



Description of cryptic taxa within the *Alpheus bouvieri* A. Milne-Edwards, 1878 and *A. hebes* Kim and Abele, 1988 species complexes (Crustacea: Decapoda: Alpheidae)

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Abstract

Alpheus bouvieri A. Milne-Edwards, 1878 and *A. hebes* Kim and Abele, 1988 are reviewed based on morphological and genetic data. *Alpheus bouvieri*, previously believed to be distributed in the eastern Pacific and Atlantic, is restricted to the Atlantic populations; the eastern Pacific populations (*A. bouvieri sensu* Kim and Abele 1988) are assigned to *A. javieri* n. sp. A second new species, *A. agilis* n. sp., closely related to the eastern Pacific *A. hebes*, is described based on recently collected specimens from the eastern Atlantic (São Tomé, Cape Verde) and western Atlantic (Atol das Rocas off northeastern Brazil). The absence of *A. agilis* n. sp. (or any other representative of the *A. hebes* clade) in the Caribbean Sea is likely due to a relatively recent (~1–2 my) extinction. Genetic data (COI sequences) indicates that *A. bouvieri* and *A. javieri* n. sp., and *A. hebes* and *A. agilis* n. sp. diverged approximately 6 and 7.5 mya, respectively, i.e., around 3 my before the final closure of the Isthmus of Panama.

Key words: *Alpheus*, snapping shrimp, Alpheidae, eastern Pacific, western Atlantic, color pattern, transisthmian species, new species, extinction, Caribbean, molecular phylogeny, barcode, COI

Introduction

The snapping shrimp genus *Alpheus* Fabricius, 1798 is notorious for its extreme diversity and numerous cryptic and pseudocryptic species that can be initially detected by comparison of color patterns or by genetic analyses (Knowlton and Keller 1985; Knowlton and Mills 1992; Knowlton *et al.* 1993; Williams *et al.* 2001; Anker 2001; Nomura and Anker 2005). Problems related to transisthmian cryptic species—species pairs or complexes present on each side of the Isthmus of Panama—were addressed by Knowlton and Mills (1992), Knowlton *et al.* (1993), and in combination with a molecular phylogeny of *Alpheus* by Williams *et al.* (2001). This last study dealt with a broad selection of species from different groups of *Alpheus*, in particular the heterogeneous *A. edwardsii* (Audouin, 1826) group defined mainly by the unarmed orbital hoods and the presence of two notches (grooves) on the major chela (Banner and Banner 1982). This group was found to be polyphyletic, more precisely containing two unrelated clades of snapping shrimps with a double-notched major claw (Williams *et al.* 2001, fig. 6).

The first clade of *Alpheus* with a double-notched major claw—here clade E (for “*edwardsii*”)—is a hyperdiverse clade that includes species in which the dorsal (= superior) groove of the major chela palm

extends posteriorly on the mesial face, such as *A. nuttingi* (Schmitt, 1924) and *A. umbo* Kim and Abele, 1988 (see also Williams *et al.* 2001, fig. 1).

The second clade—hereafter Clade L (for “*leviusculus*”)—is a numerically much smaller clade that includes species, in which the dorsal groove of the major chela palm is almost abruptly rounded, not extending posteriorly on the mesial face, such as *A. bouvieri* A. Milne-Edwards, 1878 and *A. hebes* Kim and Abele, 1988 (see also Williams *et al.* 2001, fig. 1). In addition to *A. bouvieri* and *A. hebes*, the following species share this unique shape of the major chela and therefore probably belong to the Clade L: *A. leviusculus* Dana, 1852; *A. parvirostris* Dana, 1852; *A. bastardi* Coutière, 1898; *A. maindroni* Coutière, 1898; *A. chilensis* Coutière in Lenz, 1902; *A. hululensis* Coutière, 1905; *A. coutierei* De Man, 1909; *A. ladronis* Banner, 1956; *A. bannerorum* Bruce, 1987; *A. longinquus* Kim and Abele, 1988; *A. zimmermani* Anker, 2007. The present study deals mainly with the eastern Pacific-Atlantic *A. bouvieri* and *A. hebes* clades.

Alpheus bouvieri, originally described from the Cape Verde Islands in the tropical eastern Atlantic (Milne-Edwards 1878), is defined by the short, carinate rostrum; the third and fourth pereopods with unarmed ischia; the cheliped meri without a distomesial tooth; the uropod with a distinctly bilobed transverse suture; and the male minor cheliped with well developed balaeniceps fingers. Crosnier and Forest (1966) examined remnants of syntypes of *A. bouvieri* [“débris de syntypes”, “spécimens très abimés”] deposited in the Muséum national d’Histoire naturelle, Paris, France (MNHN), along with a series of specimens collected by the Calypso on the coasts of Cape Verde, São Tomé and Congo, and provided a redescription of *A. bouvieri* based on this material. These authors also mentioned occurrence of *A. bouvieri* in the western Atlantic, referring to Coutière’s (1899) reidentification of Pocock’s (1890) material from Fernando do Noronha, Brazil, originally reported as “*A. edwardsii*”. Subsequently, *A. bouvieri* was reported from the Caribbean (Chace 1972; Abele 1976), Florida (Gore *et al.* 1978), Bermuda, Brazil (Christoffersen 1979), and Ascension Island in the central Atlantic (Manning and Chace 1990).

Kim and Abele (1988) summarized records of *A. bouvieri* in the eastern Pacific, providing a detailed description and good illustrations of a male specimen from Costa Rica (Kim and Abele 1988, fig. 24). However, molecular data in Williams *et al.* (2001) showed that the eastern Pacific specimens of *A. bouvieri* (as “*A. bouvieri*—P”) were genetically distinct from the western Atlantic specimens (as “*A. bouvieri*—C” and “*A. bouvieri*—Br” for Caribbean and Brazil, respectively). For this study, we sequenced freshly collected specimens from the Pacific and Atlantic (Caribbean) coasts of Panama, as well as specimens from São Tomé in the eastern Atlantic. These new data show that there is indeed a single ampho-Atlantic species: *A. bouvieri sensu stricto*, i.e., *sensu* Milne-Edwards 1878; Crosnier and Forest 1966; Chace 1972; Christoffersen 1979 (*A. bouvieri*—C / Br in Williams *et al.* 2001), which is distinct from the eastern Pacific species, *A. bouvieri sensu* Kim and Abele 1988 (*A. bouvieri*—P in Williams *et al.* 2001). The latter taxon did not have a valid name (see complete synonymy in Kim and Abele 1988) and is therefore described as new in this study, based on freshly collected material from the Pacific coast of Panama and Costa Rica.

The eastern Pacific *Alpheus hebes*, ranging from Mexico to Ecuador, differs from both *A. bouvieri* and its eastern Pacific sister species mainly by the non-carinate, posteriorly flattening rostrum, and the ischium of the third and fourth pereopods bearing a small ventrolateral spine (Kim and Abele 1988; McClure and Wicksten 2000). A previously unreported and unnamed species, which in morphology, color pattern and ecology is remarkably similar to *A. hebes*, was recently collected in the eastern Atlantic, first in the Cape Verde Islands in 1998, then in São Tomé in 2006. The same species was also found among the alpheid material collected by Paulo S. Young (late of Museu Nacional, Rio de Janeiro, Brazil) and his collaborators at Atol das Rocas, off northeastern Brazil, in 2000. This species is herewith described as new, based on numerous specimens from both the western and eastern Atlantic. Illustrations of the most important morphological features of *A. bouvieri*, *A. hebes*, and two new species, as well as color photographs and GenBank numbers (COI) are provided.

Material and methods

Specimens were collected by hand, under rocks at low tide, or extracted from crevices in rocks, rubble, fossilized coral terraces, or from mangrove wood logs perforated by boring clams and mudshrimps. Most were photographed alive before being preserved in 70% or 95% ethanol. Specimens selected for RNA/DNA extractions were preserved in RNAlater (Ambion) or frozen; sometimes, a leg was detached from a specimen and preserved in RNAlater, while the body of the specimen was preserved in ethanol.

Carapace length (CL) and total length (TL) were measured in mm along the mid-dorsal line from the tip of the rostrum to the posterior margin of the carapace and telson, respectively. Egg size is given in mm and was measured as length x width diameter. Other abbreviations used in the text: Br—Brazil; Car—Caribbean; fcn—field collection number; EA—eastern Atlantic; EP—eastern Pacific; WA—western Atlantic. The material is deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Muséum national d'Histoire naturelle, Paris, France (MNHN); Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (FLMNH UF); Oxford University Museum of Natural History, Oxford, United Kingdom (OUMNH); and Colección de Referencia, Departamento de Biología Marina, Universidad de Panamá, Panama City, Panama (UP).

COI sequences from specimens of the *A. bouvieri* complex were obtained following the protocol described previously (see Anker *et al.* 2007). COI sequences from species of the *A. hebes* complex were generated from clones of PCR product that was amplified from cDNA. The sequenced clones produced multiple pseudogenes, suggesting that some of the nuclear pseudogenes are actually transcribed, explaining why clean sequences could not be obtained using the standard protocol. The PCR protocol used is the same as in previous studies (see Anker *et al.* 2007).

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 and 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 and Abele, 1988 / *A. chacei* Carvacho, 1979 (GenBank accession numbers AF309875, AF309876, AF309884, AF309889, AF309893, 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 and Weigt 1998). This rate differs slightly from the published rate of 1.4% (Knowlton and Weigt 1998), obtained from comparisons of COI sequences from the 3' end only.

Phylogenetic relationship of COI haplotypes were estimated using neighbor-joining (NJ), maximum likelihood (ML), and Bayesian methods. NJ analysis was performed using the software package MEGA 3.1 (Kumar *et al.* 2004) and the K2P genetic distance method. Confidence values for nodes were estimated by bootstrap (1000 replicates). The GTR+I+G was indicated as the best model of nucleotide substitution for our dataset using a hierarchical likelihood ratio test and the Akaike information criterion (Akaike 1974) as performed in MrModeltest 2.2 (Nylander 2006), and was used in both ML and Bayesian analyses. Maximum likelihood analysis was performed with the software program PAUP 4.0b10 (Swofford 2002), using a heuristic search with tree bisection-reconnection (TBR) branch-swapping to search through tree space. Bayesian analysis was performed using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) with 5,000,000 generations.

Taxonomy

Genus *Alpheus* Fabricius, 1798

Alpheus bouvieri A. Milne-Edwards, 1878

Figs. 1, 5A, B

Alpheus Bouvieri Milne-Edwards 1878: 231; Coutière 1898: 131 (part., specimens from Congo); Coutière 1899 (part., for page numbers see Chace and Forest 1970).

Alpheus bouvieri—Rathbun 1900: 312 (part.); Balss 1916: 21; Sourie 1954: 253; Forest and Guinot 1958: 9; Ribeiro 1964: 5; Crosnier and Forest 1965: 606; Crosnier and Forest 1966: 273, fig. 22; Ribeiro 1968: 30, fig. 7; Uchakov 1970: 444; Fausto-Filho and Furtado 1970: 286; Chace 1972: 63; Fausto-Filho 1974: 5; Fausto-Filho 1975: 79; Fausto-Filho 1980: 113; Abele 1976: 273; Gore *et al.* 1978: 225; Christoffersen 1979: 303, figs. 2-5; Christoffersen 1980a: 37, figs. 7-10; Christoffersen 1980b: 39; Freitas-Lins 1985: 11; Abele and Kim 1986: 199, 214-215, figs. 1-d; Manning and Chace 1990: 14; Martínez-Iglesias *et al.* 1996: 33; Hernández-Aguilera *et al.* 1996: 30; Martínez-Iglesias *et al.* 1997: 404, fig. 6; Christoffersen 1998: 357; Santos and Coelho 1998: 74; McClure 2005: 133 (part., not fig. 8); Coelho *et al.* 2006: 1221; Almeida *et al.* 2006: 9.

Crangon (Alpheus) bouvieri—Monod 1933: 462, figs. 1A-C.

Alpheus leviusculus bouvieri—Banner and Banner 1982: 250 (part.).

Not *Alpheus Bouvieri*—Coutière 1898: 131 (part., specimens from Pacific coast of Panama = *A. javieri* **n. sp.**); Coutière 1905: 907 (part, other species).

Not *Alpheus bouvieri*—Holthuis 1951: 81; Holthuis 1952b: 43 (possibly = *A. holthuisi* Ribeiro, 1964; see Crosnier and Forest 1966); Monod 1927: 594 (= *A. pontederiae* Rochebrune, 1883; see Crosnier and Forest 1966); Chace 1962: 610 (possibly = *A. longinquus* Kim and Abele, 1988; see Kim and Abele 1988); Christoffersen 1979: 303 (part., specimens from Eastern Pacific); Kim and Abele 1988: 58, fig. 24; Wicksten and Hendrickx 1992: 4; Ricaurte *et al.* 1995: 81, 84; Vargas and Cortés 1999: 899; McClure and Wicksten 2000: 966, fig. 2; Wicksten and Hendrickx 2003: 63; McClure 2005: 134 (part., fig. 8 only) (= *A. javieri* **n. sp.**); Hickman and Zimmerman 2000: 35 (= *Alpheus* sp.).

Not *Alpheus leviusculus bouvieri*—Christoffersen and Ramos 1988: 63 (= *A. javieri* **n. sp.**)

Not *Alpheus bouvieri* var. *chilensis* (not *sensu* Coutière 1902)—Schmitt 1924a: 162 (= *A. javieri*, **n. sp.**).

Alpheus Edwardsii (not *sensu* Audouin 1826)—Dana 1852: 542; Dana 1855: 11, pl. 34, fig. 2a-f; Bate 1888: 542, pl. 97, fig. 1; Pocock 1890: 518 (part.) (see Crosnier and Forest 1966).

Alpheus heterochaelis (not *sensu* Say 1818)—Kingsley 1878: 194 (part.); Rathbun 1900: 152 (part.); Luederwaldt 1919: 429 (part.) (see Christoffersen 1979).

Alpheus nuttingi var. ? (not *sensu* Schmitt 1924b)—Schmitt 1936: 368.

Alpheus sp.—Santos 1974: 7 et seq., figs. 1-16, 18g; Santos 1981: 319 et seq., figs. 1-16, 18g.

Material examined.—São Tomé. 1 male (CL 4.8), 2 ovig. females (CL 5.2, 6.4), USNM 1123843, ST 1, Boca do Inferno, rocky intertidal, under consolidated volcanic rocks and coralline algae, coll. A. Anker and N. Knowlton, 29 Jan 2006 [fcn 06-008 (male), 06-007, 06-009 (females)]; 1 female (CL 4.0), USNM 1123845, ST 2, Praia Lagarto, near São Tomé town hospital, intertidal, sand with *Montastraea*, zoanthids and rocks embedded in sand, coll. N. Knowlton and A. Anker, 30 Jan 2006 [fcn 06-026]; 1 male (CL 3.9), 1 ovig. female (CL 4.6), USNM 1123846, ST 3, 200 m west of Lagoa Azul, rocky intertidal with coralline algae, from holes and under rocks, coll. A. Anker and N. Knowlton, 31 Jan 2006 [fcn 06-073 (male), 06-072 (female)]; 1 male (CL 4.2), 1 female (CL 5.5), 1 ovig. female (CL 4.5), MNHN-Na 17182, ST 2A, Praia Lagarto, near São Tomé town hospital, intertidal, sand with *Montastraea*, zoanthids and rocks embedded in sand, coll. N. Knowlton and A. Anker, 2 Feb 2006 [fcn 06-132 (male), 06-131, 06-133 (females)]; 1 ovig. female (CL 5.7), USNM 1123847, ST 11, Kia dive site off Ilha das Cabras, depth about 10 m, under rocks, coll. N. Knowlton, 8 Feb 2006 [fcn 06-189].

Cape Verde. 1 male (CL 5.3), 1 female (CL 7.9), USNM 1123848, São Vicente, Baía das Gatas, coll. N. Knowlton *et al.*, 28 Mar 1998; 7 males (CL 4.2-5.4), 8 females, including 7 ovig. females (CL 3.9-6.9), USNM 1123849, Santiago, Praia, beach near Club Nautics, coll. N. Knowlton *et al.*, 5 Apr 1998; 1 ovig. female (CL not measured), MNHN-Na 13674, Terrafal, in tide pool, coll. P. Wirtz, Feb 2000.

Panama (Caribbean coast). 3 males (CL 5.4, CL 6.1, 7.4), 2 ovig. females (CL 6.1, 8.2), USNM 1123850, Bocas del Toro, Isla Colón, Bocas del Drago, shallow subtidal (less than 0.5 m), from crevices in rocks and rubble, coll. C. Hurt, 16 Sep 2006 [06-474, 06-475, 06-517 (males), fcn 06-473, 06-476 (females)]; 1 male (CL 6.7), 1 ovig. female (CL 7.3), USNM 1123851, Bocas del Toro, Isla Colón, between Big Creek and Playa Bluff, from crevices in rocks and fossilized coral platform, coll. A. Anker, A. Baeza and J.A. Vera-Caripe, 19 Nov 2006 [fcn 06-612 (male, specimen dissected), 06-611 (female)]; 1 male (CL 8.2), 2 ovig. females (CL 7.1, 8.7), UP, same collection data as for previous specimens [fcn 06-616 (male), 06-614, 06-615 (females)].

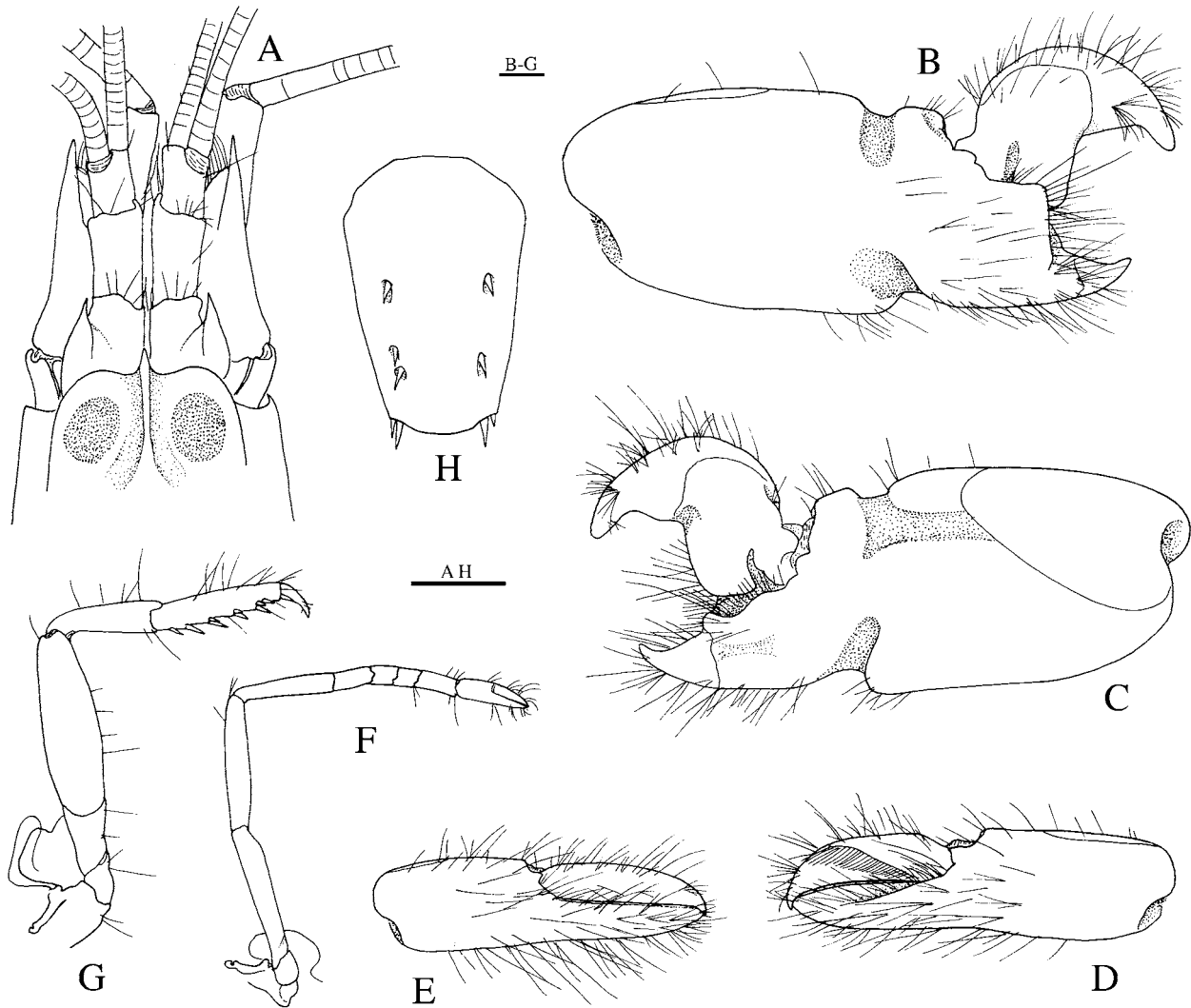


FIGURE 1. *Alpheus bouvieri* A. Milne-Edwards, 1878; male (A–D, F–H) and female (E) from Bocas del Toro, Panama (USNM 1123851): A, frontal region, dorsal view; B, major chela, mesial view; C, same, lateral view; D, male minor chela, mesial view; E, female minor chela, mesial view; F, second pereopod, lateral view; G, third pereopod, lateral view; H, telson, dorsal view. Scale bars: 1 mm.

Mexico (Gulf of Mexico). 1 male (CL not measured), FLMNH UF Arthropoda 16557, Los Alacranes Reef off Yucatan Peninsula, under rocks, coll. N. Simões, 2008 [fcn ALA068 = 08-253].

Brazil. 1 male (CL 6.1), 9 females (CL 4.6–9.6), 3 juveniles (CL not measured), USNM 1123852, Pernambuco, mouth of Rio Formoso, Carneiro reef, Tomandaré, under rocks, coll. N. Knowlton *et al.*, 17 Sep 1998; 1 ovig. female (CL 10.1), USNM 1123853, Rio de Janeiro, Ilha Grande, coll. N. Knowlton *et al.*, 26 Sep 1998; 1 male (CL 7.4), USNM 1123854, Rio de Janeiro, Cabo Frio, coll. N. Knowlton *et al.*, 18 Sep 1998; 1 ovig. female (CL 5.1), MNRJ 20843, LT 719, Atol das Rocas, Canal da Barretão, coll. P.S. Young, P.C. Paiva

and A.A. Aguiar, 10 Oct 2000 [specimen dissected]; 1 ovig. female (CL 7.1), MNRJ 20844, Atol das Rocas, in front of Ilha do Farol, under rocks, coll. P.S. Young, P.C. Paiva and A.A. Aguiar, 14 Oct 2000.

Diagnosis. Species of *Alpheus leviusculus* group (Clade L). Frontal margin of carapace with distinct, short, narrow, distally acute rostrum; rostral carina sharply delimited, extending to level of eyes, gradually flattening; orbital hoods unarmed, rounded, swollen, gently sloping into shallow orbitorostral grooves. Antennule with second peduncular segment less than twice as long as wide; stylocerite with acute tip, reaching distal margin of first segment. Antenna with basicerite armed with sharp distoventral tooth; scaphocerite with strong distolateral tooth extending well beyond broad blade, reaching end of antennular peduncle; carpocerite overreaching both scaphocerite and end of antennular peduncle. Third maxilliped not particularly broadened, unarmed. Major cheliped with merus lacking sharp distomesial tooth; chela somewhat compressed, dorsal groove broad, deep, extending mesially as contrasting rounded depression and laterally as well defined, posteriorly extending groove; dorsal shoulder rounded, not overhanging; ventral groove broad and deep, adjacent shoulder rounded, slightly protruding; adhesive disks small; fingers about half-length of palm; plunger of dactylus well developed. Minor cheliped sexually dimorphic; palm without grooves or notches in both sexes; fingers somewhat broadened and balaeniceps in males, subconical and non-balaeniceps in females. Second pereopod with first carpal segment slightly more than twice as long as second. Third pereopod with unarmed ischium, merus and carpus; propodus with row of stout spines, most paired; dactylus stout, simple, conical. Male second pleopod with typical appendices masculina and interna. Uropod with protopod laterally projecting as acute tooth; exopod with distolateral spine bordered laterally by sharp distolateral tooth; transverse suture sinuous, consisting of two rounded lobes and subtriangular tooth adjacent to distolateral spine; both exopod and endopod furnished with row of spinules distally. Telson broad, tapering distally, with two pairs of dorsal spines; posterior margin slightly convex, with two pairs of spines at each posterolateral angle.

Description. See Crosnier and Forest (1966) for description and figures of eastern Atlantic specimens, and Christoffersen (1979) for description and figures of western Atlantic (Brazilian) specimens. Complementary figures are provided in Fig. 1.

Size. Eastern Atlantic: largest male from Cape Verde at CL 5.4 mm and TL 13.7 mm; largest female from Cape Verde at CL 7.9 mm and TL 20.1 mm (Crosnier and Forest's (1966) specimens were comparable, with a TL of 8–22 mm); western Atlantic: largest male from Panama at CL 8.2 mm and TL 23.9 mm; largest female from Brazil at CL 10.1 mm and TL 26.6 mm; egg size: about 0.6 x 0.5 mm (average from 3 eggs from largest ovigerous female).

Color pattern. Opaque-whitish with broad transverse bands varying from brown-green to dark-brown (combination of gray-blue and red chromatophores), two on carapace and one along posterior half of each pleomere; uropods and telson white proximally, brown distally; walking legs whitish with red chromatophores; minor chela pale brown to green-brown; major chela olive-green to pale brown mesially, with more or less marked whitish patch ventroproximally; dorsal and ventral grooves paler brown to almost white; distal half of pollex and dactylus whitish or pink; rostrum and rostral carina region brown or brown-green; antennular peduncles brown; scaphocerite of antenna with brown lateral margin and distolateral tooth; antennal and antennular flagella pale yellow; eggs or ovaries in females yolk-yellow (Fig. 5A, B).

Type locality. Cape Verde (Milne-Edwards 1878); type specimens in MNHN.

Distribution. Amphi-Atlantic. Eastern Atlantic: Cape Verde; Senegal; Guinea; Ghana; São Tomé; Cameroon; Gabon; Congo (e.g., Balss 1916; Sourie 1954; Crosnier and Forest 1966; Ribeiro 1968; present study); Central Atlantic: Ascension Island (Manning and Chace 1990); Western Atlantic: Florida; Bermuda; Caribbean (Cuba, Panama, Antigua, Guadeloupe, Grenada, Grenadines, Tobago); Gulf of Mexico; Brazil (Ceará to Rio Grande do Sul, including Atol das Rocas and Fernando do Noronha) (e.g., Chace 1972; Abele 1976; Gore *et al.* 1978; Christoffersen 1979, 1998; McClure 2005; present study).

Ecology. Intertidal or shallow subtidal, probably to a depth of about 5 m; under rocks or in rock and rubble crevices, on sand and mixed sand-mud substrates; sometimes in crevices of sabellariid reefs (Gore *et al.* 1978); usually encountered in male-female pairs.

Remarks. *Alpheus bouvieri* is most closely related to *A. javieri* **n. sp.** (see below). However, the only species, with which it can be confused in the Atlantic, e.g., in Brazil or in West Africa, is *A. agilis* **n. sp.** (see below).

GenBank access number. FJ013876 (Panama, fcn 06-502, 206572334 5'), FJ013875 (Panama, fcn 06-495, 206572332 5'), FJ013874 (Panama, fcn 06-493, 206572330 5'), FJ013873 (São Tomé, fcn 06-008, 206572328 5'), FJ013873 (São Tomé, fcn 06-008, 206572328 5').

***Alpheus javieri* n. sp.**

Figs. 2, 5C, D

Alpheus Bouvieri (not *sensu* Milne-Edwards 1878)—Coutière 1898: 131 (part., specimens from Pacific coast of Panama).

Alpheus bouvieri (not *sensu* Milne-Edwards 1878)—Christoffersen 1979: 303 (part., specimens from Eastern Pacific); Kim and Abele 1988: 58, fig. 24; Wicksten and Hendrickx 1992: 4; Ricaurte *et al.* 1995: 81, 84; Vargas and Cortés 1999: 899; McClure and Wicksten 2000: 966, fig. 2; Wicksten and Hendrickx 2003: 63; McClure 2005: 134 (part., fig. 8 only).

[?] *Alpheus bouvieri* (not *sensu* Milne-Edwards 1878)—Hickman and Zimmerman 2000: 35.

Alpheus leviusculus bouvieri (not *sensu* Milne-Edwards 1878)—Christoffersen and Ramos 1988: 63.

Alpheus bouvieri var. *chilensis* (not *sensu* Coutière 1902)—Schmitt 1924a: 162.

Type material. Panama (Pacific coast). Holotype: 1 male (CL 8.0), USNM 1123855, Río Mar, rocky intertidal, under rocks and from crevices in rocky reef platform, coll. A. Anker, J. Jara and E. Gómez, 3 Mar 2006 [fcn 06-300a]. Paratypes: 1 ovig. female (CL 8.5), USNM 1123856, same collection data as for holotype, mated pair [fcn 06-300b]; 1 ovig. female (CL 4.9), USNM 1123857, same collection data as for holotype [fcn 06-255]; 1 male (CL 6.5), OUMNH-ZC 2006-10-010, same collection data as for holotype [fcn 06-384]; 1 male (CL 6.0), USNM 1123858, same collection data as for holotype [fcn 06-258]; 1 male (CL 7.7), 2 ovig. females (CL 7.2, 9.4), USNM 1123859, Panama City, Altos de Diablo, intertidal with some mangroves, under rocks on mud, coll. D. Roche, 20 Feb 2007 [fcn 07-084, male specimen dissected]; 1 ovig. female (CL 7.7), MNHN-Na 17183, about 15 km west of Panama City, rocky intertidal, under rocks, coll. T. Lamy, 1 Jun 2006 [fcn 06-424]; 1 male, 1 ovig. female (CL not measured), UP, Río Mar, rocky intertidal, in rock crevices, coll. A. Anker, J. Jara and I. Marin, 3 Mar 2006 [fcn 07-122].

Additional material examined. Panama (Pacific coast). 1 ovig. female (CL 5.8), FLMNH UF Arthropoda 16555, Las Perlas Islands, Saboga, large intertidal rocks, from rock crevices, coll. A. Anker, J. Jara and C. Hurt, 15 Nov 2005 [fcn 05-148]; 1 ovig. female (CL 5.6), USNM 1123860, Las Perlas Islands, small island off Contadora, rocky intertidal, from crevices in rock platform, coll. A. Anker, C. Hurt, E. Gómez, J. Jara and E. Tóth, 31 Mar 2006 [fcn 06-368]; 2 females (CL 4.1, 4.8), USNM 1123861, Coiba Marine National Park, Isla Coiba, Ensenada Santa Cruz on NW coast, intertidal mudflat, from perforated wood on mud, coll. A. Anker, J. Jara, E. Gómez, E. Tóth and I. Marin, 21 Mar 2007 [fcn 07-121, 07-146]; 1 male (CL 6.5), USNM 1123862, Chame Peninsula, Chame Bay estuary, from perforated wood on mud near mangrove, coll. A. Anker and J.A. Vera-Caripe, 7 Nov 2006 [fcn 06-519, specimen with abnormal (regenerated) chelipeds]; 1 specimen (sex and CL not determined), Panama City, Amador causeway, Naos, Punta Culebra, rocky intertidal, under rocks, coll. A. Anker and C. Hurt, 2 Mar 2006 [fcn 06-253, specimen in RNA later, not deposited].

Costa Rica (Pacific coast). 1 male (CL 6.1), USNM 1123863, Punta Morales, intertidal, under rocks on sand-mud near mangroves, coll. A. Anker, 22 Nov 2005 [fcn 05-147]; 1 specimen (sex and CL not determined), Nicoya Peninsula, Curu, rock-sand intertidal, on sand under rock, coll. A. Anker, 25 Nov 2005 [fcn 05-018, specimen in RNA later, not deposited, photograph available].

Diagnosis. Species of *Alpheus leviusculus* group (Clade L). Frontal margin of carapace with distinct, short, narrow, distally acute rostrum; rostral carina well marked, extending to level of eyes, gradually

flattening; orbital hoods unarmed, rounded, swollen, gently sloping into shallow orbitorostral grooves. Antennule with second peduncular segment less than twice as long as wide; stylocerite with acute tip, reaching distal margin of first segment. Antenna with basicerite armed with sharp distoventral tooth; scaphocerite with strong distolateral tooth extending well beyond broad blade, reaching end of antennular peduncle; carpocerite overreaching both scaphocerite and end of antennular peduncle. Third maxilliped not particularly broadened, unarmed. Major cheliped with merus lacking sharp distomesial tooth; chela somewhat compressed, dorsal groove relatively broad, deep, extending mesially as contrasting rounded depression and laterally as well defined, posteriorly extending groove; dorsal shoulder rounded, not overhanging; ventral groove broad and deep, adjacent shoulder rounded, slightly protruding; adhesive disks small; fingers about half-length of palm; plunger of dactylus well developed. Minor cheliped sexually dimorphic; palm without grooves or notches in both sexes; fingers somewhat broadened, balaeniceps in males, subconical and non-balaeniceps in females. Second pereopod with first carpal segment nearly twice as long as second. Third pereopod with unarmed ischium, merus and carpus; propodus with row of stout, often brown-colored spines, most in pairs; dactylus stout, simple, conical. Male second pleopod with typical appendices masculina and interna. Uropod with protopod laterally projecting as acute tooth; exopod with distolateral spine bordered laterally by sharp distolateral tooth; transverse suture sinuous, consisting of two rounded lobes and subtriangular tooth adjacent to distolateral spine; both exopod and endopod furnished with row of spinules distally. Telson broad, tapering distally, with two pairs of dorsal spines; posterior margin slightly convex, with two pairs of spines at each posterolateral angle.

Description. See Kim and Abele (1988) and McClure and Wicksten (2000), both as *Alpheus bouvieri*. Complementary figures are provided in Fig. 2.

Size. Largest male, holotype at CL 8.0 mm and TL 22.7 mm; largest female at CL 9.4 mm and 28.8 TL mm; egg size: about 0.5 x 0.6 mm (average from 3 eggs from largest ovigerous female).

Color pattern. Opaque-whitish with broad transverse bands varying from blue-green to brown-green (combination of gray-blue and red chromatophores), two on carapace and one along posterior half of each pleomere; uropods and telson white proximally, blue-green distally; walking legs semitransparent with red chromatophores; minor chela green or greenish-brown; major chela olive-green or blue-green mesially, without well marked whitish patch ventroproximally; dorsal and ventral grooves paler brown; distal half of pollex and dactylus whitish or pink; rostrum and rostral carina region brown-green; antennular peduncles green-brown; scaphocerite of antenna with green lateral margin and distolateral tooth; antennal and antennular flagella pale yellow; eggs or ovaries in females yolk-yellow (Fig. 5C, D). See also color description in McClure and Wicksten (2000). Color photograph of “*A. bouvieri*” from Galapagos (Hickman and Zimmerman 2000, p. 35) is probably not *A. javieri* n. sp. (see remarks below).

Etymology. The species is named after our friend and colleague, Javier Jara (Naos, STRI), for his invaluable help in field trips and preparation of manuscripts.

Type locality. Río Mar (80 km west of Panama City) and vicinity of Panama City, Pacific coast of Panama.

Distribution. Eastern Pacific: Costa Rica; Panama; Colombia; Galapagos (Kim and Abele 1988; Christoffersen and Ramos 1988; McClure and Wicksten 2000; present study).

Ecology. Intertidal and shallow subtidal, probably to at least 5 m; rocky and mixed sand-rock bottoms, under rocks and in rock crevices, apparently capable of boring tunnels into hard rocks using its major cheliped (Ricaurte *et al.* 1995); also in estuaries and mangroves, under rocks or debris in muddy sand or mud, sometimes in or under perforated chunks of wood (e.g., specimens from Chame Bay and Coiba in present study); usually encountered in male-female pairs; feeds mostly on algae growing on burrow walls (Ricaurte *et al.* 1995).

Remarks. *Alpheus javieri* n. sp. differs from its closest relative, *A. bouvieri*, by the slightly narrower and deeper dorsal groove on the palm of the major chela (compare Figs. 1B, C and 2B, C) and the slightly shorter first carpal segment in the second pereopod (compare Figs. 1F and 2F). Furthermore, in *A. javieri* n. sp., the spines on the propodus of the third and fourth pereopods are often tan or brown-colored (Fig. 2G), whereas in

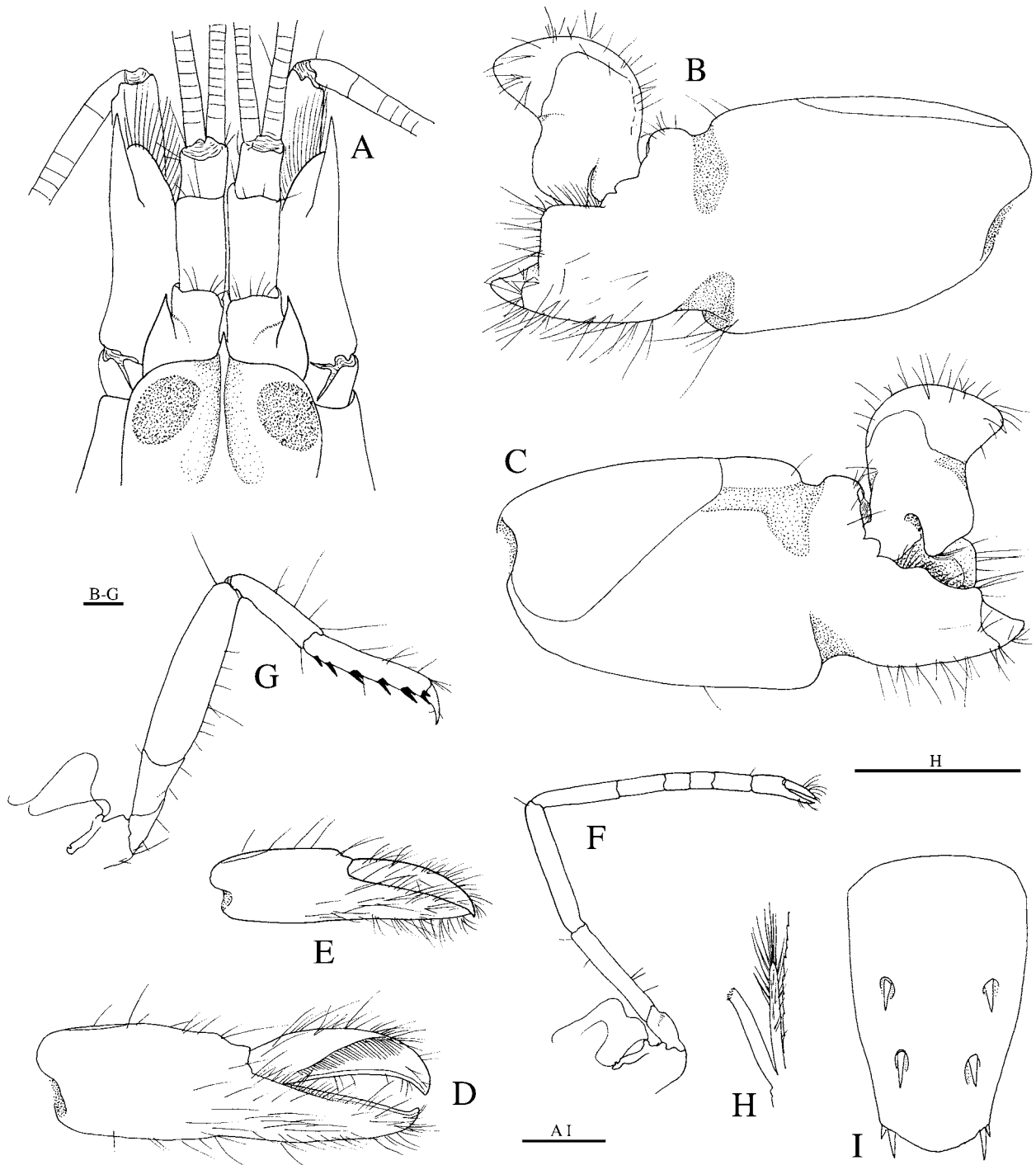


FIGURE 2. *Alpheus javieri* n. sp.; paratype male (A–D, F–I) and paratype female (E) from Panama Canal zone (USNM 1123859): A, frontal region, dorsal view; B, major chela, mesial view; C, same, lateral view; D, male minor chela, mesial view; E, female minor chela, mesial view; F, second pereopod, lateral view; G, third pereopod, lateral view; H, appendix masculina and appendix interna of second pleopod; I, telson, dorsal view. Scale bars: 1 mm.

A. bouvieri, these spines are typically uncolored (cf. Fig. 1G). The color patterns of the two species are very similar (Fig. 5A–D), although in *A. javieri* n. sp., the pale patch on the mesial face of the major chela appears to be less marked compared to that in *A. bouvieri*.

Hickman and Zimmerman (2000) provided two color photographs of a shrimp from Galapagos identified as “*Alpheus bouvieri*”. The color pattern of this individual somewhat differs from that of Panamanian

specimens (*A. javieri* **n. sp.**), especially in that the bands on the abdomen are broader and also more brown, giving the shrimp an almost uniform brownish appearance. Hickman and Zimmerman (2000) also noted that the specimens from Galapagos rarely exceeded 11 mm TL, whereas specimens elsewhere may reach 19 mm TL. These observations suggest that “*A. bouvieri*” of Hickman and Zimmerman (2000) may not be the same species as *A. javieri* **n. sp.** (*A. bouvieri sensu* Kim and Abele 1988). Only a careful reexamination of Galapagos material will allow to resolve this uncertainty.

In the tropical eastern Pacific, *A. javieri* **n. sp.** may be confused with *A. hebes* and *A. longinquus*, but it can be distinguished from the first species by the absence of a spine on the ischium of the third and fourth pereopods, and from the second by the relatively shorter palm of the major chela and the presence of balaeniceps setae on the minor chela in males (see also Kim and Abele 1988).

GenBank access number. FJ013871 (fcn 06-521, 206572324 5'), FJ013870 (fcn 06-520, 206572322 5'), FJ013869 (fcn 06-253, 206572320, 5'), FJ013868 (fcn 05-008, 206572318 5').

***Alpheus hebes* Kim and Abele, 1988**

Figs. 3, 5E

Alpheus hebes Kim and Abele 1988: 62, fig. 26; Ríos Gonzalez 1989: 118, pl. 22; Ríos 1992: 5; Wicksten and Hendrickx 1992: 5; Hernández-Aguilera and Martínez-Guzmán 1992: 4; Vargas and Cortés 1999: 900; McClure and Wicksten 2000: 965, fig. 1; Hickman and Zimmerman 2000: 37; Wicksten and Hendrickx 2003: 64.

[?] *Alpheus Bouvieri* var. *Bastardi* (not *bouvieri sensu* Milne-Edwards 1878; not *bastardi sensu* Coutière 1898) Coutière 1898: 133 (part., specimens from Panama).

Material examined. Panama (Pacific coast). 1 male (CL 6.5), USNM 1123864, Las Perlas Islands, small island off Contadora, rocky intertidal, from rock crevices, coll. A. Anker, C. Hurt, E. Gómez, J. Jara and E. Tóth, 31 Mar 2006 [fcn 06-369, specimen dissected]; 1 ovig. female (CL 6.0), MNHN-Na 17184, Las Perlas Islands, Isla del Rey, sta. 2, coll. N. Knowlton *et al.*, 1998.

Diagnosis. Species of *Alpheus leviusculus* group (Clade L). Frontal margin of carapace with short, subtriangular rostrum; rostral carina not delimited, postrostral area flattened; orbital hoods unarmed, rounded, swollen, markedly but not steeply sloping into shallow orbitorostral grooves. Antennule with second peduncular segment less than twice as long as wide; stylocerite with blunt or subacute tip, not reaching distal margin of first segment. Antenna with basicerite armed with sharp distoventral tooth; scaphocerite with strong distolateral tooth extending only slightly beyond broad blade, not reaching end of antennular peduncle; carpocerite greatly overreaching both scaphocerite and end of antennular peduncle. Third maxilliped not particularly broadened, unarmed. Major cheliped with merus lacking sharp distomesial tooth; chela somewhat compressed, dorsal groove relatively broad and deep, extending mesially as contrasting rounded depression and laterally as well defined, posteriorly extending groove; dorsal shoulder rounded, not overhanging; ventral groove broad and deep, adjacent shoulder rounded, not protruding; adhesive disks small; fingers slightly less than half-length of palm; plunger of dactylus well developed. Minor cheliped sexually dimorphic; palm with very shallow dorsal groove; fingers somewhat broadened and balaeniceps in males, subconical and non-balaeniceps in females. Second pereopod with first carpal segment about twice as long as second. Third pereopod with ischium armed with small ventrolateral spine, merus and carpus unarmed; propodus with row of stout spines, most paired; dactylus stout, simple, conical. Male second pleopod with typical appendices masculina and interna. Uropod with protopod laterally projecting as acute tooth; exopod with distolateral spine bordered laterally by sharp distolateral tooth; transverse suture sinuous, consisting of two rounded lobes and subtriangular tooth adjacent to distolateral spine; both exopod and endopod furnished with row of spinules distally. Telson broad, tapering distally, with two pairs of dorsal spines; posterior margin convex, with two pairs of spines at each posterolateral angle and row of spinules in-between.

Description. See Kim and Abele (1988) and McClure and Wicksten (2000). Complementary figures are provided in Fig. 3.

Size. Male at CL 6.5 mm and TL 19.3 mm; ovigerous female at CL 6.0 mm and TL 19.0 mm; egg size: 0.5 x 0.65 mm (average from 3 eggs).

Color pattern. Opaque-whitish with broad transverse bands of brown (combination of gray-blue and red chromatophores), two on carapace separated by halfmoon-shaped patch, and one along posterior half of each pleomere; uropods and telson brown except for whitish most proximal part; walking legs semitransparent with red chromatophores; minor chela pale brown; major chela orange-brown mesially, without paler ventroproximal patch and dorsal and ventral grooves; distal half of pollex and dactylus pink, tip whitish; rostrum and rostral carina region brown; antennular peduncles brown; scaphocerite of antenna mostly whitish; antennal and antennular flagella pale yellow (Fig. 5E). See also color description in McClure and Wicksten (2000) and color photographs in Hickman and Zimmerman (2000).

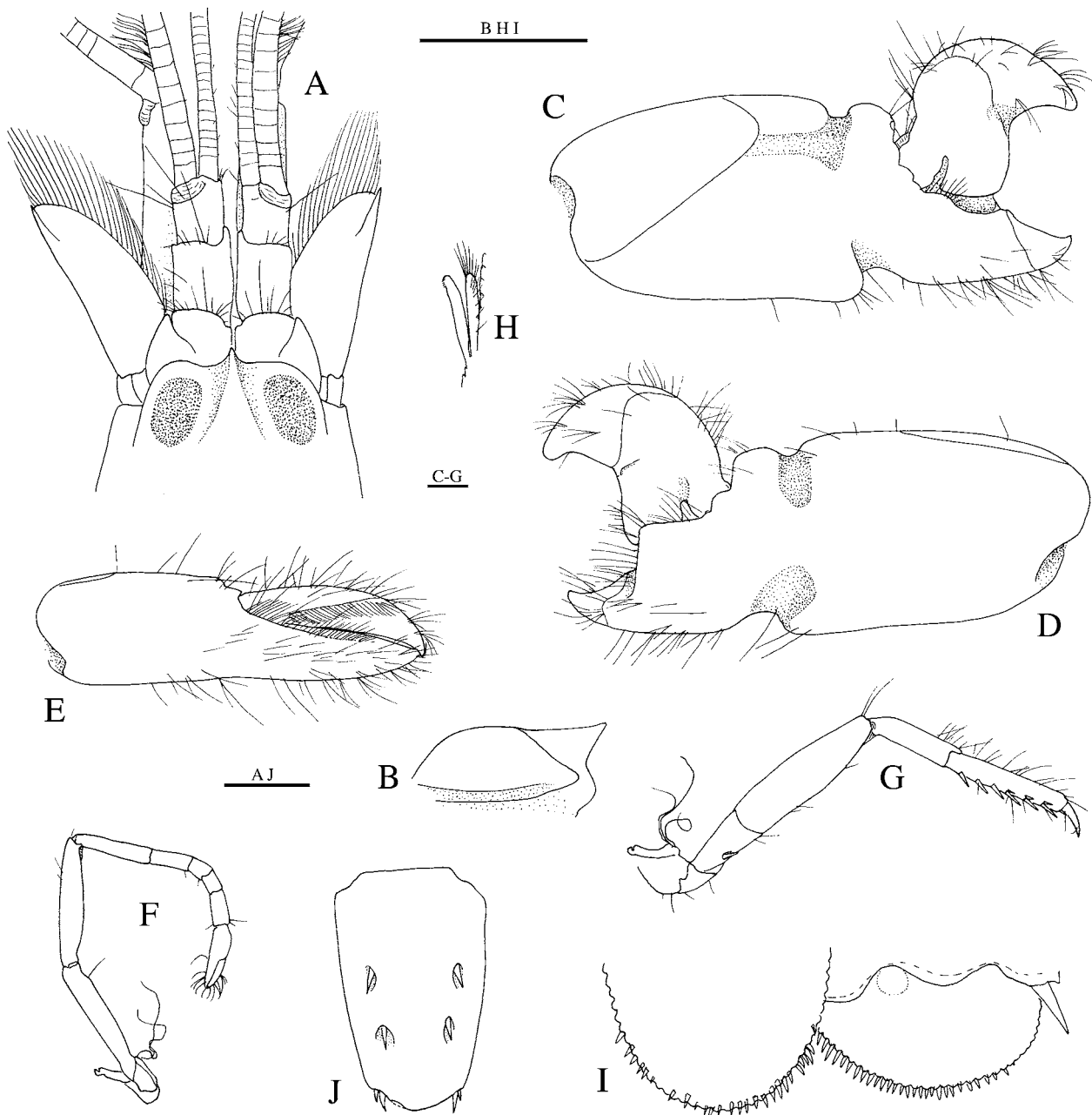


FIGURE 3. *Alpheus hebes* Kim and Abele, 1988; male from Las Perlas, Panama (USNM 1123864): A, frontal region, dorsal view; B, stylocerite of antennule, ventrolateral view; C, major chela, lateral view; D, same, mesial view; E, male minor chela, mesial view; F, second pereopod, lateral view; G, third pereopod, lateral view; H, appendix masculina and appendix interna of second pleopod; I, uropod, distal region; J, telson, dorsal view. Scale bars: 1 mm.

Type locality. James Island, Galapagos (Kim and Abele 1988); type specimens in USNM.

Distribution. Eastern Pacific: Gulf of California; Clarion Island; western Mexico; Costa Rica; Panama; Colombia; Ecuador; Galapagos (Kim and Abele 1988; McClure and Wicksten 2000).

Ecology. Mid-intertidal, under rocks on sand (McClure and Wicksten 2000; present study).

Remarks. *Alpheus hebes* is most closely related to the below described new species (see under *A. agilis* n. sp.). In the tropical eastern Pacific, *A. hebes* may be confused with *A. javieri* n. sp. and *A. longinquus*, differing from both of them by the shape of the rostrum and post-rostral region, a short, distally blunt or subacute stylocerite, and the presence of a spine on the ischium of the third and fourth pereopods; in addition, male specimens of *A. hebes* may be easily distinguished from *A. longinquus* by the balaeniceps minor chela (see also Kim and Abele 1988).

GenBank access number. FJ937717 (fcn 07-163), FJ937718 (fcn 07-164).

Alpheus agilis n. sp.

Figs. 4, 5F

Type material. São Tomé. Holotype: 1 male (CL 5.0), USNM 1123865, ST 3, 200 m west of Lagoa Azul, rocky intertidal with coralline algae, from rock crevices and under rocks, coll. A. Anker and N. Knowlton, 31 Jan 2006 [fcn 06-067]. Paratypes: 1 male (CL 4.6), 2 ovig. females (CL 4.4, 4.7), USNM 1123866, same collection data as for holotype [06-068 (male), 06-069, 06-071 (females)]; 1 male (CL 5.9), USNM 1123867, ST 8, near Porto Alegre, rocky intertidal with cemented basaltic rocks and coralline algae, depth about 30 cm, under rocks on coarse sand, coll. A. Anker, 5 Feb 2006 [fcn 06-152, specimen dissected]; 1 male (CL 4.4), 2 ovig. females (CL 4.5, 4.7), MNHN-Na 17185, ST 8A, near Porto Alegre, rocky intertidal with cemented basaltic rocks and coralline algae, depth about 30 cm, under rocks on coarse sand, coll. A. Anker, 14 Feb 2006 [fcn 06-221]; 1 ovig. female (CL 5.5), FLMNH UF Arthropoda 16556, ST 4, 2 km west of Lagoa Azul, near ship wreck, rocky cliffs, under rocks in tide pool, coll. N. Knowlton and A. Anker, 1 February 2006 [fcn 06-114].

Additional material examined. Cape Verde. 2 males (CL 4.6, 6.7), 4 juveniles (CL not measured), USNM 1123868, São Vicente, between Baia das Gatas and Praia Grande, coll. N. Knowlton *et al.*, 25 Mar 1998; 6 juvenile specimens (CL not measured), USNM 1123869, São Vicente, Calhau, in tide pools, coll. N. Knowlton *et al.*, 26 Mar 1998; 1 specimen (CL not measured) of unknown sex (chelipeds and abdomen missing), not deposited, Santiago, Praia, beach near Club Nautics, coll. N. Knowlton *et al.*, 5 April 1998.

Brazil: 4 males (CL 5.8, 6.2, 7.2, 7.3), 2 ovig. females (CL 7.2, 8.0), 2 immature females (CL 4.0, 4.1), MNRJ 20845, Atol das Rocas, Ilha do Cemitério, in tide pools, coll. P.S. Young, P.C. Paiva and A.A. Aguiar, 13 Oct 2000.

Diagnosis. Species of *Alpheus leviusculus* group (Clade L). Frontal margin of carapace with short, subtriangular rostrum; rostral carina not delimited, postrostral area flattened; orbital hoods unarmed, rounded, swollen, markedly but not steeply sloping into shallow orbitorostral grooves. Antennule with second peduncular segment less than twice as long as wide; stylocerite with acute tip, reaching or slightly overreaching distal margin of first segment. Antenna with basicerite armed with sharp distoventral tooth; scaphocerite with strong distolateral tooth extending only slightly beyond broad blade, not reaching end of antennular peduncle; carpcerite greatly overreaching both scaphocerite and end of antennular peduncle. Third maxilliped not particularly broadened, unarmed. Major cheliped with merus lacking sharp distomesial tooth; chela somewhat compressed, dorsal groove relatively broad and deep, extending mesially as contrasting rounded depression and laterally as well defined, posteriorly extending groove; dorsal shoulder rounded, not overhanging; ventral groove broad and deep, adjacent shoulder rounded, not protruding; adhesive disks small; fingers slightly less than half-length of palm; plunger of dactylus well developed. Minor cheliped sexually dimorphic; palm with very shallow dorsal groove; fingers somewhat broadened and balaeniceps in males, subconical and non-balaeniceps in females. Second pereopod with first carpal segment nearly twice as long

as second. Third pereopod with ischium armed with small ventrolateral spine, merus and carpus unarmed; propodus with row of stout spines, most paired; dactylus stout, simple, conical. Male second pleopod with typical appendices masculina and interna. Uropod with protopod laterally projecting as acute tooth; exopod with distolateral spine bordered laterally by sharp distolateral tooth; transverse suture sinuous, consisting of two rounded lobes and subtriangular tooth adjacent to distolateral spine; both exopod and endopod furnished with row of spinules distally. Telson broad, tapering distally, with two pairs of dorsal spines; posterior margin convex, with two pairs of spines at each posterolateral angle and row of spinules in-between.

Description. Carapace smooth, not setose, laterally not compressed. Rostrum short slender, subtriangular, slightly descendant, distally subacute (Fig. 4A, B), not reaching half length of first segment of antennular peduncle; postrostral area flattened, broadening posteriorly to level of posterior margin of corneas (Fig. 4A); adrostral grooves shallow, not abruptly delimited from either orbital hoods or postrostral area; orbito-rostral process feebly developed. Orbital hoods inflated, distally rounded, unarmed (Fig. 4A); anterior margin between rostrum and orbital hoods feebly concave. Pterygostomial angle rounded (Fig. 4B). Eyes completely concealed in dorsal and lateral views, partly visible in frontal view, with small subacute tooth on anteromesial margin; cornea well developed. Ocellar beak conspicuously protruding between eyes.

Antennular peduncles rather stout, second segment only slightly longer than broad; stylocerite with acute tip, slightly overreaching distal margin of first segment in dorsal view (Fig. 4A, C); mesioventral carina of first segment with blunt, broadly subtriangular tooth (Fig. 4E); lateral flagellum with numerous tufts of aesthetascs approximately on 8th to 16th segments, secondary ramus rudimentary (Fig. 4D). Antenna with basicerite bearing strong, acute ventrolateral tooth (Fig. 4B); carpocerite stout, reaching far beyond distolateral tooth of scaphocerite (Fig. 4A); scaphocerite with nearly straight lateral margin, reaching distal margin of antennular peduncle; distolateral tooth of scaphocerite moderately strong, reaching distinctly beyond blade; cleft between blade and distolateral tooth relatively deep (Fig. 4A).

Mouthparts typical for *Alpheus* in external view. Third maxilliped moderately stout (Fig. 4F); lateral plate with subacute point; antepenultimate segment subtriangular in cross-section; penultimate segment slender, more than twice as long as wide; ultimate segment distally tapering (Fig. 4F).

Male major cheliped with short ischium and stout merus; ventromesial margin of merus straight, ending bluntly distally; distodorsal margin also blunt; carpus short, cup-shaped; chela (Fig. 4G, H) laterally somewhat compressed; dorsal and ventral margins of palm with broad transversal grooves; dorsal groove extending to mesial face in form of well delimited, rounded depression, latter not extending posteriorly; same dorsal groove continuing to lateral face as well marked rounded depression, however, extending from here posteriorly to linea impressa (Fig. 4H); dorsal shoulder rounded, gently sloping, not overhanging groove (Fig. 4G); ventral groove broad, deep, oblique, extending to both mesial and lateral face; ventral shoulder rounded, not protruding (Fig. 4G, H); linea impressa well marked; adhesive disks small; fingers about half-length of palm; proximal margin of pollex forming large, nearly 90° angle on mesial face (Fig. 4G); dactylus reaching slightly beyond pollex, with small transverse ridge near base of plunger; plunger well developed, stout (Fig. 4G, H). Female major cheliped generally similar to male major cheliped; chela usually smaller, more slender, and with somewhat different proportions.

Male minor cheliped with short ischium and stout merus; ventromesial margin of merus straight, unarmed distally; carpus short, cup-shaped; chela (Fig. 4I) subcylindrical, without sculpture; palm slightly longer than fingers; dactylus slightly expanded, with rows of balaeniceps setae (Fig. 4I), cutting edges sharp, blade-like; pollex proximally with row of setae. Female minor cheliped similar in general proportions, but chela (Fig. 4J) without row of balaeniceps setae on fingers.

Second pereopod (Fig. 4K) slender; ischium subequal to merus; carpus five-segmented, first segment longest, ratio of carpal segments (from proximal to distal) approximately 4 : 2.5 : 1 : 1 : 2; chela longer than second segment, simple, with fingers subequal to palm. Third and fourth pereopods similar in shape and length; third pereopod (Fig. 4L) with ischium armed with small ventrolateral spine; merus unarmed, about five times as long as wide; carpus unarmed, distinctly slenderer than merus; propodus with about six slender ventral spines, often in pairs, and two distoventral spines (Fig. 4L); dactylus simple, conical, gradually

curved, with acute tip, 0.4 length of propodus. Fifth pereopod smaller and slenderer than third and fourth pereopods; ischium unarmed ventrally; propodus with six-seven ventral spines (including distoventral spine); distolateral margin with about six rows of grooming setae; dactylus simple, conical, similar to that of third or fourth pereopods.

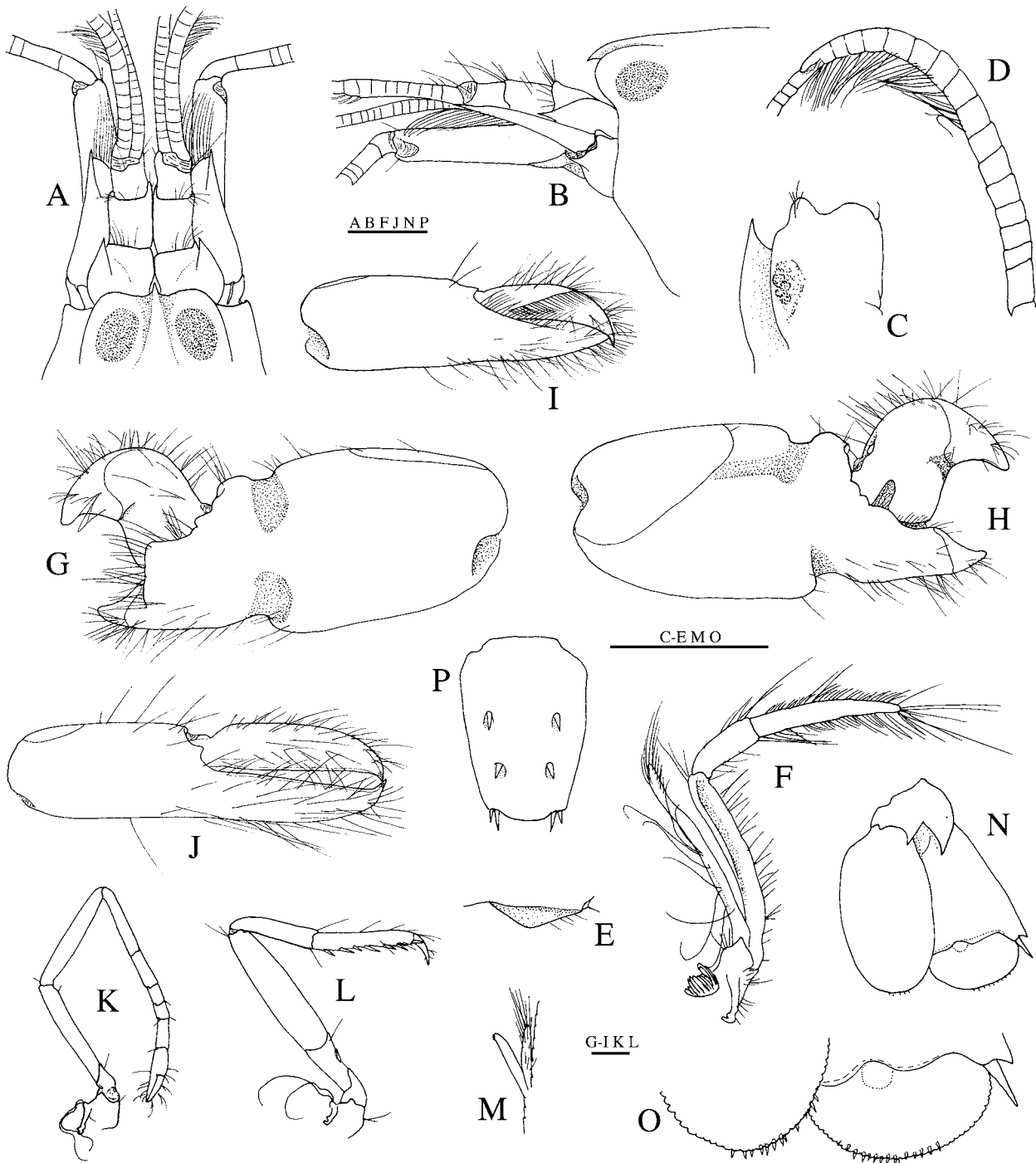


FIGURE 4. *Alpheus agilis* n. sp.; paratype male (A–I, K–P) (USNM 1123867) and paratype ovigerous female (J) (USNM 1123866) from São Tomé; A, frontal region, dorsal view; B, same, lateral view; C, stylocerite of antennule, ventrolateral view; D, lateral antennular flagellum; E, ventromesial tooth on first antennular segment; F, third maxilliped, lateral view; G, major chela, mesial view; H, same, lateral view; I, male minor chela, mesial view; J, female minor chela, mesial view; K, second pereopod, lateral view; L, third pereopod, lateral view; M, appendix masculina and appendix interna of second pleopod; N, uropod, lateral view; O, same, distal region; P, telson, dorsal view. Scale bars: 1 mm.

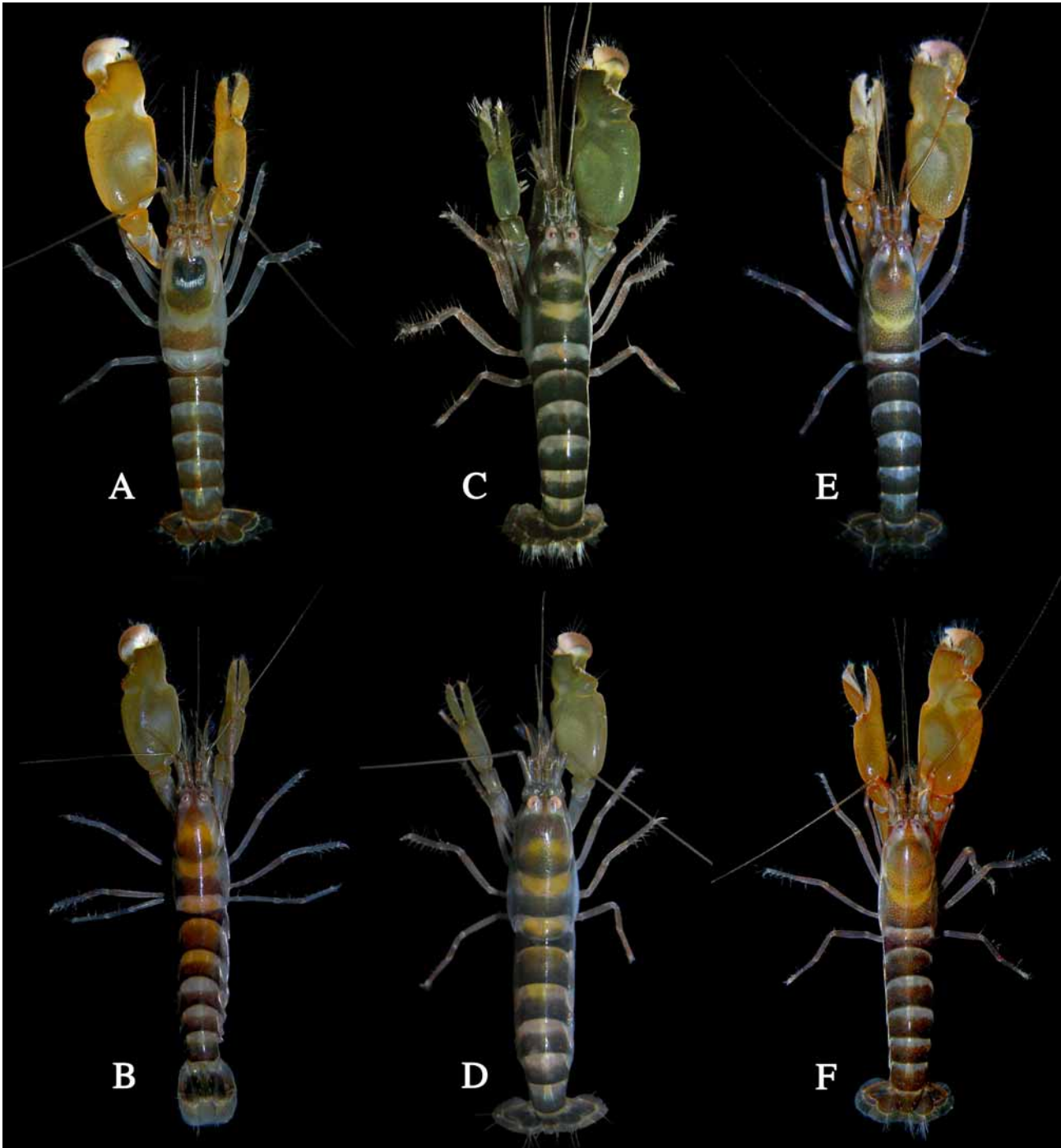


FIGURE 5. Color patterns of *Alpheus bouvieri* A. Milne-Edwards, 1878 [western Atlantic] (A); *Alpheus bouvieri* [eastern Atlantic] (B); *Alpheus javieri* n. sp. (C, D); *Alpheus hebes* Kim and Abele, 1988 (E); and *Alpheus agilis* n. sp. [eastern Atlantic] (F): A, male from Bocas del Toro, Panama; B, female from São Tomé; C, male from Punta Morales, Costa Rica; D, female from Las Perlas, Panama; E, male from Las Perlas, Panama; F, male from São Tomé.

Abdominal somites (pleurites) broadly rounded posteroventrally; sixth pleuron without articulated flap. Male second pleopod with appendix masculina subequal to appendix interna, furnished with slender setae on tip and along margins (Fig. 4M). Uropod with protopod armed with two large acute distal teeth; exopodal diaeresis with two broad rounded lobes (Fig. 4N, O); distolateral spine long, slender; distal margin of endopod and exopod with row of spinules (Fig. 4O). Telson relatively broad (Fig. 4P), subrectangular, tapering posteriorly; dorsal surface with two pairs of moderately strong spines, situated at some distance from lateral

margins, first pair slightly anterior to mid-length, second pair well posterior to telson mid-length (Fig. 4P); posterior margin broadly rounded, with two pairs of posterolateral spines, mesial much longer than lateral, apparently without row of spinules between mesial spines (Fig. 4P); anal tubercles moderately developed. Gill/exopod formula typical for *Alpheus*.

Size. Eastern Atlantic: largest male from Cape Verde at CL 6.7 mm and TL 17.3 mm; largest ovigerous female from São Tomé at CL 5.5 mm and TL 16.5 mm; western Atlantic (Atol das Rocas, Brazil): largest male at CL 7.3 mm and TL 24.1 mm; largest ovigerous female at CL 8.0 mm and TL 22.2 mm; egg size: about 1.1 x 1.2 mm (average from 3 eggs from a 4.7 mm CL ovigerous female from São Tomé).

Color pattern. Nearly identical to that of *A. hebes* (see description above and Fig. 5F).

Etymology. The species' name refers to shrimp's agility (*agilis*, Latin for agile, quick), which makes them somewhat hard to collect, even at low tide.

Type locality. São Tomé Island in the Gulf of Guinea.

Distribution. Eastern Atlantic: presently known only from São Tomé and Cape Verde.

Ecology. Mid-intertidal, under rocks on sand; usually in male-female pairs. The shrimps are very agile and almost restless, crawling quickly over the bottom both in or out of water.

Remarks. *Alpheus agilis n. sp.* is most closely related to the eastern Pacific *A. hebes*. The main difference between these two species lies in the stylocerite, which is sharp and exceeding the distal margin of the first segment of the antennular peduncle in *A. agilis n. sp.* (Fig. 4A–C) and usually blunt (sometimes subacute) and not exceeding this margin in *A. hebes* (Fig. 3A, B). Further, possibly consistent but even more subtle differences, are the ratio of the carpal segments in the second pereopod, e.g., the relatively longer second segment in *A. agilis n. sp.* (compare Figs. 4K and 3F), the relative width of the flattened postrostral area (compare Figs. 4A and 3A), and the width of the dorsal notch of the major chela (compare Figs. 4G, H and 3C, D). Remarkably, the color patterns of *A. agilis n. sp.* and *A. hebes* are quasi-identical (compare Figs. 5F, E). The western Atlantic (Atol das Rocas) specimens are also quasi-identical with the eastern Atlantic specimens. In the field, e.g., in Brazil or in West Africa, *A. agilis n. sp.* may be confused with *A. bouvieri*, differing from the latter species by the presence of a spine on the ischium of the third and fourth pereopods.

GenBank access number. FJ937719 (Brazil, fcn AA-Ag-001), FJ937720 (Brazil, AA-Ag-002), FJ937721 (São Tomé, fcn 06-068).

Discussion

The *Alpheus bouvieri* species complex presently contains two species, *A. javieri n. sp.* in the eastern Pacific, and *A. bouvieri* in the western, central and eastern Atlantic. Based on our molecular analyses (Fig. 6), the eastern Atlantic clade of *A. bouvieri* (*A. bouvieri* EA) is nested within the western Atlantic clade (*A. bouvieri* WA). In addition, Williams *et al.* (2001) obtained low values of genetic distance between *A. bouvieri* C (Caribbean) and *A. bouvieri* Br (Brazil) (see Williams *et al.* 2001, fig. 3). The absence of clear-cut differences in color pattern or morphology between *A. bouvieri* C and *A. bouvieri* EA (Fig. 5A, B), the presence of *A. bouvieri* in the central Atlantic (Ascension Island), and the paraphyletic relationship of COI haplotypes (Fig. 6) all suggest recent gene flow between the eastern and western Atlantic populations, thus supporting the designation of *A. bouvieri* as an amphi-Atlantic species, ranging from the Caribbean south to Brazil across the central Atlantic to West Africa. In contrast, the eastern Pacific *A. javieri n. sp.* is genetically clearly distinct from *A. bouvieri* (Fig. 6); this is corroborated by slight differences in morphology and color pattern (Fig. 5). The K2P COI distance between the two transisthmian sister species is about 8.0%, which, based on a previously established molecular clock (see Material and methods), corresponds to slightly less than 6 my of separation.

The related *A. hebes* species complex also includes two sister species, the eastern Pacific *A. hebes* and the amphi-Atlantic *A. agilis, n. sp.*; however, the latter species is present only in Brazil and West Africa and is absent from the Caribbean. Therefore, unlike the *A. bouvieri* clade with the “classic” transisthmian distribution

(species present on both sides of the Isthmus of Panama), the *A. hebes* clade shows a “disjunct-transisthmian” distribution (isthmian species present on the eastern Pacific side only, with the closest sister taxa being in Brazil and the eastern Atlantic). The K2P COI distance between *A. hebes* and *A. agilis* n. sp. is 10.6%, corresponding to ~7.5 my of separation. Like *A. bouvieri* and *A. javieri* n. sp., *A. hebes* and *A. agilis* n. sp. diverged only slightly in morphology and retained essentially the same color pattern (Fig. 6E, F). Within the Atlantic Ocean, the eastern Atlantic populations of *A. agilis* n. sp. (*A. agilis* EA in Fig. 6) differ genetically from the western Atlantic, or more precisely Brazilian populations (*A. agilis* WA-Brazil in Fig. 6), with a K2P COI distance of 3.7%; this distance is below the value obtained between the two genetically least diverged transisthmian sister species of *Alpheus* (see Anker *et al.* 2007), but is sufficiently large to suggest a process of incipient speciation.

Thus, genetic data show that in both the *A. bouvieri* and *A. hebes* clades, transisthmian speciation occurred well before the final closure of the Isthmus of Panama generally dated about 3 mya. The absence of *A. agilis* or another member of the *A. hebes* clade in the Caribbean presumably reflects an extinction event, since for millions of years there was a single neotropical sea basin. The fossil record documents similar Caribbean extinctions in many other groups (see review in Budd *et al.*, 1996).

The relationships between *A. bouvieri* and *A. hebes* clades cannot be addressed without considering other presumed species of the Clade L; indeed it remains unconfirmed that the *A. bouvieri* and *A. hebes* clades actually form sister clades within the Clade L, since a number of other morphologically similar taxa from the Pacific have yet to be studied genetically. The average K2P COI genetic distance between the *A. bouvieri* and *A. hebes* clades is 19.0 %, based on which the estimated divergence time would be around 11 mya.

As mentioned above, several other species may be assigned to the Clade L based on the above-mentioned unique features of the major chela: *A. chilensis* and *A. longinquus* in the eastern Pacific; *A. zimmermani* in the western Atlantic; *A. leviusculus*, *A. bastardi*, *A. hululensis*, *A. coutierei*, *A. ladronis*, *A. parvirostris*, *A. bannerorum* and *A. maindroni* in the Indo-West Pacific. These species, as well as *A. holthuisi* (which has been incorrectly allied with *A. bouvieri*) are briefly discussed below.

Alpheus chilensis Coutière in Lenz, 1902

Alpheus chilensis differs from *A. bouvieri* (and also from *A. hebes*) by the flattened, non-carinate postrostral region; the second male pleopod with a reduced appendix masculina; the third maxilliped with a dorsodistally projecting antepenultimate segment; and the distomesial margins of the cheliped meri armed with a small acute tooth (Coutière 1902; Holthuis 1952a; Kim and Abele 1988). The redescription of *A. chilensis* by Holthuis (1952a) does not mention the presence or absence of a spine on the ischium of the third pereopod, although his drawings suggest that this spine is absent (see also Kim and Abele 1988). The above combination of features indicates that this species forms a distinct lineage within the Clade L, distantly related to *A. bouvieri* and *A. hebes* clades. DNA sequencing will eventually confirm that *A. chilensis* is indeed a member of the Clade L, as strongly suggested by the shape of the major chela. The color pattern of *A. chilensis*, briefly described by Holthuis (1952a) as gray-brownish green with reddish legs needs to be documented in more detail. Holthuis (1952a) also suggested that earlier reports of *A. chilensis* from Galapagos (Schmitt 1924a; Boone 1930) are misidentifications. Generally, all records of *A. chilensis* outside its type locality in southern Chile (Calbuco, south of Puerto Montt) are more or less doubtful and require verification; this also includes a record of *A. chilensis* from the isolated Easter Island (Retamal 2004).

Alpheus longinquus Kim and Abele, 1988

Alpheus longinquus, ranging from Mexico to Galapagos (Kim and Abele, 1988), appears to be morphologically very close to *A. bouvieri*. This species may be separated from all other eastern Pacific members of the Clade L, viz., *A. bouvieri*, *A. hebes* and *A. chilensis*, by the absence of balaeniceps setae on the male minor chela and the comparatively longer and slenderer palm of the major chela (Kim and Abele 1988). The striped color pattern of *A. longinquus* in Hickman and Zimmerman (2000) does not fully correspond to the more uniform grayish color pattern of a specimen from Panama tentatively identified as *A.*

longinquus by one of us (NK); unfortunately, this specimen could not be located and examined. Therefore, a reliable illustration of the color pattern and genetic data are also desirable for this species.

Alpheus zimmermani Anker, 2007

Alpheus zimmermani is a very distinct species known from a single specimen from the Caribbean Sea, distinguishable from all other species of the Clade L (and also from all other species of *Alpheus*) by the marked dorsal carina and the unique and conspicuous red-white color pattern (Anker 2007). It differs specifically from *A. bouvieri* by the presence of a spine on the ischium of the third pereopod, and possibly the non-balaeniceps fingers of the male minor cheliped. This remarkable species may form a very distinct lineage within the Clade L; however, this also needs to be confirmed genetically.

Alpheus leviusculus Dana, 1852 (incl. *A. bastardi* Coutière, 1905)

Alpheus leviusculus, the nominal species of the Clade L, ranges from the Red Sea and western Indian Ocean to Wake Island in the Central Pacific (Chace 1988). Banner and Banner (1964) provided a good redescription and illustrations of *A. leviusculus*. Later, Banner and Banner (1982) provided additional figures of *A. leviusculus*, placed *A. bastardi* in synonymy of *A. leviusculus*, and suggested treating *A. bouvieri* as a subspecies of *A. leviusculus*, although this latter idea of “*A. leviusculus bouvieri*” was not supported by Kim and Abele (1988) because of clear morphological differences in morphology between *A. bouvieri* (+ *A. javieri* n. sp.) and *A. leviusculus* (see Banner and Banner 1982, fig. 77). In addition, Banner and Banner (1982) reported morphological variation in *A. leviusculus*, which is often the first indication for the presence of several species (in which case the status of *A. bastardi* would need a re-examination).

Alpheus ladronis Banner, 1956; *Alpheus coutierei* De Man, 1910; *Alpheus hululensis* Coutière, 1905

Alpheus ladronis differs from *A. leviusculus* and *A. bouvieri* mainly by the non-balaeniceps minor chela (Banner 1956). *Alpheus coutierei* differs from all the other species of the Clade L by the rugose mesial margin on the major cheliped merus (De Man 1915, pl. 22–23, fig. 97). *Alpheus hululensis* differs from *A. bouvieri* and *A. leviusculus* by the ratio of the carpal segments in the second pereopod, and by the shape and length of the rostrum (Coutière 1905; Crosnier and Forest 1966; Banner and Banner 1982). These three species are putatively assigned to Clade L and will require additional studies, more detailed drawings, documentation of color patterns, and DNA sequencing; some of them may be convergent lineages, not or only distantly related to the Clade L.

Alpheus parvirostris Dana, 1852; *Alpheus bannerorum* Bruce, 1987; *Alpheus maindroni* Coutière, 1898

Alpheus parvirostris and *A. bannerorum* differ from all other species of Clade L by the somewhat twisted dorsal notch of the major claw and the elongate distoventral tooth of the antennal basicerite (Banner and Banner 1982; Bruce 1987). In addition, *A. parvirostris* bears a strong distoventral tooth on the meri of the third and fourth pereopods. The main diagnostic feature of *A. maindroni* is a conspicuously elevated area in front of the dorsal notch of the major claw (Coutière 1898; Banner and Banner 1982). These three species are probably closely related, especially *A. parvirostris* and *A. bannerorum* (Bruce 1987). However, their assignment to Clade L is again tentative, awaiting additional genetic studies.

Alpheus holthuisi Ribeiro, 1964

The eastern Atlantic *A. holthuisi* Ribeiro, 1964 was previously considered to be a close relative of *A. bouvieri* (Ribeiro 1964; Crosnier and Forest 1966), and has even been confused a few times with *A. bouvieri* in the past (Holthuis 1951). However, based on Crosnier and Forest’s figures and our observation of recently collected material, *A. holthuisi* is not a species from Clade L. Most importantly, the major chela of *A. holthuisi* has a posteriorly extending dorsal groove on the mesial face, making it a member of Clade E (see above). Therefore, *A. holthuisi* will be treated in detail elsewhere.

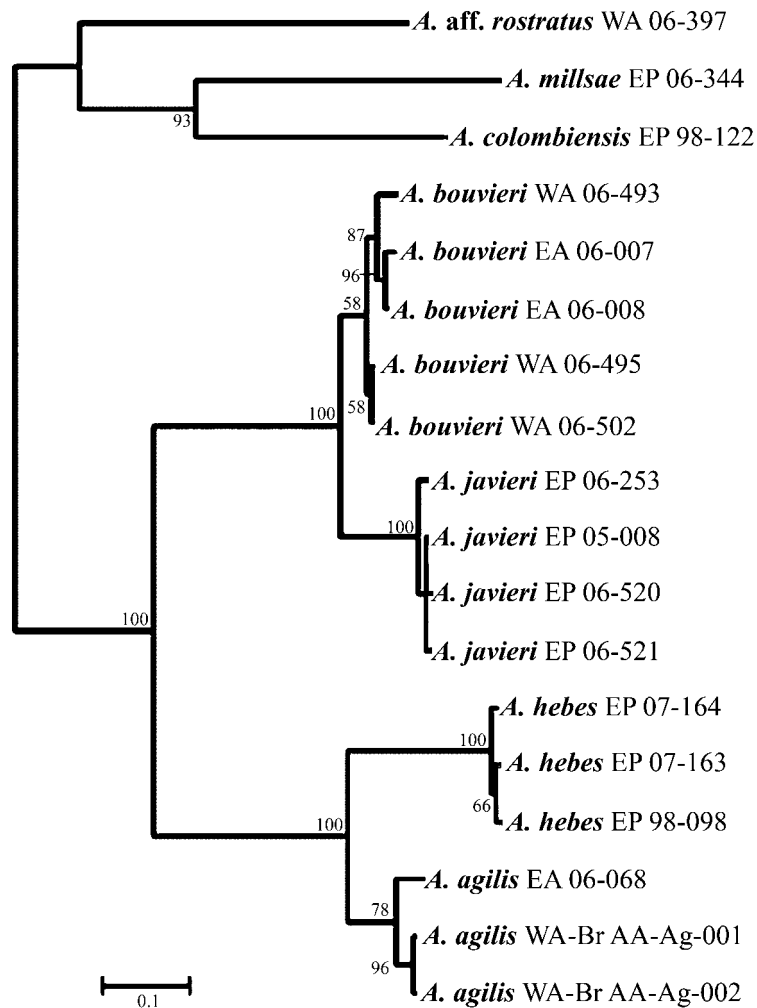


FIGURE 6. Bayesian tree from mitochondrial COI sequences for the *Alpheus bouvieri* A. Milne-Edwards, 1878 and *A. hebes* Kim and Abele, 1988 species complexes. Numbers at nodes indicate posterior probability values. Results from maximum likelihood and neighbor-joining analyses produced very similar trees (not shown). Field collection numbers (numbers associated with each terminal) correspond to specimens from various localities on the Pacific coast of Panama (EP), Atlantic (Caribbean) coast of Panama (WA), Atol das Rocas, Brazil (WA-Br), and São Tomé (EA). The tree is rooted with three species of *Alpheus* not closely related to the species of Clade L.

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