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Revision of the *Alpheus websteri* Kingsley, 1880 species complex (Crustacea: Decapoda: Alpheidae), with revalidation of *A. arenensis* (Chace, 1937)

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Abstract

The *Alpheus websteri* Kingsley, 1880 species complex is revised. *Alpheus websteri s. str.* is redefined and restricted to the western Atlantic, ranging from the type locality in the Florida Keys to northeastern Brazil. The eastern Pacific *A. arenensis* (Chace, 1937), formerly a synonym of *A. websteri*, and the eastern Atlantic *A. fagei* Crosnier and Forest, 1966, are shown to be distinct from *A. websteri* morphologically, genetically and also by color pattern. Morphology, genetics and color patterns all suggest that *A. websteri* and *A. arenensis* are transisthmian sister species, with *A. fagei* being their closest relative. Complete synonymy, color photographs and GenBank barcodes (COI) are provided for all three species.

Key words: *Alpheus*, snapping shrimp, species complex, transisthmian taxa, color pattern, eastern Pacific, Atlantic, Caribbean, molecular phylogeny, barcode, COI

Introduction

The largest alpheid genus, *Alpheus* Fabricius, 1798, includes seven species groups first defined by Coutière (1899, 1905) and widely used by most subsequent workers (e.g., Banner & Banner 1982; Chace 1988). One of these species groups is the fairly large (over 30 species) *A. sulcatus* Kingsley, 1878 group, defined by orbital hoods usually armed with acute teeth, the major cheliped lacking marked dorsal and ventral notches, and the uropod bearing a stout, usually dark-colored (black to tan-brown) distolateral spine (e.g., Banner & Banner 1982). Based on molecular data, Williams *et al.* (2001) suggested that the *A. sulcatus* group, as currently defined, is polyphyletic. However, within this group, all species with a stout and dark-colored uropodal spine appear to form a monophyletic clade (Williams *et al.* 2001), which includes *A. websteri* Kingsley, 1880.

Alpheus websteri was originally described without illustrations from Key West, Florida (Kingsley 1880). The type of *A. websteri* was deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM). *Alpheus websteri* can be separated from all other western Atlantic species by the following features: (1) small, acute, dorsally rounded rostrum, furnished with stiff setae; (2) broad rostral carina, extending posteriorly well beyond orbital hoods; (3) acute orbital teeth inserted on the anterior margin of the orbital hoods; (4) major chela bearing a shallow transverse constriction on the dorsal margin of the palm, near the dactylus; (5) merus of the major cheliped with an acute distal tooth on the ventromesial margin; (6) minor cheliped with non-balaeniceps fingers in both sexes; (7) third to fifth pereiopods without spine on

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the ventrolateral margin of the ischium, without distoventral tooth on the merus, and with a biunguiculate dactylus; (8) uropodal exopod with a broad, black-colored distolateral spine, and with a doubled distolateral tooth (i.e, with two teeth lateral to the distolateral spine), a feature found only in a few other species of *Alpheus*.

Two other nominal species from the *A. websteri* complex were described from the western Atlantic: *A. ridleyi* Pocock, 1890 from Fernando do Noronha, Brazil, and *A. nigrospinatus* Rankin, 1898 from the Bahamas (Pocock 1890; Rankin 1898). Rankin's *A. nigrospinatus* was recognized as junior synonym of *A. ridleyi* (Crosnier & Forest 1966; Chace 1972). Chace (1972) listed *A. ridleyi* in his key to the western Atlantic species, but strangely did not mention *A. websteri*, except in the index: "*websteri*, *Alpheus*—see *A. formosus*, [p.] 67"; however, *A. websteri* is not listed under synonymy of *A. formosus* Gibbes, 1850 or elsewhere.

Chace (1937) described and illustrated an eastern Pacific species from the *Alpheus sulcatus* group under the name *Crangon arenensis* Chace, 1937—now *Alpheus arenensis*. Chace did not compare *A. arenensis* with *A. websteri* or *A. ridleyi*, but instead with the Indo-West Pacific *A. gracilis* Heller, 1861.

Crosnier & Forest (1965, 1966) described and illustrated the eastern Atlantic *Alpheus fagei* Crosnier & Forest, 1965. These authors provided a comparative table of morphological characters that allow separation of *A. fagei* from its most closely related species, *A. ridleyi* and *A. arenensis*, as well as from *A. rugimanus* A. Milne Edwards, 1878 (see below). Hendrix & Gore (1973) described *Alpheus thomasi* Hendrix & Gore, 1973 from the Indian River region in Florida, and noted that this species may be closely related to *A. ridleyi* and *A. fagei*.

Wicksten (1983) examined specimens of the *A. websteri* complex from the eastern Pacific (Gulf of California to Galapagos), western Atlantic (Caribbean, Florida) and eastern Atlantic (São Tomé), and concluded that *A. ridleyi*, *A. arenensis* and *A. fagei* should all be treated as synonyms of a single widespread species—*A. websteri*. In the most important study of the eastern Pacific species of *Alpheus*, Kim & Abele (1988) concurred with Wicksten (1983) on the synonymy of *A. ridleyi* and *A. arenensis*, reporting the eastern Pacific form as *A. websteri*. However, they noted that in the eastern Pacific specimens, the distal tooth on the ventromesial margin of the merus of the chelipeds was minute or absent, whereas in the western Atlantic specimens, this tooth was rather strong. Nevertheless, *A. websteri* was the name listed in the most recent checklist of the Caridea of the eastern Pacific (Wicksten & Hendrickx 2003). On the other hand, Kim & Abele (1988) did not agree with Wicksten's (1983) synonymy of *A. fagei*, treating it as distinct from *A. websteri*.

The recent DNA analyses by Williams *et al.* (2001) showed that *A. websteri*-P (E Pacific, correspoding to *A. arenensis*) and *A. websteri*-C (Caribbean) are genetically distinct forms, suggesting that they actually represent two transisthmian sibling species. The eastern Atlantic *A. fagei* was not included in their study.

The present work is the first revision of the *A. websteri* species complex. We collected, photographed and morphologically examined specimens from the eastern Pacific (Panama), western Atlantic (Panama, Honduras, Dominican Republic, Guadeloupe, Brazil) and eastern Atlantic (São Tomé); some of them were also sequenced (COI). The presently available data leaves no doubt that there are three species—one in each of the three oceanic provinces: *A. arenensis* (= *A. websteri sensu* Wicksten 1983, part., *A. websteri sensu* Kim & Abele 1988) in the eastern Pacific, *A. websteri* (= *A. ridleyi*, *A. nigrospinatus*) in the western Atlantic, and *A. fagei* (= *A. websteri sensu* Wicksten 1983, part.) in the eastern Atlantic. Therefore, *A. arenensis* is formally resurrected from the synonymy proposed by Wicksten (1983) and followed by Kim & Abele (1988). The specific status of *A. fagei* is confirmed, supporting Kim & Abele's (1988) conclusions. The nominal species, *A. websteri*, is redefined below on the basis of newly collected Caribbean material. Updated synonymy, color pattern photographs and GenBank barcodes (COI) are provided for all three species.

Material and methods

Specimens were collected under rocks at low tide or from crevices of coral rocks at depths of 1–3 m. Most were photographed alive and preserved in 70% or 95% ethanol. Specimens selected for RNA extractions

were preserved in RNAlater (Ambion) or frozen; in some cases, a leg was detached from a specimen and preserved in RNAlater, while the body of the specimen was preserved in ethanol. All drawings were made with the aid of a camera lucida under the dissecting microscope.

The 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); Oxford University Museum of Natural History, Oxford, UK (OUMNH), Colección de Referencia, Departamento de Biología Marina, Universidad de Panamá, Panama City, Panama (UP), and Museu Nacional, Rio de Janeiro, Brazil (MNRJ). Abbreviations used in the text: Mxp—maxilliped; P—pereiopod; CL—carapace length (measured in mm along the mid-dorsal line from the tip of the rostrum to the posterior margin of the carapace); TL—total length (measured in mm along mid-dorsal line from the tip of the rostrum to the posteror 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 Panamanian isthmus (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 websteri Kingsley, 1880

Figs. 1, 2, 3A–D, 4A

Alpheus websteri Kingsley 1880: 416; Abele & Kim 1986: 197, 208–209, fig. a; Martínez-Iglesias *et al.* 1993: 11; Martínez-Iglesias *et al.* 1996: 34; Martínez-Iglesias *et al.* 1997: 425, fig. 18; Salazar-Rosas 1995: 59, pl. 17; Christoffersen 1998: 361; McClure 2005: 156 (not fig. 24); Coelho *et al.* 2006: 52.

Not *Alpheus websteri*—Wicksten 1983: 42 (part.); Wicksten & Hendrickx 1985: 572; Kim & Abele 1988: 28, fig. 11; Villalobos Hiriart *et al.* 1989: 17; Wicksten & Hendrickx 1992: 5 (part.); Wicksten 1993: 151; Hendrickx 1993a: 306; Hendrickx 1993b: 6; Hendrickx 1995: 432; Camacho 1996: 64; Vargas & Cortés 1999: 902; Villalobos 2000: 66, fig. 33; Wicksten & Hendrickx 2003: 65 (part.); McClure 2005: 157, fig. 24 (= *A. arenensis* (Chace, 1937)).

Alpheus Ridleyi Pocock 1890: 518.

Alpheus ridleyi—Crosnier & Forest 1966: 230, 232, 233, 236, 237; Chace 1972: 69; Coelho & Ramos 1972: 150; Fausto Filho 1974: 5; Fausto Filho 1980: 113; Rodríguez 1980: 149, fig. 42d–f; Cubit & Williams 1983: 24; Rodríguez 1986: 153; Márquez 1988: 35, fig. 22; Hernández Aguilera *et al.* 1996: 34.

Not *Alpheus ridleyi*—Grajal & Laughlin 1984: 224 (= *A. cf. armatus* Rathbun, 1901, see Rodríguez 1986).

Alpheus nigro-spinatus Rankin 1898: 249, pl. 30, fig. 6.

Crangon nigrospinatus—Schmitt, 1924: 71.

Material examined.—Dominican Republic. 1 male (CL 7.9), MNHN-Na 16362, Bayahibe, from crevices in coral rocks, depth 1–2 m, coll. A. Anker, 5 Jan 2005 [fcn 05-020, specimen sequenced]. Guadeloupe. 1 male (CL 9.2), MNHN-Na 16241, Grand Cul de Sac, shallow subtidal, coll. F. Fasquel, 2002 [02-006]. Panama (Caribbean coast). 1 ovig. female (CL 7.2), USNM 1109181, Isla Grande, south of Miraculo, from coral rocks, coll. N. Knowlton *et al.*, 15–16 Jun 1995 [fcn C-1403, B-421, specimen dissected]; 1 male (CL 8.6), 1 ovig. female (CL 6.9), USNM 1109182, same collection data as previous specimen [fcn C-1398 + C-1399, B-426]; 1 male (CL 7.5), 1 ovig. female (CL 6.4), USNM 1109183, same collection data as previous specimens [fcn C-1401 + C-1402, B-428]; 1 male (CL 9.5), USNM 1109184, same collection data as previous specimens [fcn C-1410, B-432]; 1 ovig. female (CL 6.9), USNM 1109185, Isla Grande, from coral rocks, coll. N. Knowlton *et al.*, 15 Nov 1991 [fcn C-171, B-36]; 1 male (CL 7.5), USNM 1109186, same collection data as previous specimen [fcn C-172, B-37]; 1 male (CL 4.7), OUMNH-ZC 2007-13-033, Isla Grande, NE side, exposed rocky platform, from crevices in rocks, coll. A. Anker, J. Luque and J. Vera Caripe, 16 Sep 2007 [fcn 07-263]; 1 male (CL 8.7), 1 ovig. female (CL 7.3), UP, Panama, Caribbean coast, N. Knowlton *et al.* coll. 15–16 Jun 1995 [fcn B-427, B-430]; 1 specimen (sex and CL not determined), Panama, Bocas del Toro, Isla Colon, Bocas del Drago [fcn 06-500, specimen preserved in RNAlater and sequenced, not deposited]. Honduras. 1 male (CL 4.4), OUMNH-ZC 2007-20-002, Bay Islands, Utila, southern shore, Coral View reef, 1605.326' N 086°54.652' W, hand collecting, from coral rocks, depth 1 m, coll. A. Anker and S. De Grave, 5 Jul 2007 [fcn H173]. Brazil. 1 ovig. female (CL 9.5), MNRJ 20149, Atol das Rocas, Piscina das Rocas, in calcareous algae, coll. P.S. Young, P.C. Paiva and A.A. Aguiar, 26 Oct 2000 [specimen dissected and sequenced].

Comparative material of *Alpheus thomasi*: Panama (Caribbean coast). 1 male (CL 5.8), USNM 1109187, Bocas del Toro, Isla Colón, between Big Creek and Playa Bluff, from crevices in coral rocks, depth 1–2 m, coll. A. Anker, 18 Oct 2005 [fcn 05-158]; 1 ovig. female (CL 7.7), USNM 1109188, Bocas del Toro, hospital Point, under large rock, depth 0.5–1 m, coll. A. Anker, 16 Oct 2005 [05-159]; 2 males (CL 8.0, 7.3), 2 ovig. females (CL 8.1, 7.8), MNHN-Na 16707, Bocas del Toro, Isla Colón, Boca del Drago, from crevices in coral rocks, depth 0.5–1 m, coll. A. Anker, 20 Oct 2005 [fcn 05-160]; 1 ovig. female (CL 6.5), USNM 1109189, Bocas del Toro, Isla Colón, Boca del Drago, from crevices in coral rocks, depth 0.5–1 m, coll. A. Anker, 20 Oct 2005 [fcn 05-157]; 1 ovig. female (CL 7.9), OUMNH-ZC 2007-13-032, Isla Grande, southern shore, from coral rubble conglomerate, depth 0.5–1 m, coll. A. Anker, 4 Sep 2006 [fcn 06-430].

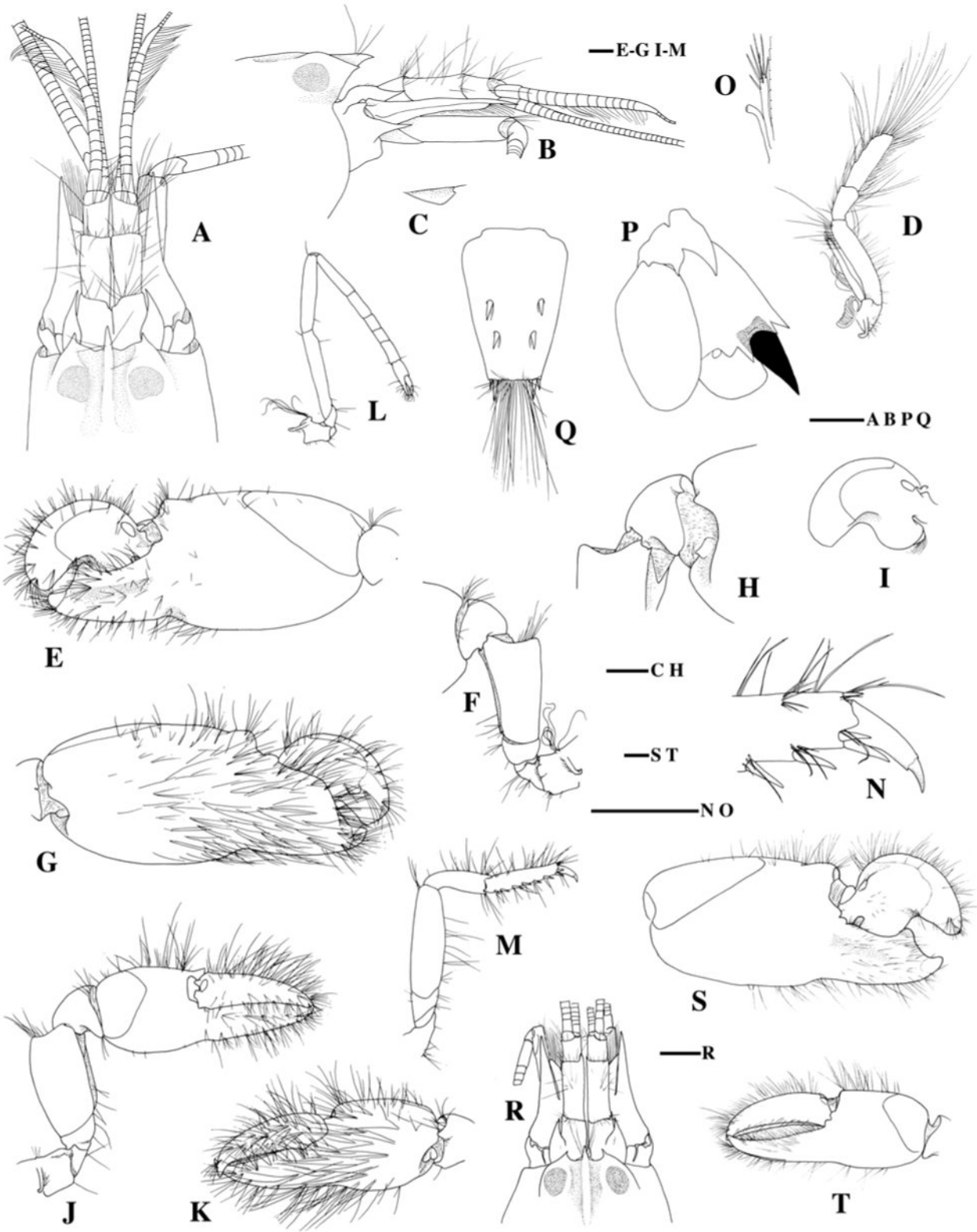

FIGURE 1. *Alpheus websteri* Kingsley, 1880, male from Isla Grande, Caribbean coast of Panama (USNM 1109181) (A–Q), male from Guadeloupe (MNHN-Na 16241) (R–T); A, frontal region, dorsal view; B, same, lateral view; C, tooth on ventromesial carina of first segment of antennular peduncle, lateral view; D, third maxilliped, lateral view; E, major cheliped, chela, lateral view; F, same, coxa to carpus, lateral view; G, same, chela, mesial view; H, same, detail of mesioventral margin of merus and carpus, mesial view; I, same, dactylus, lateral view; J, minor cheliped, lateral view; K, same, chela, mesial view; L, second pereiopod, lateral view; M, third pereiopod, lateral view; N, same, distal propodus and dactylus, lateral view; O, second pleopod, appendix masculina and appendix interna, mesial view; P, right uropod, dorsal view; Q, telson, dorsal view; R, frontal region, dorsal view; S, major chela, lateral view; T, minor chela, lateral view. Scale bars: 1 mm.

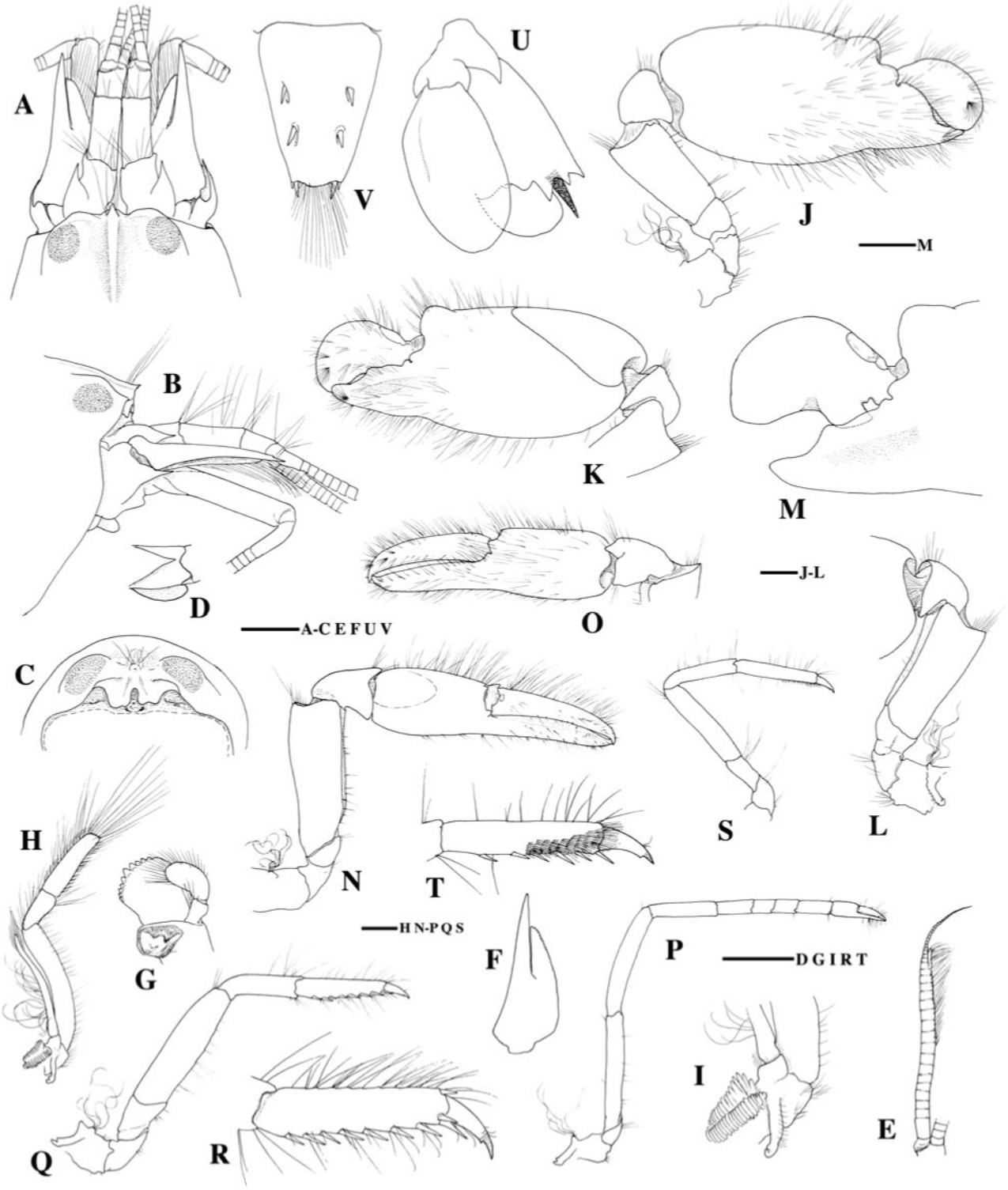

FIGURE. 2. *Alpheus websteri* Kingsley, 1880, ovigerous female from Atol das Rocas, Brazil (MNRJ 20149); A, frontal region, dorsal view; B, same, lateral view; C, orbito-rostral process, frontal view; D, tooth on ventromesial carina of first segment of antennular peduncle, lateral view; E, lateral antennular flagellum, lateral view; F, scaphocerite of antenna, dorsal view; G, mandible, mesial view; H, third maxilliped, lateral view; I, same, detail of coxa and arthrobranch; J, major cheliped, mesial view; K, same, chela and carpus, lateral view; L, same, coxa to carpus, lateral view; M, same, detail of pollex and dactylus with setae omitted, lateral view; N, minor cheliped, lateral view; O, same, chela and carpus, mesial view; P, second pereiopod, lateral view; Q, third pereiopod, lateral view; R, same, propodus and dactylus, lateral view; S, fifth pereiopod, lateral view; T, same, propodus and dactylus, ventrolateral view; U, right uropod, dorsal view; V, telson, dorsal view. Scale bars: 1 mm.

Description.—Carapace smooth, not setose, laterally not compressed. Rostrum relatively short, tip slightly descendant, subacute distally, fringed with long setae (Fig. 1A); rostral carina bluntly rounded, broad, reaching beyond eyes posteriorly (Fig. 1A); orbito-rostral process well developed, broadly W-shaped in frontal view, with deep, rounded median notch (Fig. 2B, C). Orbital hoods moderately inflated, distally with acute teeth (Fig. 1A), rarely without teeth (Fig. 2A). Frontal margin between orbital teeth and rostrum concave and sometimes slightly angular (Fig. 1A, R). Adrostral grooves moderately deep and narrow, not abruptly delimited from rostrum and orbital hood (Fig. 1A, R). Pterygostomial angle rounded, not protruding (Fig. 1B); cardiac notch well developed. Eyes completely concealed in dorsal, lateral and frontal view. Ocellar beak partly concealed by orbito-rostral process, vertically protruding towards rostrum, not visible in lateral view.

Antennular peduncles relatively stout, second segment distinctly longer than first, twice or more as long as wide (Fig. 1A, R); stylocerite distally subacute, usually reaching or slightly overreaching distal margin of first segment (Fig. 1A), sometimes reaching only to about 4/5 length of first segment (Fig. 2A); mesioventral carina of first segment with minute subacute tooth as illustrated (Fig. 1C), sometimes blunt (Fig. 2D); lateral flagellum with numerous tufts of aesthetascs (Fig. 1B), secondary ramus rudimentary, composed of one or two fused segments (Fig. 2E). Antenna with basicerite bearing strong, acute ventrolateral tooth, reaching to level of stylocerite tip (Fig. 1B); carpocerite stout, reaching slightly beyond distolateral spine of scaphocerite; distolateral tooth of scaphocerite strong, exceeding distal margin of antennular peduncle, and reaching well beyond blade (Figs. 1A, 2F); lateral margin of scaphocerite slightly concave (Fig. 1A); blade narrow, subtriangular, separated from distolateral tooth by deep cleft (Figs. 1A, 2F).

Mouthparts (mandible, maxillule, maxilla, first and second maxillipeds) typical for *Alpheus*; mandible with incisor process bearing 10–11 rounded or subtriangular distal teeth (Fig. 2G). Third maxilliped moderately stout (Fig. 1D); antepenultimate segment slightly flattened, ventral margin straight; penultimate segment twice as long as wide, slightly broadening distally; ultimate segment setose, with very long setae, especially on apex (Fig. 1D); coxa with lateral plate ear-shaped distally, furnished with small setae (Fig. 1D); exopod almost reaching penultimate segment; arthrobranch well developed.

Male major cheliped (Fig. 1F–I, S) with short, robust ischium; merus stout, about three times as long as wide proximally, dorsal margin distally blunt (Fig. 1F, H); ventrolateral and ventromesial margins straight, latter distally with small acute tooth (Fig. 1H), rarely without tooth (Fig. 2J); carpus cup-shaped, without pronounced distal lobes (Fig. 1F); chela ovate, slightly compressed laterally; mesial surface of palm smooth, very setose (Fig. 1G); lateral surface of palm with shallow, longitudinal depression near pollex (Fig. 1E, S), ventral and dorsal margins of palm with shallow transverse constrictions subdistally, near fingers (Fig. 1E); linea impressa conspicuous (Fig. 1E); fingers about half-length of palm; dactylus distally rounded, with relatively short plunger, latter distally with stamen-shaped sensillae (Fig. 1I); adhesive discs large (Fig. 1E, S). Female major cheliped (Fig. 2J–M) similar to male major cheliped except for proportions of fingers to palm and general shape of palm. Male minor cheliped with merus about 2.5 times as long as wide proximally, ventrolateral and ventromesial margins straight, distally unarmed; carpus cup-shaped, distal margin with blunt process dorsomesially (Fig. 1K); chela palm with smooth mesial and lateral surfaces, mesial surface very setose (Fig. 1K); distomesial margin with triangular tooth (Fig. 1J, K); linea impressa conspicuous (Fig. 1J); fingers slightly longer than palm, not balaeniceps, with sharp, blade-like cutting margins (Fig. 1T), tips crossing when chela closed. Female minor cheliped (Figs. 2N, O) with merus about three times as long as wide proximally (Fig. 2N); carpus and chela as in male but distinctly more slender (Fig. 2O).

Second pereiopod slender (Fig. 1L); ischium slightly shorter than merus (Fig. 1L); carpus five-segmented, ratio of carpal segments (from proximal to distal) approximately equal to 5 : 3 : 1.5 : 1.4 : 2.2 (Figs. 1L, 2P); chela simple, with fingers slightly longer than palm. Third and fourth pereiopods similar in shape and length; third pereiopod with ventrally unarmed ischium (Figs. 1M, 2Q); merus unarmed, about four times as long as wide; carpus unarmed; propodus armed with seven spines on ventral margin, one spine on distodorsal margin and two spines on distoventral margin (Figs. 1N, 2R); dactylus conical, gradually curved towards acute tip,

biunguiculate, secondary unguis situated on flexor margin at about 3/4 of dactylus length (Figs. 1N, 2R). Fifth pereiopod (Fig. 1S) smaller and more slender than third and fourth pereiopods; ischium unarmed ventrally; merus about six times as long as wide; propodus ventrally with six spines (including distoventral spine (Fig. 2T), ventrolaterally with at least nine rows of grooming setae (Fig. 2T); dactylus biunguiculate, conical, as in third and fourth pereiopods (Fig. 2T).

Abdominal segments with posteroventral margins broadly rounded; sixth segment without articulated flap, posterior margin straight, dorsolateral projections rounded; preanal plate rounded. Male second pleopod with appendix masculina reaching far beyond appendix interna, with slender, mostly apical setae (Fig. 1O); in larger males setae present along outer margin, from about mid-length to apex. Uropod (Fig. 1P) with protopod bearing one robust acute lateral tooth and one subacute mesial tooth distally; exopod with lateral portion of diaeresis bearing four teeth: one blunt tooth at about mid-length, one strong acute tooth mesial to distolateral spine and two acute teeth lateral to distolateral spine = doubled distolateral tooth (Fig. 1P); distolateral spine very stout, especially in males, reaching beyond posterior margin of exopod, black or dark brown (Figs. 1P, 2U); distal margins of exopod without spinules. Telson (Figs. 1Q, 2V) moderately broad, more or less tapering towards posterior margin; dorsal surface without median groove, with two pairs of strong dorsal spines, situated at some distance from lateral margins, anterior and posterior to telson mid-length, respectively (Figs. 1Q, 2V); posterior margin almost straight (Fig. 1Q) to slightly convex (Fig. 2V), with two pairs of posterolateral spines, mesial being three times longer than lateral; anal tubercles well developed. Gill formula typical for *Alpheus*.

Color pattern.—Background color pale grey to cream whitish; carapace with two broad transverse brown bands, one band at about mid-length, extending anteriorly on mid-dorsal line, and one more posterior band, extending anteriorly dorsolaterally (Fig. 3A); both bands abruptly changing direction on carapace flanks (Fig. 3D); two small short brown bands present anterolaterally, ventrally and posteroventrally to orbital hoods (Fig. 3D); rostral area also brownish, in particular rostral carina; inner organs visible through carapace dorsally as large brownish patch; abdomen with six broad (except first) straight transverse brown bands extending to ventral margin of pleurae, abruptly changing direction laterally (towards posterior); second abdominal band bifurcating laterally, reverse V-shaped (Fig. 3D); sixth abdominal somite almost completely brown; white bands between bands with sparse but quite large spots of egg-yellow chromatophores (Fig. 3A, C); tail fan mostly purple-brown, with large white areas and bright egg-yellow spots, proximal portion of telson and uropods whitish, with egg-yellow spots, dorsal spines yellowish or whitish; distolateral spine black; walking legs and second pereiopods appearing pinkish semitransparent speckled with minute red chromatophores except on articulations; cheliped merus and carpus brown laterally; mesial face of palm of major chela mostly pale brown with white areas and brown patches and fairly large dark brown spots on distal half (Fig. 3B, D), most proximal portion of palm white; pollex brown with whitish tip; dactylus brown-white with dark spots proximally, pink distally (Fig. 3B); palm of minor chela brown-orange, with white areas and brown spots; fingers dark brown, white towards tip (Fig. 3B, D); antennular peduncles brown distally, whitish proximally; basicerite and scaphocerite mostly whitish, with occasional brown-orange spots, lateral margin and distolateral tooth of scaphocerite brown-orange; antennular and antennal flagella pale brown; corneas grey-brown (Fig. 3A–D); juveniles similar, but with more contrasting pattern on chelae and narrower bands on abdomen (Fig. 4A).

Size.—The two largest examined specimens are a male from Isla Grande, Panama, with CL 9.5 mm and TL 25.3 mm, and the aberrant female from Atol das Rocas, Brazil with CL 9.5 mm and TL 30 mm.

Ecology.—Intertidal and shallow subtidal, probably to about 10 m, in coral and rock crevices on sand and coral-sand bottoms.

Type locality.—Florida Keys, Florida, USA.

Distribution.—Western Atlantic: southeastern USA: Florida Keys (Kingsley 1880); Bahamas: New Providence (Rankin 1898); eastern Mexico: Quintana Roo (Bahía de la Ascensión, Bahía del Espíritu Santo)

and Cozumel (Chace 1972; Hernández Aguilera *et al.* 1996; McClure 2005); Honduras: Utila (present study); Cuba: Batabano Gulf (Martínez-Iglesias *et al.* 1997); Dominican Republic: Bayahibe; Panama: Bocas del Toro, Isla Grande, Colón (Cubit & Williams 1983; present study); Venezuela: Los Roques and Distrito Federal (Rodríguez 1980); Lesser Antilles: Anguilla, Antigua, Saint Lucia, Tobago (Chace 1972); Guadeloupe (present study); Barbados (Schmitt 1924); northeastern Brazil: Fernando do Noronha (Pocock 1890) and Atol das Rocas (present study). An unpublished record from Alagoas, Brazil (Souza 2001) needs confirmation; the almost schematic illustrations in this study may actually represent *A. thomasi* and not *A. websteri* (A. Anker, pers. obs.).

Remarks.—The ovigerous female from Atol das Rocas (MNRJ 20149) (Fig. 2) is remarkable in lacking orbital teeth (Fig. 2A), bearing a short, ascendant rostrum (Fig. 2B) and having no trace of a distomesial tooth on the merus of the major cheliped (Fig. 2J). In all other features of the chelipeds (Fig. 2J–O), second to fifth pereiopods (Fig. 2P–S), tail fan (Fig. 2U, V), third maxilliped (Fig. 2H, I), antennules and antenna (Fig. 2A, B, F), this specimen agrees well with the Caribbean *A. websteri* specimens.

The more slender minor chela (Fig. 2N, O) and the less stout uropodal spine (Fig. 2U) appear to occur generally in females of *A. websteri*. Moreover, the color of the uropodal spine in females of *A. websteri* apparently varies from brown, as in the female from Atol das Rocas (Fig. 2U), to shiny black, as in most Caribbean females (Fig. 1P). The shape of the ventromesial carina of the first segment of the antennular peduncle – blunt in the specimen from Atol das Rocas (Fig. 2D) vs. with small subacute tooth in the specimen from Panama (Fig. 1C) – may be somewhat variable, as observed in other specimens of *A. websteri* from the Caribbean, as well as other *Alpheus* species (A. Anker, pers. obs.). A comparison of the COI gene sequence between the Caribbean specimens and the female from Atol das Rocas resulted in the latter falling within the variation range of the Caribbean samples. Therefore, this single specimen is considered as an aberrant individual of *A. websteri*. The lack of distinct orbital teeth and distomesial tooth on the chelipeds in large specimens could be due to wearing away from use or from bluntening (polishing) during molting (see also under *A. rugimanus*). The abnormal frontal region can also be result of a physical damage (injury). Unfortunately, no other specimens of *A. websteri* were collected at Atol das Rocas.

In the field, *A. websteri* may be confused with the sympatric *A. thomasi*, which ranges from southern Florida to Panama and Brazil (Hendrix & Gore 1973; Christoffersen 1998; present study). However, the latter species can be easily distinguished from *A. websteri* by the frontal margin between the rostrum and the orbital hoods being more deeply notched; the slenderer major and minor chelae; the uropod with a distinctly narrower distolateral spine and with a simple distolateral tooth on the diaeresis (doubled in *A. websteri*); and several features on the third pereiopod, including the distinctly slenderer merus, a simple dactylus (biunguiculate in *A. websteri*), and most importantly, the presence of a ventrolateral spine on the ischium (absent in *A. websteri*) (see Hendrix & Gore 1973). *Alpheus thomasi* can also be distinguished from *A. websteri* by several details of the color pattern, the most important being the absence of spots on the major chela (compare Figs. 5D, E and 4A–D).

GenBank number.—EU339467 [05-020, MNHN-Na 16362, Dominican Republic], EU339468 [06-500, not deposited, Panama], EU339469 [F119, not deposited, Panama], EU339470 [AA-AC-42, MNRJ 20149, Atol das Rocas, Brazil].

Alpheus arenensis (Chace, 1937)

Figs. 3E, 4B

Crangon arenensis Chace 1937: 119, fig. 4.

Alpheus arenensis—Crosnier & Forest 1966: 236; Rodríguez de la Cruz 1977: 29; Carvacho & Ríos 1982: 282; Rodríguez de la Cruz 1987: 43.

Alpheus websteri (not *sensu* Kingsley 1880)—Wicksten 1983: 42 (part.); Wicksten & Hendrickx 1985: 572; Kim & Abele 1988: 28, fig. 11; Villalobos Hiriart *et al.* 1989: 17; Wicksten & Hendrickx 1992: 5 (part.); Wicksten 1993:

151; Hendrickx 1993a: 306; Hendrickx 1993b: 6; Hendrickx 1995: 432; Salazar-Rosas 1995: 59, pl. 17; Camacho 1996: 64; Vargas & Cortés 1999: 902; Villalobos 2000: 66, fig. 33; Wicksten & Hendrickx 2003: 65 (part.); McClure 2005: 157, fig. 24 (reproduced from Kim & Abele 1988).

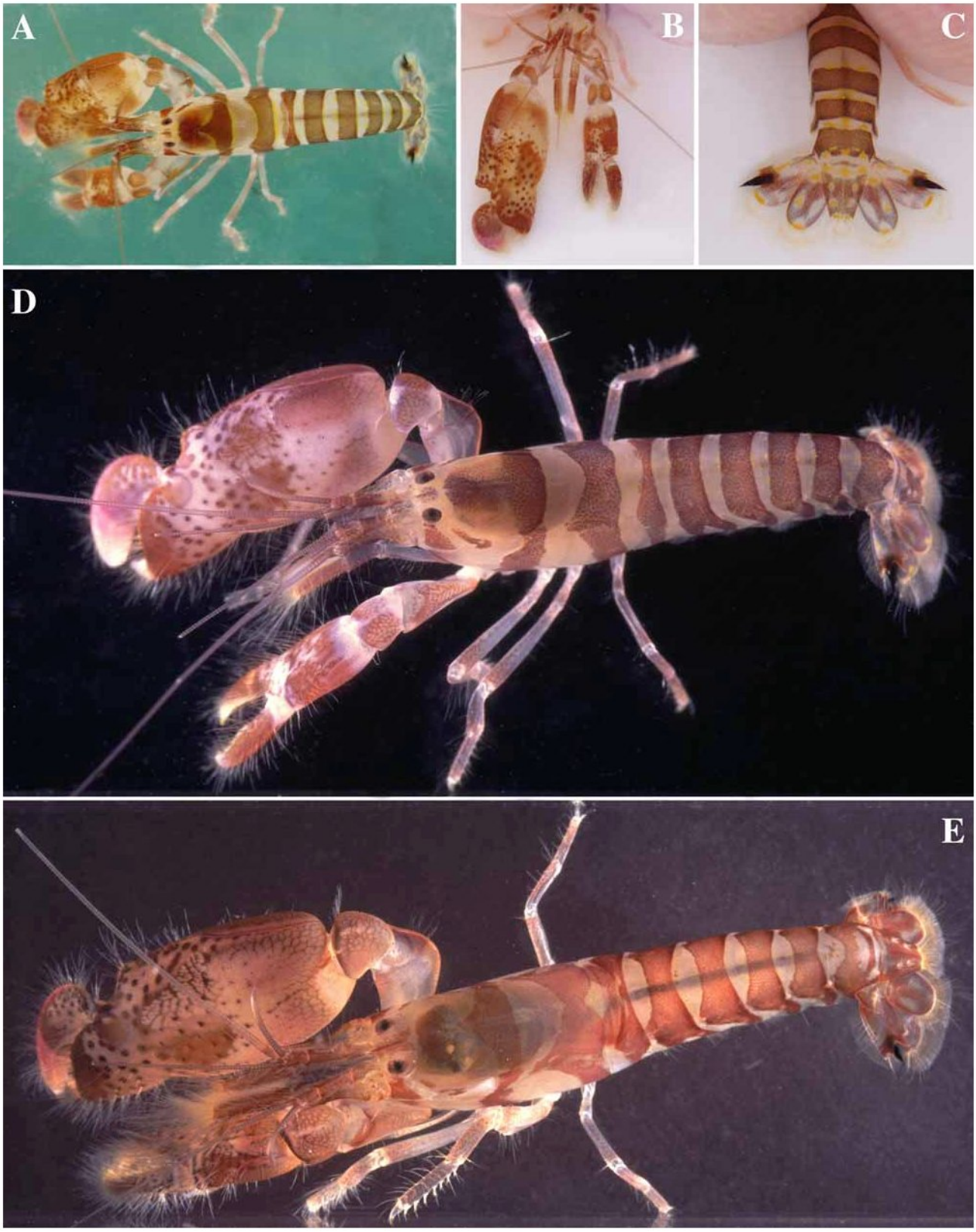

FIGURE. 3. Color patterns of adult males of *Alpheus websteri* Kingsley, 1880 (A–D) and *Alpheus arenensis* (Chace, 1937) (E); A–C, specimen from Dominican Republic (MNHN-Na 16362), A, general view, B, chelipeds, C, tail fan; D, specimen from Isla Grande, Caribbean coast of Panama; E, specimen from Isla Perico, Pacific coast of Panama.

Material examined.—Panama (Pacific coast). 1 male (CL 4.1), USNM 1109190, Las Perlas Islands, Saboga, shallow subtidal, from rock crevices, coll. A. Anker, J. Jara and C. Hurt, 15 Nov 2005 [fcn 05-156]; 1 male (CL 9.7), 1 female (CL 9.3), USNM 1109191, Amador Causeway near Panama City, Isla Perico, intertidal, coll. N. Knowlton *et al.*, 22 Jan 1992 [fcn C-292 and C-293, B-68]; 1 male (CL 9.3), USNM 1109192, Río Mar, intertidal, coll. N. Knowlton *et al.*, 16–20 Feb 1992 [fcn C-367, B-103]; 1 male (CL 8.7), USNM 1109193, same collection data as previous specimen [fcn C-363, B-99]; 1 male (CL 6.7), USNM 1109194, same collection data as previous specimen [fcn C-365, B-101]; 1 ovig. female (CL 6.5), MNHN-Na 16387, Coiba Marine National Park, Coibita, mud-rock intertidal, under rock, coll. A. Anker, I. Marin, J. Jara, E. Gómez and E. Tóth, 20 Mar 2007 [fcn 07-111].

Description.—See Chace (1937) as *Crangon arenensis*; Kim & Abele (1988) as *Alpheus websteri*.

Color pattern.—Background color cream white or pale grey; carapace with two broad transverse chestnut to brown bands, one band at about mid-length, extending anteriorly on mid-dorsal line, and one more posterior band, constricted on anterior and posterior margins, and extending anteriorly dorsolaterally, almost reaching first band (Fig. 3E), defining "bikini" pattern in dorsal view; both bands abruptly changing direction on carapace flanks (Fig. 3E); two small short brown bands present anterolaterally, ventrally and posteroventrally to orbital hoods (Fig. 3E); rostral area also brownish, in particular rostral carina; inner organs visible through carapace dorsally as large brownish patch; articulation zone between carapace and abdomen and posterior carapace sharing white rhomboid patch on brown background (Fig. 3E); abdomen with six broad (except first) chestnut to brown transverse bands with concave margins, extending to ventral margin of pleurae, abruptly changing direction laterally (towards posterior) and nearly touching on flanks (Fig. 3E); second abdominal band bifurcating laterally, reverse V-shaped (Fig. 3D); sixth abdominal somite almost completely brown except for transversely elongate white patch (Fig. 3E); white bands between brown bands with sparse spots of pale-yellow chromatophores; tail fan mostly purple-brown with large white areas, proximal portion of telson and uropods whitish, dorsal spines whitish; distolateral spine black; walking legs and second pereiopods appearing pinkish semitransparent speckled with minute red chromatophores except on articulations; cheliped merus and carpus brown laterally; mesial face of palm of major chela mostly pale brown with white areas and brown patches and fairly large dark brown spots on distal half (Fig. 3E), most proximal portion of palm white; pollex brown with whitish tip; dactylus brown-white with dark spots proximally, pink distally (Fig. 3E); palm of minor chela brown-orange, with white areas and brown spots; fingers dark brown, paler towards tip; antennular peduncles brown distally, whitish proximally; basicerite and scaphocerite mostly whitish with occasional brown-orange spots, lateral margin and distolateral tooth of scaphocerite brown; antennular and antennal flagella pale brown; corneas dark brown-grey (Fig. 3E); juveniles similar, but with more contrasting pattern on chelae, carapace, abdomen and tail fan; yellow chromatophores more intense and forming transverse bands fringing brown-grey bands on carapace and abdomen (Fig. 4B).

Size.—The largest specimen from the Pacific coast of Panama is a male from Isla Perico with CL 9.7 mm, TL 24.8 mm. The CL of the Gulf of California specimens ranged from 4.4 to 8.0 mm, and TL from 17.0 to 21.6 mm (Villalobos 2000).

Ecology.—Intertidal to about 6 m (Wicksten 1983); in crevices of rocks and under coral rubble on sand or mixed sand-coral bottoms.

Type locality.—Arena Bank, Gulf of California, Mexico.

Distribution.—Eastern Pacific: Mexico: central and southern Gulf of California (e..g., Arena Bank, Sonora) and Revillagigedo Islands (Socorro) (Chace 1937; Carvacho & Ríos 1982; Wicksten 1983; Wicksten & Hendrickx 2003); Costa Rica: Guanacaste, Puntarenas (Kim & Abele 1988); Panama: Las Perlas (Kim & Abele 1988; present study); Colombia (Wicksten 1983); Galapagos (Wicksten 1993; Wicksten & Hendrickx 2003).

Remarks.—The only noticeable morphological difference between *A. websteri* and *A. arenensis* lies in the development of the small distal tooth on the ventromesial margin of the major cheliped merus: acute in *A.*

websteri (Fig. 1H) and blunt or absent in *A. arenensis* (see Kim & Abele 1988, fig. 11f). A side by side comparison of two large adults of each species revealed two further, although very subtle differences: the orbital grooves appear to be deeper in *A. arenensis* compared to those of *A. websteri*, while the scaphocerite blade is shorter in *A. arenensis* compared to that of *A. websteri*, reaching to about 3/5 of the scaphocerite length (vs. 3/4 in *A. websteri*). Differences in color between the two species are more numerous both in adults (Fig. 3D, E) and juveniles (Fig. 4A, B), including the more concave margins of the abdominal bands in *A. arenensis* (vs. almost straight in *A. websteri*); the "bikini"-shaped posterior band on the carapace (this band is subrectangular in *A. websteri*); and the presence of a white dorsomedian patch on the sixth abdominal somite (absent in *A. websteri*) (see also Table 1).

GenBank number.—EU339466 [99-041, not deposited, Panama].

TABLE 1. Differences among the three species of the *A. websteri* Kingsley complex: *A. websteri* Kingsley, 1880; *A. arenensis* (Chace, 1937); and *A. fagei* Crosnier and Forest, 1965. Abbreviations: EA – eastern Atlantic, EP – eastern Pacific; WA – western Atlantic; P – pereiopod.

Feature	*A. websteri* (WA)	*A. arenensis* (EP)	*A. fagei* (EA)
Distoventral tooth of basicerite	reaching or slightly exceeding stylocerite	slightly exceeding stylocerite	not reaching stylocerite
Major chela: distal (mesioventral) tooth on merus	small, acute	small, blunt or absent	small, subacute
Male minor chela height/length ratio	~3.0	~3.0	~2.5
P3 propodus: distodorsal spines	1–2	1–2	0
P3 dactylus	biunguiculate	biunguiculate	simple
Color: sixth abdominal somite	without white dorsal patch	with white dorsal patch	without white dorsal patch
Color: abdominal transverse bands 1	with straight margins	with concave margins	with straight margins
Color: abdominal transverse bands 2	approaching laterally	almost touching laterally	approaching laterally
Color: palm of major chela	white-brown marbled with brown spots	white-brown marbled with brown spots	brown-orange with pale bands and whitish streak
Color: posterior band on carapace	subrectangular	bikini-shaped	subrectangular
Color: carapace-abdomen region	white band	brown with white median patch	white band

Alpheus fagei Crosnier & Forest, 1965

Figs. 4C, 5A–C

Alpheus fagei Crosnier & Forest 1965: 603, fig. 1; Crosnier & Forest 1966: 233, fig. 8; Wicksten 1983: 42; Kim & Abele 1988: 30.

Material examined.—São Tomé. 1 female (CL 5.0), USNM 1109195, ST 5, Lagoa Azul, shallow bay with rocky shore, from coralline algae and rocks, depth 1–3 m, coll. N. Knowlton and A. Anker, 3 Feb 2006 [fcn 06-139]; 1 male (CL 7.4), 1 ovig. female (CL 9.6), USNM 1109196, ST 10, Ilha das Cabras, off beach near

light house, depth about 2 m, coarse sand and rubble, under rocks and rock crevices, coll. A. Anker, 8 Feb 2006 [fcn 06-179]; 1 ovig. female (CL 5.8), USNM 1109197, ST 5A, Lagoa Azul, shallow bay with rocky shore, from coralline algae and rocks, depth 1–3 m, coll. N. Knowlton and A. Anker, 6 Feb 2006 [fcn 06-163]; 1 male (CL 5.1) 1 ovig. female (CL 6.6), USNM 1109198, same collection data as previous specimen [fcn 06-161, 06-162]; 1 ovig. female, CL 10.1, USNM 1109199, ST 3, 200 m west of Lagoa Azul, rocky shore with coralline algae, from holes and under rocks, intertidal, extreme low tide, coll. N. Knowlton and A. Anker, 31 Jan 2006 [fcn 06-065]; 1 male (CL 8.7), 1 ovig. female (CL 9.1) MNHN-Na 16708, ST 6A: São Tome town, near fortress, shallow bay with sand-mud and scattered rocks, under rocks, depth 0.5–1 m, coll. N. Knowlton and A. Anker, 4 Feb 2006 [fcn 06-168, 06-167]; 1 juvenile (CL not measured), USNM 1109200, ST 2, Praia Lagarto, near hospital, sand with *Montastraea*, zoanthids and rocks embedded in sand, intertidal (extreme low tide), coll. N. Knowlton and A. Anker, 30 Jan 2006 [fcn 06-051].

Description.—See Crosnier & Forest (1965, 1966).

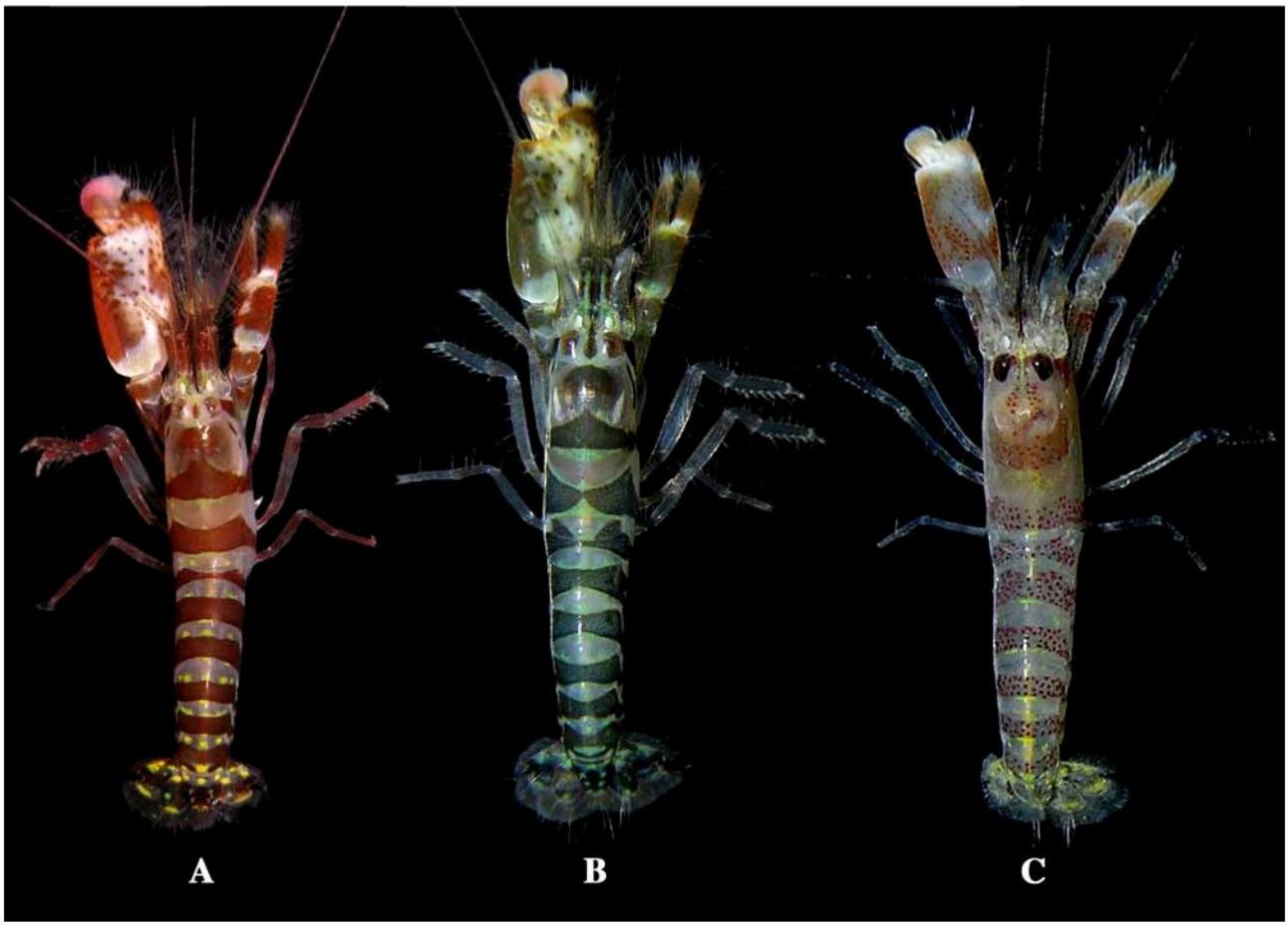

FIGURE. 4. Color patterns of juveniles of *Alpheus websteri* Kingsley, 1880 (A); *Alpheus arenensis* (Chace, 1937) (B); *Alpheus fagei* Crosnier and Forest, 1966 (C); A, specimen from Utila, Honduras (OUMNH 2007-20-002); B, specimen from Las Perlas Islands, Pacific coast of Panama (USNM 1109190); C, specimen from São Tomé (USNM 1109200).

Color pattern.—Background color cream white or pale grey; carapace with two broad transverse brown bands, one band at about mid-length, somewhat extending anteriorly on mid-dorsal line (Fig. 5A, B), and one more posterior band, with concave anterior margin and more or less sinuous posterior margin (Fig. 5A, B), and extending anteriorly dorsolaterally, but not reaching first band (Fig. 5C), both bands abruptly changing direction on carapace flanks (Fig. 5C); anterolateral areas of carapace below orbital hoods dark brown (Fig. 5C); rostral area also brownish, with pale greenish-brown rostral carina; inner organs visible through carapace dorsally as large purple-brown patch; abdomen with six broad dark brown or chocolate brown transverse

bands with slightly concave posterior margins, extending to ventral margin of pleurae, abruptly changing direction laterally (towards posterior) but not touching on flanks (Fig. 5C); second abdominal band bifurcating laterally, reverse V-shaped (Fig. 5C); sixth abdominal somite almost completely dark brown except for large yellow spot posteriorly (Fig. 5A, B); white bands between brown bands with intense egg-yellow bands anteriorly, fringing posterior margins of brown bands (Fig. 5A, B); tail fan mostly purple-brown, with large white areas and spots of yellow chromatophores, proximal portion of telson and uropods whitish, dorsal spines whitish; distolateral spine black; walking legs and second pereiopods pinkish semitransparent speckled with minute red chromatophores except on articulations; cheliped merus and carpus orange-brown laterally; mesial face of palm of major chela orange-brown with paler areas (Fig. 5B) and sometimes transverse white streaks (Fig. 5A); pollex darker orange-brown with whitish tip; dactylus brown-grey proximally, pink distally (Fig. 5A); palm of minor chela brown-orange, white proximally; fingers dark brown, pale grey towards tip; antennular peduncles brown distally, whitish proximally; basicerite and scaphocerite mostly whitish with occasional brown-orange spots, lateral margin and distolateral tooth of scaphocerite brown; antennular and antennal flagella pale brown; corneas grey (Fig. 5A–C); juveniles with paler bands but more contrasting pattern, especially marked white patches on major chela (Fig. 4C).

Size.—The largest examined specimen is an ovigerous female with CL 10.1 mm and TL 27.9 mm.

FIGURE. 5. Color patterns of adults of *Alpheus fagei* Crosnier & Forest, 1966 (A–C) and *Alpheus thomasi* Hendrix & Gore, 1973 (D, E); A, female from São Tomé (USNM 1109199); B, C, male from São Tomé (MNHN-Na 16708); D, male from Bocas del Toro, Caribbean coast of Panama (MNHN-Na 16707); E, ovigerous female from Bocas del Toro, Caribbean coast of Panama (USNM 1109188). Notice similarities, especially in the presence of narrow yellow bands fringing brown bands and the bifurcating band on the second abdominal somite.

Ecology.—Lower intertidal to about 35 m (Crosnier & Forest 1966); hard bottoms, in crevices of calcareous algal crusts and overgrown rocks, also in coral rubble and under rocks on mixed sand-rock bottoms.

Type locality.—São Tomé, Gulf of Guinea.

Distribution.—Eastern Atlantic: Ivory Coast; Gulf of Guinea: São Tomé and Principe (Crosnier & Forest 1966).

Remarks.—*Alpheus fagei* differs from *A. websteri* and *A. arenensis* mainly by the shorter basicerite, not reaching level of stylocerite (vs. reaching to or slightly beyond stylocerite in *A. websteri* and *A. arenensis*); the third pereiopod bearing a simple dactylus (vs. biunguiculate in *A. websteri* and *A. arenensis*); and in life, by the palm of the major chela lacking dark spots (vs. with spots in *A. websteri* and *A. arenensis*) (see also Table 1). The color pattern of *A. fagei* is remarkably similar to that of the western Atlantic *A. thomasi* (Fig. 5). The main color differences between the two species are the relatively broader bands on the carapace in *A. fagei*, and a brighter, more contrasting pattern on the major claw in *A. thomasi*. In addition to these, *A. fagei* may be easily separated from *A. thomasi* by the same morphological criteria as *A. websteri* (see above).

GenBank number.—EU339464 [06-086, not deposited, São Tomé], EU339465 [06-119, not deposited, São Tomé].

Discussion

The *Alpheus websteri* species complex now includes three allopatric species: the western Atlantic *A. websteri*, the eastern Pacific *A. arenensis* and the eastern Atlantic *A. fagei*. These three species share, in addition to the above-listed morphological characters, a very characteristic color pattern, consisting of dark transverse bands fringed by yellow bands on the abdomen, with the band on the second pleuron bifurcating laterally (divided into two oblique bands thus forming a reverse V).

Alpheus websteri and *A. arenensis* are morphologically quasi-identical (cf. Table 1), diverging only slightly in color patterns (cf. Fig. 3); they therefore clearly represent a pair of transisthmian sister species. This is strongly corroborated by molecular data: the K2P genetic distance for the 5' end of COI between *A. websteri* and *A. arenensis* is 8.8% which is slightly below the mean value of distances observed in other transithmian *Alpheus* pairs: in 13 other comparisons, distances ranged from 6.4 % to 20.1 % and averaged 10.6 % (Williams *et al.* 2001; C. Hurt, pers. obs.). Using Knowlton & Weigt's (1998) molecular clock, based on 3' COI sequence data in *Alpheus*, the timing of divergence between these two species may be estimated at about 6 mya.

Alpheus fagei differs rather insignificantly in morphology from *A. websteri* and *A. arenensis* (see Table 1); however, differences in the color pattern are more marked, especially on the major chela (cf. Figs. 3, 5A–C). Therefore, the eastern Atlantic species appears to form a sister clade to the *A. websteri* – *A. arenensis* clade. Molecular data supports this assumption: the K2P distance (COI 5') between *A. fagei* and *A. websteri* or *A. arenensis* is 18.3%. Based on these values (see methods), the estimated time of divergence between *A. fagei* and the *A. websteri* – *A. arenensis* clade would be approximately 12 mya.

As mentioned above, the *A. websteri* complex is part of clade III of Williams *et al.* (2001), which includes the majority of species of the polyphyletic *A. sulcatus* species group. However, the affinities of the *A. websteri* complex to other species of the clade III are unclear. Crosnier & Forest (1966) included the eastern Atlantic *A. rugimanus* in their comparative table of species of the *A. websteri* complex. However, our data (morphology, genetics and color patterns) does not support a close relationship between the *A. websteri* complex and *A. rugimanus*. Therefore, the latter species will be treated in more detail elsewhere.

On the other hand, the western Atlantic *Alpheus thomasi* may well be part of the *A. websteri* complex *sensu lato*. This species is morphologically close to the three species of the *A. websteri* complex (Hendrix & Gore 1973) and also shares with them the presence of dark transverse bands fringed by yellow bands and the

laterally divided band on the second abdominal pleuron (cf. Fig. 5D, E). Thus color and to lesser extent morphological data support a sister clade position of *A. thomasi* to the *A. websteri* complex *sensu stricto* [(*A. websteri* – *A. arenensis*) – *A. fagei*]. However, preliminary molecular data (Hurt *et al.*, in prep.) suggests that *A. thomasi* rather forms a separate lineage within a subclade of the clade III, which includes the *A. websteri* complex and at least two other subclades. These results are somewhat different from those obtained by Williams *et al.* (2001), where *A. thomasi* forms the most basal lineage of the clade III (see Williams *et al.* 2001, fig. 6).

Chace (1937) believed that the Indo-West Pacific *A. gracilis* (also a species complex, A. Anker, pers. obs.) was the closest relative of *A. arenensis*. We did not have specimens of *A. gracilis* for direct comparison of color patterns or molecular studies, but based on published records (e.g., Banner & Banner 1982), *A. gracilis* appears not to be closely related to the *A. websteri* complex. Molecular analyses of the entire clade III (Hurt *et al.*, in prep.), including some important Indo-West Pacific taxa, are needed to elucidate phylogenetic affinities of the *A. websteri* complex, *A. thomasi*, *A. rugimanus* and the *A. gracilis* complex.

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