Zootaxa 1577: 41–60 (2007)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Revision of the *Alpheus nuttingi* (Schmitt) species complex (Crustacea: Decapoda: Alpheidae), with description of a new species from the tropical eastern Pacific

ARTHUR ANKER*[1], CARLA HURT[1, 3], NANCY KNOWLTON[1,2,4]

[1]*Instituto Smithsonian de Investigaciones Tropicales, Apartado 0843–03092, Balboa, Ancón, Panamá, República de Panamá / Smithsonian Tropical Research Institute, Naos Unit 0948, APO AA 34002, USA*

[2]*Center for Marine Biodiversity and Conservation-0202, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, 92093-0202, USA*

[3]*Present address: University of Miami, Department of Biology, Coral Gables, FL, 33124-9118, USA*

[4]*Future address: National Museum of Natural History, Smithsonian Institution, Washington DC, 20013-7012 USA*

**Corresponding author: ankera@si.edu*

Abstract

The *Alpheus nuttingi* (Schmitt, 1924) species complex consists of three species. The only western Atlantic species, *A. nuttingi*, occurs from the southeastern United States to Brazil. The two eastern Pacific species are *A. galapagensis* Sivertsen, 1933 (synonyms: *A. canalis* Kim & Abele, 1988; *A. cryptodentatus* Christoffersen & Ramos, 1988), which occurs from the Gulf of California to Colombia and Galapagos, and *A. millsae*, n. sp., presently known only from a few localities in Panama. The three species differ morphologically, genetically, and in color pattern. The two eastern Pacific species both can be found in the intertidal, but *A. millsae*, n. sp. occurs slightly deeper, suggesting the possibility of ecological speciation. All evidence shows that *A. nuttingi* and *A. millsae*, n. sp. are transisthmian sister species, with *A. galapagensis* forming their sister clade. Genetic differentiation between the transisthmian sister species suggests a divergence time of approximately 6 mya, well before the final closure of the Isthmus of Panama.

Key words: *Alpheus*, snapping shrimp, species complex, transisthmian taxa, color pattern, eastern Pacific, western Atlantic, sibling species, COI, barcode

Introduction

The largest and morphologically most heterogenous species group within the speciose genus *Alpheus* Fabricius, 1798 is the *A. edwardsii* (Audouin, 1826) group (Coutière, 1899), with at least 95 described species worldwide (Anker, 2001b). This group is characterized mainly by the unarmed orbital hoods and the presence of two notches on the major chela: one on the dorsal margin and one on the ventral margin of the palm (e.g., Banner & Banner, 1982). However, based on molecular data, Williams *et al.* (2001) suggested that this configuration of the major chela may have evolved independently more than once within *Alpheus*, i.e., the *A. edwardsii* group may be polyphyletic. One of these clades contains the majority of species of the *A. edwardsii* group, including the western Atlantic *A. nuttingi* (Schmitt, 1924) and an eastern Pacific taxon that has had several names (see below), including *A. galapagensis* Sivertsen, 1933 and *A. canalis* Kim & Abele, 1988. These two closely related species differ from all the other American species of the *A. edwardsii* group by the sharply carinate rostrum; the deep adrostral furrows, not abruptly delimited from the orbital hoods or rostrum; the simple conical dactyli on the walking legs; the merus of the major cheliped with a minute distomesial tooth; the minor cheliped with fingers neither expanded nor balaeniceps, and with sharp, proximally some-

Accepted by J. Goy: 20 Jul. 2007; published: 7 Sept. 2007

what convex cutting edges; and the distal margin of the telson and uropodal endopod bearing a row of spinules.

Knowlton & Mills (1992) and Knowlton *et al.* (1993) documented the presence of two distinct forms in the eastern Pacific that they called *A. canalis* sp-a and *A. canalis* sp-b. The two eastern Pacific forms differed from each other as well as from the western Atlantic *A. nuttingi* in color pattern (Knowlton & Mills, 1992) and genetics (proteins, mitochondrial DNA) (Knowlton *et al.*, 1993). Pairing tests showed that these three forms were also reproductively isolated (Knowlton *et al.*, 1993). Williams *et al.* (2001) confirmed genetic and color differences, calling the two eastern Pacific forms *A. canalis* "blue" (or "blue antennae") and *A. canalis* "orange" (or "orange antennae"). However, their taxonomic status was never formally established.

McClure & Wicksten (2000) concluded that *A. canalis* is a junior synonym of *A. galapagensis* Sivertsen, 1933, based on reexamination of the type material of the latter species [two ovigerous female paratypes deposited in the collections of the Zoological Museum of Oslo (ZMO F.89)]. The illustrated minor chela (found loose in the vial together with the body of one of the paratypes; see McClure & Wicksten, 2000, fig. 3H) appears to belong to another specimen of a different species (see discussion in McClure & Wicksten, 2000).

Wicksten & Hendrickx (2003) suggested that *Alpheus cryptodentatus* Christoffersen & Ramos, 1988 described from Ensenada de Utría on the Pacific coast of Colombia (Christoffersen & Ramos, 1988) may be another junior synonym of *A. galapagensis*. We examined a specimen of *A. galapagensis* from Las Perlas Islands, about 250 km from the type locality of *A. cryptodentatus*, and contrasted it to the description and illustrations of *A. cryptodentatus* in Christoffersen & Ramos (1988). We found that our specimen from Las Perlas agrees in all important features with *A. cryptodentatus*, especially in the presence of a minute tooth on the mesioventral margin of the major cheliped merus (the origin of the name *A. cryptodentatus*), a very large and stout plunger on the major chela dactylus, and the sharp, proximally convex cutting edges of the pollex of the non-balaeniceps minor chela. Therefore, *A. cryptodentatus* should also be regarded as a junior synonym of *A. galapagensis*.

Alpheus galapagensis bears a small spine on the ischium of the third pereiopod (see McClure & Wicksten, 2000, fig. 3J; see also Kim & Abele, 1988, fig. 30j, as *A. canalis*; Christoffersen & Ramos, 1988, fig. 2F, as *A. cryptodentatus*), a feature also present in *A. canalis* sp-a (orange antennae) of Knowlton & Mills (1992), Knowlton *et al.* (1993) and Williams *et al.* (2001). In contrast, both *A. canalis* sp-b (blue antennae) and *A. nuttingi* lack this spine. The previously reported reproductive incompatibility and differences in color and genetics between *A. canalis* sp-b and *A. nuttingi* (Knowlton & Mills, 1992; Knowlton *et al.*, 1993; Williams *et al.*, 2001) leave no doubt that the two forms represent distinct, transisthmian, cryptic sister species. Therefore, *A. canalis* sp-b, a hitherto undescribed form, is described below as *A. millsae*, n. sp. Diagnostic features of the three species are summarized, and illustrations are provided for the new species and *A. nuttingi*, for which the only good drawings available were those of Schmitt (1924, fig. 4–6, frontal region and major claw) and Hendrix (1971, pls. 14, 15, extensive drawings in an unpublished thesis). The color patterns of *A. galapagensis*, *A. nuttingi* and *A. millsae*, n. sp. are illustrated. An updated synonymy and all known records of the three species of the *A. nuttingi* complex are provided. GenBank barcodes (COI) are provided for voucher specimens of each species.

Material and methods

Most specimens were collected intertidally under rocks. Selected specimens were photographed and preserved in 95% EtOH or RNAlater (Ambion) for DNA/RNA sequencing. All drawings were made under a dissecting microscope with the aid of a camera lucida. The type material is deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM); Muséum

national d'Histoire naturelle, Paris, France (MNHN); Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (RMNH); and Colección de Referencia, Departamento de Biología Marina, Univesidad de Panamá, Panama City, Panama (UP); additional specimens are deposited in the USNM, MNHN, UP and Oxford University Museum of Natural History, Oxford, UK (OUMNH-ZC). Barcode voucher specimens will be deposited in the USNM. Other abbreviations used in the text: A1—antennule / antennular; Abd—abdomen / abdominal; Mxp—maxilliped; P—pereiopod; CL—carapace length (measured along mediodorsal line from the tip of the rostrum to the posterior margin of the carapace); TL—total length (measured from the tip of the rostrum to the posterior margin of the telson); fcn—field collection number.

COI sequences were obtained from cDNA rather than from direct amplification of genomic DNA, in order to reduce the risk of amplification of nuclear pseudogenes, previously shown to be pervasive within the genus *Alpheus* (Williams & Knowlton, 2001). Total RNA was extracted using the SV Total RNA Isolation System (Promega) following manufacturers' instructions. First-strand synthesis of cDNA was performed using MuLV reverse transcriptase and RNase inhibitor (Applied Biosystems) and a T_{18} Reverse Primer. The resulting cDNA was then used as template in polymerase chain reaction (PCR) using universal primers HCOI/LCOI from Folmer *et al*. (1994) to amplify 665 bp from the 5' end of the mitochondrial COI gene (corresponding to the target region for the COI Barcode) [www.barcodinglife.org], and primers COIF / COI(10) (Williams & Knowlton, 2001) to amplify the adjacent 677 bp from the same gene, for a total of 1224 bp (sequences overlapped slightly).

PCR amplifications were carried out in 30-µL volumes containing 0.1 µM forward and reverse primer, 200 µM each dNTP, 2.0 mM $MgCl^{2+}$, 1.5 units of Amplitaq Gold DNA polymerase, and 3 µL Amplitaq 10X PCR Buffer II. Thermocycler parameters were as follows: 95°C for 10 min; 30 cycles of 95° C for 30 s, 50°C for 30 s, 72°C for 1 min + 2 s/cycle; with a 10 min final extension at 72°C. PCR products were gel excised on a 1% (w/v) low-melt agarose gel and extracted using the Wizard SV Gel and PCR Clean-UP System (Promega), following manufacturers' instructions. An aliquot (2 µl) of the purified PCR product was quantified by electrophoresis on an analytical gel, and DNA concentrations were determined by comparison of fluorescence with a standard DNA mass ladder. Cycle sequencing reactions were performed using 50–100ng DNA and BigDye terminator v3.1 (Applied Biosystems) following manufacturers' instructions for cycle sequencing. Reaction products were separated from unincorporated dye-terminators by centrifugation through Sephadex G-50 columns in a 96-well filter plate (Millipore). Products of sequencing reactions were run on a 3700 Applied Biosystems automated capillary sequencer.

Genetic distances were calculated using the Kimura-2-Parameter (K2P) distance method as implemented in Mega v3.1 in order to facilitate comparisons with alpheid distances obtained previously (Knowlton *et al*., 1993; Knowlton & Weigt, 1998). A rate of 1.5 % sequence divergence per million years was used to estimate the timing of divergence of sister taxa. This rate was estimated by averaging the K2P genetic distances for both 5' and 3' COI sequences obtained from the transisthmian sister species pair *Alpheus antepaenultimus* Kim & Abele, 1988 / *A. chacei* Carvacho, 1979 (GenBank accession numbers AF309875, AF309876, AF309884, AF308989, AF308983, EF532616—EF532619). This geminate species pair has the smallest observed genetic distance of all transisthmian comparisons, and its divergence is likely to correspond to the final closing of the Isthmus of Panama approximately three million years ago (Knowlton & Weigt, 1998). This rate differs slightly from the published rate of 1.4% (Knowlton & Weigt, 1998), obtained from comparisons of COI sequences from the 3' end only.

Taxonomy

Alpheus Fabricius, 1798

Alpheus nuttingi (Schmitt, 1924)

Figs. 1, 5A, 6A, 7A–C, 8A

Crangon nuttingi Schmitt, 1924: 78, pl. 2, figs. 4–6

Alpheus nuttingi – Hendrix, 1971: 111, pls. 14, 15; Chace, 1972: 68; Christoffersen, 1979: 304; Christoffersen, 1980: 92, figs. 21–23; Santos, 1981: 342, figs. 17f, g, 18a, b, f; Abele & Kim, 1986: 199, 214, 215, figs. e, h; Knowlton & Mills, 1992: 2; Hernández-Aguilera *et al.*, 1996: 33; Martínez-Iglesias *et al.*, 1997: 425; Christoffersen, 1998: 360; Santos & Coelho, 1998: 76, fig. 16; McClure, 2005: 147, fig. 18.

Alpheus nutting (lap. cal.) – Spivak, 1997: 72.

Not *Alpheus nuttingi* var. ? – Schmitt, 1936: 368 (= *A.* cf. *bouvieri* A. Milne-Edwards, 1878)

Alpheus heterochaelis (not Say 1818) – Smith, 1871: 23 (part.); Rathbun, 1900: 152 (part.); Luederwaldt, 1919: 429 (part.) (see Christoffersen, 1984).

Crangon heterochaelis (not Say, 1818) – Schmitt, 1939: 28 (part.) (see Christoffersen, 1984).

Material examined.—**Panama**: 1 male, USNM 1100678, Bocas del Toro, Isla Carenero, near Bucaneer, under rocks on sand/silt, depth: 0.5–1 m, coll. A. Anker, 25 Oct 2005 [fcn 05-143]; 1 female, USNM 1100679, same collection data as previous specimen [fcn 05-138]; 1 male, USNM 1100680, Bocas del Toro, Hospital Point, under rocks on sand/silt, depth: 0.5–1 m, coll. A. Anker, 16 Oct 2005 [fcn 05-140]; 1 ovig. female, MNHN-Na 16364, Bocas del Toro, Isla Colon, between Big Creek and Playa Bluff, from crevices in coral rocks, depth: 1–2 m, coll. A, Anker, 18 Oct 2005 [fcn 05-142]; 2 males, USNM 1100682, Bocas del Toro, Isla Colon, Bocas del Drago, from coral rocks, depth: 0.5–1 m, coll. A. Anker, 20 Oct 2005 [fcn 05-141]; 1 male, USNM 1100681, Coco Solo, near Colón, under rocks, coll. N. Knowlton lab, 22 Feb 1995 [fcn B331, C-1239]. **Costa Rica**: 1 male, MNHN-Na 16365, Cahuita, Puerto Vargas, under rocks and coral rubble, among seagrass roots, depth: 0.5–1 m, coll. A. Anker, 26–27 Nov 2005 [fcn 05-144]. **Aruba**: 1 male, 1 female, MNHN-Na 16366, southern coast east of international airport, Pos Chiquito, from coral rocks, depth: 0.5–1 m, coll. A. Anker, 7–8 Dec 2003 [fcn 03-013].

Description.—For complete description see Schmitt (1924) and Hendrix (1971). An adult male from Panama is illustrated in Fig. 1 for comparison with the below-described *A. millsae*, n. sp.

Size.—The largest examined male is 12.7 mm CL and 36.8 mm TL. Hendrix (1971) gave the size range for Florida specimens as 5.5–10.0 mm CL for males and 6.0–9.16 mm CL for females.

Color.—Body greenish (combination of reddish and bluish chromatophores) speckled with numerous pale yellow or greenish dots, some interconnected, forming chains and small reticulations; flanks of carapace dull greenish to whitish; legs reddish with some spots and white patches marking articulations; third and fourth abdominal somite occasionally with a pair of minute dark-brown dorsolateral spots; fifth somite occasionally with one minute brown mediodorsal spot; major and minor chelae mesially greenish-brown with numerous whitish spots and patches, many of them interconnected, especially on distal half of palm and fingers; pale orange or yellow areas marking palmar depressions; dactylus of major chela pinkish-white distally; antennular and antennal flagella pale blue (Fig. 7A, B); ovigerous females with yellow-orange eggs (Fig. 8A); young individuals paler, more reticulated (Fig. 7C). A similar color description was provided by Hendrix (1971).

Type locality.—Pelican Island, Barbados (Schmitt, 1924).

Distribution.—Western Atlantic: from southern Florida (Abele & Kim, 1986) and southwestern Gulf of Mexico (McClure, 2005) throughout Caribbean Sea (Chace, 1972) to Santa Catarina, southern Brazil (Christoffersen, 1998). Brazilian specimens are genetically distinct from the Caribbean specimens (Williams *et al.*, 2001; see also below) despite having the same color pattern (A. Anker, pers. obs., based on color photographs by E. Mossolin).

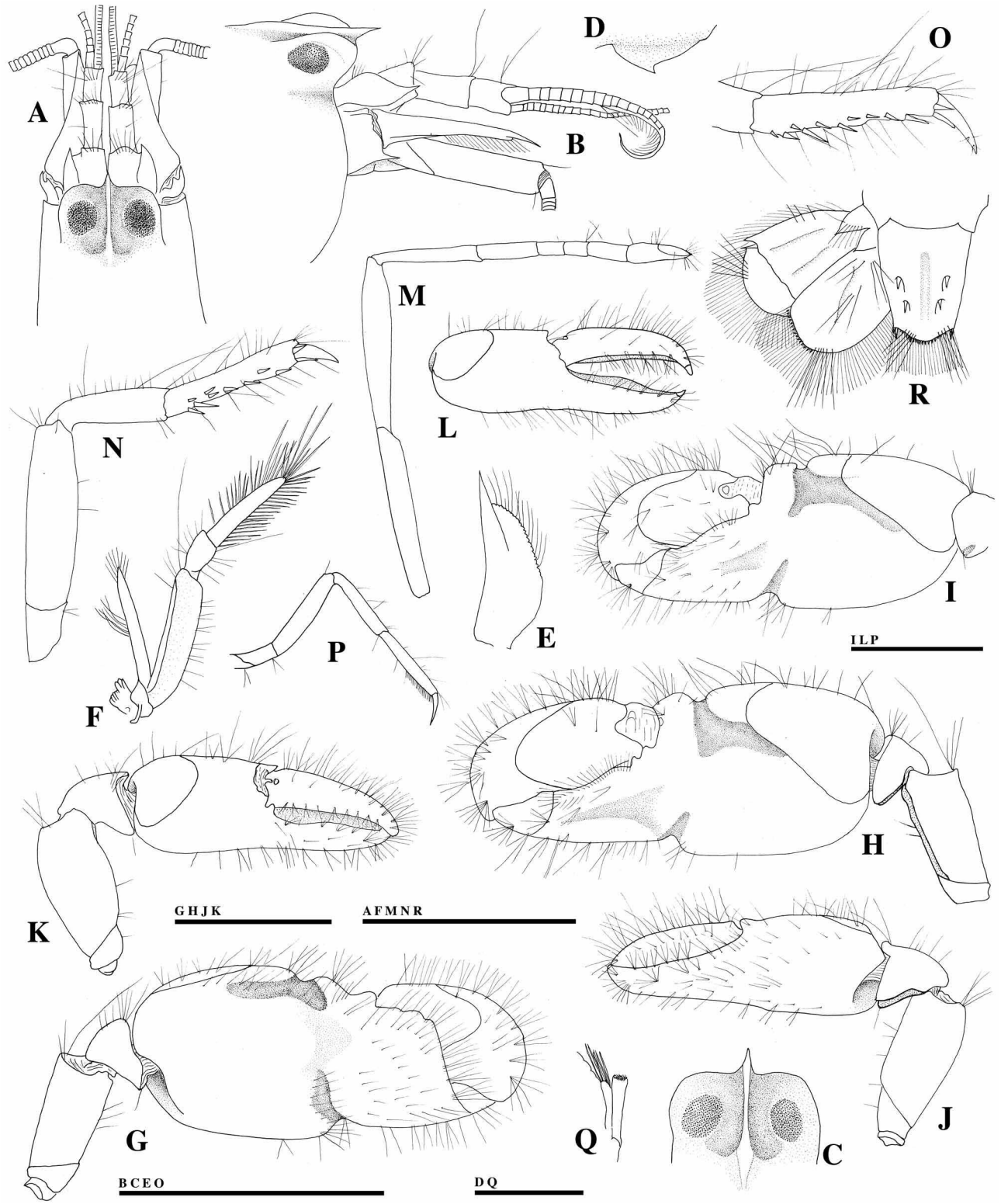

FIGURE 1. *Alpheus nuttingi* (Schmitt, 1924), male specimen from Colón, Panama (USNM 1100681): A, frontal region, dorsal view; B, same, lateral view; C, orbital hoods and rostrum, dorsal view; D, tooth on ventromesial carina of first segment of antennular peduncle, lateral view; E, scaphocerite of antenna, dorsal view; F, third maxilliped, lateral view; G, major cheliped, mesial view; H, same, lateral view (chela slightly dorsolateral); I, same, chela, lateral view; J, minor cheliped, mesial view; K, same, lateral view; L, chela with opened fingers, lateral view; M, second pereiopod, lateral view; N, third pereiopod, lateral view; O, same, propodus and dactylus; P, fifth pereiopod, lateral view; Q, second pleopod, appendix masculina and appendix interna, mesial view; R, left uropod and telson, dorsal view. Scale bars: 5 mm (AFMNR, BCEO, GHJK, ILP), 1 mm (DQ).

Ecology.—*Alpheus nuttingi* is a very common *Alpheus* species in the Caribbean region and along the Brazilian coast. It occurs mostly on sandy bottoms with abundant coral rubble and rocks, often near *Thalassia* beds; in crevices of coral rocks; among sandy reefs of sabellariid polychaetes; in clumps of *Halimeda* and similar habitats in depths ranging from the intertidal to about 5 m (Hendrix, 1971; Chace, 1972; Christoffersen, 1998).

Remarks.—*Alpheus nuttingi* differs from the closely related *A. millsae*, n. sp. (see description below) mainly by the shorter rostral carina (Fig. 1C); the larger and more robust plunger of the dactylus of the major chela (Fig. 5A); the broader dorsal notch on the palm of the major chela (Fig. 5A); the relatively thicker fingers of the minor chela (Fig. 6A); and by the color pattern, especially by the pale dots being mostly chained or interconnected (vs. isolated in *A. millsae*, n. sp., cf. Fig. 7) (see also Table 1). It differs from *A. galapagensis* by the absence of a spine on the ischium of the third pereiopod (Fig. 1N), which is always present in *A. galapagensis* (see Kim & Abele, 1988, fig. 30j), and by the color pattern, especially the blue antennal and antennular flagella (orange in *A. galapagensis*, cf. Fig. 7) (see also Table 1).

TABLE 1. Summary of variable features within the *Alpheus nuttingi* species complex. The features 1–4, 8 and 9 (marked with an *) appear to be consistent and are therefore diagnostic. The features 5-7 and 10 are less reliable, but can be used as supporting characters in combination with other features. EP – Eastern Pacific; WA – Western Atlantic.

Character	*A. nuttingi* [WA]	*A. millsae*, n. sp. [EP]	*A. galapagensis* [EP] Synonyms: *A. canalis*, A. cryptodentatus
1. Spine on ischium of P3*	absent	absent	present
2. Rostral carina*	extending slightly beyond orbital hoods	extending far beyond orbital hoods	extending slightly beyond orbital hoods
3. Finger of minor chela in large males*	thick relative to palm	slender relative to palm	thick relative to palm
4. Plunger of dactylus of male major chela*	very large	moderately large, distally truncated	very large
5. Dorsal notch of male major chela, width/height*	ratio ~2 (notch broader)	ratio < 2 (notch narrower)	ratio < 2 (notch narrower)
6. Color: dark spots on abdominal somites 3–5	feebly marked or absent	well marked	feebly marked or absent
7. Color: pale patches on major claw	may be present in large individuals	may be present in large individuals	usually present (always in large individuals)
8. Color: antennular and antennal flagella*	pale blue	pale blue	pale orange
9. Color: pale spots on carapace/abdomen*	most interconnected or chained	most isolated	most isolated
10. Color: blue/white spots on major claw	irregular, densely spaced, often interconnected	irregular, densely spaced, often interconnected	usually rounded, widely spaced and not interconnected
11. Color of freshly-laid eggs in females	orange	olive-green (? eggs developed)	bright green

The presence or absence of small dark (blackish or dark brown) spots on the third (two dorsolateral), fifth (one median) and occasionally fifth (one median) abdominal somites is shown here not to be a reliable character. These spots are always present in *A. millsae*, n. sp. (Fig. 7G, H) and are usually absent in *A. nuttingi* (Fig.

7A, C); however, at least two examined specimens of the latter species have feebly marked brown spots on the abdomen (Fig. 7B), thus making this feature too ambiguous to be used for species discrimination. The color of freshly-laid eggs (orange in one photographed female of *A. nuttingi*, cf. Fig. 8A), if shown to be constant, may also separate *A. nuttingi* from the two eastern Pacific species, in particular from *A. galapagensis*, in which the eggs are bright green (cf. Fig. 8B).

The shape of the tooth on the mesioventral carina of the first segment of the antennular peduncle appears to be variable in *A. nuttingi* and other species of the complex (see below). This tooth usually bears an acute or subacute point (Fig. 1D), but is bluntly subtriangular in some specimens, resembling the tooth in *A. galapagensis* illustrated by Kim & Abele (1988, fig. 30c). The minor chela is more slender in younger males and females compared to larger adult males.

A minor detail that Hendrix (1971) overlooked in his otherwise very detailed description of *A. nuttingi* is the presence of spinules on the distal margin of the telson and uropodal endopod (Fig. 1R); these spinules are also present in *A. galapagensis* (Kim & Abele, 1988, fig. 30l) and *A. millsae*, n. sp. (Fig. 4R, see below).

GenBank number.—COI 5' EF092281 (fcn 05-127), EF092282 (fcn 06-417); COI 3' AF309922 (fcn 98-330) AF309921 (fcn 98-282), AF309000 (fcn 98-282).

Alpheus galapagensis Sivertsen, 1933

Figs. 2, 5B, 6B, 7D–F, 8B

Alpheus strenuus var. *galapagensis* Sivertsen, 1933: 3, pl. 1, figs. 1–5; Banner & Banner, 1982: 228.
Alpheus galapagensis—Kim & Abele, 1988: 102, fig. 43; Wicksten & Hendrickx, 1992: 5; McClure & Wicksten, 2000: 968, fig. 3; Hickman & Zimmerman, 2000: 36; Wicksten & Hendrickx, 2003: 64.
Alpheus canalis Kim & Abele, 1988: 72, fig. 30; Villalobos Hiriart *et al.*, 1989: 20; Ríos, 1989: 105, pl. 20; Ríos, 1992: 4; Flores-Hernández, 1991: 106; Lemaitre & Alvarez-Leon, 1992: 42; Wicksten & Hendrickx, 1992: 4; Hernández Aguilera & Martínez Guzman, 1992: 4; Hendrickx, 1992: 9; Hendrickx, 1993a: 306; Hendrickx, 1993b: 6; Hendrickx, 1995: 432; Camacho, 1996: 80; Vargas & Cortés, 1999: 899; Villalobos, 2000: 43, fig. 21; McClure & Wicksten, 2000: 968, fig. 3 (part., not fig. 3H).
Alpheus canalis sp-a—Knowlton & Mills, 1992: 2.
Alpheus canalis sp. a—Knowlton *et al.*, 1993: 1630.
Alpheus canalis "orange" – Williams *et al.*, 2001: 377.
Alpheus canalis "orange antennae" —Williams *et al.*, 2001: 385.
Alpheus cryptodentatus Christoffersen & Ramos, 1988: 61, figs. 1, 2.

Material examined.—**Panama**: 1 male, USNM 1100683, Las Perlas, small island facing Contadora, rocky intertidal, under rocks on coarse sand, extreme low tide, coll. A. Anker, C. Hurt, E. Gómez, J. Jara and E. Tóth, 31 Mar 2006 [fcn 06-382]; 1 male, 1 ovig. female, MNHN-Na 16367, Amador, Punta Culebra, rocky intertidal, under large rocks on sand, low tide, coll. A. Anker and C. Hurt, 2 Mar 2006 [fcn 06-284]; 1 male, USNM 1100684, same collection data as previous specimen [fcn 06-301]; 1 ovig. female, MNHN-Na 16367, same collection data as previous specimen [fcn 06-286]; 1 male, 1 ovig. female, MNHN-Na 16368, Río Mar, intertidal, under rocks on silt/sand, low tide, coll. A. Anker, C. Hurt, J. Jara and E. Gómez, 3 Mar 2006 [fcn 06-298]; 1 ovig. female, USNM 1100685, same collection data as previous specimen [fcn 06-256]; 1 male, OUMNH-ZC 2006-10-0005, Pacific coast of Panama near Panama City, rocky intertidal, coll. J. Jara, Jan 2006 [fcn 06-285]; 1 female, UP, Amador Causeway, Isla Naos, Punta Culebra, under rocks at low tide, coll. A. Anker and I. Marin, 17 Apr 2004 [fcn 07-123]. **Costa Rica**: 1 male, 1 ovig. female, MNHN-Na 16384, Punta Morales, Playa Blanca, rocky intertidal, under oyster-covered rocks on coarse sand, low tide, coll. A. Anker, 22 Nov 2005 [fcn 05-145].

Description.—For complete description see Sivertsen (1933), Kim & Abele (1988, as *A. canalis*), Christoffersen & Ramos (1988, as *A. cryptodentatus*) and McClure & Wicksten (2000).

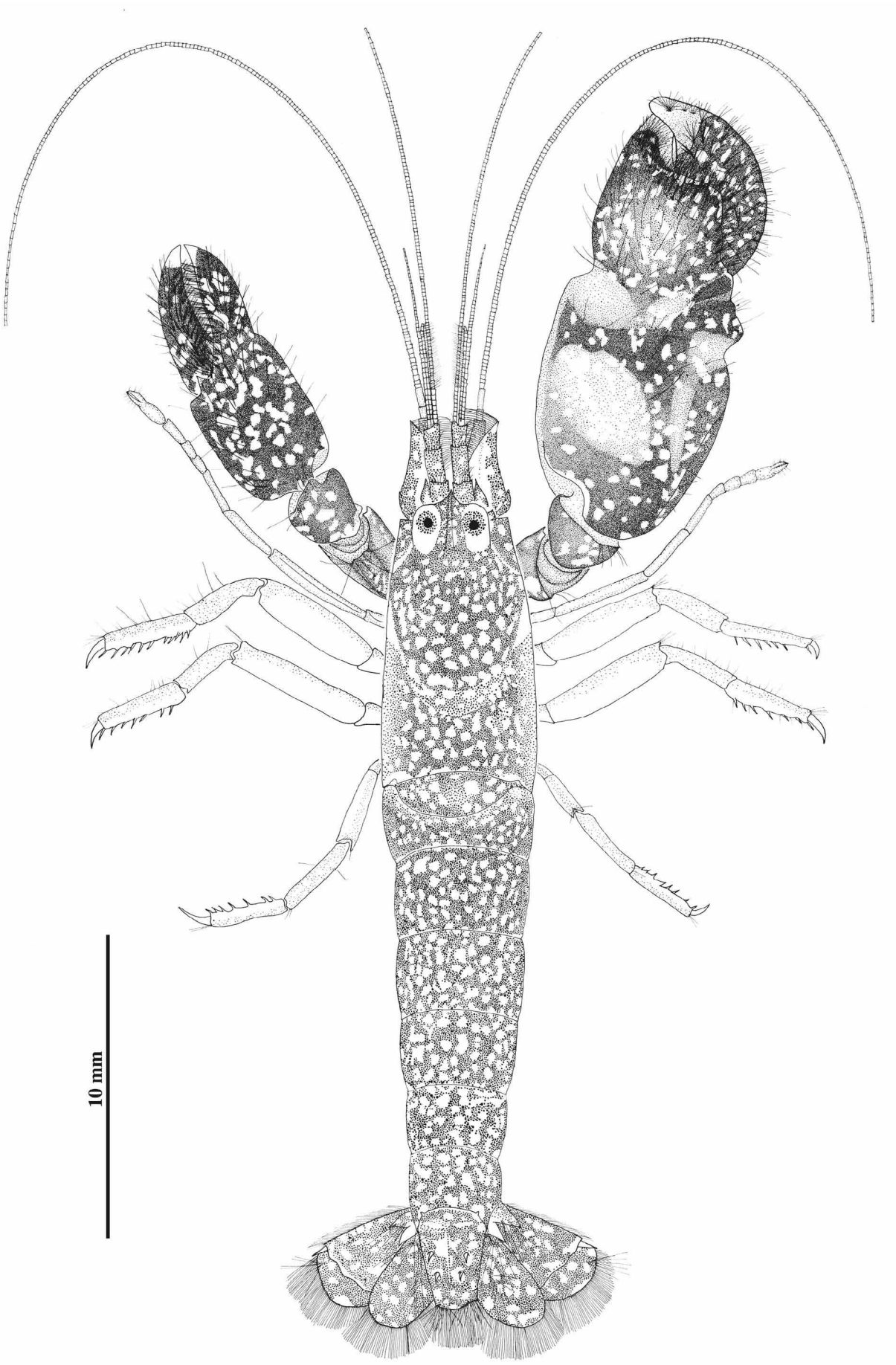

FIGURE 2. *Alpheus galapagensis* Sivertsen, 1933, color pattern, drawn from living male specimen from Playa Corona, Panama.

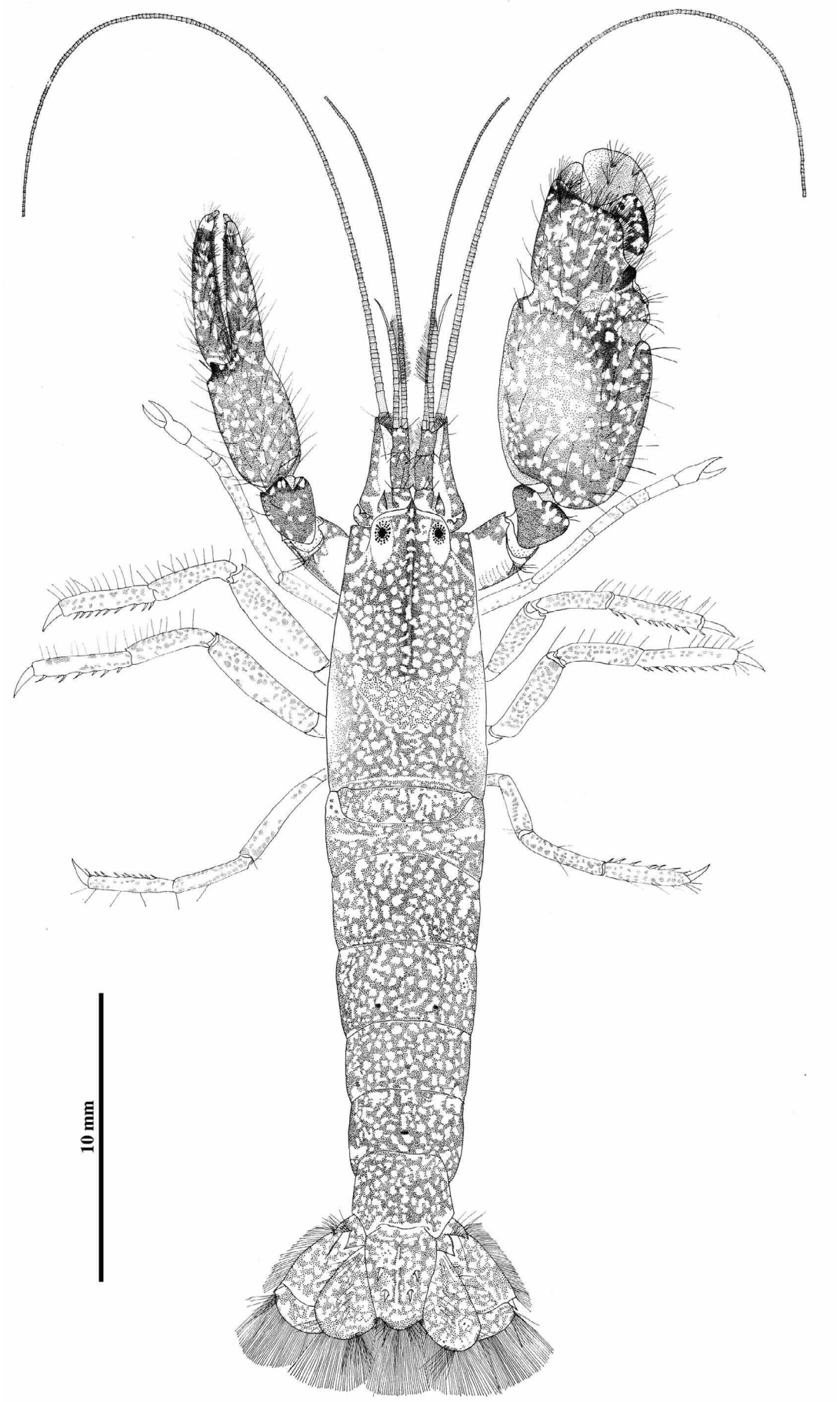

FIGURE 3. *Alpheus millsae*, n. sp., color pattern, drawn from living female specimen from Casco Viejo, Panama.

Size.—The largest examined male from Panama (fcn 06-284) is 13.2 mm CL and 40.0 mm TL. Kim & Abele (1988) gave the size range for their specimens as following: males, 5.8–15.1 mm CL; females, 5.2–14.1 mm CL; ovigerous females, 6.1–15.0 mm CL.

Color.—Body greenish (combination of reddish and bluish chromatophores) speckled with numerous pale yellow dots or small yellowish spots, most of them isolated and not interconnecting; flanks of carapace dull greenish or whitish; legs reddish with some spots and white patches marking articulations; third and fourth abdominal somite usually with a pair of minute dark dorsolateral spots; fifth somite usually with one minute brown mediodorsal spot; major and minor chelae mesially greenish-brown with numerous whitish or pale bluish spots and dots, most isolated, not interconnecting; large yellow areas marking palmar depressions in larger specimens; dactylus of major chela pinkish distally; antennular and antennal flagella pale orange (Fig. 2, 7D–F); ovigerous females with bright green eggs (Fig. 8B). A similar color description was provided by Christoffersen & Ramos (1988, as *A. cryptodentatus*); a color photograph of a specimen from Galapagos was published by Hickman & Zimmerman (2000).

Type locality.—Floreana, Galapagos (Sivertsen, 1933).

Distribution.—Eastern Pacific: from central Gulf of California through western Mexico, El Salvador, Costa Rica and Panama to Colombia and Galapagos (Sivertsen, 1933; Kim & Abele, 1988; Christoffersen & Ramos, 1988; McClure & Wicksten, 2000; Villalobos, 2000; Wicksten & Hendrickx, 2003).

Ecology.—*Alpheus galapagensis* is a common snapping shrimp on the rocky and mixed rocky-sandy intertidal of the tropical eastern Pacific. It occurs on sand, mud, silt and rock bottoms, under rocks and rubble, in tidal lava pools, occasionally also in crevices of rocks and corals (Villalobos, 2000; Wicksten & Hendrickx, 2003; present study). The depth range of this species extends from the mid-intertidal to about 15 m, exceptionally as deep as 37 m (Villalobos, 2000). Some specimens were found under rocks together with fire worms (Amphinomidae), a facultative, protective association that is also observed in some other shallow water *Alpheus* species throughout the world (A. Anker, pers. obs.).

Remarks.—*Alpheus galapagensis* may be easily distinguished from both *A. nuttingi* and *A. millsae*, n. sp. (see description below) by the presence of a small spine on the ischium of the third pereiopod (see Kim & Abele, 1988, fig. 30j), and in life by the less densely spaced, usually rounded spots on the mesial face of the major claw (vs. more densely spaced, irregularly shaped and often interconnecting in the other two species, cf. Fig. 7), and the orange antennal and antennular flagella (vs. blue in the other two species, cf. Fig. 7) (see also Table 1). Like in *A. nuttingi*, the shape of the tooth on the mesioventral carina of the first segment of the antennular peduncle appears to be variable in *A. galapagensis*; it may be blunt (cf. Kim & Abele, 1988, fig. 30c) or bear a minute acute point, as in some of the present specimens. The color of freshly-laid eggs (green in one photographed female of *A. galapagensis*, cf. Fig. 8B), if shown to be constant, may separate *A. galapagensis* from *A. nuttingi*, in which the eggs are orange (cf. Fig. 8B).

The synonymy of *A. cryptodentatus* with *A. galapagensis*, although very likely, needs confirmation by examination of the type specimens of *A. cryptodentatus* deposited in the collections of the Universidade Federal da Paraíba in João Pessoa, Brazil (UFPB).

GenBank number.—COI 5' EF092284 (fcn JJ-AC-28); COI 3' AF309883 (fcn 98-089).

***Alpheus millsae*, n. sp.**
Figs. 3, 4, 5C, 6C, 7G–H, 8C

Alpheus canalis sp-b— Knowlton & Mills, 1992: 2.
Alpheus canalis sp. b—Knowlton *et al.*, 1993: 1630.
Alpheus canalis "blue"—Williams *et al.*, 2001: 377.
Alpheus canalis "blue antennae"—Williams *et al.*, 2001: 385.

Material examined.—1 male, holotype, CL 13.7 mm, USNM 1100686, Panama, Panama City, off Casco Viejo, rocky intertidal, near extreme low tide mark, under rocks on coarse sand, coll. A. Anker, C. Hurt, J. Jara and E. Tóth, 30 Mar 2006 [fcn 06-343]; 1 male, 1 ovig. female, paratypes, USNM 1100687, same collection data as for holotype [fcn 06-346]; 1 male, 1 ovig. female, paratypes, MNHN-Na 16369, same collection data as for holotype [fcn 06-345]; 1 ovig. female, paratype, RMNH D 51746, same collection data as for holotype [fcn 06-344]; 1 male, USNM 1100688, Río Mar, rocky intertidal, under rocks, coll. N. Knowlton lab., 19–20 Feb 1992 [fcn B-112, C-391, dissected]; 1 ovig. female, USNM 1100689, same collection data as previous specimen [fcn B-112, C-392]; 1 female, 2 ovig. females, USNM 1100690, Panama, Panama City, off Casco Viejo, rocky intertidal, under rocks, coll. N. Knowlton lab., Feb 1999; 1 male, 1 ovig. female, UP, Panama, Río Mar, under large rocks at low tide, coll. A. Anker, I. Marin and J. Jara, 19 Apr 2007 [fcn 07-121].

Description.—Carapace smooth, not setose, laterally not compressed. Rostrum moderately long, slender, subtriangular, horizontal or slightly ascendant (Fig. 4B), subacute distally (Fig. 4A, C), not reaching half length of first segment of antennular peduncle (Fig. 4A); rostral carina sharply delimited between orbital hoods, broadening and becoming blunt posterior to orbital hoods, continuing as very flat, barely noticeable ridge to half length of carapace (Fig. 4A, C); adrostral furrows deep, markedly (but not abruptly) delimited posteriorly (Fig. 4A, C); orbito-rostral process rather feebly developed, with V-shaped median notch. Orbital hoods inflated, distally rounded, unarmed (Fig. 4A, C), sloping gradually into adrostral furrows; margin between rostrum and orbital hoods not protruding. Pterygostomian angle broadly rounded, not protruding (Fig. 4B); cardiac notch well developed. Eyes completely concealed in dorsal, lateral and frontal view. Ocellar beak dorsally projecting between eyes, fitting into V-shaped notch of the orbito-rostral process.

Antennular peduncles moderately slender, second segment slightly more than twice as long as first; stylocerite with acute tip, reaching to distal margin of segment (Fig. 4A); mesioventral carina of first segment with tooth usually bearing small acute point (Fig. 4D); lateral flagellum with numerous tufts of aesthetascs, secondary ramus rudimentary. Antenna with basicerite bearing strong, acute ventrolateral tooth (Fig. 4B); carpocerite stout, reaching slightly beyond distolateral tooth of scaphocerite; scaphocerite not reaching distal margin of antennular peduncle (Fig. 4A), distolateral tooth of scaphocerite reaching far beyond relatively narrow blade (Fig. 4E), lateral margin slightly concave (Fig. 4E).

Mouthparts (mandible, maxillule, maxilla, first and second maxillipeds) typical for *Alpheus*. Third maxilliped moderately stout (Fig. 4F); lateral plate with blunt apex (Fig. 4G); antepenultimate segment subtriangular in cross-section, lateral surface flattened, ventral margin straight; penultimate segment about twice as long as wide, distally widening; ultimate segment particularly setose, distally tapering (Fig. 4F).

Male major cheliped (Fig. 4I–J, 5C) with short ischium and stout merus; merus about twice as long as proximally wide; ventral surface flattened; dorsal margin distally bluntly projecting (Fig. 4I); ventromesial margin straight, distally with small blunt tooth (Fig. 4H); carpus short, cup-shaped; chela ovate, laterally somewhat compressed; dorsal and ventral margins of palm with broad transversal grooves, dorsal groove about half as high as long, adjacent shoulder rounded, not overhanging groove, sloping with angle of about 80° into groove (Fig. 4J); ventral groove broad, deep, oblique, adjacent shoulder rounded, not protruding, sloping with angle of about 90° into groove (Fig. 4J); lateral surface of palm with deep longitudinal groove extending from dorsal groove to linea impressa (Fig. 4I, J); deep oblique-transversal groove extending from ventral groove onto lateral surface (Fig. 4, I, J); very shallow depression extending from pollex to area between longitudinal and oblique-transversal grooves (Fig. 4J); mesial face with longitudinal groove extending from dorsal groove ventrally and posteriorly to below linea impressa (Fig. 4H); deep oblique-transversal groove extending from ventral groove onto mesial surface; linea impressa well marked; adhesive disks small (Fig. 4J); fingers about half-length of palm; pollex with mesiodorsal margin forming large blunt angle (Fig. 4H), distally without ridge; dactylus reaching slightly beyond pollex, proximally with longitudinal ridge or crest on mesial face (Fig. 4H–J); plunger moderately large, distally truncate (Fig. 5C), with stamen-shaped sensillae. Female major cheliped similar to male major cheliped, but smaller and more slender, chela also with somewhat different proportions (Fig. 4S).

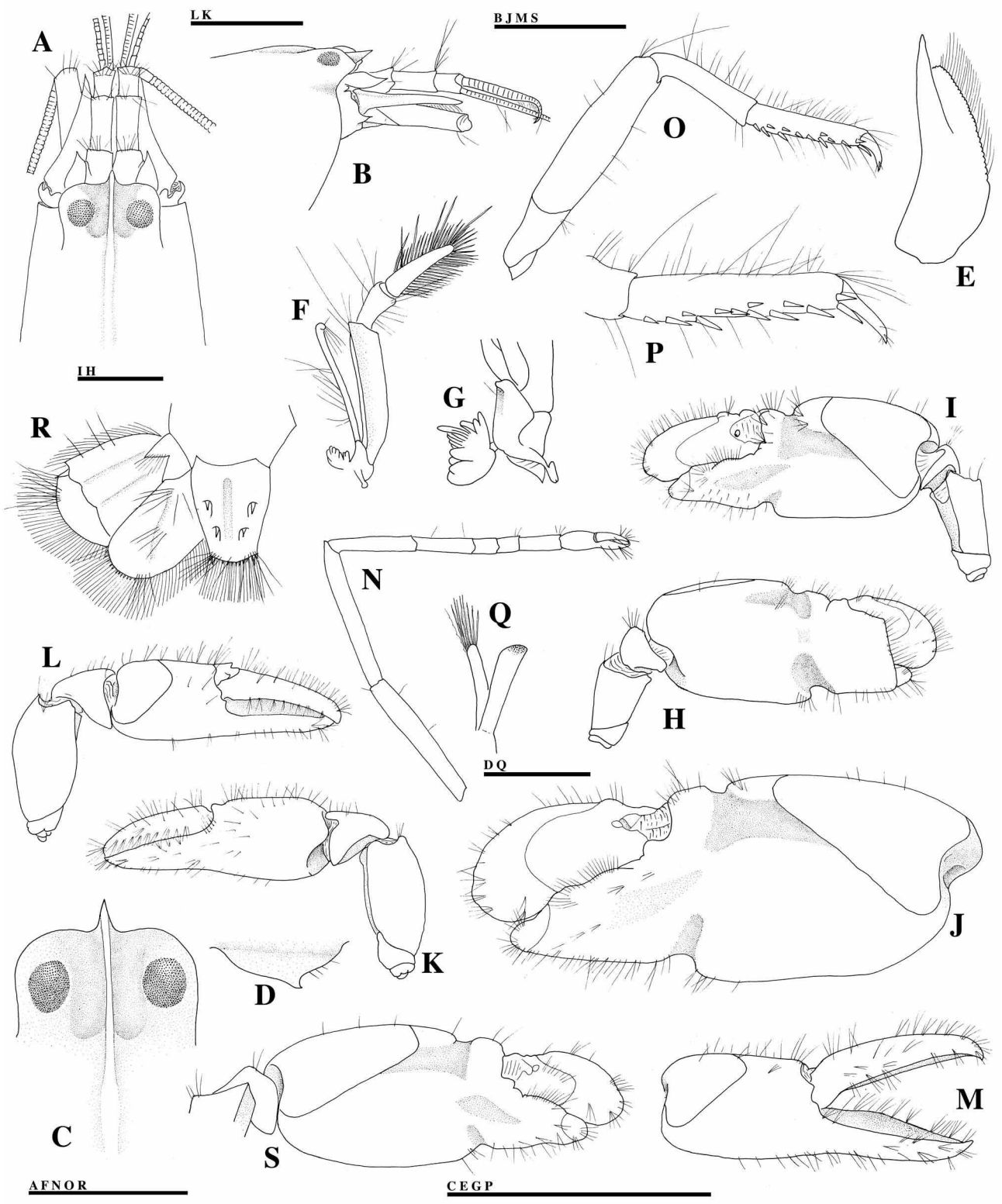

FIGURE 4. *Alpheus millsae*, n. sp., male paratype (USNM 1100688) (A–R) and female paratype (USNM 1100689) (S) from Río Mar, Panama: A, frontal region, dorsal view; B, same, lateral view; C, orbital hoods and rostrum, dorsal view; D, tooth on ventromesial carina of first segment of antennular peduncle, lateral view; E, scaphocerite of antenna, dorsal view; F, third maxilliped, lateral view; G, same, detail of coxa and arthrobranch; H, major cheliped, mesial view; I, same, lateral view (chela slightly dorsolateral); J, same, chela, lateral view; K, minor cheliped, mesial view; L, same, lateral view; M, chela with opened fingers, lateral view; N, second pereiopod, lateral view; O, third pereiopod, lateral view; P, same, propodus and dactylus; Q, second pleopod, appendix masculina and appendix interna, mesial view; R, left uropod and telson, dorsal view; S, female major chela, lateral view. Scale bars: 5 mm (AFNOR, BJMS, CEGP, IH, LK), 1 mm (DQ).

Male minor cheliped (Fig. 4K–M) with very short ischium; merus dorsally and ventrally somewhat inflated, about three times as long as wide proximally, ventromesial margin straight, distally blunt, without acute tooth; carpus cup-shaped, more elongated than carpus of major cheliped, distally with dorsomesial lobe (Fig. 4K); chela with palm slightly longer than fingers (Fig. 4M, 6C), without sculpture, distomesial margin of palm with blunt tooth (Fig. 4K, L), ventral margin slightly concave below base of pollex; linea impressa well marked; adhesive disks inconspicuous; fingers elongate, slender, about half of palm height, without rows of balaeniceps setae (Fig. 4K–M), cutting edges sharp, blade-like, that of pollex proximally slightly convex (Fig. 4M). Female minor cheliped similar, but with more slender fingers.

Second pereiopod (Fig. 4N) slender; ischium subequal to merus; carpus five-segmented, first segment longest, ratio of carpal segments (from proximal to distal) approximately 5 : 3 : 1 : 1 : 2; chela as long as second segment, simple, with fingers equal to palm (Fig. 4N). Third and fourth pereiopods similar in shape and length; third pereiopod with ischium ventrally without spine (Fig. 4O); merus with unarmed distoventral margin, about four times as long as wide; carpus with unarmed ventral margin, more slender than merus; propodus armed with about 10 spines or pairs of spines on ventral margin, and two spines on distoventral margin (Fig. 4P); dactylus simple, conical, gradually curved towards subacute tip, about one third length of propodus (Fig. 4P). Fifth pereiopod smaller and more slender than third and fourth pereiopods; ischium ventrally unarmed; propodus ventrally with at least nine spines (including distoventral spine), distolaterally with numerous rows of grooming setae; dactylus simple, conical [see Fig. 1P for almost identical fifth pereiopod in *A. nuttingi*].

Abdominal segments with broadly rounded posteroventral margins; sixth segment without articulated flap, posterior margin straight, dorsolateral projections rounded; preanal plate rounded. Male second pleopod with appendix masculina subequal to appendix interna, apex furnished with at least eight stiff, elongated setae (Fig. 4Q). Uropod with sympodite bearing distally two large subacute teeth; exopod with diaeresis bearing two large rounded lobes on lateral half (Fig. 4R), distolateral spine moderately long, slender; distal margin of endopod with row of spinules (Fig. 4R). Telson broad, tapering posteriorly; dorsal surface with median depression and two pairs of strong spines, situated far from lateral margins, anterior and posterior to telson mid-length, respectively (Fig. 4R); posterior margin broadly rounded, with two pairs of small posterolateral spines, mesial longer than lateral, and row of spinules between mesial spines (Fig. 4R); anal tubercles well developed. Gill/exopod formula typical for *Alpheus*.

Size.—The largest examined male is the holotype with 13.7 mm CL and 41.8 mm TL; the largest paratype female is 12 mm CL and 36.2 mm TL.

Color.—Body greenish-brown or greenish (combination of reddish and bluish chromatophores) speckled with numerous pale green or yellow dots or small yellowish spots, most of them isolated and not interconnecting; flanks of carapace whitish; legs reddish with some spots and white patches marking articulations; third and fourth abdominal somite with pair of minute dark dorsolateral spots; fifth somite with one minute brown mediodorsal spot; major and minor chelae mesially brown-greenish or olive-green with numerous irregular white spots and dots, most isolated, not interconnecting; pale orange areas marking palmar depressions; dactylus of major chela pink and white distally; antennular and antennal flagella pale blue or bluish-greenish (Figs. 3, 7G, H); ovigerous females with olive-green eggs (Fig. 8C).

Type locality.—Casco Viejo, Panama.

Distribution.—Eastern Pacific: presently known only from the Pacific coast of Panama, near Panama City (Amador, Casco Viejo) and Río Mar.

Ecology.—*Alpheus millsae*, n. sp. is ecologically similar to *A. galapagensis*, but appears to occur in slightly deeper water; all specimens were collected near extreme low tide mark on rocky shores, under rocks on coarse sand, locally also silt and various debris (shells, urchin tests etc.). Some specimens were found under rocks together with fire worms (Amphinomidae).

Remarks.—*Alpheus millsae*, n. sp. may be distinguished from its transisthmian sister species, *A. nuttingi*,

and from the sympatric *A. galapagensis*, by the higher and posteriorly further extending rostral carina (Figs. 4C) and shorter plunger of the dactylus on the major chela (Fig. 5C); from *A. nuttingi* by the mostly non-interconnected pale-greenish dots (vs. interconnected in *A. nuttingi*) (cf. Fig. 7); from *A. galapagensis* by the absence of a small spine on the ischium of the third pereiopod (Fig. 4O), which is always present in *A. galapagensis* (Kim & Abele, 1988, fig. 30j), the more densely spaced, often irregular and interconnecting spots on the mesial face of the major claw (vs. less densely spaced, rounded spots in *A. galapagensis*), and the bluish (vs. orange in *A. galapagensis*) antennal and antennular flagella (cf. Fig. 7) (see also Table 1).

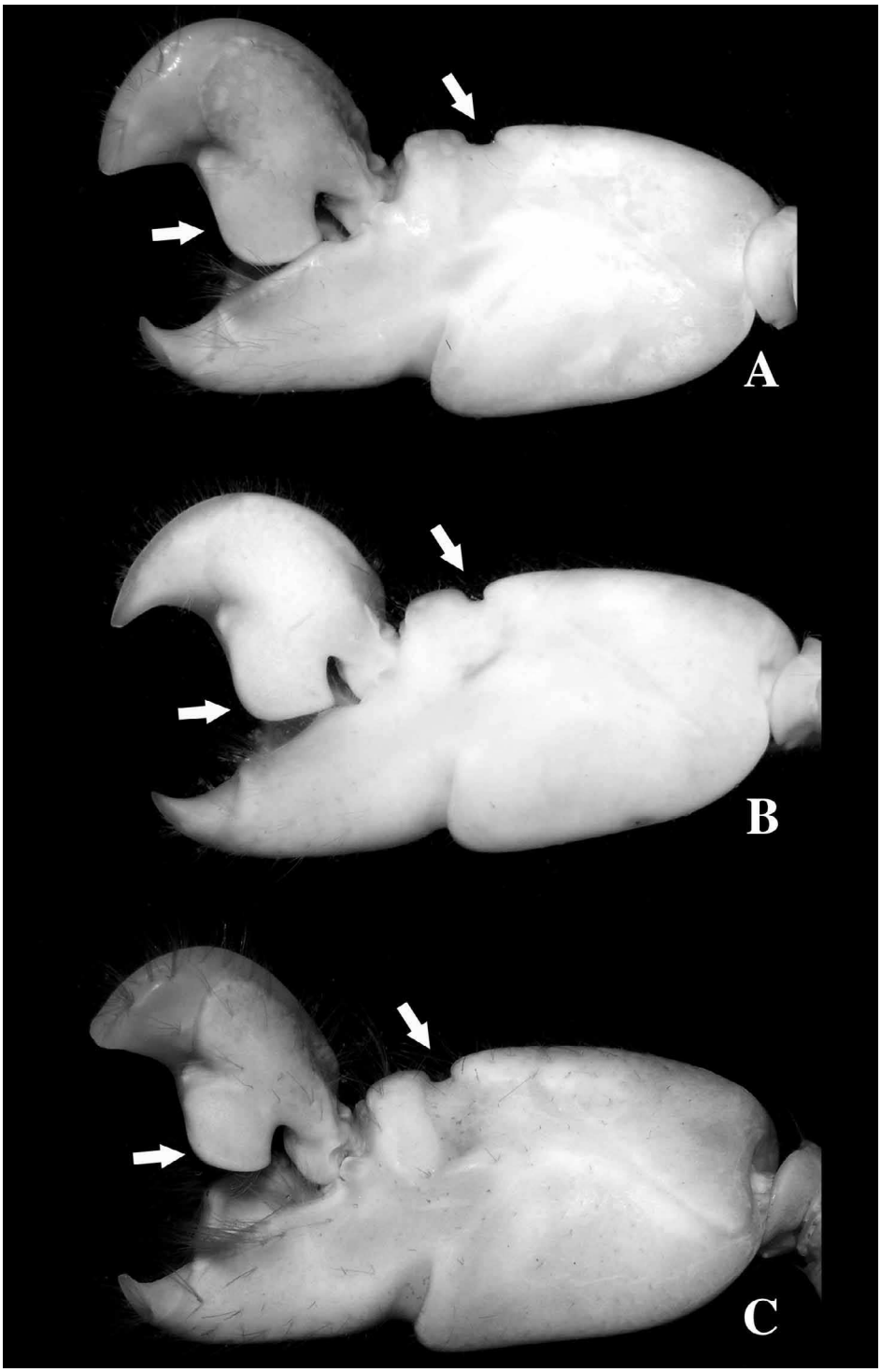

FIGURE 5. Major chelae of large male specimens of *Alpheus nuttingi* (Schmitt, 1924) (A), *Alpheus galapagensis* Sivertsen, 1933 (B) and *Alpheus millsae*, n. sp. (C), showing differences in the shape of the dactylus plunger and dorsal notch of the palm (see arrows); A, male from Cahuita, Costa Rica (MNHN-Na 16365); B, male from Las Perlas, Panama (USNM 1100683); C, male from Casco Viejo, Panama (holotype, USNM 1100686).

The color of freshly laid eggs of *A. millsae*, n. sp. was not recorded; the developing eggs are dull olive-green (Fig. 8C). Thus it remains to be confirmed whether egg color in *A. millsae*, n. sp. can be used as a diagnostic character to distinguish it from *A. galapagensis* and *A. nuttingi*.

Etymology.—The species is named after DeEtta K. Mills, in recognition of her help in earlier studies of neotropical cryptic species of *Alpheus*.

GenBank number.—COI 5' EF092283 (fcn 06-334); COI 3' AF309881 (fcn 99-004), AF309882 (fcn 99-005).

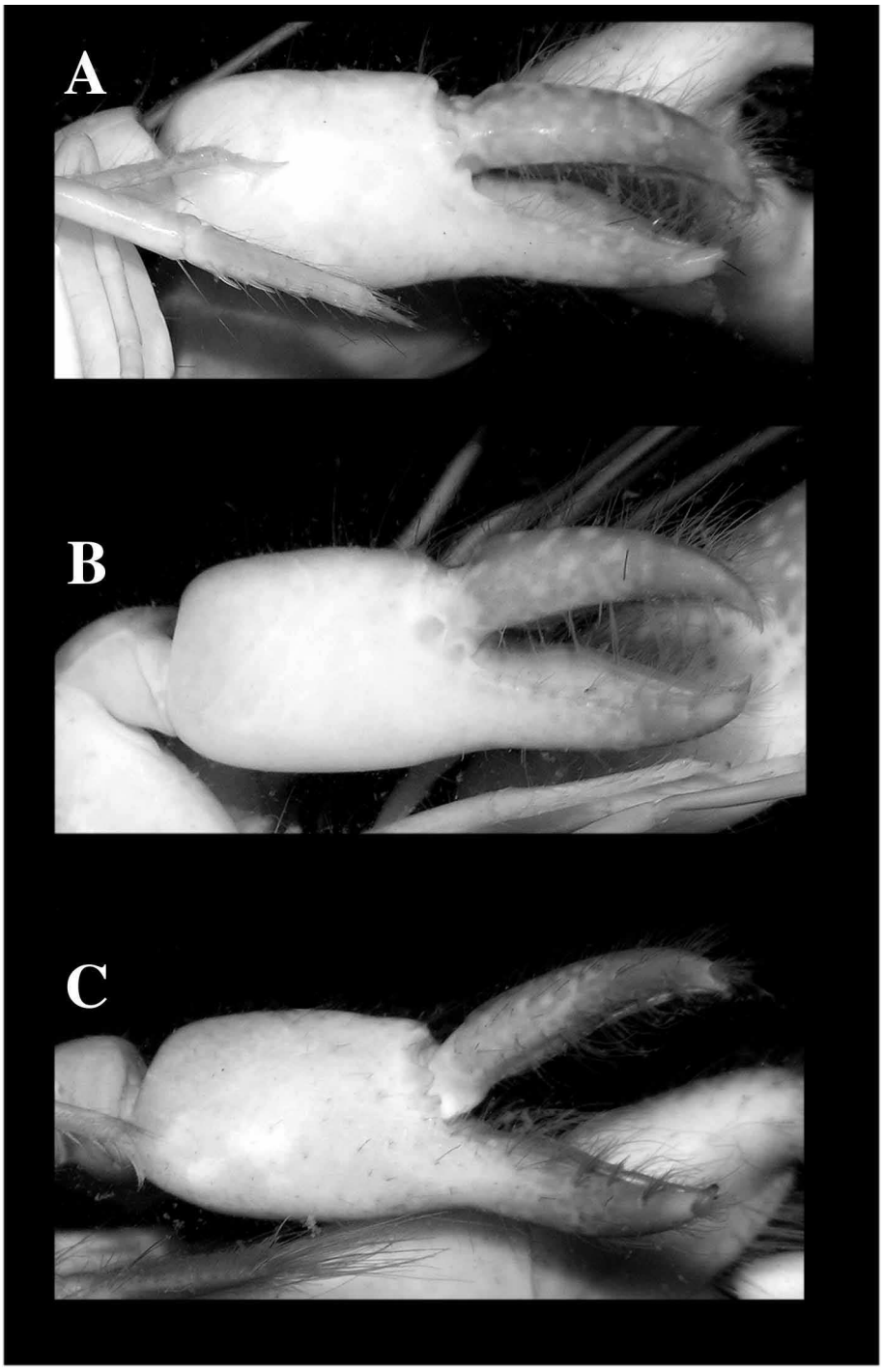

FIGURE 6. Minor chela of large male specimens of *Alpheus nuttingi* (Schmitt, 1924) (A), *Alpheus galapagensis* Sivertsen, 1933 (B) and *Alpheus millsae*, n. sp. (C) showing slight differences in the relative thickness of the fingers; A, male from Cahuita, Costa Rica (MNHN-Na 16365); B, male from Las Perlas, Panama (USNM 1100683); C, male from Casco Viejo, Panama (holotype, USNM 1100686).

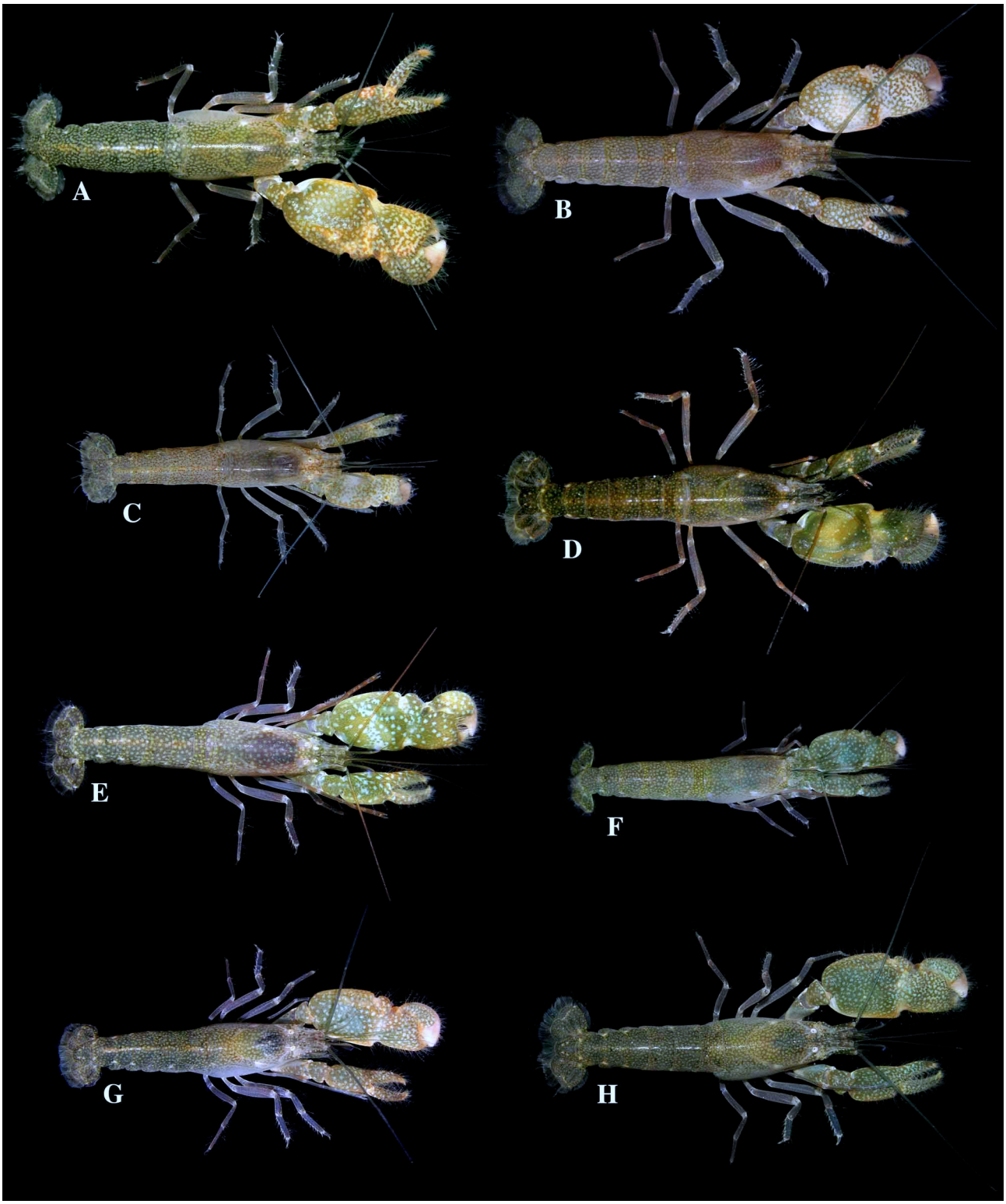

FIGURE 7. Color patterns, in dorsal view, of *Alpheus nuttingi* (Schmitt, 1924) (A-C), *Alpheus galapagensis* Sivertsen, 1933 (D–F) and *Alpheus millsae*, n. sp. (G, H): A, large adult male from Cahuita, Costa Rica (MNHN-Na 16365); B, adult male from Bocas del Toro, Panama (USNM 1100678); C, subadult female from Bocas del Toro, Panama (USNM 1100679); D, large adult male from Punta Culebra, Panama (OUMNH-ZC 2006-10-0005); E, adult male from Las Perlas, Panama (USNM 1100683); F, ovigerous female from Río Mar, Panama (MNHN-Na 16368); G, adult male from Casco Viejo, Panama (paratype, MNHN-Na 16369); H, large adult male from Casco Viejo (holotype, USNM 1100686).

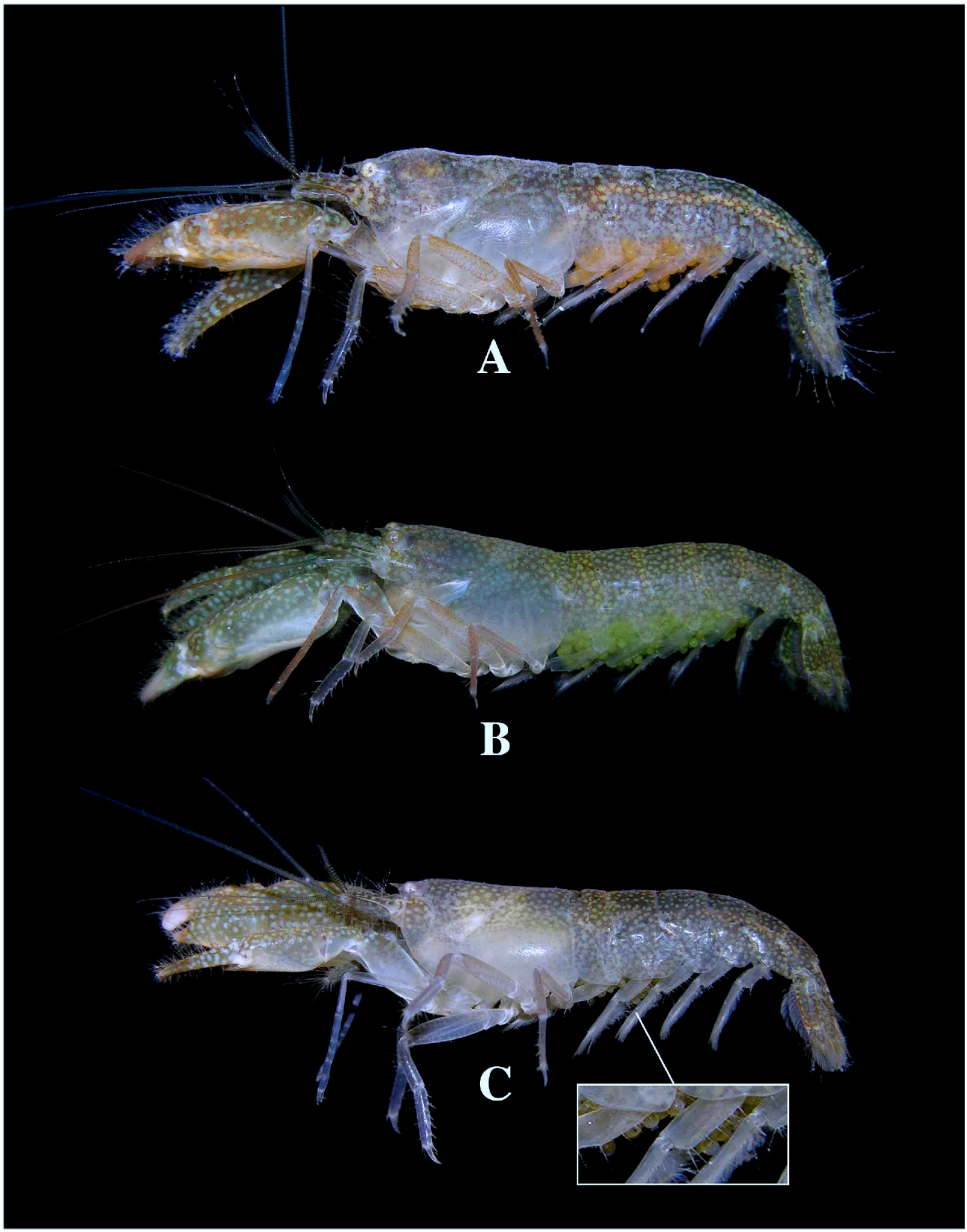

FIGURE 8. Color patterns, in lateral view, of ovigerous females of *Alpheus nuttingi* (Schmitt, 1924) (A), *Alpheus galapagensis* Sivertsen, 1933 (B), and *Alpheus millsae*, n. sp. (C), showing color of eggs: A, specimen from Bocas del Toro, Panama (MNHN-Na 16364); B, specimen from Río Mar, Panama (MNHN-Na 16368); C, specimen from Casco Viejo, Panama (paratype, MNHN-Na 16369). Note that in the female of *A. millsae*, n. sp., eggs (see insert) started to develop and so their color cannot be used for direct comparison with *A. nuttingi* and *A. galapagensis*.

Discussion

The *Alpheus nuttingi* species complex has both allopatric and sympatric representatives. Within *Alpheus*, this situation is common in the Indo-West Pacific (e.g., Bruce, 1987; Anker, 2001a; Nomura & Anker, 2005) and not uncommon also in the western Atlantic and eastern Pacific (e.g., Knowlton & Keller, 1985; Knowlton & Mills, 1992; Knowlton *et al.*, 1993). The present study underlines once more the importance of four approaches for detecting cryptic species: a careful examination of morphology, photography of living specimens, ecological data, and genetic analyses. Our genetic results confirm those obtained by Williams *et al.* (2001), suggesting that *A. galapagensis* forms a sister group to the transisthmian clade containing *A. nuttingi* and *A. millsae*, n. sp. This is mostly corroborated by morphology and color, e.g., by the absence of spine on the P3 ischium in both *A. nuttingi* and *A. millsae*, n. sp. (vs. present in *A. galapagensis*), and by the blue antennal flagella in both *A. nuttingi* and *A. millsae*, n. sp. (vs. orange in *A. galapagensis*).

These three species appear to have diverged somewhat before the closure of the Isthmus of Panama. The average COI genetic distance between *A. nuttingi* and *A. millsae*, n. sp. is 9%, between *A. nuttingi* and *A. galapagensis* 12.4%, and between *A. galapagensis* and *A. millsae*, n. sp. 11.6%. Assuming a rate of sequence divergence of 1.5% per million years (see Methods), divergences times were approximately 6 mya for the transisthmian sister taxa, and 8 mya for the sympatric eastern Pacific taxa. The fact that the two Pacific species seem to differ ecologically primarily in the depth distribution (with *A. millsae*, n. sp. typically restricted to the very lowest part of the intertidal and *A. galapagensis* slightly higher) suggests that some form of ecological speciation may be involved (*sensu* Rundle & Nosil, 2005).

Despite similarity in color pattern and morphology, Brazilian specimens of *A. nuttingi* are genetically distinct from Caribbean specimens, with an average K2P genetic distance of 3.5% (3' end of COI) between the two groups, compared to 0.7% among individuals within the Caribbean (Williams *et al.*, 2001). This value is smaller than genetic differences estimated from other transisthmian pairs, which ranged from 5% to 19% (Knowlton & Weigt, 1998). However, they are substantially more distinct than other Brazilian/Carribean species pairs; for instance, Brazilian/Caribbean K2P genetic distances were 0.4% and 0.2% for *A. bouvieri* A. Milne Edwards, 1878 and *A. formosus* Gibbes, 1850, respectively. In laboratory trials, even the least divergent transisthmian pairs showed evidence of substantial reproductive isolation and are therefore considered distinct biological species. Brazilian/Carribean *A. nuttingi* COI distances fall just short of transisthmian values, suggesting that they are likely at an incipient stage of speciation.

Acknowledgments

We thank Javier Jara (Naos, STRI, Panama City), who prepared most of the drawings used in this study, including the detailed line drawings of color patterns of the two transisthmian species, and also assisted in the field, together with Eyda Gómez and Eva Tóth (Naos, STRI, Panama City, Panama). Sammy De Grave (OUMNH) helped to obtain rare literature. Emerson Mossolin (Universidade de São Paulo, São Paulo, Brazil) shared photographs of Brazilian specimens. The present study was supported by the John Dove Isaacs Professorship of Natural Philosophy and the Scripps Instutition of Oceanography, La Jolla, USA, and is also a part of the Census of Marine Life/CReefs Project. We are also grateful to the Autoridad National del Ambiente (ANAM) for collection permits in Panama. The work was accomplished at the Smithsonian Tropical Research Institute (STRI) facilities at Naos, Panama City, Republic of Panama.

References

Abele, L.G. & Kim, W. (1986) An illustrated guide to the marine decapod crustaceans of Florida. *Technical Series Department of Environmental Regulations*, 8, parts 1 and 2, 760 pp.

Anker, A. (2001a) Two new species of snapping shrimps from the Indo-Pacific, with remarks on color patterns and sibling species in Alpheidae (Crustacea: Caridea). *Raffles Bulletin of Zoology*, 49, 57–72.

Anker, A. (2001b) Taxonomie et évolution des Alpheidae (Crustacea, Decapoda). Thèse de Doctorat, Muséum national d'Histoire naturelle, Paris. 2 vols, 547 + 331 pp.

Banner, D.M. & Banner, A.H. (1982) The alpheid shrimp of Australia, part III: the remaining alpheids, principally the genus *Alpheus*, and the family Ogyrididae. *Records of the Australian Museum*, 34, 1–357.

Bruce, A.J. (1987) A new species of alpheid shrimp, *Alpheus bannerorum*, from northern Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Science*, 4, 61–72, pl. 1.

Camacho, M.E. (1996) Aspectos taxonómicos y distribución geográfica de cinco familias de camarones carídeos (Crustacea: Decapoda), en Nayarit, México. Tesis Licenciatura, Facultad de Ciencias (Biología), Universidad Nacional Autónoma de México, México, 161 pp.

Chace, F.A. Jr. (1972) The shrimps of the Smithsonian-Bredin Caribbean expeditions with a summary of the West Indian shallow-water species (Crustacea: Decapoda: Natantia). *Smithsonian Contributions to Zoology*, 98, i–x + 1–179.

Christoffersen, M.L. (1979) Decapod Crustacea: Alpheoidea. Campagnes de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961–1962). I. *Résultats Scientifiques de la Campagne de la Calypso*, 11, 297–377.

Christoffersen, M.L. (1980) Taxonomia e distribuição geográfica dos Alpheoidea (Crustacea, Decapoda, Natantia) do Brasil, Uruguay e norte da Argentina, incluindo considerações sobre a divisão do sul do continente em províncias biogeográficas marinhas. PhD Thesis, Universidade do São Paulo, São Paulo, 467 pp.

Christoffersen, M.L. (1984) The western Atlantic snapping shrimps related to *Alpheus heterochaelis* Say (Crustacea Caridea), with the description of a new species. *Papéis Avulsos de Zoologia, São Paulo*, 35, 189–208.

Christoffersen, M.L. (1998) Malacostraca. Eucarida. Caridea, Crangonoidea and Alpheoidea (except Glyphocrangonidae and Crangonidae). In: Young, P.S. (ed.), Catalogue of Crustacea of Brazil. pp. 351–372. Museu Nacional, Rio de Janeiro, Brazil. 717 pp.

Christoffersen, M.L. & Ramos, G.E. (1988) A new species of *Alpheus* (Caridea, Alpheidae) from the Pacific coast of Colombia. *Revista Nordestina de Biologia*, 6, 61–65.

Coutière, H. (1899) Les "Alpheidae", morphologie externe et interne, formes larvaires, bionomie. *Annales des Sciences Naturelles, Zoologie*, série 8, 9, 1–560, pls. 1–6. Masson et Cie, Paris.

Flores-Hernández, P. **(**1991) Taxonomía y distribución geográfica de tres familias de camarones carídeos (Crustacea: Decapoda) intermareales de la islas del Golfo de California, México. Tesis Profesional. Facultad de Ciencias, Universidad Nacional Autónoma de México, México, 225 pp.

Folmer O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Hendrickx, M.E. (1992) Distribution and zoogeographic affinities of decapod crustaceans of the Gulf of California, Mexico. *Proceedings of the San Diego Society of Natural History*, 20, 1–12.

Hendrickx, M.E. (1993a). Crustáceos decápodos del Pacífico Mexicano. In: Salazar-Vallejo, S.I. & González, N.E. (eds.), Biodiversidad marina y costera de México. CONABIO-CIQRO, México, pp. 271–318.

Hendrickx, M.E. (1993b). Crustáceos decápodos bentonicos del sur de Sinaloa, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Zoología*, 64, 1–16.

Hendrickx, M.E. (1995). Camarones. In: Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K.E. & Niem, V.H. (eds.), Guía FAO para la identificación de especies para los fines de la pesca. Pacífico centro-Oriental. Vol. 1. Plantas e invertebrados, pp. 417–537. FAO, Rome, Italy, 646 pp.

Hendrix, G.Y. (1971). A systematic study of the genus *Alpheus* (Crustacea: Decapoda: Alpheidae) in South Florida. PhD Dissertation, University of Miami, Coral Gables, Florida, USA. 184 pp., 24 pls.

Hernández Aguilera, J.L. & Martínez Guzman, L.A. (1992). Notas acerca de la distribución de los estomatópodos y decápodos de aguas someras de Isla Clarión, Archipiélago Revillagigedo, Colima, México. *Proceedings of the San Diego Society of Natural History*, 19, 1–6.

Hernández Aguilera, J.L., Toral Almazán, R.E. & Ruiz Nuño, J.A. (1996). Especies catalogadas de crustáceos estomatópodos y decápodos para el Golfo de México, Río Bravo, Tamps. a Progreso, Yuc. Dirección de Oceanografía, Dirección General de Oceanografía Naval, Secretaria de Marina, México, i–xiii, 1–132.

Hickman, C.P. Jr. & Zimmerman, T.L. (2000) A field guide to crustaceans of Galapagos—Guía de campo de los crustáceos de Galápagos. Sugar Spring Press, Lexingon, Virginia, U.S.A. 156 pp.

Kim, W. & Abele, L.G. (1988) The snapping shrimp genus *Alpheus* from the eastern Pacific (Decapoda: Caridea: Alpheidae). *Smithsonian Contributions to Zoology*, 454, 1–119.

Knowlton, N. & Keller, B.D. (1985) Two more sibling species of alpheid shrimp associated with the Caribbean sea anemones *Bartholomea annulata* and *Heteractis lucida*. *Bulletin of Marine Science*, 37, 893–904.

Knowlton, N. & Mills, D.K. (1992) The systematic importance of color and color pattern: evidence for complexes of sibling species of snapping shrimp (Caridea: Alpheidae: *Alpheus*) from the Caribbean and Pacific coasts of Panama. *Proceedings of the San Diego*

Society of Natural History, 18, 1–5.
Knowlton N. & Weigt, L.A. **(**1998) New dates and new rates for divergence across the Isthmus of Panama. *Proceedings of the Royal Society of London, Biological Sciences*, 265, 2257–2263.
Knowlton, N., Weigt, L.A., Solorzano, L.A., Mills, D.K., & Bermingham, E. (1993) Divergence in proteins, mitochondrial DNA, and reproductive compatibility across the Isthmus of Panama. *Science*, 260, 1629–1632.
Lemaitre, R. & Alvarez-Leon, R. (1992) Crustáceos decápodos del Pacifico colombiano: lista de especies y consideraciones zoogeográficas. *Anales del Instituto de Investigaciónes Marinas de Punta Betín*, 21, 33–76.
Luederwaldt, H. (1919) Lista dos crustáceos superiores (Thoracostraca) do Museum Paulista que foram encontrados no estado de São Paulo. *Revista do Museu Paulista*, 11, 427–435.
Martínez-Iglesias, J.C., Ríos, R. & Carvacho, A. (1997) Las especies del género *Alpheus* (Decapoda: Alpheidae) de Cuba. *Revista de Biología Tropical*, 44/45, 401–429.
McClure, M.R. (2005) Alpheidae. In: Hernández Aguilera, J.L., Ruiz Nuño, J.A., Toral Almazán, R.E. & Arenas Fuentes, V. (eds.), Camarones, langostas y cangrejos de la costa este de México. Volume 1., pp. 119–202. Estudio y Conservación de la Naturaleza, A.C. y CONABIO, Mexico 350 pp.
McClure, M.R. & Wicksten, M.K. (2000) Taxonomic studies of snapping shrimp of the *Alpheus* "*edwardsii*" group from the Galapagos Islands. *Proceedings of the Biological Society of Washington*, 113, 964–973.
Nomura, K. & Anker, A. (2005) The taxonomic identity of *Alpheus gracilipes* Stimpson, 1860 (Decapoda: Caridea: Alpheidae), with description of five new cryptic species from Japan. *Crustacean Research*, 34, 104–139.
Rathbun, M.J. (1900) The decapod and stomatopod Crustacea, Part I. In: Results of the Branner-Agassiz Expedition to Brazil. *Proceedings of the Washington Academy of Sciences*, 2, 133–156, pl. 8.
Ríos R. (1989) Un catálogo de camarones carídeos de Mulegé y Bahía Concepción, B.C.S. con anotaciones acerca de su biología, ecología, distribución geográfica y taxonomía. Tesis, Ensenada, B.C., México, 208 pp.
Ríos, R. (1992) Camarones carídeos del Golfo de California. VI. Alpheidae del estuario de Mulegé y de Bahía Concepcion, Baja California Sur, México (Crustacea: Caridea). *Proceedings of the San Diego Society of Natural History*, 14, 1–13.
Rundle, H.D. & Nosil, P. (2005) Ecological speciation. *Ecology Letters*, 8, 336–352.
Santos, M.A. (1981) Estágios larvais de três espécies de *Alpheus* (Crustacea, Decapoda, Natantia) do litoral do estado de São Paulo. In: Anonymous (ed.), Seminários de Biologia Marinha, pp. 319–348. Academia Brasileira de Ciências, Rio de Janeiro, 383 pp. [not seen]
Santos, M.A.C. & Coelho, P.A. (1998) Camarões (Crustacea, Decapoda) do litoral de Jaboato dos Guararapes, Pernambuco - Brasil. *Trabalhos Oceanográficos da Universidade Federal do Pernambuco, Recife*, 26, 63–83.
Schmitt, W.L. (1924) Report on Macrura, Anomura and Stomatopoda collected by the Barbados-Antigua Expedition from the University of Iowa in 1918. *Studies of Natural History, Iowa University*, 10, 65–99, pls. 1–5.
Schmitt, W.L. (1936) Macruran and anomuran Crustacea from Bonaire, Curaçao and Aruba. Zoologische Ergebnisse einer Reise nach Bonaire, Curaçao und Aruba im Jahre 1930. Nr 16. *Zoologische Jahrbücher, Abteilung für Systematik, Oekologie und Geographie der Tiere*, 67, 363–378, pls. 11–13.
Schmitt, W.L. (1939) Decapod and other Crustacea collected on the Presidential Cruise of 1938 (with introduction and station data). *Smithsonian Miscellaneous Collections*, 98, 1–29, 3 pls.
Sivertsen, E. (1933) Littoral Crustacea Decapoda from the Galapagos Islands, Part VII. The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebaek. *Meddelelser fra det Zoologiske Museum, Oslo*, 38, 1–23, pls. 1–4.
Smith, S.I. (1871) Notice of the Crustacea collected by Prof. C.F. Hart on the coast of Brazil in 1867. *Transactions of the Connecticut Academy of Arts and Sciences*, 2, 1–44, pl. 1.
Spivak, E.D. (1997) Los crustáceos decápodos del Atlántico sudoccidental (25º–55ºS): distribución y ciclos de vida. *Investigaciones Marinas, Valparaíso*, 25, 69–91.
Vargas, R. & Cortés, J. (1999) Biodiversidad marina de Costa Rica: Crustacea: Decapoda (Penaeoidea, Sergestoidea, Stenopodidea, Caridea, Thalassinidea, Palinura) del Caribe. *Revista de Biología Tropical*, 47, 887–911.
Villalobos, J.L. (2000) Estudio monográfico de los crustáceos decápodos no braquiuros de la zona intermareal de las islas del Golfo de California, México. Tesis de Maestría, Ciencias (Biología). Universidad Nacional Autónoma de México, México, 312 pp.
Villalobos Hiriart, J.L., Nates-Rodríguez, J.C., Cantu Díaz-Barriga, A., Valle Martínez, M.D., Flores Hernández, P., Lira Fernandez, E. & Schmidtsdorf-Valencia, P. (1989) Listados faunísticos de México. I. Crustáceos estomatópodos y decápodos intermareales de las islas del Golfo de California. Instituto de Biología, Universidad Nacional Autónoma de México, México, i–ix + 1–101.
Wicksten, M.K. & Hendrickx, M.E. (1992) Checklist of penaeoid and caridean shrimps (Decapoda: Penaeoidea, Caridea) from the eastern tropical Pacific. *Proceedings of the San Diego Society of Natural History*, 9, 1–11.
Wicksten, M.K. & Hendrickx, M.E. (2003) An updated checklist of benthic marine and brackish water shrimps (Decapoda: Penaeoidea, Stenopodidea, Caridea) from the eastern tropical Pacific. In : Hendrickx, M. (ed.), Contribuciónes al estudio de los crustáceos del Pacifico Este, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autonoma de México, México, pp. 49–76.
Williams, S.T. & Knowlton, N. **(**2001) Mitochondrial pseudogenes are pervasive and often insidious in the snapping shrimp genus *Alpheus*. *Molecular Biology and Evolution*, 18, 1484–1493.
Williams, S.T., Knowlton, N., Weigt, L.A. & Jara, J.A. (2001) Evidence for three major clades within the snapping shrimp genus *Alpheus* inferred from nuclear and mitochondrial gene sequence data. *Molecular Phylogenetics and Evolution*, 20, 375–389.