

A New Species of *Lysmata* (Crustacea, Decapoda, Hippolytidae) from the Pacific Coast of Panama, with Observations of Its Reproductive Biology

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Arthur Anker, Juan Antonio Baeza, and Sammy De Grave (2009) A new species of *Lysmata* (Crustacea: Decapoda: Hippolytidae) from the Pacific coast of Panama, with observations of its reproductive biology. *Zoological Studies* 48(5): 682-692. *Lysmata holthuisi* sp. nov., a new peppermint shrimp, is described from Taboga I., on the Pacific coast of Panama. In addition to the type locality, *L. holthuisi* sp. nov. occurs in the vicinity of Panama City and around some islands relatively close to the mainland (Las Perlas and Coiba). The new species can be distinguished from other species of *Lysmata* by the rostrum bearing 6 (occasionally 5 or 7) dorsal and 2 (rarely 3) ventral teeth; the presence of setae between the dorsal rostral teeth; an acute well-developed pterygostomial tooth; a stylocerite overreaching the 1st antennular segment; the accessory branch of the lateral antennular flagellum consisting of 6 or 7 free segments; the marked segmentation of the merus of the 2nd pereopod; the absence of a posteroventral tooth on the 4th pleuron; and by its diagnostic color pattern, characterized by red longitudinal stripes on the carapace and abdomen, and conspicuous bright yellow and red markings on or near the accessory branch of the lateral antennular flagellum. Among the eastern Pacific species, *L. holthuisi* sp. nov. appears to be most closely related to *L. argentopunctata* Wicksten and *L. chica* Wicksten. Anatomical observations, field population studies, and laboratory experiments indicate that *L. holthuisi* sp. nov. is a protandric simultaneous hermaphrodite, with an early male phase followed by a functional simultaneous hermaphroditic phase. <http://zoolstud.sinica.edu.tw/Journals/48.5/682.pdf>

Key words: *Lysmata*, Shrimp, New species, Eastern Pacific, Hermaphroditism.

The genus *Lysmata* Risso, 1816 presently contains 36 described species (Chace 1997, Rhyne and Lin 2006, Rhyne and Anker 2007, Baeza and Anker 2008), although several other species are currently under study or in the process of being described, and more species can be expected to be found, as revisionary studies progress (Rhyne and Lin 2006). The genus occurs worldwide in tropical, temperate, and cool-temperate seas, usually on rocky boulder slopes and reefal habitats, with the majority of species being concentrated in the Indo-

West Pacific (Chace 1997). Protandry (a sex change from male to female) is relatively common among hippolytids. However, in both *Lysmata* and *Exhippolysmata*, protandric simultaneous hermaphroditism (PSH) has been reported and documented (Bauer 2000, Braga et al. 2007).

The eastern Pacific presently contains 8 species of *Lysmata* (Wicksten 2000a b): *L. argentopunctata* Wicksten, 2000 (Mexico, Gulf of California, and the Galapagos); *L. californica* (Stimpson, 1866) (California to Mexico); *L. chica*

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Wicksten, 2000 (the Galapagos); *L. galapagensis* Schmitt, 1924 (Baja California to Panama, and the Galapagos); *L. gracilirostris* Wicksten, 2000 (Mexico and the Galapagos); *L. nayaritensis* Wicksten 2000 (Mexico to Panama); *L. porteri* (Rathbun, 1907) (Chile); and *L. trisetacea* (Heller, 1861) (Mexico to Colombia). Taxonomic confusion surrounds *L. trisetacea*, and the true status of the eastern Pacific populations currently recorded under this name must await a study on the validity of *L. chiltoni* Kemp, 1914 and *L. paucidens* (Rathbun, 1906), both currently considered to be junior synonyms of *L. trisetacea*. Although *L. intermedia* (Kingsley, 1878) was reported from the eastern Pacific, both Wicksten (2000) and d'Udekem d'Acoz (2000) consider this to be a tropical western Atlantic species.

In 2005 and 2006, the 1st author (A. Anker) made extensive collections of various caridean shrimps on the Pacific coast of Panama, among which were several species of *Lysmata*. One of them appeared to be particularly common in rocky intertidal areas, including at Punta Culebra, a few hundred meters from the Naos Laboratories of the Smithsonian Tropical Research Institute (STRI), and off Casco Viejo, the historical part of Panama City. Surprisingly, this species could not be assigned to any previously described species and is herein described as new. The diagnostic color pattern of the new species is illustrated. As many *Lysmata* species are known to be protandric simultaneous hermaphrodites (e.g., Bauer and Holt 1998, Lin and Zhang 2001, Zhang and Lin 2004, Bauer and Newman 2004, Rhyne and Lin 2006, Baeza et al. 2007, Baeza 2008, Baeza and Anker 2008), one of us (J.A. Baeza) conducted experiments to investigate the presence of hermaphroditism in the new species. The population abundance, sex ratios, and size distribution of the different sexes at different sampling localities are also reported.

MATERIALS AND METHODS

For taxonomic studies, shrimp were collected between 2005 and 2007 along the Pacific coast of Panama at Punta Culebra (Amador causeway near Panama City), Casco Viejo (off Panama City), Saboga (Las Perlas Is.), Taboga (Taboga Is.), and Coibita (Coiba Marine National Park). Most specimens were collected from small pools under larger rocks with the aid of a small aquarium hand-net while walking in rocky

intertidal areas at low tide. All specimens were subsequently preserved in 70%-90% ethanol. To document color patterns, some specimens were photographed alive on different backgrounds prior to preservation. Drawings were made under a dissecting microscope equipped with a camera lucida. Microphotographs were made under a light microscope with a mounted digital camera. Postorbital carapace length (pocl, in mm) was measured from the postorbital margin to the posterior margin of the carapace. Materials are deposited in the collections of the National Museum of Natural History, Washington DC, USA (USNM); Oxford University Museum of Natural History, Oxford, UK (OUMNH); Colección de Referencia, Departamento de Biología Marina, Universidad de Panamá, Panama City, Panama (UP); and Nationaal Natuurhistorisch Museum (Naturalis), Leiden, the Netherlands (RMNH).

For studies of reproduction and behavior, shrimp were collected from Dec. 2006 to Apr. 2007 at 4 sites along the Pacific coast of Panama: Playa Venao (8°53'30.51"N, 79°35'44.92"W), Taboga I. (8°46'56.11"N, 79°33'28.18"W), Playa Río Mar (8°27'08.54"N, 79°58'23.67"W), and Playa Chumical (8°53'06.37"N, 79°38'42.27"W). Shrimp were collected in the afore-mentioned way during the daytime, and transported to Naos Laboratories (STRI), where they were maintained in 21 L aquaria at 26-31°C and 34-36 ppt salinity, and were fed every other day with commercial fish food (Clorofin Sinking Granules) before being measured and sexed, and were selected for dissection or experiments to determine their sexual system.

The reproductive anatomy was examined in a total of 6 specimens: 3 small individuals expected to be males (CL 3.9, 4.0, and 4.1 mm) and 3 presumed hermaphrodites carrying embryos beneath their abdomen (CL 6.2, 6.7, and 7.1 mm). Specimens were defined as males or hermaphrodites by the presence (males) or absence (hermaphrodites) of coupling hooks (cincinnuli) and appendices masculina on the endopods of the 1st and 2nd pleopods, respectively. When male gonopores were observed on individuals, the sperm mass contained in the ejaculatory ducts was retrieved by electro-ejaculation, following Baeza (2006), resulting in the ejaculation of spermatophores by individuals. Each individual was then dissected to extract the gonads, and the presence of ovarian and/or testicular tissue was examined under a microscope. Finally, the 1st and 2nd pleopods were dissected out, and the presence or absence

of appendices interna and masculina was recorded.

Experiments were conducted to determine: (1) whether brooding shrimp can function as males, (2) whether brooding hermaphrodites can fertilize themselves, and (3) whether males do mature as hermaphrodites later in life. To determine if shrimp reproducing as females (brooding embryos) can function as males, 3 replicate pairs of brooding individuals were maintained in 21 L aquaria (experiment 1). To determine if shrimp are capable of self-fertilization, 6 brooding individuals were each maintained alone during a full molting cycle (experiment 2). To determine if males mature into hermaphrodites, 3 pairs of males (small non-brooding individuals with no externally visible female gonads but with cincinnuli and appendices masculina) were maintained separately in 21 L aquaria for at least 50 d (experiment 3). All treatments were examined daily for hatching of embryos, the presence of exuvia from molting, development of mature oocytes in the gonads (visible through the carapace), and spawning of a new batch of eggs. In order to determine if embryos were fertilized, 5 d after spawning, developing embryos were carefully examined for the presence of cleavage.

The rationale for the 3 above-described experiments is as follows. If ovigerous individuals, which are paired together produce normally developing broods, we inferred that either the other ovigerous shrimp in the aquarium acted as a male to inseminate its partner, or the shrimp are capable of self-fertilization, with both cases demonstrating functional hermaphroditism. However, if shrimp in isolation failed to successfully produce and brood normally developing eggs, we could eliminate the possibility that the shrimp can self-fertilize. Finally, if male shrimp at the beginning of the experiment develop an ovarian portion of the ovotestis and produce eggs, we could infer that maturing male shrimp can transform into hermaphrodites. The results from the above 3 experiments taken together demonstrate PSH in the studied species.

TAXONOMY

Family Hippolytidae Dana, 1852

Genus *Lysmata* Risso, 1816

Lysmata holthuisi sp. nov.

(Figs. 1-5)

Type material: Pacific coast of Panama: Holotype: ovigerous (ov) hermaphrodite (pool 6.0), Taboga I., intertidal, low tide, under rocks and coral rubble, leg. A. Anker et al., 21 Feb. 2007, USNM 1115553. Paratypes: 3 ov hermaphrodites (5.0, 5.4, and 5.5), same data as for holotype, UP; ovigerous hermaphrodite (5.9, specimen photographed), Playa Venao, rocky intertidal, low tide, in pools under rocks, leg. A. Baeza, 18 Apr. 2007, USNM 1115554; 2 ov hermaphrodites (5.9 and 6.2, latter specimen dissected), Playa Venao, rocky intertidal, low tide, in pools under rocks, leg. A. Anker, C. Hurt, and A. Baeza, 5 Dec. 2006, USNM 1115555; 1 non-ov hermaphrodite (4.7), 1 ov hermaphrodite (4.3), Amador Causeway near Panama City, Naos, Punta Culebra, low tide, under rocks, leg. A. Anker and C. Hurt, 2 Mar. 2006, OUMNH.ZC 2006-10-0015; 1 ♂ (4.5), 2 ov hermaphrodites (5.0 and 5.7), Casco Viejo, Panama City, rocky intertidal, low tide, leg. A. Anker et al., 31 Mar. 2006, OUMNH.ZC 2006-10-0016; 2 ov hermaphrodites (3.1 and 3.8); Las Perlas Is., Saboga, under rocks, leg. A. Anker, 16 Nov. 2005, RMNH D53042.

Additional material examined: Pacific coast of Panama: 1 ov hermaphrodite (4.5), Taboquilla, Taboga Is., Panama, rubble lifted from 15-30 m, leg. P. Barber et al., 30 Sept. 2005, OUMNH.ZC 2006-10-0017.

Etymology: The name of the new species honors Prof. L.B. Holthuis (1921-2008), in recognition of his monumental contributions to shrimp taxonomy.

Type locality: Taboga I., Pacific coast of Panama.

Distribution: Presently known with certainty only from Panama: vicinity of Panama City (Amador, Casco Viejo), Playa Veracruz, Playa Venao, Río Mar, Chumical, Taboga Is. (Taboga, Taboquilla), Las Perlas Archipelago (Saboga), and Coiba Archipelago (Coibita).

Description: Rostrum elongate, stout, about 0.5 times as long as carapace, surpassing 2nd segment of antennular peduncle; dorsal margin with 6 (occasionally 5 or 7) teeth, most-posterior tooth near middle of carapace, 3rd tooth just anterior of orbital margin; single seta present between all teeth (if not broken off); ventral margin with 2 (rarely 3) teeth, tip not subdivided. Carapace smooth, posteroventral margin rounded, pterygostomial tooth well-developed. Antennal tooth well-developed, reaching middle of cornea.

Antennular peduncle about 0.5 times as long as scaphocerite, 1st segment about 2.0-2.5 times

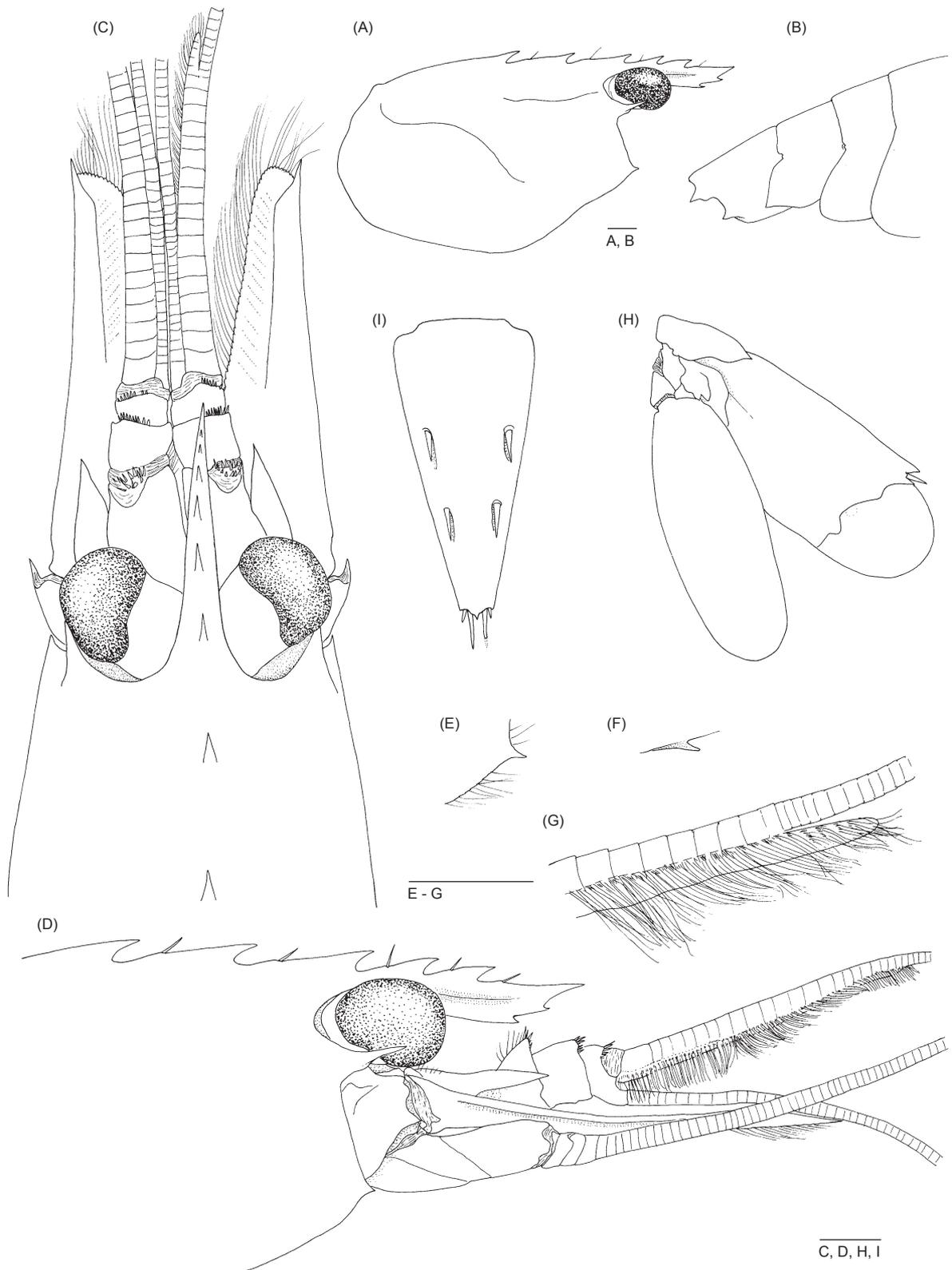


Fig. 1. *Lysmata holthuisi* sp. nov., ovigerous hermaphrodite from Taboga, paratype (USNM 1115554). (A) Carapace, lateral view; (B) posterior abdomen, lateral view; (C) frontal region, dorsal view; (D) same, lateral view; (E) pterygostomial tooth, lateral view; (F) ventromesial carina of 1st antennular segment, lateral view; (G) detail of accessory branch of lateral antennular flagellum, lateral view; (H) uropod, dorsal view; (I) telson, dorsal view. Scale bars = 1 mm.

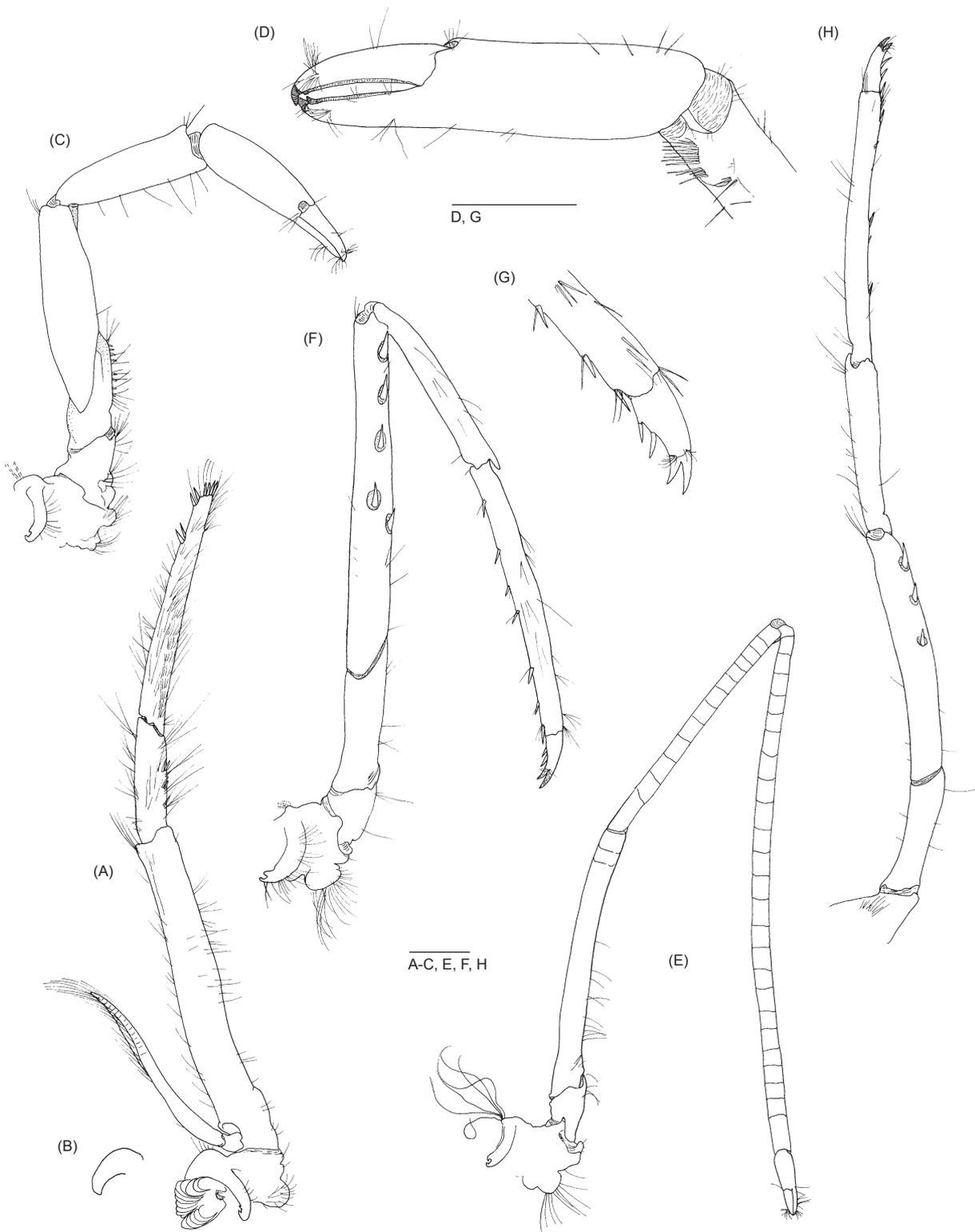


Fig. 2. *Lysmata holthuisi* sp. nov., ovigerous hermaphrodite from Taboga, paratype (USNM 111554). (A) 3rd maxilliped, lateral view; (B) same, lateral plate; (C) 1st pereopod, lateral view; (D) same, chela, mesial view; (E) 2nd pereopod, lateral view; (F) 3rd pereopod, lateral view; (G) same, distal propodus and dactylus; (H) 4th pereopod, lateral view. Scale bars = 1 mm.

as long as 2nd segment, 3rd segment about 0.6-0.7 times as long as 2nd segment; distodorsal margins of all 3 peduncular segments furnished with a series of spinules; stylocerite just overreaching 1st segment, ventromesial carina with small, anteriorly directed tooth; lateral antennular flagellum long, accessory branch with 6 or 7 free segments, free part about 0.19-0.29 times as long as fused part. Scaphocerite 4.5-5.0 times as long as wide, lateral margin straight, distolateral tooth overreaching distal margin of blade.

Third maxilliped barely overreaching scaphocerite; exopod 0.75 times as long as antepenultimate segment of endopod; penultimate segment 0.73 times as long as ultimate segment; tip with 2 subdistal and 3 distal spiniform setae.

First pereopod reaching past antennular peduncle by length of fingers when extended, ischium with row of spines along ventral margin; merus about 1.3 times as long as carpus, chela about 1.3-1.4 times as long as carpus, palm about 1.8-1.85 times as long as dactylus, tip of dactylus simple, tip of pollex bifid. Second pereopods slender, subequal in length, fully extended overreaching scaphocerite by 0.3-0.5 length of carpus; ending in small, simple chelae; merus (in holotype) with 12 (left) and 15 segments (right), carpus twice as long as merus, (in holotype) with 25 (left) and 28 segments (right).

Third to 5th pereopods similar, decreasing in length from 3rd to 5th; 3rd pereopod overreaching scaphocerite by 0.5-0.7 length of propodus, merus (in holotype) with 4 spines, about 2.5-2.9 times as long as ischium; carpus about 1/2 as long as merus, unarmed; propodus about 1.4-1.5 times as long as carpus, ventrally with 7 spiniform setae (holotype); dactylus about 0.2 times as long as propodus, biunguiculate, dorsal unguis slightly larger than ventral one, flexor margin of dactylus with 2 spines; 4th pereopod similar to 3rd, (in holotype) with 5 spines on merus and 7 spiniform setae on propodus; 5th pereopod similar, (in holotype) with 1 spine on merus and 6 spiniform setae on propodus.

First 3 abdominal somites ventrally rounded, 4th somite without posterolateral tooth; 5th somite with poorly developed posterolateral tooth; 6th somite about 1.35 times as long as 5th, with blunt posteroventral tooth. Telson about 2.5 times as long as wide, tapering posteriorly, dorsal surface with 2 pairs of spines, approximately inserted at 0.3 and 0.6 of telson length; posterior margin medially acute, furnished with 2 pairs of spiniform setae, mesial 2.5 times as long as lateral. Uropods

without specific features, as figured.

Morphological variation: Regarding rostral teeth, the current material exhibits little variation with the majority of specimens possessing 6 dorsal and 2 ventral teeth; a single individual has 3 ventral teeth, while 2 individuals differ in the number of dorsal teeth, with 5 and 7 respectively (Fig. 3). The meral segmentation of the 2nd pereopod ranges between 12 and 18 segments, with often a minor difference between the left and right pereopods. Similarly, carpal segmentation ranges 22-29, and frequently differs by 1-3 segments between the left and right pereopods. Some variation was noted in the number of spines on the meri of the ambulatory pereopods: 4-7, 4-7, and 1-2 on the 3rd, 4th, and 5th pereopods, respectively, in approximately 1/2 of individuals, there was a difference of 1 or 2 spines between the left and right pereopods. The number of spiniform setae on the propodus of the ambulatory pereopods is also not constant, ranging 6-8, 5-7, and 4-6 on the 3rd, 4th, and 5th pereopods, respectively, again with a frequent difference between the left and right pereopods.

Color in life: Generally semitranslucent with narrow red longitudinal lines (Fig. 4); carapace with several narrow red longitudinal and oblique lines, with scattered or grouped red dots in between, and 1 mediodorsal V-shaped band crossing the most-posterior post-rostral tooth; abdominal pleura with red longitudinal lines, nearly continuous across entire abdomen, broader and more-diffuse transverse bands along posterior margin, and red spots arranged in broad bands between red lines; accessory branch of lateral flagellum conspicuously bright yellow, adjacent segments deep red; pereopods semitransparent with red dots; telson and uropods with red and yellow dots arranged in bands and lines; ovaries or eggs greenish.

Taxonomic remarks: Based on the last revision of the eastern Pacific species of *Lysmata* (Wicksten 2000b), *L. holthuisi* sp. nov. can be immediately distinguished from *L. californica*, *L. gracilirostris*, *L. nayaritensis*, and *L. porteri* by the stylocerite overreaching the 1st antennular peduncle (vs. shorter in the other species) and the accessory branch of the lateral antennular flagellum consisting of 6 or 7 free segments (vs. fused or vestigial in the other species). Among the remaining 4 eastern Pacific species, *L. holthuisi* sp. nov. can be distinguished from *L. galapagensis* and *L. trisetacea* sensu Wicksten (2000) by the presence of a well-developed pterygostomial tooth in *L. holthuisi* sp. nov., which is absent from both

L. galapagensis and *L. trisetacea* sensu Wicksten (2000b). In life, *L. holthuisi* sp. nov. can easily be separated from *L. californica* (cf. Debelius 1999), *L. galapagensis* (cf. Hickman and Zimmerman 2000), *L. nayaritensis*, and *L. gracilirostris* (A. Anker and A. Baeza, pers. obs.) by its unique color pattern (Fig. 3).

Lysmata holthuisi sp. nov. is morphologically more similar and perhaps phylogenetically closer to *L. argentopunctata* and *L. chica*, both from the *L. intermedia* species complex. This complex further includes the western Atlantic *L. intermedia*, several undescribed forms in the western Atlantic (A. Rhyne, pers. comm.; A. Anker, pers. obs.), and possibly the eastern Atlantic *L. seticaudata* (Risso, 1816) (d'Udekem d'Acoz 2000). *Lysmata holthuisi* sp. nov. differs from *L. argentopunctata* in its rostral formula, a well-developed pterygostomial tooth (vs. small or minute in *L. argentopunctata*), the presence of setae between the dorsal rostral teeth (absent in *L. argentopunctata*), and the relative development of the accessory branch of the lateral antennular flagellum (0.19-0.29 of the fused part in *L. holthuisi* sp. nov. vs. 0.5 in *L. argentopunctata*). In life, both species can easily be separated by their characteristic color patterns, which in *L. argentopunctata* consists of broad red longitudinal stripes on the carapace and abdomen, interspersed with lines of silvery-white spots (Kerstitch 1989 [as *L. intermedia*], Hickman and Zimmerman 2000). *Lysmata holthuisi* sp. nov. differs from *L. chica* by the presence of a well-

developed pterygostomial tooth (vs. minute or absent in *L. chica*); the absence of a posteroventral tooth on the 4th pleuron (vs. present in *L. chica*); the presence of setae in between the dorsal rostral teeth (vs. absent in *L. chica*); and the segmentation on the merus of the 2nd pereopod, which is very faint and poorly delineated in *L. chica*. Wicksten (2000b) described the color pattern of *L. chica* as transversely banded with brown to cream and pink bands; this description matches the color pattern of the shrimp identified as *L. chica* in Hickman and Zimmerman (2000), and markedly contrasts to the color pattern of *L. holthuisi* sp. nov. (Fig. 3).

REPRODUCTIVE BIOLOGY

Dissections demonstrated that all examined individuals (brooding or non-brooding) had male gonopores located at the coxae of the 5th pair of pereopods (Fig. 5A), storing a spermatophore containing sperm cells, which resemble inverted umbrellas (Figs. 5B, C), and had ovotestes containing sperm (Figs. 5D, E). The ovotestes of non-brooding shrimp had a poorly developed female portion full of immature colorless oocytes (Fig. 5D). In contrast, the ovotestes of brooding individuals had a relatively large anterior female portion full of green vitellogenic oocytes (Fig. 5E). In both brooding and non-brooding individuals, the vas deferentia and oviducts extended laterally from the male and female gonads, respectively (Fig.

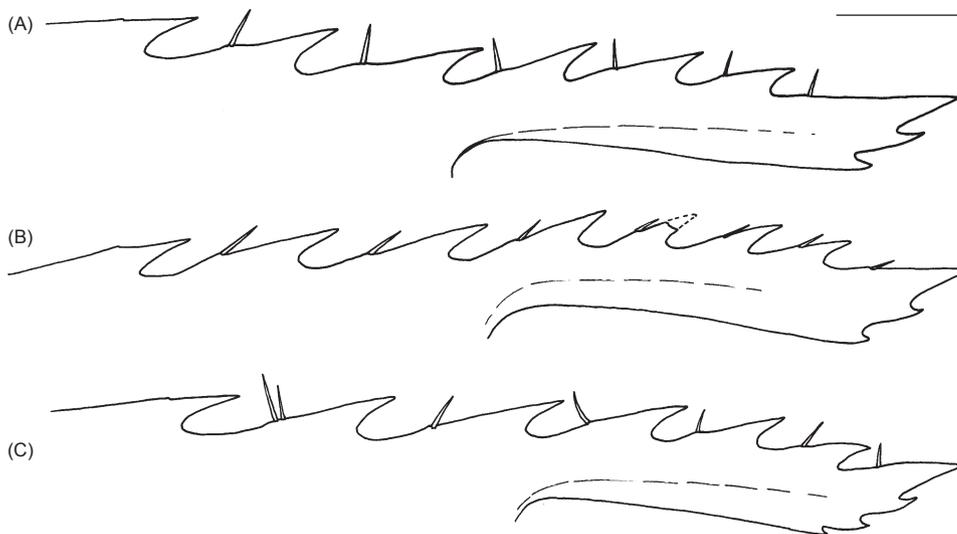


Fig. 3. *Lysmata holthuisi* sp. nov., rostral variation in specimens from Taboga. (A) Holotype, ovigerous hermaphrodite (USNM 111555); (B, C) 2 paratypes, ovigerous hermaphrodites. Scale bar = 1 mm.

5D). Embryo-brooding individuals lacked cincinnuli and appendices masculina on the endopod of the 1st and 2nd pereopods, respectively. In contrast, cincinnuli and appendices masculinae (the latter bearing long setae) were observed on the endopod of the 1st and 2nd pleopods, respectively, of non-brooding individuals (Figs. 5F, G). These anatomical observations indicate that populations of *L. holthuisi* sp. nov. are indeed composed of smaller functional males and larger functional hermaphrodites.

The first 2 experiments demonstrated that brooding individuals are able to fertilize each other and do not self-fertilize. All 6 brooding animals retained in isolation produced eggs after molting, but these eggs disappeared after the

first 2 d, suggesting that they did not develop. These individuals were capable of normal female reproduction since their previous broods had hatched normally. In contrast, all 6 brooding shrimp in the paired treatment spawned and retained eggs that developed normally. These results demonstrate that the 2nd individual in the pair probably acts as a male and fertilizes its partner.

The 3rd experiment demonstrated that males do mature as simultaneous hermaphrodites later in life. All males in all 3 replicates of paired males matured as functional hermaphrodites in less than 50 d. Invariably, the largest of the 2 males in each replicated pair was the 1st maturing as a hermaphrodite, as indicated by the development



Fig. 4. *Lysmata holthuisi* sp. nov., color pattern of hermaphrodite specimen from Punta Culebra, paratype (OUMNH.ZC 2006-10-0015). (A) Dorsal view; (B) lateral view.

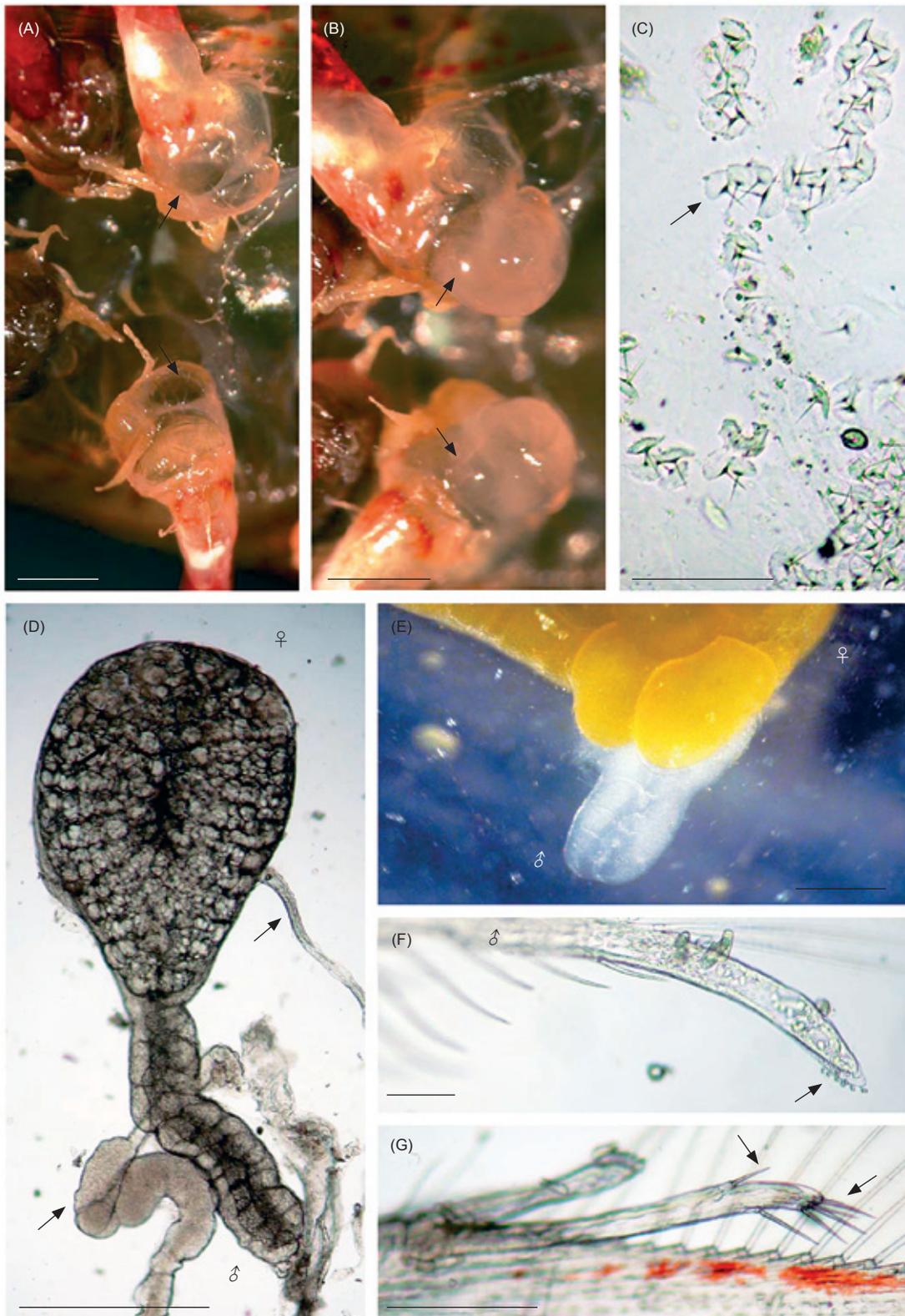


Fig. 5. *Lysmata holthuisi* sp. nov., anatomical and morphological differences between males and hermaphrodites. (A) Gonopores of hermaphrodite; (B) spermatophore retrieved from gonopores of hermaphrodite; (C) sperm from hermaphrodite; (D) ovotestes dissected from male (female and male portions labeled in the photograph); (E) ovotestes dissected from female (female and male portions labeled in the photograph); (F) endpod of male 1st pleopod (arrow points to cincinnuli); (G) endpod of male 2nd pleopod (arrows point to setae on appendix masculina). Scale bars: A, B, G = 500 μ m, C = 20 μ m, D, E = 1000 μ m, F = 100 μ m.

of the female gonad, molting when the gonad was full of mature oocytes (indicated by the green-colored gonad visible through the carapace), and subsequently spawning and brooding their eggs. The results from all experiments and the dissections demonstrate that *L. holthuisi* sp. nov. is indeed a protandric simultaneous hermaphrodite. After recruitment to the benthic population, individuals invariably mature and first reproduce exclusively as males, only later in life becoming functional simultaneous hermaphrodites, capable of both male and female reproduction.

Population abundance of the new species at the different sampling localities was high, with a minimum of 30 and a maximum of 43 individuals captured per hour of collecting (at Venao and Chumical, respectively), with a mean value of 38.50 (standard deviation (SD), 5.80). Invariably, the populations were biased toward males, with an overall 61.3% (138 of 225) of the collected shrimp being male (Fig. 6).

In terms of size distribution, males (mean pool, 2.99 mm; SD, 0.72; range, 1.50-4.70 mm) were

almost always smaller than hermaphrodites (mean pool, 5.17 mm; SD, 0.69; range, 4.10-6.30 mm), with only a few (28 in total, i.e., 12.4%) individuals of the 2 sexes overlapping in size, within a range of 4.10-4.70 mm. At each locality, a few individuals (12 in total, i.e., 5.3%) were intermediate in size between males and hermaphrodites (mean pool, 4.18 mm; SD, 0.20; range, 4.00-4.60 mm) had male external characters, but also presented a developing ovary (with small white oocytes visible through the carapace). These “transitional” individuals most likely were close to becoming hermaphrodites during their next molt (Fig. 6).

Overall, the present study demonstrates that *L. holthuisi* sp. nov. is a protandric simultaneous hermaphrodite, as has been reported for all species of *Lysmata* for which the sexual biology has been studied (e.g., Fiedler 1998, Bauer and Holt 1998, d’Udekem d’Acoz 2003, Bauer and Newman 2004, Baeza et al. 2007, Baeza 2008, Baeza and Anker 2008). PSH may well represent a conserved character within the genus *Lysmata* and other closely related genera (*Lysmatella* and

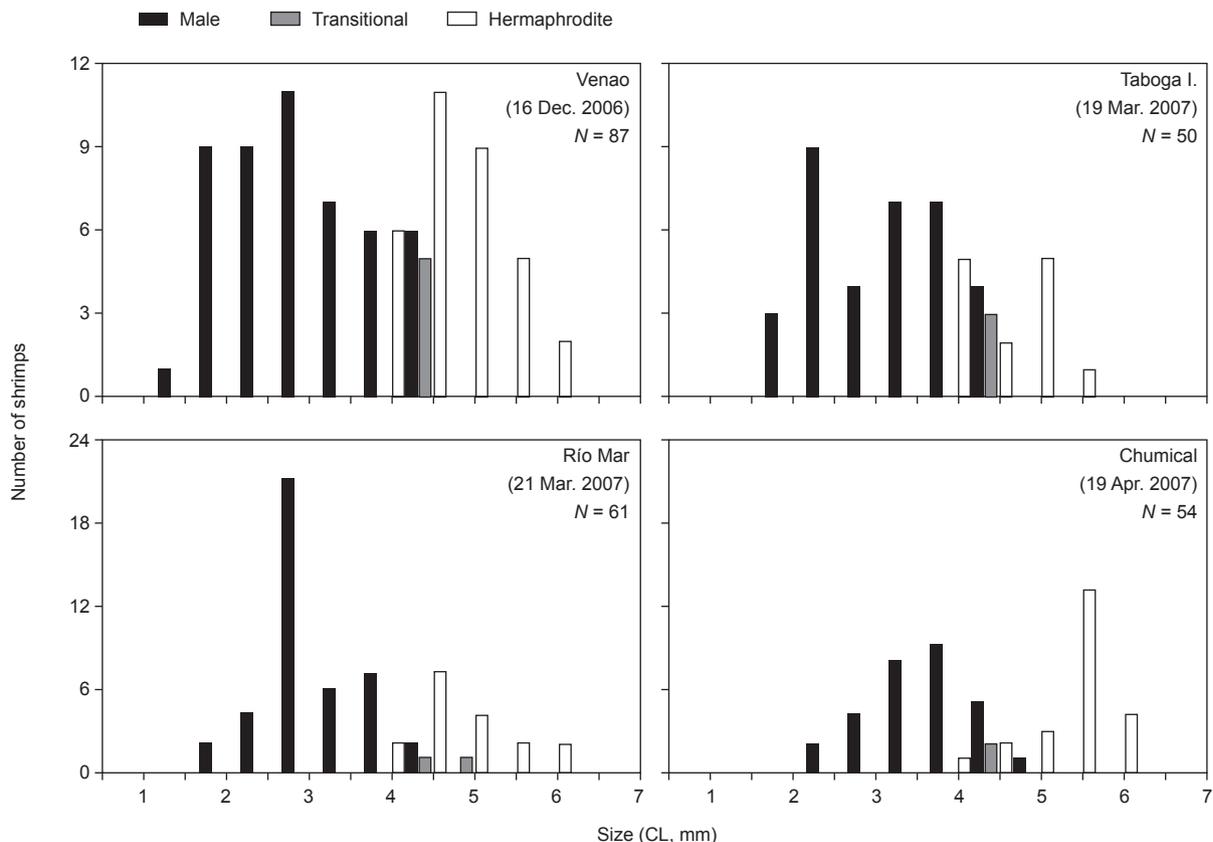


Fig. 6. Population structure of *Lysmata holthuisi* sp. nov. at different localities on the Pacific coast of Panama, from sampling conducted in Dec. 2006-Apr. 2007 (males light gray, transitional phase dark gray, hermaphrodites black).

Exhippolysmata). Phylogenetic studies within the genus *Lysmata*, a well as a genus-level analysis of the Hippolytidae sensu lato will shed more light onto the evolutionary origins of protandric simultaneous hermaphroditism.

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