



Revision of the *Alpheus formosus* Gibbes, 1850 complex, with redescription of *A. formosus* and description of a new species from the tropical western Atlantic (Crustacea: Decapoda: Alpheidae)

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Abstract

The *Alpheus formosus* Gibbes, 1850 complex is revised based on materials from the eastern Pacific and western Atlantic. Three species are recognized: *Alpheus panamensis* Kingsley, 1878 in the eastern Pacific, ranging from the Gulf of California to the Galapagos Archipelago; *A. formosus* Gibbes, 1850 (synonym: *A. poeyi* Guérin Méneville, 1857) in the western Atlantic, ranging from North Carolina and throughout the Caribbean to southern Brazil; and *A. paraformosus* n. sp., presently known only from the southwestern Caribbean (Panama) in the western Atlantic. *Alpheus paraformosus* n. sp. differs from *A. formosus* and *A. panamensis* by the distinctly shorter rostral furrows, the absence of balaeniceps setae on the fingers of the minor chela, and also several subtle but discrete features in the color pattern. *Alpheus formosus* is redescribed based on recently collected material. A female specimen from Florida Keys is designated as neotype of *A. formosus*. Morphology, color and genetics all suggest that *A. formosus* and *A. panamensis* are transisthmian sister species, with *A. paraformosus* n. sp. being their nearest relative.

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

Introduction

The western Atlantic *Alpheus formosus* Gibbes, 1850 and the eastern Pacific *A. panamensis* Kingsley, 1878 are among the most common intertidal and shallow subtidal snapping shrimps on the American tropical and subtropical coasts (Chace 1972; Kim & Abele 1988). They differ from other species of *Alpheus* by the combination of the following features: the orbital teeth arising from the anterodorsal margin of the orbital hood; the well developed, dorsally flattened rostrum; the deep adrostral furrows, abruptly delimited from the rostrum; the subcylindrical major chela, without sculpture and with well developed adhesive plaques; the minor chela with acute distomesial tooth on the palm, and with rows of balaeniceps setae on the fingers in both sexes (more developed in males); the third pereopod with simple conical dactylus, unarmed merus, and ischium bearing ventrolateral spine; and the more or less dark-colored distolateral spine of the uropodal exopod. The two species also display a very characteristic color pattern, which consists of a dark brown-red background; a broad yellow mediodorsal band running from the tip of the rostrum to the telson; a narrow irregular white lon-

gitudinal band on each side of the abdomen; and bluish to purplish walking legs and antennular / antennal flagella.

Alpheus formosus and *A. panamensis* are morphologically very similar, to such an extent that *A. panamensis* was treated as a junior synonym of *A. formosus* by Christoffersen (1979). However, Kim & Abele (1988) pointed out that *A. panamensis* should be treated as distinct from *A. formosus*, listing two subtle but consistent morphological differences between the two species, in addition to the somewhat different color of the uropodal spine.

Knowlton & Mills (1992) suspected the presence of two cryptic species—*A. formosus*-a and *A. formosus*-b—occurring sympatrically on the Caribbean coasts of Panama. These authors provided a detailed table listing differences in color pattern between *A. formosus*-a, *A. formosus*-b and *A. panamensis* (Knowlton & Mills 1992, Table 1). Subsequent studies of proteins, DNA and reproductive compatibility (Knowlton *et al.* 1993; Williams *et al.* 2001) confirmed that *A. formosus*-a and *A. formosus*-b (listed as *A. formosus* sp. a and *A. formosus* sp. b in Knowlton *et al.* 1993; and as *A. formosus* A and *A. formosus* B in Williams *et al.* 2001) are two genetically distinct species. Furthermore, *A. formosus*-a was found to more closely related to *A. panamensis* than to *A. formosus*-b (Williams *et al.* 2001). However, until now, *A. formosus*-a and *A. formosus*-b were not formally distinguished taxonomically.

Alpheus formosus was originally described by Gibbes (1850) from Key West, Florida. Gibbes' type specimens of *A. formosus* could not be traced in any major museum and are considered as lost (see also Hendrix 1971). Manning & Reed (2006) listed a specimen of *A. formosus* from Florida deposited by William Stimpson in the collections of the Zoological Museum, Copenhagen (ZMC); however, the type status of this specimen was not confirmed. In 2004, one of us (AA) collected and photographed a complete female specimen of *A. formosus* in the Big Pine Key, Florida Keys, only about 50 km from the type locality. In morphology and color pattern, this specimen corresponds to *A. formosus*-a of Knowlton & Mills (1992) and Williams *et al.* (2001), and also to *A. formosus* of Hendrix (1971), apparently the only species found in Florida. This strongly suggests that *A. formosus*-a of Knowlton & Mills (1992) and Williams *et al.* (2001), as well as *A. formosus* of Hendrix (1971) are actually the same species: *A. formosus sensu stricto* (*sensu* Gibbes 1850). Thus, the taxonomic identity of *A. formosus* is finally determined; the female specimen from Big Pine Key is designated as neotype of *A. formosus*. Detailed drawings of a male specimen from Atol das Rocas, Brazil, as well as some drawings of the female neotype are provided. Additional drawings of *A. formosus* from Florida may be found in Hendrix (1971).

Guérin-Méneville (1857) described *Alpheus poeyi* Guérin-Méneville, 1857 from an unknown locality in Cuba. Coutière (1899) noted that judging from Guérin's short description and drawings, *A. poeyi* was probably the same as *A. formosus*. One of us (NK) examined the dried holotype of *A. poeyi* in the collections of the Academy of Natural Sciences, Philadelphia, USA (ANSP), and confirmed that *A. poeyi* is morphologically identical with *A. formosus*. We compared Guérin's surprisingly informative figure of the frontal region of *A. poeyi* with the frontal region of *A. formosus* (*A. formosus*-a) and *A. formosus*-b, and came to the conclusion that *A. poeyi* matches the former species. Therefore, *A. poeyi* should be treated as a junior synonym of *A. formosus*, as suggested by Coutière (1899).

On the other hand, *Alpheus formosus*-b of Knowlton & Mills (1992) and Williams *et al.* (2001) appears to be an undescribed form. A careful comparison between specimens of *A. formosus* (= *A. formosus*-a) from Florida, Caribbean and Brazil and *A. formosus*-b from Panama yielded at least two morphological features that enable one to distinguish preserved specimens of *A. formosus*-b from those of *A. formosus* (*A. formosus*-a). Based on these morphological differences, as well as subtle but consistent differences in color patterns (Knowlton & Mills 1992) and a clear genetic divergence (Williams *et al.* 2001), *A. formosus*-b is herewith described as a new species. Color photographs and GenBank (COI) numbers are provided for all three species of the *A. formosus* complex.

Material and methods

Specimens were collected under rocks at low tide or from crevices of coral rocks and coral rubble at depths of 0.5–2 m; 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; in some cases, a leg was detached from a specimen and preserved in RNAlater, while the body of the specimen was preserved in ethanol.

The holotype and paratypes of the new species and the neotype of *A. formosus* are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM). Additional specimens are deposited in the USNM, Muséum national d'Histoire naturelle, Paris, France (MNHN), Museu Nacional, Rio de Janeiro, Brazil (MNRJ), Natural History Museum of Los Angeles County, Los Angeles, USA (LACM), Oxford University Museum of Natural History, Oxford, UK (OUMNH), and Colección de Referencia, Departamento de Biología Marina, Universidad de Panamá, Panama City, Panama (UP). Carapace length (CL, in mm) and total length (TL, in mm) were measured along the mid-dorsal line from the tip of the rostrum to the posterior margin of the carapace and telson, respectively. Other abbreviations used in the text: fcn—field collection number; EP—eastern Pacific; WA—western Atlantic.

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 T₁₈ 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- μ L volumes containing 0.1 μ M forward and reverse primer, 200 μ M each dNTP, 2.0 mM MgCl²⁺, 1.5 units of Amplitaq Gold DNA polymerase, and 3 μ L 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 μ l) 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, AF309889, 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

Genus *Alpheus* Fabricius, 1798

Alpheus panamensis Kingsley, 1878

Figs. 7a, b

Alpheus panamensis Kingsley 1878a: 192; Kingsley 1878b: 58; Lockington 1878: 473; Kingsley 1883: 113; Coutière 1899 (for page numbers see Chace & Forest 1970); Holthuis 1954: 160; Abele 1976: 271, 273; Abele & Patton 1976: 37; Kim & Abele 1988: 38; Wicksten & Hendrickx 1992: 5; Knowlton & Mills 1992: 1; Knowlton *et al.* 1993: 1630; Hickman & Zimmerman 2000: 44; Hermoso-Salazar & Hernández-Alcántara 2003: 1279; Wicksten & Hendrickx 2003: 64; Hendrickx & Hermoso-Salazar 2005: 433.

Crangon panamensis—Rathbun 1910: 607.

Alpheus formosus (not *sensu* Gibbes 1850)—Christoffersen 1979: 314 (part., specimens from E Pacific).

Not *Alpheus panamensis*—Pocock 1890: 519; Zimmer 1913: 391; Fausto-Filho 1974: 5 (= *A. formosus* Gibbes, 1850).

Material examined.—Panama (Pacific coast). 1 male (CL 13.2), USNM 1100691, Panama City, Casco Viejo, rocky intertidal, under rocks at extreme low tide, coll. A. Anker, C. Hurt, J. Jara and E. Tóth, 30 Mar 2006 [fcn 06-326]; 1 ovig. female (CL 14.5), USNM 1100692, same collection data as previous specimen (mated pair) [fcn 06-326]; 1 male (CL 8.9), 1 ovig. female (CL 10.5), USNM 1100693, Río Mar, rocky intertidal, under rocks at extreme low tide, coll. A. Anker, E. Gómez and J. Jara, 3 Mar 2006 [fcn 06-299]; 1 male (CL 7.6), 1 female (CL 8.6), USNM 1100694, Panama City, Casco Viejo, rocky intertidal, under rocks at low tide, coll. A. Anker *et al.*, 30 Mar 2006 [fcn 06-303]; 1 male (CL 9.5), 1 ovig. female (CL 9.5), USNM 1100695, same collection data as previous specimens [fcn 06-302]; 15 specimens: males, females, ovig. females (CL 4.7–8.1), MNHN-Na 16358, Taboga Islands, Taboguilla, rock-rubble bottom, subtidal (less than 30 m), from rock crevices, coll. P. Barber *et al.*, 30 Sep 2005 [fcn 05-098]; 1 juvenile specimen (sex and CL not determined), USNM 1100696, Panama City, Amador Causeway, low tide, on muddy sand under rocks, coll. N. Knowlton, A. Anker, C. Hurt and J. Jara, 29 Mar 2006 [fcn 06-310]; 1 female (CL not measured), UP, Playa Venao, rock-sand intertidal, under rocks at low tide, coll. K. Kerr, Mar 2007 [fcn 07-132].

Description.—See Kim & Abele (1988).

Size.—The largest specimen examined is an ovigerous female from Casco Viejo, Panama City, with CL 14.5 mm and TL 48.2 mm.

Color pattern.—Body brownish, with more or less intense yellow mediodorsal band extending from rostral tip to posterior margin of sixth abdominal somite; carapace with white lateral band extending from anterolateral margin to cardiac notch, continued by zigzag white band ending at sixth abdominal somite; rostrum yellow bordered by reddish brown on margins; carapace flanks below white band pale; telson and uropods brown with large yellow patches and spots; walking legs and second pereopods purple to bluish; antennular and antennal peduncles brown with pale areas, flagella pale bluish; chelipeds orange brown to dark brown; major chela with pale patch near articulation with dactylus; dactylus and pollex distally ivory-pinkish; minor chela mostly orange-brown (Fig. 7a, b); eggs orange-yellow (Fig. 7b).

Ecology.—Rocky intertidal and shallow subtidal, to about 10 m; under rocks on mud/sand bottoms, in tide pools (Hickman and Zimmerman 2000; present study); also among corals, *Pocillopora damicornis* (Linnaeus, 1758) (Abele 1976; Abele & Patton 1976).

Type locality.—The original type localities were “Acajutla, Central America” (El Salvador), and “Panama”, (Kingsley 1878a). Three syntype specimens were recently located in the collections of the Museum of Comparative Zoology, Harvard University (MCZ 4988). Based on the original label accompanying these specimens, the type locality of *A. panamensis* should be restricted to Las Perlas Islands, Panama.

Distribution.—Eastern Pacific: Mexico: Michoacan (Hermoso-Salazar & Hernández-Alcántara 2003); Oaxaca (Hendrickx & Hermoso-Salazar 2005); Costa Rica: Guanacaste and Nicoya Gulf, Puntarenas (Kim &

Abele 1988); Panama: vicinity of Panama City (Casco Viejo, Amador, Punta Paitilla), Venado, Río Mar, Taboga and Las Perlas Islands (Kim & Abele 1988; present study); Ecuador: La Libertad (Kim & Abele 1988), Galapagos (Hickman & Zimmerman 2000; Wicksten & Hendrickx 2003).

Remarks.—*Alpheus panamensis* is closely related to *A. formosus* but can be separated from the latter by the orbitorostral (= adrostral) grooves extending posteriorly to the base of the orbital hoods (vs. to the level of eye base in *A. formosus*); the rostral plate being slightly broader at base; and the paler distolateral spine on the uropod (only distally tan in *A. panamensis* vs. usually entirely black in *A. formosus*) (see also Kim & Abele, 1988). *Alpheus panamensis* also differs from the below-described new species, e.g., by the presence of bal-
aeniceps setae on the fingers of the minor chela and by further posterior extension of the orbitorostral grooves (see below).

GenBank number.—EF532611 (fcn 98-163), EF532612 (fcn 05-015, to be deposited in USNM), EF532613 (fcn 05-017), AF309923.

Alpheus formosus Gibbes, 1850

Figs. 1–4, 7c–e

Alpheus formosus Gibbes 1850: 196; Kingsley 1878a: 190; Heilprin 1888: 322; Heilprin 1889: 151; Coutière 1899 (for page numbers see Chace & Forest 1970); Coutière 1910: 485; Verrill 1900: 579; Rathbun 1900: 152; Rathbun 1901: 106; Verrill 1922: 84; Balss 1924: 177; Boone 1930: 166; Chace 1956: 146; Hazlett 1962: 82; Bullis & Thompson 1965: 8; Williams 1965: 64; Fausto-Filho 1970: 56; Hendrix 1971: 83; Chace 1972: 67; Corrêa 1972: 3; Coelho & Ramos 1972: 148; Ray 1974: 104; Abele 1976: 273; Camp *et al.* 1977: 25; Gore *et al.* 1978: 225; Christoffersen 1979: 314 (part.); Corredor *et al.* 1979: 32; Christoffersen 1980a: 65; Christoffersen 1980b: 39; Rodríguez 1980: 145; Fausto-Filho 1980: 113; Morgado 1980: 33; Reed *et al.* 1982: 768; Carvacho 1982: 18; Cubit & Williams 1983: 24; Williams 1984: 94; Lemaitre 1984: 426; Young 1984: 29; Freitas-Lins 1985: 39; Young 1986: 106; Sterrer 1986: 325; Rodríguez 1986: 143; Abele & Kim 1986: 197, 206; Kim & Abele 1988: 39, 40; Márquez 1988: 34; Markham *et al.* 1990: 421; Martínez-Iglesias *et al.* 1996: 33; Hernández Aguilera *et al.* 1996: 32; Martínez-Iglesias *et al.* 1997: 423; Hobbs 1998: 906; Santos & Coelho 1998: 73; Posey *et al.* 1998: 154; Christoffersen 1998: 358; Vargas & Cortés 1999: 901; Morgado & Tanaka 2001: 177; Coelho *et al.* 2006: 51; Manning & Reed 2006: 289.*

Alpheus formosus-a—Knowlton & Mills 1992: 2.

Alpheus formosus sp. a—Knowlton *et al.* 1993: 1630.

Alpheus formosus A—Williams *et al.* 2001: 377.

Alpheus formosus (lap. cal.)—McClure 2005: 142, fig. 14, pl. 4, fig. A.*

Crangon formosus—Hay & Shore 1918: 384; Schmitt 1924a: 65; Schmitt 1924b: 73; Pearse 1932: 107; Schmitt 1935: 144; Schmitt 1936: 368; Schmitt 1939: 28; Pearse 1950: 150; Pearse & Williams 1951: 143.*

Crangon formosum—Manter 1933: 177.*

Alpheus Poeyi Guérin-Méneville 1857: 19.

Alpheus panamensis (not *sensu* Kingsley 1878)—Pocock 1890: 519; Zimmer 1913: 391; Fausto-Filho 1974: 5.*

Not *Alpheus formosus*—Christoffersen 1979: 315 (part., specimens from E Pacific) (= *A. panamensis* Kingsley, 1878); Frische 2003: 38 (color photograph, = *Alpheus* sp.).

*Remark: Two species were previously confused under the name “*Alpheus formosus*”; therefore, some of the above-listed records may actually refer to the new species and not to *A. formosus*.

Type material.—USA, Florida. Neotype, ovig. female (CL 9.7), USNM 1100697, USA, Florida, Big Pine Key, Bahia Honda State Park, shallow subtidal (less than 1.5 m), under rocks, coll. A. Anker, 18 Apr 2004 [fcn 04-010].

Additional material examined.—Panama (Caribbean coast). 1 male (CL 5.6), 1 female (CL 6.0), USNM 1100699, Bocas del Toro, Isla Bastimentos, shallow subtidal (0.5–1 m), from coral rocks, coll. A. Anker, 21

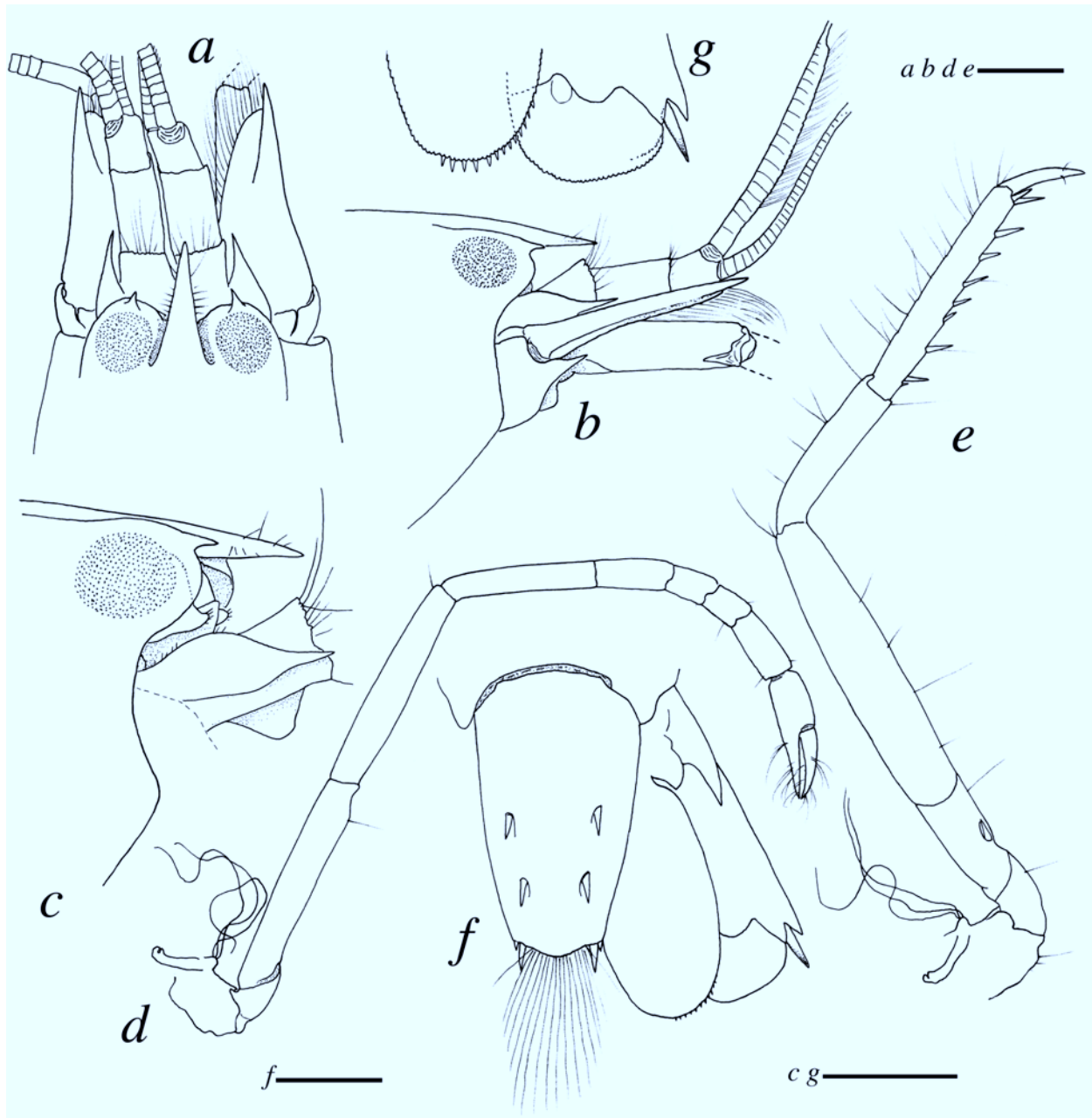


FIGURE 1. *Alpheus formosus* Gibbes, 1850, male from Atol das Rocas, Brazil (MNRJ 20755): a, frontal region, dorsal; b, same, lateral; c, same, detail of orbital hoods, rostrum and first segment of antennular peduncle; d, second pereopod, lateral; e, third pereopod, lateral; f, telson and uropod, dorsal (fringing setae on uropod omitted); g, uropod, distal region of exopod and endopod, dorsal (setae omitted). Scale bars = 1 mm.

Oct 2005 [fcn 05-103]; 1 male (CL 7.8) USNM 1100700, Isla Grande, southern shore, shallow subtidal (0.5–1.5 m), from coral rubble, coll. A. Anker, 21 Apr 2006 [fcn 06-425]; 1 juvenile (CL not measured), USNM 1100701, Isla Grande, western point, from coral rocks, shallow subtidal (0.5–1m), coll. A. Anker and C. Hurt, 6 Oct 2005 [fcn 05-101]; 1 male (CL 6.9), USNM 1100702, same collection data as previous specimen [fcn 06-392]. Costa Rica (Caribbean coast). 3 males (CL 5.8, 6.6, 6.5), 1 ovig. female (CL 6.7), USNM 1100698, Cahuita, shallow subtidal (0.5–1.5 m), from rock crevices and *Halimeda* clumps, coll. A. Anker, I.S. Wehrmann and L. Harris, 26–27 Nov 2005 [fcn 05-100]; 1 male (CL 10.3), MNHN-Na 16385, same collection data as previous specimens [fcn 05-102]. Aruba. 2 males (CL 5.3, 6.3), 1 female (CL 6.2), 1 ovig. female (CL 7.1), MNHN-Na 16360, Baby Beach, shallow subtidal (1–1.5 m), from crevices in coral rubble, coll. A. Anker, 6

Dec 2003 [fcn 03-011]. Guadeloupe. 1 female (CL not measured), MNHN-Na 13715, Le Moule, depth 2 m, coll. F. Fasquel, 29 Oct 1999; 1 male (CL not measured), MNHN-Na 16386, same collection data as for previous specimen. Brazil. 2 males (CL 6.7, 7.8), 1 ovig. female (CL 7.9), MNRJ 20755, LT 702, Atol das Rocas, between Piscina das Tartarugas and Piscina das Rocas, in pools, among calcareous algae, coll. P.S. Young, P.C. Paiva and A.A. Aguiar, 28 Oct 2000 [1 male dissected]; 1 male (CL 5.7), MNRJ 20756, Atol das Rocas, Piscina do Cemitério, in calcareous algae, coll. P.S. Young *et al.*, 1 Jan 2001; 1 male (CL 9.5), 1 ovig. female (CL 9.4), MNRJ 20757, Atol das Rocas, near Pedra do Garapira, in tide pool, coll. P.S. Young, P.C. Paiva and A.A. Aguiar, 14 Oct 2000; 1 male (CL 11.0), MNRJ 20758, Atol das Rocas, Piscina das Rocas, in calcareous alga, coll. P.S. Young *et al.*, 26 Oct 2000; 1 male (CL not measured), MNHN-Na 16359, Pernambuco, Rio Formozo, coll. A.C. Branner Hartt, Dec 1875 [specimen lacking all pereopods]. USA, Florida. 1 male (CL 11.5), OUMNH-ZC 2007-13-034, USA, Florida, near Marineland, 5 km south of Sebastian Inlet, shallow subtidal, coll. J.A. Baeza, 15 Jul 2007 [fcn 07-240; specimen somewhat desiccated during transport, rehydrated in EtOH]. British Virgin Islands. 1 juvenile (CL not measured), Guana Island, coll. Guana Marine Invertebrate Project, 2000 [fcn Vc 0600] [specimen missing minor cheliped, identification tentative based on length of adrostral furrows; specimen will be deposited in LACM].

Redescription.—Carapace glabrous, non-setose, somewhat compressed laterally. Rostrum well developed, dorsally flattened; margins fringed with setae directed up- or sideways (Fig. 1a, b); tip acute, reaching to or slightly beyond distal margin of first segment of antennular peduncle (Fig. 1a); rostral carina absent; orbito-rostral process broad, round W-shaped. Orbital hoods with acute teeth inserted at some distance from anterior margin (Fig. 1a). Adrostral furrows deep, narrow, abruptly delimited from rostrum, posteriorly extending almost to level of cornea base (Fig. 1a). Pterygostomial angle rounded, somewhat protruding anteriorly (Fig. 1b, c); cardiac notch well developed. Eyes completely concealed in dorsal, lateral and partly in frontal view. Ocellar beak vertically protruding towards rostrum, more or less visible in lateral view (Fig. 1c).

Antennular peduncles relatively stout, second segment longer than dorsally visible portion of first, about 1.5 times as long as wide (Fig. 1a); stylocerite with acute tip, slightly overreaching distal margin of first segment (Fig. 1a, b); mesioventral carina of first segment with large, bluntly protruding tooth (Fig. 1c); lateral flagellum with numerous tufts of aesthetascs, accessory ramus rudimentary (Fig. 1b). Antenna with stout basicerite bearing strong acute ventrolateral tooth, its tip not reaching level of stylocerite tip (Fig. 1b); carpo-cerite stout, reaching slightly beyond distolateral spine of scaphocerite; scaphocerite with very strong distolateral tooth separated from narrow blade by deep cleft (Fig. 1a), tip of distolateral tooth reaching far beyond blade and exceeding end of antennular peduncle (Fig. 1a); lateral margin of scaphocerite very slightly concave at mid-length (Fig. 1a).

Mouthparts (mandible, maxillule, maxilla, first and second maxillipeds) typical for *Alpheus*. Third maxilliped moderately stout; coxa with distally subacute lateral plate; exopod reaching penultimate segment; antepenultimate segment slightly flattened, ventral margin straight; penultimate segment about 2.5 times as long as wide; arthrobranch well developed (third maxilliped generally very similar to that of *A. panamensis*, cf. Kim & Abele, 1988: fig. 15d, and to that of below-described new species, cf. Fig. 5d).

Male major cheliped (Fig. 2) with short, stout ischium; merus stout, about 2.5 times as long as wide proximally, dorsal margin distally protruding (Fig. 2a, c); ventrolateral margin straight, ventromesial margin rugose, with spinules, distally with acute tooth (Fig. 2c); carpus very short, cup-shaped; chela large, subcylindrical, broadly oval in cross-section; palm smooth, moderately setose distally; distomesial margin with strong acute tooth (Fig. 2b); linea impressa conspicuous (Fig. 2a); adhesive discs relatively large (Fig. 2a); fingers more than half-length of palm, dactylus usually reaching beyond pollex, with large plunger, latter distally with stamen-shaped sensillae (Fig. 2a). Female major cheliped similar to that of male, except for somewhat smaller size and different proportions of fingers to palm (Fig. 4b). Mesiodistal tooth on merus sometimes (Fig. 4b, c), independently of sex, with two acute teeth: one larger and stronger tooth, and one much smaller tooth.

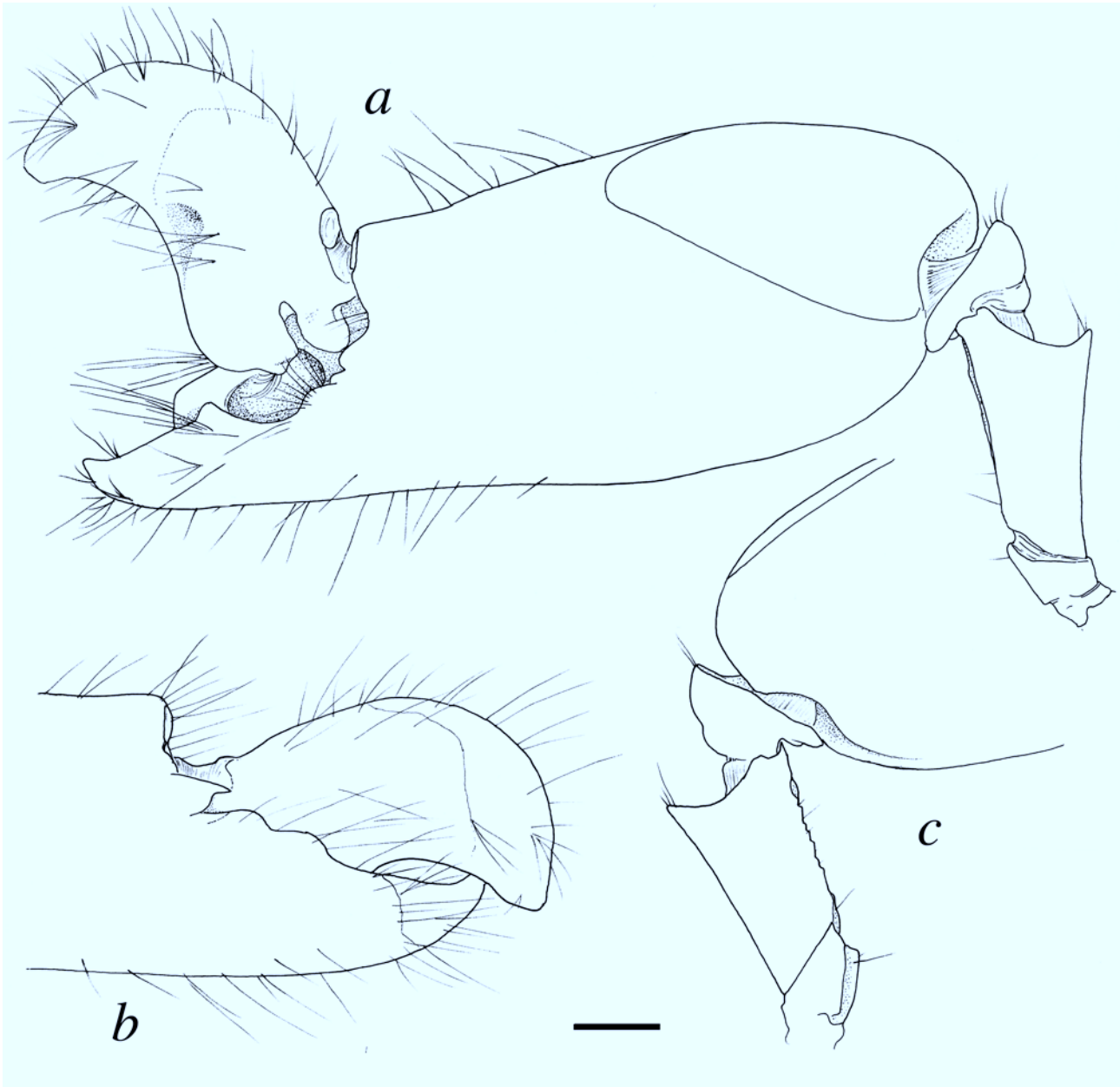


FIGURE 2. *Alpheus formosus* Gibbes, 1850, male from Atol das Rocas, Brazil (MNRJ 20755): a, major cheliped, lateral; b, same, distal portion of chela, mesial; c, same, detail of ischium, merus and carpus, mesial. Scale bar = 1 mm.

Male minor cheliped (Fig. 3) with short, stout ischium; merus about three times as long as wide proximally; ventrolateral margin straight; ventromesial margin somewhat rugose, usually with spinules; distally with acute tooth (Fig. 3d); carpus cup-shaped; chela smooth, ovate in cross-section, somewhat setose mesially (Fig. 3b); distomesial margin of palm with strong acute tooth (Fig. 3a, b); linea impressa conspicuous (Fig. 3a); adhesive discs small (Fig. 3a); fingers about as long as palm, with well developed rows of balaeniceps setae (Fig. 3a–c), tips strongly curved, crossing when chela closed. Female minor cheliped similar to that of male; chela with well developed rows of balaeniceps setae (Fig. 4d).

Second pereiopod with ischium subequal to merus (Fig. 1d); carpus five-segmented, ratio of carpal segments (from proximal to distal) approximately: 6/3/1.5/1.5/3 (Fig. 1d); chela simple, with fingers slightly longer than palm. Third pereiopod with ischium bearing small ventrolateral spine (Fig. 1e); merus unarmed, about six times as long as wide; carpus unarmed; propodus with stout spines or pairs of spines along ventral

margin and two spines distoventrally near articulation with dactylus (Fig. 1e); dactylus about 1/3 propodus length, simple, conical, gradually curved towards acute tip, with some setae (Fig. 1e). Fourth pereopod similar to third pereopod. Fifth pereopod smaller and slenderer than third and fourth pereopods; ischium unarmed; propodus with row of spines and at least eight rows of grooming setae distolaterally; dactylus conical, as in third pereopod.

Abdominal pleura with posteroventral margins broadly rounded; sixth somite without articulated flap, dorsolateral projections on each side of telson bluntly rounded. Male second pleopod with appendix masculina reaching somewhat beyond appendix interna, with numerous slender apical and subapical setae. Uropod with protopod bearing elongate acute distolateral tooth (Fig. 1f); exopod with strong acute distolateral tooth adjacent to distolateral spine; diaeresis bearing strong lateral tooth, mesial to distolateral spine (Fig. 1f, g); distolateral spine stout, usually black to tan-brown (Figs. 4e, 7e), sometimes pale in alcohol (Fig. 1f, g); distal margins of endopod with row of spinules (Fig. 1g). Telson moderately broad, subrectangular, tapering towards posterior margin (Fig. 1f); dorsal surface without median groove, with two pairs of strong dorsal spines, situated at some distance from lateral margins, both pairs situated in posterior 2/3 length of telson (Fig. 1f); posterior margin convex centrally, with two pairs of posterolateral spines, mesial being much longer than lateral (Fig. 1f); anal tubercles well developed. Gill formula typical for *Alpheus*.

Size.—The largest Caribbean specimen is a male from Cahuita, Costa Rica, with CL 10.3 mm and TL 33.5 mm; the CL of remaining adult specimens range from 5.3 mm to 7.8 mm. The CL of the neotype (ovigerous female) from Florida Keys is 9.7 mm; the maximum CL of Florida specimens was 14.7 mm (Hendrix 1971). The largest specimen from Brazil is a male from Atol das Rocas with 11.0 mm CL and 35.7 mm TL.

Color pattern.—Body red-brown to purple-brown, with more or less intense yellow mediodorsal band extending from rostrum tip to posterior margin of sixth abdominal somite; carapace with white lateral band extending from anterolateral margin to cardiac notch, continued by zigzag white band ending at sixth abdominal somite; rostrum entirely yellow, usually not bordered by reddish brown on margins; carapace flanks below white band pale; telson and uropods red-brown with large yellow patches and spots; walking legs and second pereopods bluish, sometimes intense magenta blue; antennular peduncles yellow-brown; antennal scaphocerite brown with white areas, flagella pale bluish; chelipeds pale brown to intense orange brown, major chela with pale patch near articulation with dactylus; dactylus and pollex distally pinkish; minor chela mostly pale brown to orange brown (Fig. 7c–e); distolateral spine on uropodal exopod usually brown to almost black (Fig. 7e); eggs orange-reddish (Fig. 7d).

Ecology.—Intertidal to about 40 m (Sterrer 1986), commonly associated with reef-fringing habitats, in crevices of rocks, dead and living corals and coral rubble (Verrill 1922; present study); mixed sand-rubble bottoms among turtle grass (*Thalassia testudinum*), under rocks and coral rubble; in crevices on reefs of the sabellariid polychaete *Phragmatopoma* sp. (Camp *et al.* 1977; Gore *et al.* 1978); in empty conch shells (*Strombus*) on the outer fringing reefs near *Thalassia* beds (Hendrix 1971); occasionally in sponges, e.g., *Callyspongia*, *Ircinia* (Pearse 1950; Chace 1956), among bryozoan colonies, *Schizoporella* sp. (Christoffersen 1979; Morgado & Tanaka 2001), and in living corals, e.g., *Oculina* and *Porites* (Chace 1972; Reed *et al.* 1982); occasionally entering sea-connected cave systems (Hobbs 1998).

Type locality.—Key West, Florida (Gibbes 1850).

Distribution.—Western Atlantic: North Carolina (Hay & Shore 1918; Williams 1965, 1984; Christoffersen 1979); reefs of South Carolina (Pearse & Williams 1951); Florida: southern and central-eastern Florida (e.g., Fort Pierce, Sainte-Lucie, Hutchinson Island, Sebastian Inlet), Florida Keys (e.g., Key West, Big Pine Key, Cedar Key), Dry Tortugas (Gibbes 1850; Coutière 1910; Zimmer 1913; Balss 1924; Boone 1930; Pearse 1932; Hendrix 1971; Camp *et al.* 1977; Gore *et al.* 1978; Reed *et al.* 1982; Posey *et al.* 1998; present study); Bermuda (Heilprin 1888; Verrill 1922; Sterrer 1986); US Virgin Islands (Hendrix 1971); St. John (Zimmer 1913); British Virgin Islands: Guana (present study); Bahamas: Bimini, Cay Sal Bank (Pearse 1950; Lemaitre

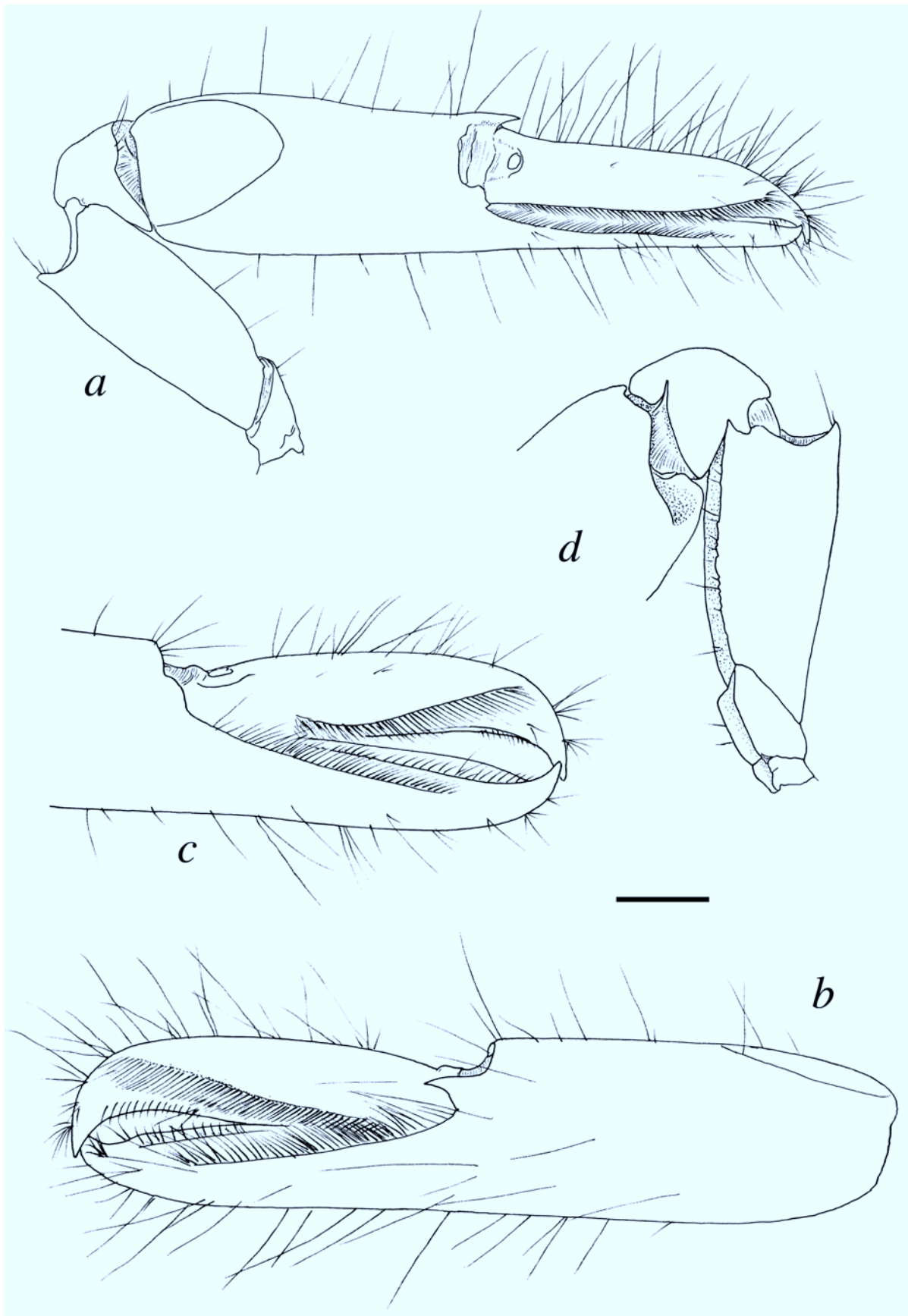


FIGURE 3. *Alpheus formosus* Gibbes, 1850, male from Atol das Rocas, Brazil (MNRJ 20755): a, minor cheliped, lateral; b, same, chela, mesial; c, distal portion of chela, lateral; d, same, detail of ischium, merus and carpus, mesial. Scale bar = 1 mm.

1984), Blue Holes Cave System (Hobbs 1998); Puerto Rico; Culebra (Rathbun 1901; Schmitt 1935; Ray 1974); French Antilles: Martinique, Guadeloupe (Carvacho 1982; present study); Tobago (Chace 1972); Barbados (Zimmer 1913; Schmitt 1924b); Netherlands Antilles: Aruba, Curaçao, Bonaire (Schmitt 1924a, 1936; present study); Venezuela: Los Roques, Tucacas, Isla Margarita, Arrecifes (Chace 1956; Rodríguez 1980; Rodríguez 1986); Colombia: Providencia (Schmitt 1939); Panama: Isla Grande, Colón, Bocas del Toro (Abele 1976; Cubit & Williams 1983; present study); Costa Rica: Limón, Cahuita (Vargas & Cortés 1999; present study); Honduras: Utila (A. Anker, pers. obs.); Mexico: Quintana Roo (Chace 1972), Veracruz, Campeche (Hernández-Aguilera *et al.* 1996), Puerto Morelos, Punta Estrella (Markham *et al.* 1990); Jamaica: Kingston (Zimmer 1913); Cuba: Gulf of Batabano (Martínez-Iglesias *et al.* 1996, 1997); Brazil: Natal, Rio Grande do Norte, Pernambuco, Alagoas, Bahia (including Abrolhos Islands), Ceara, Espírito Santo, Rio de Janeiro, São Paulo (Rathbun 1900; Fausto-Filho 1970; Corrêa 1972; Christoffersen 1979, 1998; Coelho *et al.* 2006), Fernando do Noronha (Pocock 1890); Atol das Rocas (present study). Some of the above-listed literature records may actually refer to the below-described new species, and not to *A. formosus*, as the two species were not distinguished in the past.

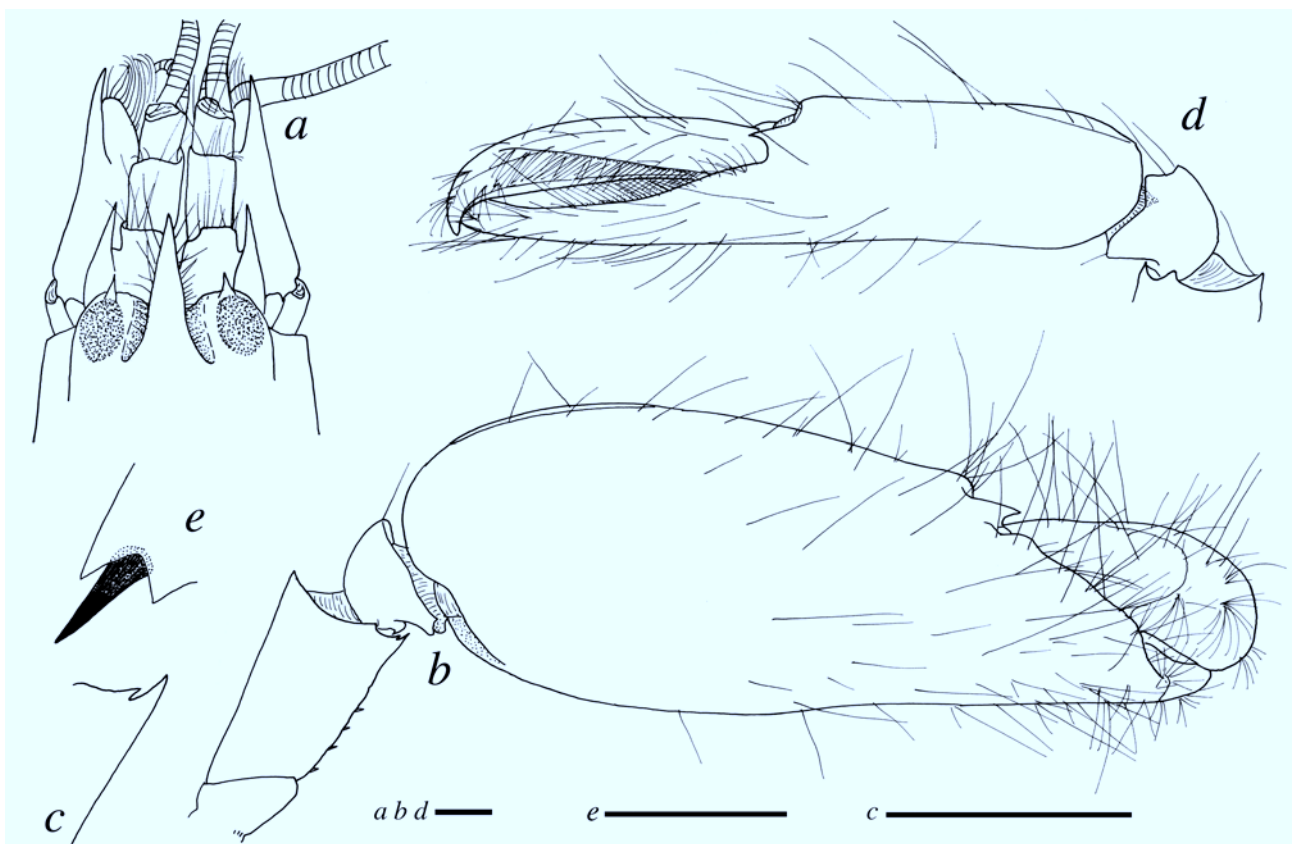


FIGURE 4. *Alpheus formosus* Gibbes, 1850, neotype female from Big Pine Key, Florida Keys (USNM 1100697): a, frontal region, dorsal; b, major cheliped, mesial; c, same, detail of distomesial tooth; d, minor chela and carpus, mesial; e, detail of distolateral spine of uropod, dorsal. Scale bars = 1 mm.

Remarks.—*Alpheus formosus* is closely related to *A. panamensis* but can be distinguished from the latter by the orbitorostral grooves extending to the level of eye base posteriorly (vs. to the base of the orbital hoods in *A. panamensis*); the rostral plate being slightly narrower at base; and the usually much darker distolateral spine on the uropod (black in *A. formosus* vs. pale, distally tan in *A. panamensis*) (see also Kim & Abele 1988). The color of the uropodal spine may be lighter if the animal has recently molted. For instance, some alcohol-preserved specimens from Atol das Rocas, including the illustrated male specimen, have a pale spine, without trace of black pigment (Fig. 1f). Most individuals, however, including the neotype, have a dark

brown to blackish spine in life and in alcohol (Fig. 4e). *Alpheus formosus* can be distinguished from the below-described new species by the presence of balaeniceps setae on the fingers of the minor chela in both sexes (more developed in males), the posteriorly more extending orbitorostral grooves and several features of the color pattern (see below).

GenBank number.—EF532605 (fcn 98-163), EF532606 (fcn 98-189), EF532607 (fcn 98-190), EF532608 (fcn 05-101, USNM 1100701), EF532609 (fcn 06-414), EF532610 (06-499), AF309903, AF309904.

***Alpheus paraformosus* n. sp.**

Figs. 5, 6, 7f–h

Alpheus formosus-b—Knowlton & Mills 1992: 2.

Alpheus formosus sp. b—Knowlton *et al.* 1993: 1630.

Alpheus formosus B—Williams *et al.* 2001: 377.

Type material.—Panama (Caribbean coast). Holotype: 1 male (CL 6.6), USNM 1100703, Bocas del Toro, San Cristóbal, Punta Coco, shallow subtidal (1–1.5 m), from rock and coral rubble crevices, coll. A. Anker, 29 Oct 2005 [fcn 05-099, specimen dissected]. Paratypes: 1 ovig. female (CL 6.9), USNM 1100704, same collection data as for holotype [fcn 05-099]; 1 ovig. female (CL 7.2), USNM 1100705, Bocas del Toro, Isla Colón, Boca del Drago, from crevices in coral rubble, depth less than 2 m, coll. A. Anker and J.A. Vera Caripe, 11 Nov 2006 [fcn 06-546].

Additional material examined.—Panama (Caribbean coast). 1 male (CL 4.6), 1 ovig. female (CL 5.5), MNHN-Na 16361, Isla Grande, southern shore, shallow subtidal (1–1.5 m), from crevices in coral rubble and algal clumps, coll. A. Anker, 4 Sep 2006 [fcn 06-454]. Honduras. 1 male (CL 5.1), 1 ovigerous female (CL 5.5), OUMNH-ZC 2007-20-001, Bay Islands, Utila, southern shore, small bay towards town, 1605.458' N 086°54.533' W from rubble, depth 1 m, coll. A. Anker and S. De Grave, 3 Jul 2007 [fcn H76].

Description.—Carapace glabrous, non-setose, somewhat compressed laterally. Rostrum well developed, dorsally flattened; margins fringed with some sideways directed setae (Fig. 5a, k); tip acute, not reaching distal margin of first segment of antennular peduncle (Fig. 5a, k); rostral carina absent; orbito-rostral process broad, round W-shaped. Orbital hoods with acute teeth inserted at some distance from anterior margin (Fig. 5a, k). Adrostral furrows deep, narrow, abruptly delimited from rostrum, posteriorly extending almost to about mid-length of cornea (Fig. 5a). Pterygostomial angle rounded, slightly protruding anteriorly (Fig. 5b); cardiac notch well developed. Eyes completely concealed in dorsal, lateral and partly in frontal view. Ocellar beak vertically protruding towards rostrum, usually visible in lateral view (Fig. 5b).

Antennular peduncles relatively stout, second segment shorter than dorsally visible portion of first segment, about 1.2 times as long as wide (Fig. 5a); stylocerite with acute tip, distinctly overreaching distal margin of first segment (Fig. 5a, b); mesioventral carina of first segment with large, bluntly protruding tooth (nearly identical to that of *A. formosus*, cf. Fig. 1c); lateral flagellum with numerous tufts of aesthetascs, accessory ramus rudimentary (Fig. 5b). Antenna with stout basicerite bearing strong acute ventrolateral tooth, its tip not reaching level of stylocerite tip (Fig. 5b); carpocerite moderately stout, reaching slightly beyond distolateral tooth of scaphocerite; scaphocerite with very strong distolateral tooth separated from narrow blade by deep cleft (Fig. 5a), tip of distolateral tooth reaching far beyond blade and slightly exceeding end of antennular peduncle (Fig. 5a); lateral margin of scaphocerite straight to very slightly concave at mid-length (Fig. 5a).

Mouthparts (mandible, maxillule, maxilla, first and second maxillipeds) typical for *Alpheus*. Third maxilliped moderately stout (Fig. 5d); coxa with distally acute lateral plate; exopod reaching penultimate segment; antepenultimate segment slightly flattened, ventral margin straight; penultimate segment about three times as long as wide; arthrobranch well developed (Fig. 5d).

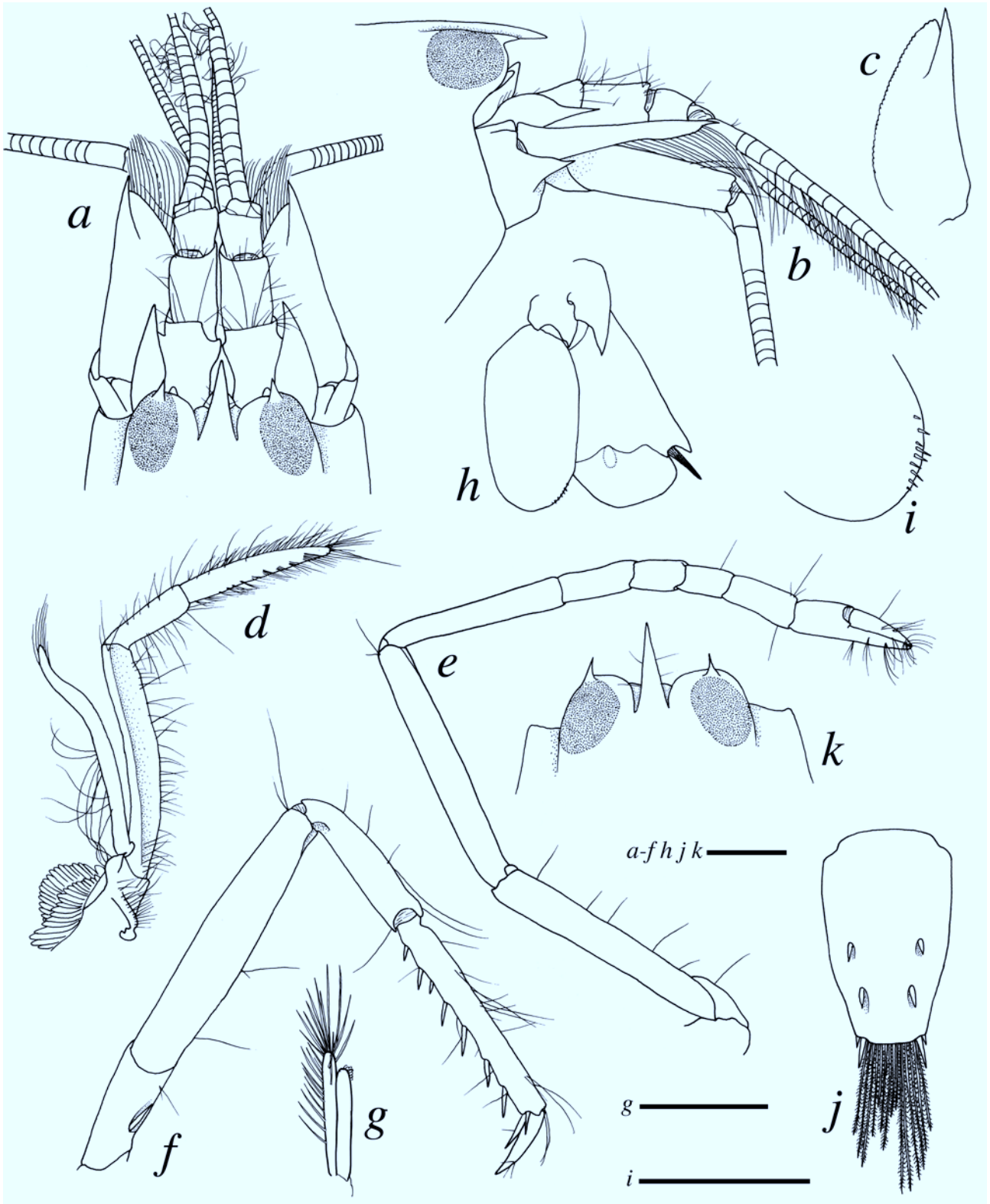


FIGURE 5. *Alpheus paraformosus* n. sp., holotype male from Bocas del Toro, Panama (USNM 1100703) [a–j]; paratype female from Bocas del Toro, Panama (USNM 1100704) [k]: a, frontal region, dorsal; b, same, lateral; c, scaphocerite, dorsal; d, third maxilliped, lateral; e, second pereopod, lateral; f, third pereopod, lateral; g, second pleopod, detail of appendix interna and appendix masculina; h, uropod, dorsal (setae omitted); i, distal margin of endopod (setae omitted); j, telson, dorsal; k, rostrum and orbital hoods, dorsal. Scale bars = 1 mm.

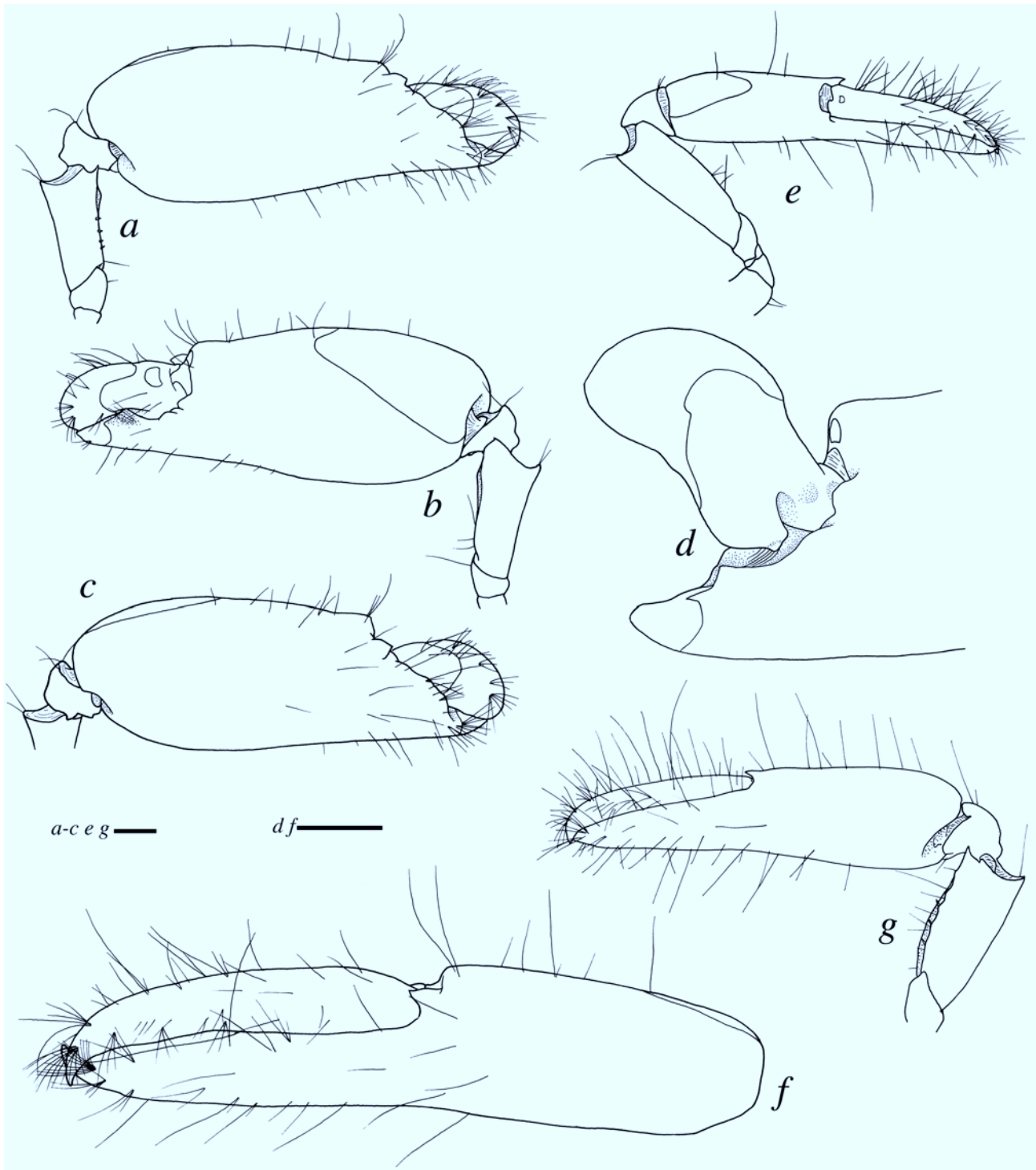


FIGURE 6. *Alpheus paraformosus* n. sp., holotype male from Bocas del Toro, Panama (USNM 1100703) [a–f]; paratype female from Bocas del Toro, Panama (USNM 1100704) [g]: a, major cheliped, mesial; b, same, lateral; c, same, chela and carpus, mesial; d, same, distal portion of chela, fingers opened (setae omitted); e, male minor cheliped, lateral; f, same, chela, mesial; g, female minor cheliped, mesial. Scale bars = 1 mm.

Male major cheliped (Fig. 6a–d) with short, stout ischium; merus stout, about 2.5 times as long as wide proximally, dorsal margin distally protruding (Fig. 6a, b); ventrolateral margin straight; ventromesial margin straight, with small spinules (Fig. 6a), distally with acute tooth (Fig. 6a); carpus very short, cup-shaped; chela large, subcylindrical, broadly oval in cross section; palm smooth, moderately setose distally; distomesial margin with blunt to subacute tooth (Fig. 6a, c); linea impressa conspicuous (Fig. 6b); adhesive discs relatively

large (Fig. 6b, d); fingers more than half-length of palm, dactylus usually reaching slightly beyond pollex, with large plunger, latter distally with stamen-shaped sensillae (Fig. 6d). Female major cheliped similar to that of male, except for somewhat smaller size and different proportions of fingers to palm.

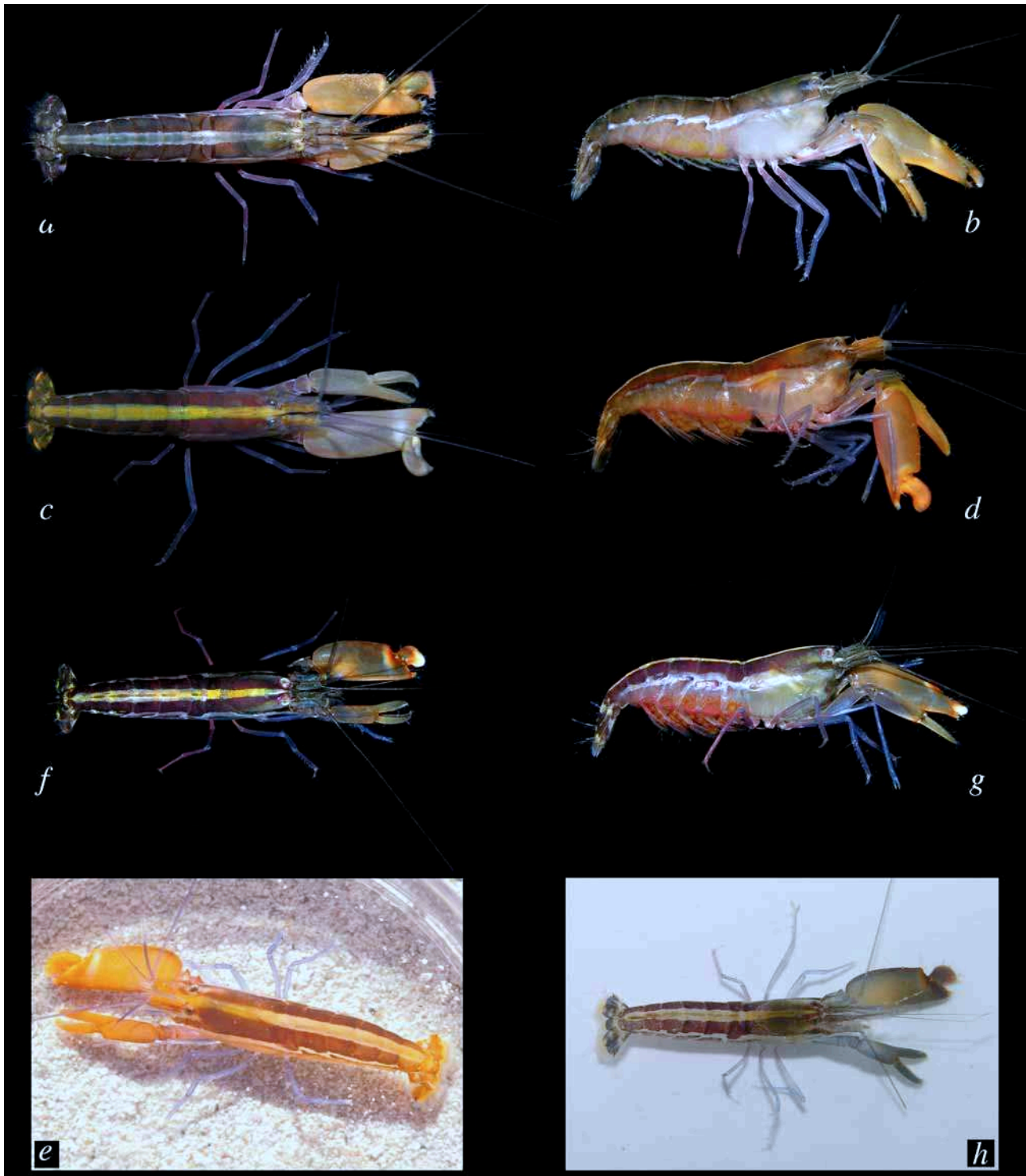


FIGURE 7. Color patterns of species of the *Alpheus formosus* Gibbes, 1850 complex: *Alpheus panamensis* Kingsley, 1878 [a, b]; *A. formosus* Gibbes, 1850 [c–e]; *A. paraformosus* n. sp. [f–h]: a, male from Río Mar, Panama (USNM 1100693); b, ovigerous female from La Chorrera, Panama (not preserved); c, male from Isla Grande, Panama (USNM 1100700); d, ovigerous female from Cahuita, Costa Rica (USNM 1100698); e, neotype female from Big Pine Key, Florida Keys (USNM 1100697); f, g, paratype ovigerous female from Bocas del Toro, Panama (USNM 1100705); h, holotype male from Bocas del Toro, Panama (USNM 1100703).

Male minor cheliped (Fig. 6e) and female minor cheliped (Fig. 6g) similar; ischium short, stout; merus more than three times as long as wide proximally; ventrolateral margin straight; ventromesial margin somewhat rugose, usually with spinules (Fig. 6g), distally with acute tooth (Fig. 6g); carpus cup-shaped; chela smooth, ovate in cross-section, moderately setose distomesially (Fig. 6f); distomesial margin of palm with strong blunt or subacute tooth (Fig. 6e, f); linea impressa well marked (Fig. 6e); adhesive discs very small; fingers about as long as palm, without distinct rows of balaeniceps setae (Fig. 6f), tips strongly curved, crossing when chela closed.

Second pereopod with ischium subequal to merus (Fig. 5e); carpus five-segmented, ratio of carpal segments (from proximal to distal) approximately: 5/2/1.5/1.5/2 (Fig. 5e); chela simple, with fingers longer than palm. Third pereopod relatively slender; ischium with ventrolateral spine (Fig. 5f); merus unarmed, about six times as long as wide; carpus unarmed; propodus with series of stout spines or pairs of spines along ventral margin and two spines distoventrally near articulation with dactylus (Fig. 5f); dactylus about 1/3 propodus length, simple, conical, gradually curved towards acute tip, with some setae (Fig. 5f). Fourth pereopod similar to third pereopod. Fifth pereopod shorter and more slender than third and fourth pereopods; ischium unarmed; propodus with row of spines and at least seven rows of grooming setae distolaterally; dactylus conical, as in third pereopod.

Abdominal pleura with posteroventral margins broadly rounded; sixth somite without articulated flap, dorsolateral projections on each side of telson bluntly rounded. Male second pleopod with appendix masculina reaching beyond appendix interna, with numerous slender setae along margins and on apex (Fig. 5g). Uropod with protopod bearing elongate acute distolateral tooth (Fig. 5h); exopod with strong acute distolateral tooth adjacent to distolateral spine; diaeresis bearing strong lateral tooth, mesial to distolateral spine (Fig. 5h); distolateral spine stout, usually tan to dark brown (Fig. 5h, 7h); distal margins of endopod with row of spinules (Fig. 5i). Telson moderately broad, subrectangular, tapering towards posterior margin (Fig. 5j); dorsal surface without median groove, with two pairs of strong dorsal spines, situated at some distance from lateral margins, both pairs situated in posterior half length of telson (Fig. 5j); posterior margin broadly rounded, with two pairs of posterolateral spines, mesial being much longer than lateral (Fig. 5j); anal tubercles well developed. Gill formula typical for *Alpheus*.

Size.—The paratype from Boca del Drago (USNM 1100705), an ovigerous female, is the largest specimen in the type series, with CL 7.2 mm and TL 20.7 mm; other specimens range from 4.6 mm to 6.9 mm in CL.

Color pattern.—Body dark purple-brown, with pale yellow mediodorsal band extending from rostrum tip to posterior margin of sixth abdominal somite; carapace with white lateral band extending from anterolateral margin to cardiac notch, continued by sinuous white band ending at sixth abdominal somite; second pleuron with white, ventrally directed oblique band; fourth pleuron with small white patch next to white band; rostrum yellow, bordered by reddish brown, posteriorly widening band on margins; carapace flanks below white band and area posterior to orbital hoods pale or whitish; telson and uropods dark purple-brown with large yellow patches and spots; walking legs and second pereopods bluish to purplish; antennular peduncles gray-brown; antennal scaphocerite mostly grayish-blue, flagella pale gray-bluish; chelipeds gray-brown; major chela with pale orange patch proximally and orange-brown patch near articulation with dactylus; dactylus gray, distally pinkish; pollex tip whitish; minor chela mostly bluish-gray (Fig. 7f–h); eggs reddish orange (Fig. 7g).

Etymology.—The specific name “*paraformosus*” reflects the great resemblance of this species—in both morphology and color pattern—to *A. formosus*.

Ecology.—Lower intertidal and shallow subtidal (0–5 m); mixed sand-rubble bottoms, in crevices of coral rocks or conglomerates of dead corals among turtle grass (*Thalassia testudinum*).

Type locality.—Bocas del Toro, Panama.

Distribution.—Western Atlantic: Panama: Bocas del Toro (type locality), Isla Grande, San Blas Islands; Honduras: Utila; probably more widespread in the Caribbean Sea to southern Florida.

Remarks.—*Alpheus paraformosus* n. sp. can be separated from both *A. formosus* and *A. panamensis* by the non-balaeniceps fingers of the minor chela in both sexes (Fig. 6e, g) and the distinctly shorter orbitorostral grooves (compare Fig. 5a and Fig. 1a). The new species also appears to be somewhat smaller than *A. formosus* and *A. panamensis* (CL range 4.4–7.2 mm for *A. paraformosus* n. sp. compared to 5.3–14.7 mm for *A. formosus* and 4.7–14.7 for *A. panamensis*). Differences in the color pattern between *A. paraformosus* n. sp., *A. formosus* and *A. panamensis* are shown in Fig. 7 and summarized in Table 1 below.

TABLE 1. Diagnostic color pattern differences among species of the *Alpheus formosus* species complex. See also Knowlton & Mills (1992) for less consistent differences (expressed in percentage of individuals).

| Features | <i>A. panamensis</i> | <i>A. formosus</i> | <i>A. paraformosus</i> |
|--------------------------|----------------------------------|-----------------------------------|--------------------------------|
| Adult rostrum | Yellow to red, margins red-brown | Usually entirely yellow | Yellow, margins red-brown |
| Juvenile rostrum | Entirely yellow | Entirely yellow | Yellow, margins red-brown |
| Mediodorsal band | With grayish band | Without grayish band | With grayish band |
| Second abdominal pleuron | Without posterior band | Without posterior band | With posterior band |
| Fourth abdominal pleuron | Without white lateral patch | Without white lateral patch | With small white lateral patch |
| Major chela | Mostly brown-orange | Mostly pale brown to orange-brown | Mostly grey or grey-brown |
| Telson and uropods | Without bluish patches | Without bluish patches | With bluish patches |
| Egg color | Yellow-orange | Orange-red | Orange-red |

GenBank number.—EF532614 (fcn 06-454, MNHN-Na 16361), EF532615 (fcn 98-266), AF308985, AF309905.

Discussion

The *Alpheus formosus* species complex, as redefined, contains three species: *A. panamensis* in the eastern Pacific, and *A. formosus* and *A. paraformosus* n. sp. in the western Atlantic. It represents a small, well defined, purely American clade within the large Clade III in Williams *et al.* (2001), the latter encompassing the majority of species of the nonmonophyletic *A. sulcatus* species group (*sensu* Banner & Banner 1982). Both previous studies and the present data suggest that *A. paraformosus* n. sp. forms a sister clade to the transisthmian clade *A. panamensis*—*A. formosus* (see also Knowlton *et al.* 1993; Williams *et al.* 2001). Morphology and color fully support molecular data: *A. paraformosus* n. sp. differs from both *A. panamensis* and *A. formosus* by two important morphological characters, viz., the absence of balaeniceps setae on the fingers of the minor chela and the short adrostral furrows, and by several differences in the color pattern (cf. Table 1), including the presence of a diagnostic, small white patch on the fourth abdominal pleuron (Fig. 7g).

The three species of the *A. formosus* complex appear to have diverged somewhat before the closure of the Isthmus of Panama. The average COI genetic distance between *A. panamensis* and *A. formosus* is 10.1%, between *A. panamensis* and *A. paraformosus* n. sp. 14.3%, and between *A. formosus* and *A. paraformosus* n. sp. 14.8%. With an estimated rate of sequence divergence of 1.5% per million years (see Methods), the time of divergence between the two transisthmian taxa, *A. panamensis* and *A. formosus*, was approximately 7 mya,

whereas the western Atlantic sympatric taxa, *A. formosus* and *A. paraformosus* n. sp. were separated for at approximately 10 mya.

Within the clade III, the closest relatives of *A. formosus*, *A. panamensis* and *A. paraformosus* n. sp. appear to be species from the *A. splendidus* Coutière, 1897 species complex, in particular the Indo-West Pacific *A. splendidus* with a strikingly similar color pattern (see Bhuti *et al.* 1975; Jeng & Chang 1985). However, *A. splendidus* and related taxa, such as the Indo-West Pacific *A. facetus* De Man, 1910, the eastern Pacific *A. confusus* Carvacho, 1988 and *A. felgenhaueri* Kim & Abele, 1988, and the eastern Atlantic *A. blachei* Crosnier & Forest, 1965, all differ from the *A. formosus* complex by the dorsally non-flattened rostra. A broad-scale phylogenetic study of the entire Clade III based on DNA/RNA studies (Hurt *et al.*, in prep.) may bring more light on the relationships between *A. formosus*, *A. splendidus* and other species complexes.

Acknowledgments

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