carried out to determine whether or not this new species was a protandric simultaneous hermaphrodite.

MATERIAL AND METHODS

Specimens were collected at night during low tide with aquarium nets from coral reef terraces at Playa Bluff, Isla Colon, Bocas del Toro, Caribbean coast of Panama, between October and November 2006. Immediately after collection, shrimps were transported to the laboratory at the Bocas del Toro Marine Research Station (9°21'N - 82°15'W) of the Smithsonian Tropical Research Institute (STRI). Shrimps were maintained in 15 L aquaria at a water temperature of 26-31°C and 34-36 ppt salinity and were fed every other day with chopped frozen clams. Some individuals were then selected for experiments conducted to determine the sexual system of this new

species (see below). After experiments, these individuals were released at the collection site.

Three adult specimens, two non-ovigerous and one ovigerous specimens, were photographed alive and preserved in 90% ethanol for species description. All drawings were made under dissecting microscope equipped with a camera lucida. The carapace length (CL, in mm) was measured along the mid-dorsal line from the postorbital margin to the posterior margin of the carapace; the length of the carapace from the tip of the rostrum to the posterior margin of the carapace (CL + R, in mm) was also determined. The holotype and the two paratypes are deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM). Other abbreviation used in the text: RMNH, Nationaal Natuurhistorisch Museum, Leiden, Netherlands.

Observations on reproductive anatomy were conducted in a total of four specimens, two potential males (CL 5.0 and 6.2 mm) and two potential hermaphrodites that carried embryos beneath the pleon (CL 8.5 and 7.9 mm). Specimens were defined as males or hermaphrodites following Fiedler (1998) and Bauer and Holt (1998), by the presence (males) or absence (hermaphrodites) of coupling hooks (cincinnuli) and appendices masculinae on the endopods of the first and second pleopods, respectively.

Abundance, size distribution of the sexes, and sex ratio (males to hermaphrodites) of the new species was described from the field. The CL and number of shrimps of each sexual phase captured on each of 15 sampling dates were recorded.

Three different experiments were conducted to test for protandric simultaneous hermaphroditism in the new species. To determine if shrimps reproducing as females (brooding embryos) could function as males, three replicated pairs of brooding shrimps were maintained separately in 15 L aquaria (Experiment 1). To determine if shrimps could self-fertilize, six brooding shrimp were each maintained in isolation from conspecifics (Experiment 2). To determine if males mature into hermaphrodite shrimp, three replicate pairs of males (small non-brooding shrimp with no externally visible female gonad and visible cincinnuli and appendices masculinae) were maintained separately in 15 L aquaria for at least 50 days (Experiment 3). In each experiment, daily observations were conducted on the occurrence of embryo hatching, the presence of exuvia from molting, development of mature oocytes in the gonad (visible through the carapace), spawning of a new batch of eggs, and development of the newly spawned embryos after four days.

If brooding hermaphrodites in the first experiment molted and successfully brooded embryos that remained attached to the pleopods and continued developing after four days, we inferred that: 1) the second brooding hermaphrodite in the aquaria acted as a male inseminating its partner, or 2) the hermaphroditic shrimp reproducing as female was capable of self-fertilization. If shrimps in isolation in the second experiment failed to successfully brood a batch of eggs, we assumed that brooding shrimps can reproduce as males but cannot self-fertilize. If males in the third experiment started developing a female gonad and spawned a batch of eggs, we inferred that male shrimps have the ability to mature as hermaphrodites later in their lives.

SYSTEMATICS

Lysmata Risso, 1816

Lysmata hochi new species

Figs. 1-3

Type Material.—Holotype: simultaneous hermaphrodite (CL 10 mm, CL + R 14.4 mm), USNM 1103074, Panama, Caribbean coast, Bocas del Toro, Isla Colon, Playa Bluff, fossil coral terraces, by night at low tide, 0.5-1 m, coll. J. A. Baeza, 1-7 Nov 2006 [fcn 06-563]. Paratypes: 1 ovigerous simultaneous hermaphrodite (CL 10.3 mm, CL + R 15.4 mm), USNM 1103078, same collection data as for holotype [fcn 06-562]; 1 simultaneous hermaphrodite (CL 10.3 mm, CL + R 16.7 mm), USNM 1103079, same collection data as for holotype, partly dissected [fcn 06-561].

Description.—Rostrum moderately long, straight, slightly curved upwards near tip (Fig. 1a, b), about 2/5 to 2/3 times

as long as carapace, tip reaching at least 1/4 length of second segment, sometimes distal margin of second segment of antennular peduncle (Fig. 1a, b); dorsal margin with three teeth (Fig. 1b), with most posterior tooth situated just anterior to postorbital margin; mid-dorsal carina with two teeth posterior to postorbital margin (Fig. 1b-d); stiff setae arising from rostral/mid-dorsal carina between teeth (Fig. 1b-d); rostrum tip usually simple (Fig. 1b, c), sometimes truncate, trifold (Fig. 1d); ventral margin of rostrum with one to three teeth (Fig. 1b-d), most proximal ventral tooth situated below most distal dorsal tooth, at various levels within length of second segment of antennular peduncle (Fig. 1b-d). Carapace smooth, with rounded posteroventral margin; antennal tooth stout, acute, somewhat separated from ventral angle of orbit (Fig. 1b); pterygostomial angle rounded, without spine (Fig. 1b). Eyes moderately large, divergent (Fig. 1a), not reaching dorsal margin of rostrum (Fig. 1b-d).

Antennular peduncle not overreaching scaphocerite; first segment with 11-12 short spinules distodorsally (Fig. 1a, b); stylocerite greatly overreaching eye, tip usually bifid (Fig. 1f), falling short of distal margin of first segment (Fig. 1a, b); spine of ventromesial carina small, acute, anteriorly directed; second segment slightly shorter than wide, with five to six (sometimes less) spinules distodorsally (Fig. 1a); third segment with one or two distodorsal spinules; lateral antennular flagellum with aesthetascs extending from first segment to accessory branch (Fig. 1g); accessory branch consisting of one unguis-shaped segment (Fig. 1h). Antenna with basicerite bearing acute distolateral tooth (Fig. 1b); scaphocerite subrectangular, about three times as long as wide distally, with inconspicuously concave lateral margin, distolateral tooth stout, acute, distinctly overreaching blade (Fig. 1i).

Mouthparts not dissected, appearing typical for genus externally (see Chace, 1972, 1997; Rhyne and Lin, 2006). Third maxilliped greatly overreaching scaphocerite in full extension, very setose (Fig. 1j); lateral plate of coxa ear-shaped, posterior angle produced (Fig. 1j); exopod about 1/2 length of antepenultimate segment; penultimate segment less than 1/2 length of antepenultimate segment; ultimate segment less than twice as long as penultimate segment, tip armed with circle of stout spines (Fig. 1k).

First pereopod (P1) relatively short, ending in simple chela (Fig. 1l, m); ventral margin of ischium with small inconspicuous spinules hidden among long stiff setae (Fig. 1n); merus shorter than carpus; carpus cylindrical, with rows of grooming setae mesially as illustrated (Fig. 1o); palm about about 1.5 times longer than fingers, about twice as long as high; finger tips bifid, corneous (Fig. 1m).

Second pereopods (P2) slender, right and left subequal in length, ending in small simple chelae (Fig. 1p); merus of right and left P2 with 16-21 and 15-19 segments, respectively; carpus of right and left P2 with 21-22 and 21-24 segments, respectively.

Third to fifth pereopods similar, decreasing in length from third to fifth. Third pereopod (Fig. 1q) with unarmed ischium; merus about six times as long as wide, with two to four stout ventrolateral spines distally (Fig. 1q, s), less than twice as long as carpus; propodus slightly shorter

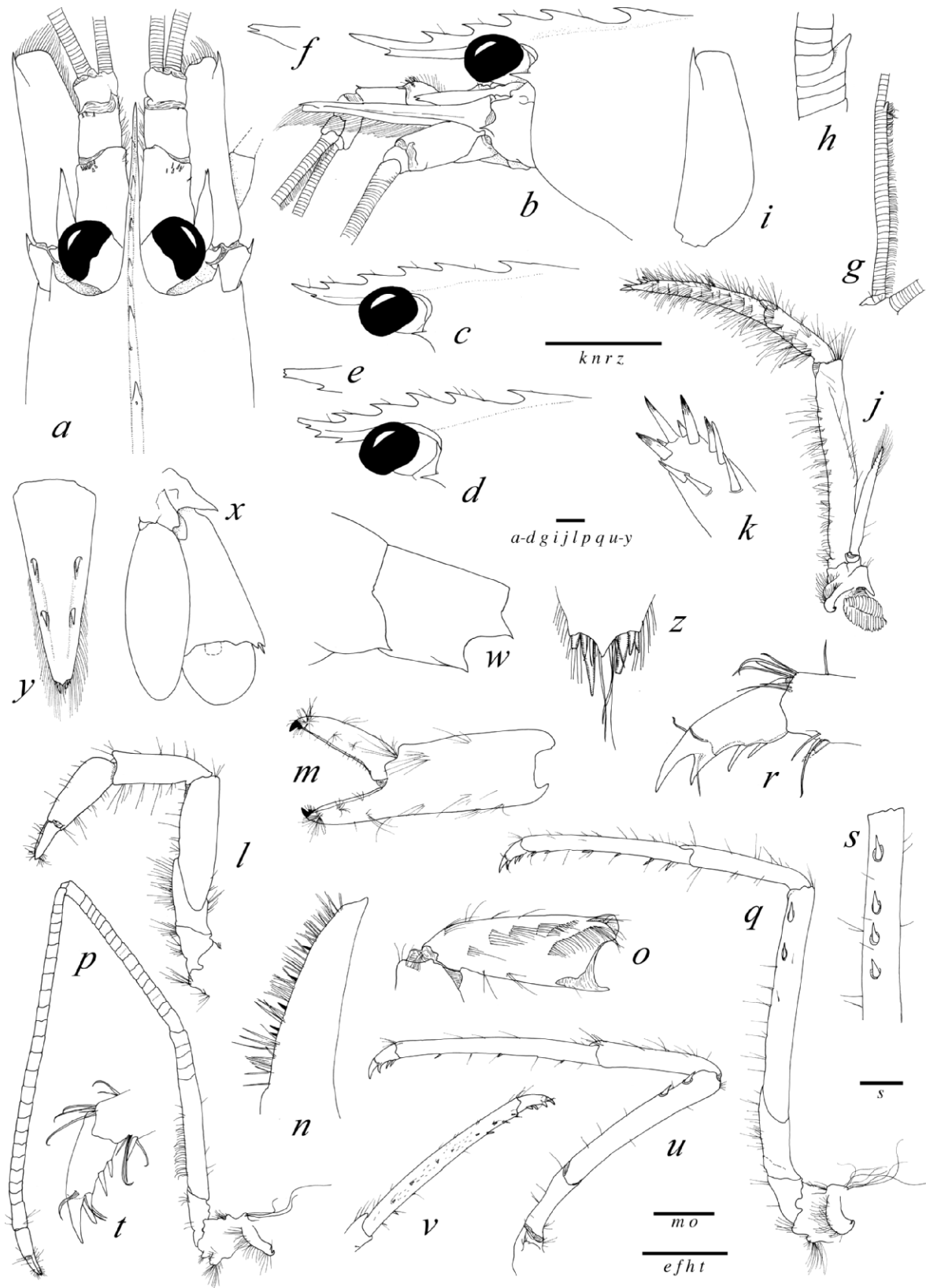


Fig. 1. *Lysmata hochi* n. sp.: paratype, simultaneous hermaphrodite (USNM 1103079) [a, b, g-r, v-z], holotype, simultaneous hermaphrodite (USNM 1103074) [c], paratype, ovigerous simultaneous hermaphrodite (USNM 1103078) [d-f, s, t]; a, frontal region, dorsal view; b, same, lateral view; c, rostrum and eye, lateral view; d, same as c; e, same as d, detail of rostrum tip; f, stylocerite tip, lateral view; g, lateral antennular flagellum, lateral view; h, same, detail of accessory branch; i, scaphocerite, dorsal view; j, third maxilliped, lateral view; k, same, tip of ultimate segment, dorsal view; l, first pereiopod, lateral view; m, same, chela with fingers opened; n, same, detail of ventrolateral margin of ischium; o, same, carpus, ventromesial view; q, third pereiopod, lateral view; r, same, dactylus; s, third pereiopod of another specimen, distal portion of merus, lateral view; t, same, dactylus; u, fifth pereiopod, lateral view; v, same, propodus and dactylus, ventromesial view; w, fifth and sixth pleomeres, lateral view; x, uropod, dorsal view; y, telson, dorsal view; z, same, detail of posterior margin. Scale bars: 1 mm.

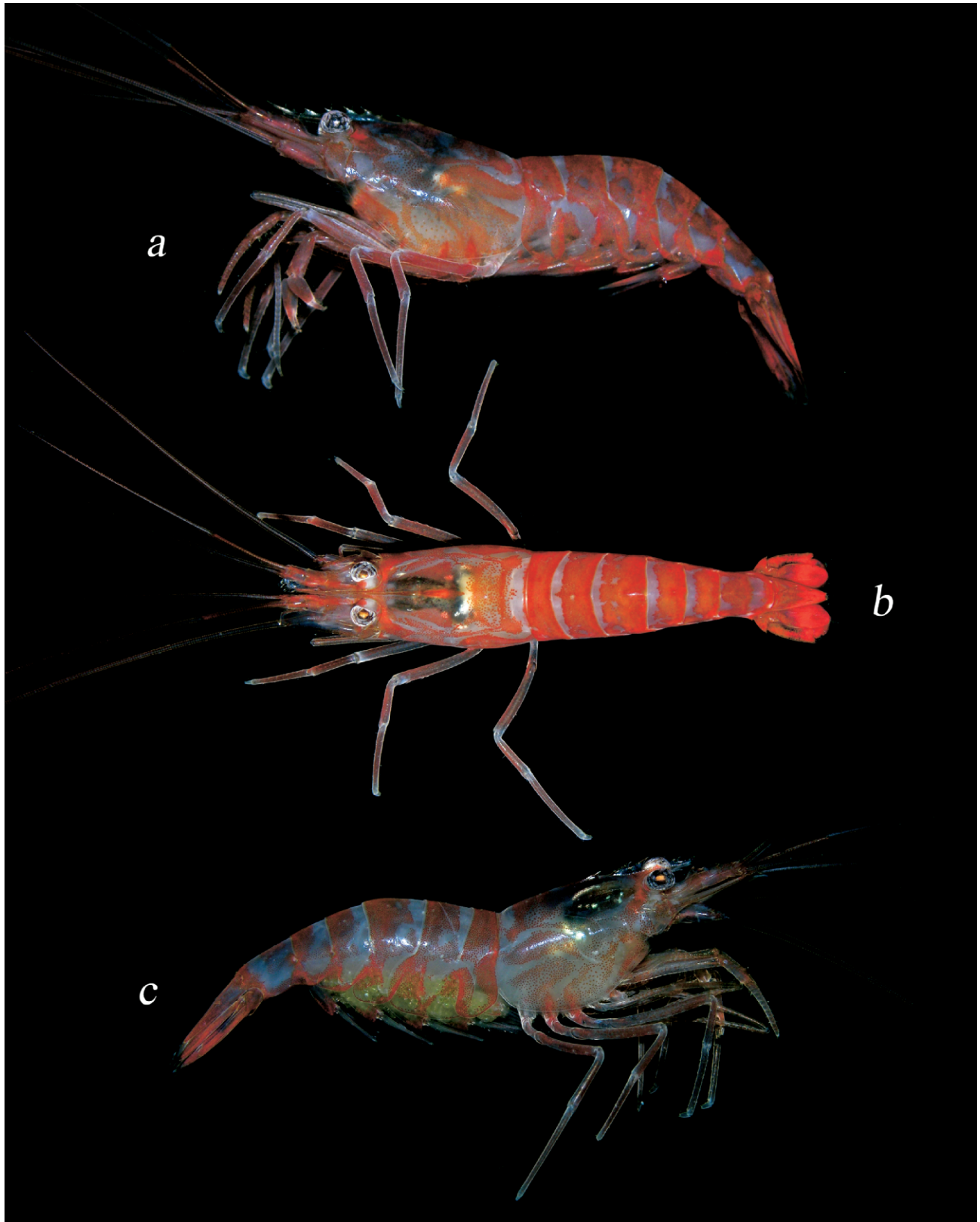


Fig. 2. *Lysmata hochi* n. sp., habitus and color pattern of two paratypes; simultaneous hermaphrodite (USNM 1103079) [a, b], ovigerous simultaneous hermaphrodite (USNM 1103078) [c]; a, c, lateral views; b, dorsal view.

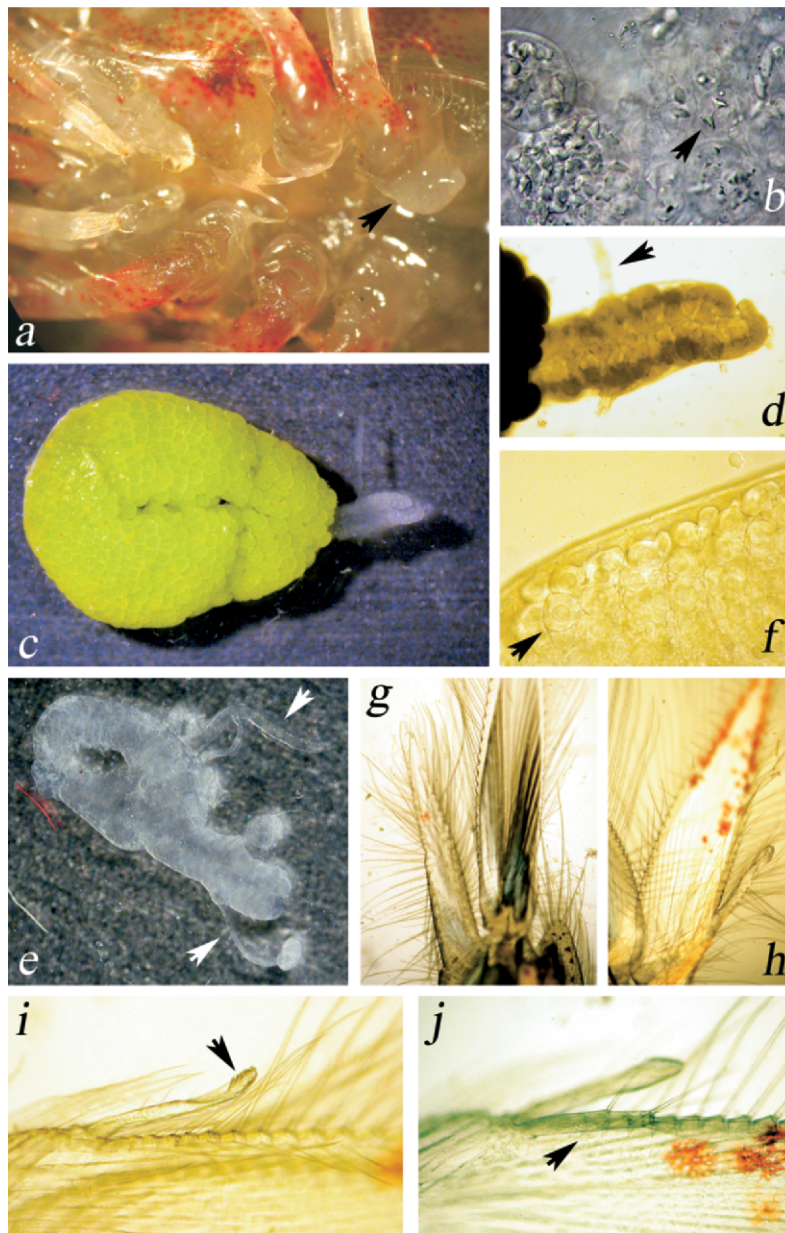


Fig. 3. *Lysmata hochi* n. sp.: anatomical and morphological differences between males and hermaphrodites; a, sperm retrieved from gonopores of hermaphrodite (arrow points at position of gonopore); b, sperm from hermaphrodite contained within ovoid capsules (arrow points at sperm cell); c, ovotestes from dissected hermaphrodite (anterior female and male portions on left and right, respectively); d, close-up of male gonad portion (arrow points at the right vas deferens); e, ovotestes from male (anterior female and male portions on left and right, respectively) (arrows on the upper right and lower left point at right oviduct and left vas deferens, respectively); f, close-up of female gonad portion in male (arrow points at immature oöcyte); g, endopod of first pleopod lacking cincinulli in hermaphrodite; h, endopod of second pleopod lacking appendix masculina in hermaphrodite; i, endopod of first pleopod in male (arrow points at cincinulli); j, endopod of second pleopod in male (arrow points at appendix masculina).

than merus, with spines or spinules along ventral and ventromesial margins; dactylus about 1/4 length of propodus (Fig. 1q), biunguiculate, in addition to two slender spines proximally on flexor margin, main (terminal) unguis longer than secondary (ventral) unguis (Fig. 1r, t). Fourth pereopod generally similar to third. Fifth pereopod with merus distinctly shorter than propodus (Fig. 1u), with two stout ventrolateral spines distally; propodus with spinules on ventral and ventromesial margins (Fig. 1v), without distinct setal rows distolaterally.

First three pleomeres with rounded margins, fourth with protruding posterolateral angle, fifth with sharp posterolateral tooth, sixth with acute posteroventral tooth and acute posterior tooth on each side of telson (Fig. 1w). Second pleopod with appendix interna and appendix masculina in primary males (Fig. 3j). Uropod with sharp lateral tooth on protopod; exopod with daeresis bearing acute tooth laterally, adjacent to distolateral spine (Fig. 1x). Telson relatively narrow, more than 2.5 times as long as wide at base, tapering posteriorly (Fig. 1y); dorsal surface with two pairs

of spines situated anterior and posterior to midlength, respectively (Fig. 1y); posterior margin subacute medially, with pair of robust long mesial spines each flanked by shorter lateral spine, sometimes two spines (Fig. 1z).

Color in Life.—Background color whitish semitransparent; carapace with complex pattern of longitudinal, oblique and transverse bands and patches (Fig. 2a-c), most conspicuous being dorsally visible reddish hexagonal patch consisting of several bands on gastric region and broadly W-shaped, white band along posterior margin (Fig. 2b); postrostral carina red; pleon with broad transverse bands, occupying at least posterior 3/4 of each pleuron (Fig. 2a-c), bands incised by white patches and oblique bands laterally (Fig. 2a, c); telson and uropods mostly red; antennular and antennal peduncles reddish with white; flagella pale reddish, fused portion of lateral flagellum intense red (Fig. 2b); legs reddish with white around articulations; eggs dull olive-green (Figs. 2c, 3c).

Size.—The CL of the three adult hermaphrodites from the type series ranges from 10.0 to 10.3 mm (for more detailed size range and population structure see under *Biology* below).

Variation.—The morphological variation among the three type specimens is considerable. The ventral margin of the rostrum may have one to three teeth, while the rostrum tip may be simple (Fig. 1b, c) or trifold, in latter case perhaps due to injury (Fig. 1e). The number of spines on the merus of the third pereopod ranges from two to four (Fig. 1q, s). The number of segments in the merus of the second pereopod ranges from 15 to 21, and in the carpus from 21 to 24. Finally, the telson may occasionally have two instead of usual one lateral spine at posteroventral angle (Fig. 1z, right side). A similar variation range of these features was documented for other species of *Lysmata* (Rhyne and Lin, 2006).

Etymology.—The new species is named after Mr. Frank Hoch, in appreciation for his support of scientific research at the Bocas del Toro station (STRI).

Type Locality.—Bocas del Toro, Caribbean coast of Panama.

Distribution.—Presently known only from Bocas del Toro, Panama (type locality) and Cahuita, Costa Rica (A. Anker, personal observation), in the southwestern Caribbean Sea, western Atlantic.

Habitat.—Fossilized coral terraces with deep channels and caves, sparsely covered with seagrass, with a drop-off about 20 m from the shore; sand bottom at about 1-3 m; plateau partly exposed during low tide.

from the gonopores by applying short electro-shocks (Fig. 3a). Sperm cells retrieved from the gonopores were shaped in the form of inverted umbrella and were contained in variable numbers within ovoid capsules (Fig. 3b). Dissection of the gonad of brooding (purportedly) hermaphroditic shrimps confirmed the presence of ovotestes, with a relatively large anterior female portion full of green vitellogenic oocytes and a relatively small posterior male gonad portion with sperm (Fig. 3c, d). The gonad dissected from male shrimps was an ovotestes (Fig. 3e), but with an undeveloped anterior female portion (full of small immature oocytes lacking color) (Fig. 3f) and a posterior male gonad containing sperm (as in Fig. 3b). In both brooding and non-brooding shrimps, vasa deferentia and oviducts extended laterally from the male and female gonad portions, respectively (Fig. 3d, e). Shrimps brooding embryos invariably lacked cincinulli and appendices masculinae in the endopod of the first and second pereopods, respectively (Fig. 3g, h). In contrast, appendices masculinae bearing large spines and numerous cincinulli on appendices interna were observed in the second and first pleopod of the two non-brooding shrimps, respectively (Fig. 3i, j). All these different anatomical characters between brooding and non-brooding shrimps indicate that the population of *L. hochi* at the study site (Playa Bluff) is indeed composed of males and hermaphrodites.

Abundance of *L. hochi* in the field was extremely low, with a mean (+/- standard deviation) of 0.35 (+/- 0.35) individuals collected per hour per sampling night. The population was highly biased towards hermaphrodites (the ratio of males to total shrimps was 0.23). Males attained sizes as small as 6.16 mm CL and as large as 8.47 mm CL. The smallest and largest hermaphrodite found was 6.82 and 11.0 mm CL, respectively.

The first two experiments demonstrated that brooding shrimps are able to fertilize each other but are not capable of self-fertilization. All six brooding shrimps maintained in isolation produced eggs after molting but these eggs disappeared after the first two days from beneath the pleon, suggesting that they did not develop. These isolated shrimps were capable of normal female reproduction since their previous broods had hatched normally. In contrast, all six brooding shrimp in the paired treatment spawned and retained eggs that developed normally. These results demonstrate that the second individual in the pair probably acts as a male and fertilizes its partner. In the third experiment in which males were maintained in pairs, at least one shrimp in each pair matured into a hermaphrodite within 50 days. Most probably, the remaining males should have matured as hermaphrodite if the experiment had lasted longer.

Taking into consideration all of the preceding information, it is possible to conclude that *L. hochi* is a protandric simultaneous hermaphrodite, incapable of self-fertilization.

Relationships with Other Species

Lysmata hochi is one of several western Atlantic species characterized by a rudimentary accessory branch on the lateral ("outer") antennular flagellum, the other species being *L. grabhami* [Gordon, 1935] *L. rathbunae* [Chace, 1970; Rhyne and Lin, 2006]; *L. rafa* [Rhyne and Anker, 2007]; *L. wurdemanni*; *L. ankeri* Rhyne and Lin, 2006; *L.*

DISCUSSION

Biology

Dissections demonstrated that all four examined shrimps (brooding or non-brooding) had male gonopores located at the coxae of the fifth pair of pereopods. From all specimens, including those brooding embryos, sperm was retrieved

boggetti Rhyne and Lin, 2006; *L. pedersenii* Rhyne and Lin, 2006; *L. bahia* Rhyne and Lin, 2006 [Rhyne and Lin, 2006]; and *L. anchisteus* Chace, 1972 [Chace, 1972].

As already noted, *L. grabhami* is a very distinctively colored cleaner shrimp (Humann and Deloach, 2002), which is not closely related to *L. hochi*. *L. rathbunae*, *L. rafa*, *L. wurdemanni*, *L. ankeri*, *L. boggetti*, *L. pedersenii* and *L. bahia* have very different, striped, "peppermint-type" color patterns, and all except for *L. bahia* also have more than two spines on the flexor margin of the dactylus on the third to fifth pereopod (Chace, 1970; Rhyne and Lin, 2006; Rhyne and Anker, 2007). *Lysmata anchisteus*, for which the color pattern remains unknown, differs from *L. hochi* by five dorsal teeth on the rostrum and one mid-dorsal tooth on the carapace posterior to the orbital margin (vs. three rostral and two mid-dorsal teeth in *L. hochi*); the somewhat stouter first pereopod; and the significantly lower number of segments in the merus (7) and carpus (13-15) of the second pereopod (vs. 15-21 and 21-24 in *L. hochi*).

The two remaining western Atlantic species, *L. intermedia* and *L. moorei*, both have a well developed accessory branch on the lateral antennular flagellum (Chace, 1972; d'Udekem d'Acoz, 2000) and differ in many other aspects from *L. hochi*, including color patterns (A. Anker, personal observation).

In the eastern Atlantic, *L. stenolepis* Crosnier and Forest, 1973, *L. olavoii* Fransen, 1991 and *L. unicoloris* Holthuis and Maurin, 1952, in addition to the ampho-Atlantic *L. grabhami* (see above), have a reduced or poorly developed accessory branch on the lateral antennular flagellum (Holthuis and Maurin, 1952; Crosnier and Forest, 1973; Fransen, 1991; Chace, 1997). Both *L. stenolepis* and *L. olavoii* are deep-water forms that are very different from *L. hochi*, e.g., by the presence of a pterygostomial tooth (*L. stenolepis*), the rostral formula (*L. olavoii*), the proportions of legs and the armature of the dactylus on the third to fifth pereopods (Crosnier and Forest, 1973; Fransen, 1991).

Lysmata unicoloris, known from Morocco, Gibraltar Strait, southern Spain (González-Gordillo et al., 2001) south to Congo (Crosnier, 1971), appears to be morphologically close to *L. hochi* n. sp., especially in the shape of the accessory branch on the lateral antennular flagellum. However, *L. unicoloris* can be separated from the new species by the presence of five spines on the merus of the third pereopod (vs. only two to four in *L. hochi*), the presence of three spines on the flexor margin of the dactylus of the third to fifth pereopod (vs. only two in *L. hochi*), and the lesser number of segments in the carpus of the second pereopod (11 in *L. unicoloris* vs. at least 15 in *L. hochi*) [Holthuis and Maurin, 1952]. Furthermore, *L. unicoloris* was collected on shallow rocky bottoms, from the shore to about 20 m (Holthuis and Maurin, 1952; Crosnier, 1971), a habitat quite different from the near-shore fossil coral terraces where *L. hochi* occurs. The brief color notes for *L. unicoloris* provided by Holthuis and Maurin (1952) are too imprecise to enable a direct comparison of color patterns.

The remaining eastern Atlantic species, *L. seticaudata* (Risso, 1816) and *L. nilita* Dohrn and Holthuis, 1950, both have a well developed accessory branch in the lateral antennular flagellum and differ from *L. hochi* in numerous

other features (Dohrn and Holthuis, 1950; d'Udekem d'Acoz, 2000), including the color pattern in *L. seticaudata* (Wirtz and Debelius, 2003, p. 120).

About 20 species of *Lysmata* are currently known in the Indo-Pacific, including at least nine species in the eastern Pacific (Chace, 1997; Wicksten, 2000; Burukovsky, 2000; A. Anker, personal observation). Only one of them, *L. kuekenthali* (De Man, 1902), ranging from South Africa to Japan and Indonesia (type locality), is morphologically very close to *L. hochi*, judging from De Man's (1902) superficial description and rather inadequate illustrations. On our request, Dr. Charles Fransen (RMNH) examined three specimens from the syntype series of *L. kuekenthali* (in total six specimens) deposited in the RMNH. The main difference between *L. hochi* and *L. kuekenthali* appears to lie in the tip of the stylocerite. In all three specimens of *L. hochi*, the stylocerite has a bifid tip (Fig. 1f) [in one specimen, the left stylocerite has traces of an injury and ends in a simple, non-bifid tip], whereas in the three examined syntypes of *L. kuekenthali*, the stylocerite has a simple tip. Chace (1997) noted that in *L. kuekenthali*, the lateral antennular flagellum has no accessory branch ("dorsal flagellum without accessory branch"). However, this statement is not correct. According to the drawing provided by C. Fransen, the lateral flagellum has a small, one-segmented accessory branch, which is only slightly shorter than the more unguis-like, one-segmented accessory branch in *L. hochi* (Fig. 1c). The color pattern of *L. hochi* (Fig. 2) is remarkably similar to the color pattern of "*L. kuekenthali*" in Debelius (2001, two color photographs on p. 126), and less similar to the possibly faded pattern of "*L. kuekenthali*" in Kamezaki et al. (1988); however, the true identities of these shrimps remain unknown.

The bifid stylocerite tip may be a key diagnostic feature of *L. hochi*; however, morphological details such as this presently remain unknown in most species of *Lysmata*.

In summary, *L. hochi* appears to be most closely related to *L. kuekenthali* and perhaps to *L. unicoloris*. This example shows that the closest relatives of a given species may not be necessarily in the same biogeographic province, in this particular case the western Atlantic. All our anatomical and behavioral observations demonstrate that *L. hochi* is a protandric simultaneous hermaphrodite, as reported for all other species of *Lysmata* in which the sexual system was previously examined (Fiedler, 1998; Bauer and Holt, 1998; Bauer and Newman 2004; d'Udekem d'Acoz, 2003). Future molecular analyses of all species of *Lysmata* will help to determine their phylogenetic relationships and shed light onto the evolutionary origins of their exceptional sexual system.

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