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TITLE:	ZOOTAXA
PUBLISHER/PLACE:	Magnolia Press Auckland, N.Z. :
VOLUME/PAGES:	2014 Dec 17;3895(4):451-91. doi: 10. 11646/zootaxa.3895.4.1 451-91
DATE:	2014
AUTHOR OF ARTICLE:	Bracken-Grisson HD;Felder DL
TITLE OF ARTICLE:	PROVISIONAL REVISION OF AMERICAN SNAPPING SHRIMP ALLIED TO A
ISSN:	1175-5326
OTHER NUMBERS/LETTERS:	NLM Unique ID: 101179386 39673549 25543582
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http://dx.doi.org/10.11646/zootaxa.3895.4.1
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Provisional revision of American snapping shrimp allied to *Alpheus floridanus* Kingsley, 1878 (Crustacea: Decapoda: Alpheidae) with notes on *A. floridanus africanus*

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Abstract

Alpheus floridanus Kingsley, 1878 has been previously treated as a single, morphologically diverse species with a broad distribution in the eastern and western Atlantic Ocean and eastern Pacific Ocean. However, variations in morphology and color patterns, in addition to genetic evidence, have prompted further investigation. Morphological characters, including curvature and length of the scaphocerite, number teeth on the incisor process of the mandible, number of pereopodal spines, proportions of the major chela, as well as color patterns, support recognition of several species in the *Alpheus floridanus* complex. *Alpheus floridanus sensu stricto* (s.s.) is redescribed based upon a lectotype selected from the former syntypic pair. The mutilated second specimen of the syntypic pair is identified as *A. platycheirus* Boone, 1927, which is fully redescribed. Three species are described as new: *A. hephaestus* sp. nov. from the eastern Pacific, and *A. roblesi* sp. nov. and *A. ulalae* sp. nov. from the western Atlantic. Morphological comparisons to the eastern Atlantic *A. floridanus africanus* Balss, 1916 are discussed, however a formal treatment of this subspecies is not the objective of this study. Our proposed taxonomic revisions of the *A. floridanus* complex are supported in a companion molecular genetic analysis (following paper, this volume).

Key words: *Alpheus*, species complex, snapping shrimp, color pattern, East Atlantic, West Atlantic, East Pacific

Introduction

Snapping shrimps of the genus *Alpheus* Fabricius, 1798 encompass a very diverse group of decapods numbering

over 286 species (De Grave & Fransen 2011). Even so, this may represent an underestimation because many species complexes of *Alpheus* appear to harbor numerous unnamed taxa (Anker *et al.* 2006). Molecular studies have identified dozens of alpheid species complexes (Anker *et al.* 2007a; 2008a; 2008b; 2008c; Anker *et al.* 2007b; Knowlton 1993; Knowlton & Mills 1992; Mathews 2006; 2007; Williams *et al.* 2001), prompting reexamination of slight morphological differences and color patterns for use as species discriminators. Taxonomists have long contended that color and its pattern are of value in discriminating between cryptic or pseudocryptic species of *Alpheus*. Color patterns have proven essential for rapid and efficient field identifications, especially for populations in the Caribbean Sea, eastern and Indo-West Pacific, and tropical eastern Atlantic (Anker 2001; Anker *et al.* 2007a; 2008a; 2008b; 2008c; Anker *et al.* 2007b; Knowlton & Mills 1992).

Alpheus floridanus Kingsley, 1878 belongs to the *A. brevisrostris* (Olivier, 1811) group which is characterized by the well-developed, unarmed orbital hoods and a compressed major chela (Chace 1988; Kim & Abele 1988). Based on previous work, *A. floridanus* appears to have a broad distribution, extending from the tropical eastern Atlantic to the Caribbean Sea, Gulf of Mexico, Florida, Brazil, and eastern Pacific (Chace 1972; Crosnier & Forest 1966; Kim & Abele 1988; Wicksten 1983; Williams *et al.* 2001; Zimmer 1913). Morphological examinations of *A. floridanus* from throughout its reported range have led previous workers to question whether this species has been mistakenly regarded as a single species, and several have proposed recognition of subspecies within this taxon (i.e. *A. floridanus floridanus* and *A. floridanus africanus* from the eastern Atlantic, Balss 1916; Crosnier & Forest 1966; Holthuis 1951). The two subspecies in the eastern Atlantic have been distinguished from one another based on marginal sinuses between the ocular hoods, major and minor chela length ratios, spines on the 3rd pereopod propodus, and antennal spine characteristics, but inconsistency in these characters has also been documented (Chace 1972). This inconsistency in morphological characters extends to western Atlantic and Pacific representatives, where researchers noted a high degree of variation in similar characters such as chela shape and size, coloration, and spination of the pereopodal articles (Chace 1972; Christoffersen 1979; Hendrix 1971; Kim & Abele 1988). In addition to morphological work, one molecular study has provided genetic evidence for the existence of at least four distinct clades within the *A. floridanus* complex (Williams *et al.* 2001) throughout the Caribbean Sea and from tropical waters of the eastern Pacific Ocean. This study suggests a scope of phylogenetic complexity among American populations that remains to be reflected in taxonomy. Lastly, a described species from Cuba, *A. platycheirus* Boone, 1927, may also be a member of the *A. floridanus* complex (e.g., Chace 1972) as morphological characteristics, such as shape of the chela, show striking similarities to *A. floridanus* (e.g., Chace 1972).

The syntypes (one male and one female) of *A. floridanus* were collected off Dry Tortugas, Florida, at 16 m depth some time prior to 1878. The original account (Kingsley 1878) provided a vague description of the species without illustrations, but the reported size measurements (body length, carapace length, and hand length) depict the male syntype. However, no holotype was designated and upon initial examination it became obvious that the syntypes displayed extreme morphological variation. This observation, along with decades of previous studies documenting variation within different population of *A. floridanus*, compelled us to examine this species complex in more detail.

Morphological comparisons of specimens that have been assigned to *A. floridanus sensu lato* (s.l.) from the western Atlantic (Caribbean Sea, Florida, Gulf of Mexico, Brazil), eastern Atlantic, and eastern Pacific are here undertaken. On the basis of these studies and simultaneous molecular phylogenetic analyses (Bracken-Griessom *et al.* this volume), a provisional taxonomic revision of the *A. floridanus* complex is presented. The syntypes of *A. floridanus* and holotype of *A. platycheirus* are re-examined in the course of our studies. Although we restrict our current focus to American species of this complex, it is obvious that morphological and color pattern similarities to illustrated specimens of close relatives in the Indo-Pacific and Mediterranean region (Hayashi & Nagata 2002; Miyake 1982; 1983; Ozcan *et al.* 2009) invite subsequent larger scale analysis of the entire group.

Material and methods

Samples were obtained from coastal and shelf habitats of the Gulf of Mexico (northern, eastern and southwestern), eastern Florida, Colombia, West Africa, and eastern Pacific waters of Costa Rica and Panama. Specimens from our own collecting efforts were obtained by vessel-deployed dredges, corers, and trawls in offshore waters or with suction (yabby) pumps in shallow subtidal or intertidal habitats. Most of this material was deposited in the

University of Louisiana at Lafayette Zoological Collections, Lafayette, USA (ULLZ). Additional specimens were obtained on loan from the Gulf Coast Research Laboratory, University of Southern Mississippi, Ocean Springs, USA (GCRL); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); and Naturalis—National Museum of Natural History, Leiden, Netherlands (RMNH), Muséum National d'Histoire Naturelle, Paris, France (MNHN), and Museum of Zoology of the University of São Paulo, São Paulo, Brazil (MZUSP). The syntypes of *A. floridanus* s.l. were loaned by the Museum of Comparative Zoology, Harvard University, Harvard, USA (MCZ). The holotype of *A. platycheirus* Boone, 1927 was made available by the Peabody Museum of Natural History, Yale University, New Haven, USA (YPM). Type material of the below described new species is deposited in USNM, ULLZ, and RMNH.

Drawings were made on a Wild M5 dissecting microscope with a camera lucida and Nikon inverted microscope with a drawing tube. Occasionally, chlorazole black staining was used to enhance contrast of some morphological features. Color photographs were made on a 35 mm digital Fuji FinePix camera with a 60 mm Nikon macrolens, using either clove-oil narcotized freshly collected animals or defrosted specimens that had been frozen shortly after collection. Carapace length (cl) was measured in millimeters (mm) from the tip of the rostrum to the posterior margin of the carapace and total length (tl) from the tip of the rostrum to the posterior margin of the telson; egg size was expressed as the mean of greatest and least dimensions. All measurements were determined ± 0.1 mm with a calibrated ocular micrometer or digital calipers.

Systematics

Family Alpheidae Rafinesque, 1815

Alpheus floridanus Kingsley, 1878

(Figures 1a–g, 3a–o, 4a–h, 5a–d)

Alpheus floridanus Kingsley 1878a: 193 (part, female syntype only).

Alpheus floridanus—Kingsley 1878b: 58; (?) Kingsley 1882: 123, plate II, fig. 8; Kingsley 1899: 717 (part); Lockington 1878: 468, 467 (part, Florida and Virgin Islands); Chace 1972: 65, fig. 17 a–e (part, Guadeloupe); Abele & Kim 1986: 199, 214–215, figs. i–k; Williams *et al.* 1989: front cover, 15, fig. 1; Karplus 1992: 275–290, fig. 1c; McLaughlin *et al.* 2005: 219, 542 fig. 1; Randall *et al.* 2005: 119–127, figs. 2–5, 7; Felder *et al.* 2009: 1057, 1091 (part, Atlantic coast of Florida).

Alpheus Floridanus—Coutière 1899: 29.

Type material. Florida: lectotype: 1 female, cl 7.5 mm (MCZ 4987), Dry Tortugas, channel north of Fort Jefferson, 16 m, Lt. W. H. Jacques.

Additional material. Florida: 1 male (ULLZ 3560), 1 ovig. female (ULLZ 5631), Ft. Pierce Inlet, sand bar with sea grass, yabby pump, 0–1 m, 21 July 1985, D. Felder and R. Manning; 1 ovig. female (ULLZ 5853), Ft. Pierce Inlet, North Inlet Park, 19 July 2002, D. Felder *et al.*; 1 male (ULLZ 5859), Ft. Pierce Inlet, South AIA Highway, mudflat, 25 March 1997, D. Felder; 1 female (ULLZ 6207), 1 male (ULLZ 6208), 1 female (ULLZ 6373), 1 ovig. female (ULLZ 6376), 3 males, 2 females (ULLZ 9581), 2 males, 1 female (ULLZ 10569), Ft. Pierce Inlet, South AIA Highway, sandy mud grassflat, 0–1 m, 25 July 2005, D. Felder *et al.*; 1 ovig. female (ULLZ 5852), Ft. Pierce Inlet, Coon Island Channel, 0–1 m, 30 July 2001, D. Felder *et al.*; 1 ovig. female (ULLZ 5856), Ft. Pierce Inlet, Little Jim Island, 0–1 m, 24 July 1995, D. Felder *et al.*; 1 male (ULLZ 5854), Ft. Pierce Inlet, 16 July 2004, D. Felder *et al.*; 1 male, 2 females (1 ovig.) (USNM 221845), Key Biscayne, West Side Flats, 28 May 1988, R. Lemaitre and R. Manning. Mexico (SW Gulf of Mexico): 1 male, (ULLZ 6203), Campeche Banks, 20°48.50'N, 92°20.35'W, stn NSF-II-043, dredge, R/V Pelican, mud, 55–54 m, 10 June 2005, D. Felder *et al.* Caribbean Sea: 1 ovig. female (ULLZ 11128), Belize, Carrie Bow Cay, 18–25 February 2009, D. Felder *et al.*; 1 ovig. female (ULLZ 12691), Panama, off Bocas Del Toro, dredge, 2004, R. Collin; 5 males, 3 ovig. females (USNM 135952), Guadeloupe, Pointe-à-Pitre, flats between Monroux and Rat Island, Smithsonian Bredin Expedition stn. 68–56, sandy mudflat, 30–31 March 1956, F. Chace and D. Nicholson. Brazil: 1 male (USNM 310856), Central American Expedition, stn. 1577, July–August 1972, A. Child *et al.*, 1 ovig. female (MZUSP 05322), Ponta de Pedra, PE, 30 August 1970, coll. P. Montouchet, det. Christoffersen 3 March 1983; 1 ovig. female (MZUSP 25380), Baja de Sepetiba, 22°55'66"S, 43°50'84"W, 05 September 1996, coll. Elaine F. Albuquerque., det. M. Tavares.

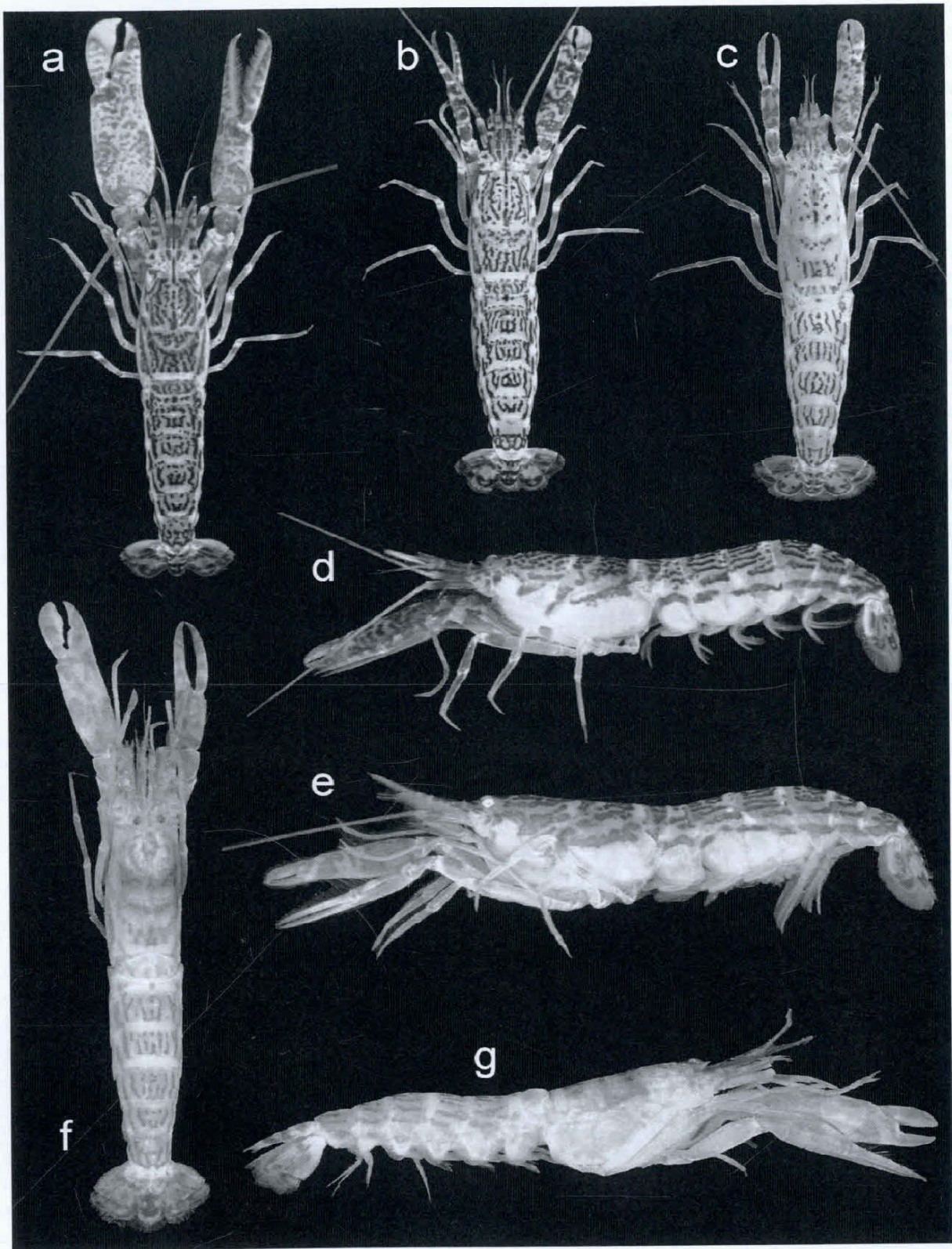


FIGURE 1. Color patterns in *Alpheus floridanus* Kingsley, 1878: a, dorsal view of male, cl 12.1 mm., Fort Pierce, Florida (ULLZ 10569A); b, dorsal view of ovigerous female, cl 12.4 mm, Fort Pierce, Florida (ULLZ 10569B); c, dorsal view of ovigerous female, cl 11.8 mm, Carrie Bow Cay, Belize (ULLZ 11128); d, lateral view of ovig. female, cl 10.3 mm, Fort Pierce, Florida (ULLZ 5631); e, lateral view of ovigerous female, cl 11.6 mm, Fort Pierce, Florida (ULLZ 6207); f, g, dorsal and lateral views of male, cl 11.0 mm, Campeche Banks, Mexico (ULLZ 6203).

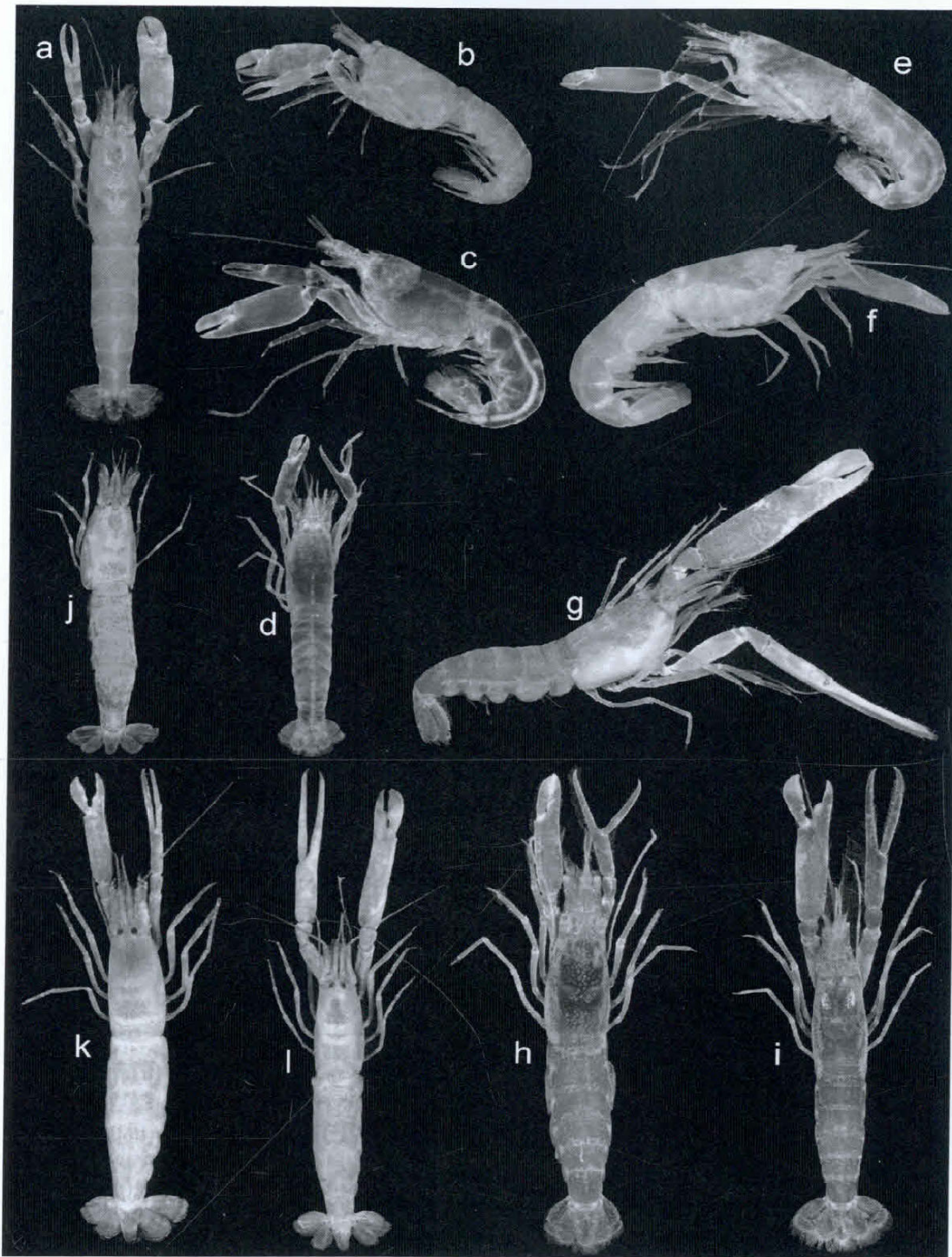


FIGURE 2. Color patterns of species allied to *Alpheus floridanus* Kingsley, 1878. *Alpheus roblesi* sp. nov.: a, b, dorsal and lateral views of male, cl 8.0 mm, Campeche Banks, Mexico (ULLZ 7197A); c, lateral view of ovigerous female, cl 7.5 mm, Campeche Banks, Mexico (ULLZ 7197B); d, dorsal view of female, cl 4.9 mm, Campeche Banks, Mexico (ULLZ 7440). *Alpheus ulalae* sp. nov.: e, f, lateral view of holotype ovigerous female, cl 7.5 mm, northeastern Gulf of Mexico (USNM 1265092 = tissue/sequence ULLZ 6815). *Alpheus hephaestus* sp. nov.: g, lateral view of male, cl 9.1 mm, Pacific coast of Costa Rica (ULLZ 6204); h, dorsal view of male, cl 7.1 mm, Pacific coast of Panama (ULLZ 8004); i, dorsal view of male, cl 8.9 mm, Pacific coast of Panama (ULLZ 9508A). *Alpheus platycheirus* Boone, 1927: j, dorsal view of damaged female, cl 7.9 mm, northern Gulf of Mexico (ULLZ 6421); k, dorsal view of ovigerous female, cl 9.0 mm, northern Gulf of Mexico (ULLZ 5858); l, dorsal view of male, cl 9.8 mm, northern Gulf of Mexico (ULLZ 5952).

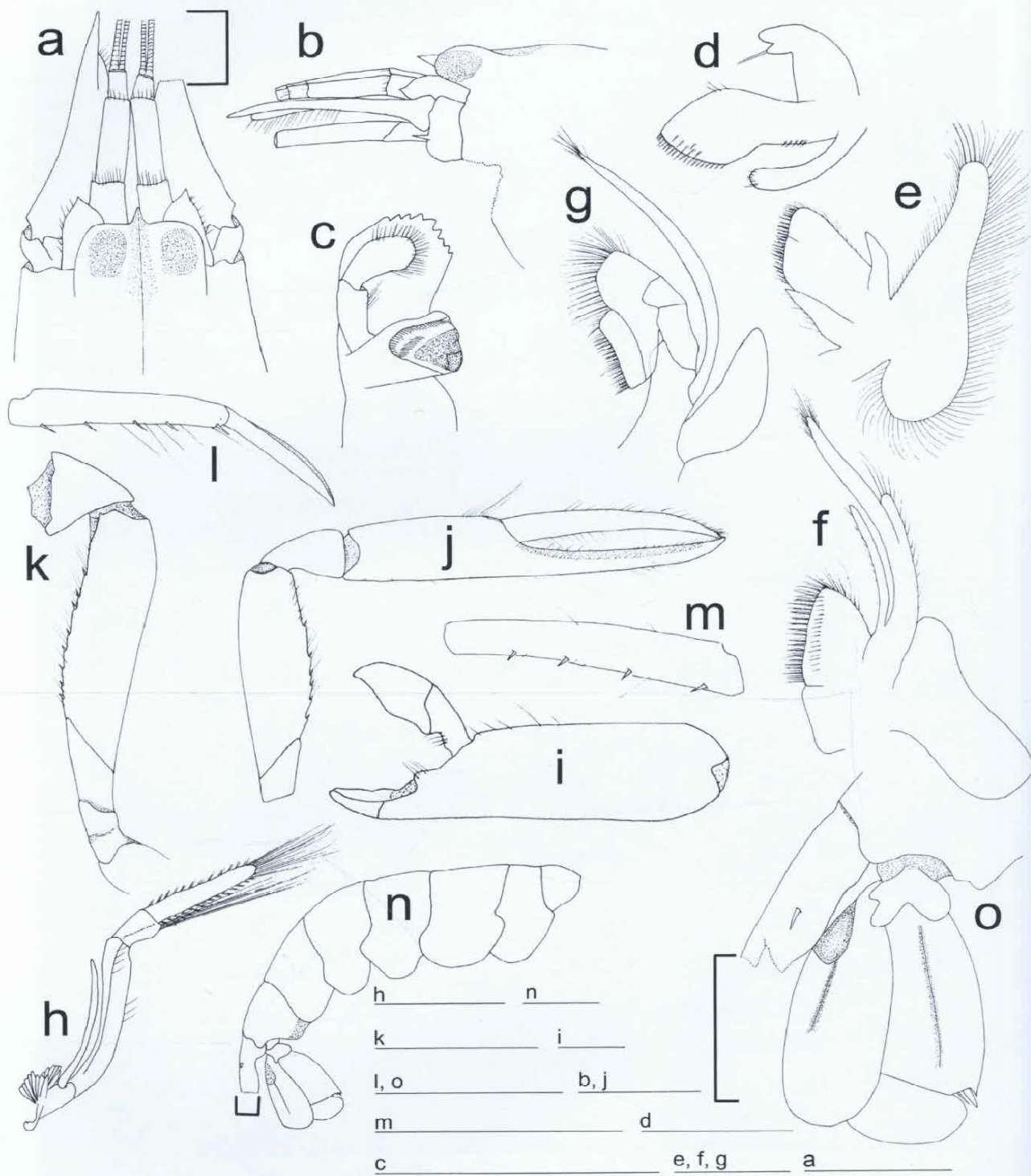


FIGURE 3. *Alpheus floridamus* Kingsley, 1878: a–o, lectotype female (MCZ 4987): a, anterior carapace, dorsal (right antennal scale broken); b, anterior carapace, left lateral view; c, left mandible, mesial; d, left maxillule, lateral; e, left second maxilla, lateral; f, left first maxilliped, lateral; g, left second maxilliped, lateral; h, right third maxilliped, lateral; i, right major chela, dactylus and propodus, lateral; j, left minor cheliped, ishium, merus, carpus, propodus, and dactylus, mesial; k, right major cheliped, coxa, basis, ishium, merus, and carpus, mesial; l, right third pereopod, lateral; m, left fourth pereopod, lateral; n, abdomen, telson (broken) and uropods, lateral; o, telson and uropods, lateral. Scale bars = 1.0 mm (d–g), 2.0 mm (a–c, h–o).

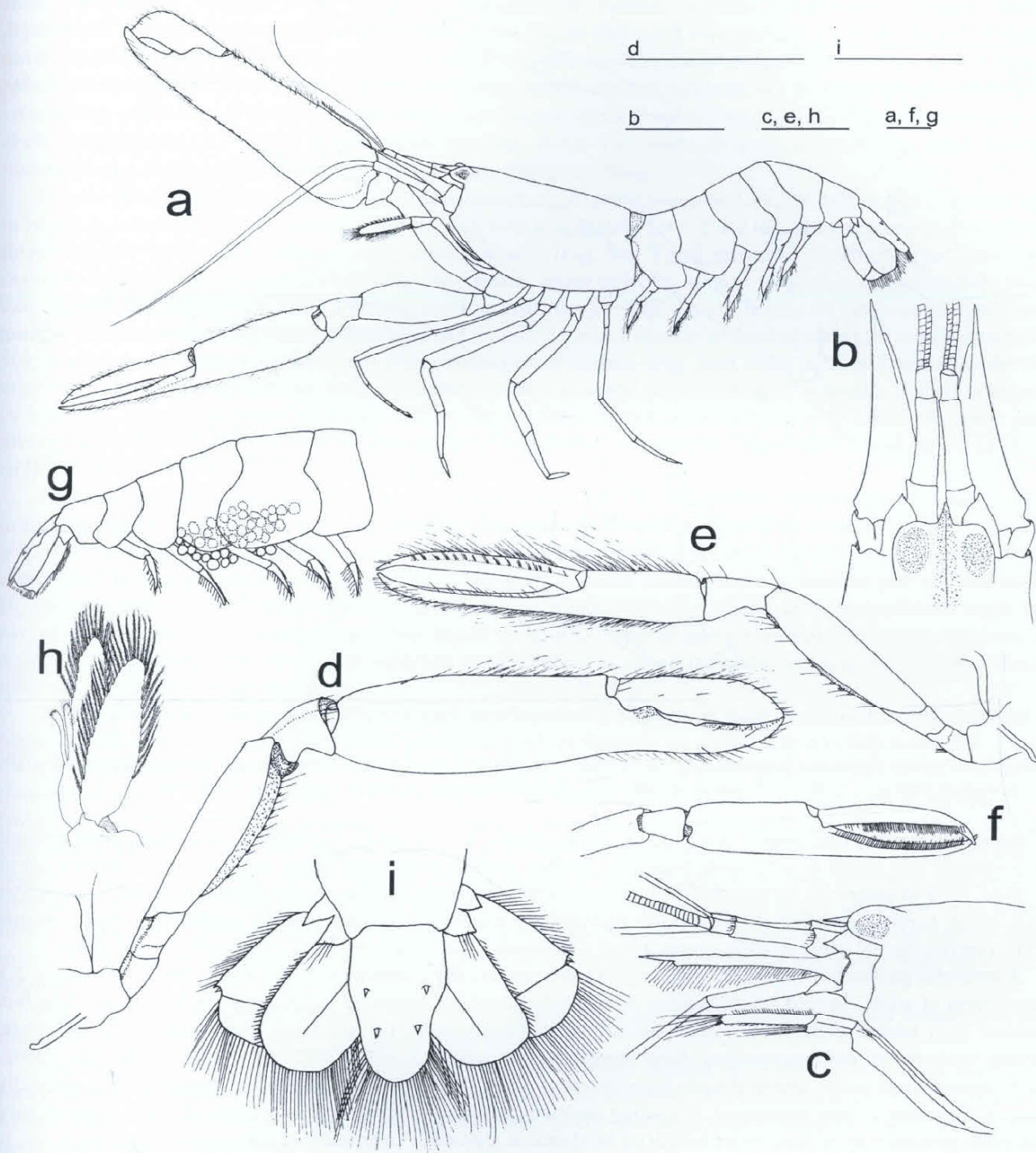


FIGURE 4. *Alpheus floridanus* Kingsley, 1878: a, h, f, male (ULLZ 6208); b–e, g, ovigerous female (ULLZ 6207); i, male (ULLZ 3560): a, habitus, lateral; b, anterior carapace, dorsal; c, anterior carapace, left lateral; d, right major cheliped, lateral; e, left minor cheliped, lateral; f, left minor cheliped, merus, carpus, propodus, and dactylus, mesial (balaeniceps setae illustrated); g, abdomen, pleopods, eggs, telson, and uropods, lateral; h, right second pleopod, appendix interna and appendix masculine; i, sixth abdominal somite, telson, and uropods, dorsal. Scale bars = 2.0 mm.

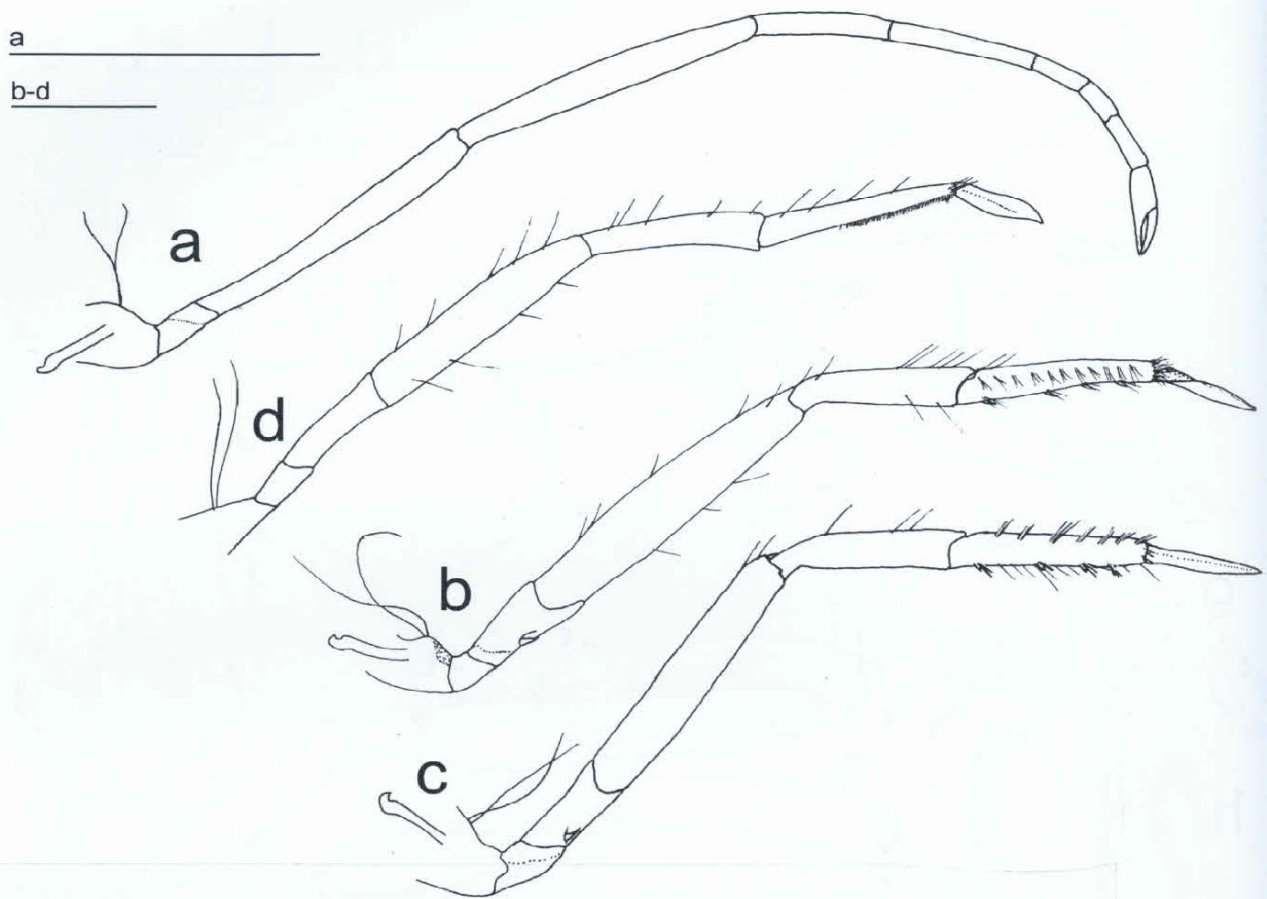


FIGURE 5. *Alpheus floridanus* Kingsley, 1878: a–d, ovigerous female (ULLZ 6207): a, right second pereopod, lateral; b, right third pereopod, lateral; c, right fourth pereopod, lateral; d, right fifth pereopod, lateral. Scale bars = 2.0 mm.

Emended description (based on lectotype unless otherwise indicated). Carapace with narrow, acute rostrum not exceeding first article of antennular peduncle, shallow median postrostral carina extending onto anterior 1/4 of carapace, flanked anteriorly by adrostral furrows reaching posteriorly to base of eyes (Figs. 3a, b; 4a, b, c); orbital hoods ovate, barely exceeding eye, unarmed; anterolateral margin of carapace weakly swollen adjacent to orbital hoods; pterygostomial angle slightly rounded (left side damaged in lectotype) (Fig. 4 c); cardiac notch deep.

Antennular peduncle first article with large ventromesial carina ending in acute tooth; first article about 2.7 times length of width, second article similar, third article about 1.4 length of width (Figs. 3a, b); mesial flagellum narrower than lateral, distal 1/2 of lateral bearing aesthetascs (broken in lectotype) stylocerite broad, lamellate, tapering to sharp tip, not overreaching distal margin of first article. Antenna with stout basicerite bearing strong, sharp, ventrolateral tooth; antennal scale (scaphocerite) (right broken in lectotype) long, lateral margin distinctly concave, distolateral spine prominent, extending distinctly beyond rounded anterior margin of blade, overreaching antennular peduncle by at least twice length of third article, distinctly overreaching carpocerite (Figs. 3a, b; 4a, b, c).

Mandible incisor process with 9 well-developed teeth distributed along full width of cutting edge, central tooth enlarged (Fig. 3c); molar process rounded, blunt; palp two-segmented Maxillule, maxilla, first and second maxilliped typical for genus (3d–g). Third maxilliped exopod long, slender, setose, not extending beyond antepenultimate article of endopod (Fig. 3h); endopod terminal article flattened, spatulate, heavily covered in thick setae; penultimate article broadening distally, bearing tuft of lengthy setae extending from ventrodiscal lip; antepenultimate article quadrate, sparsely setose.

First pereopods (chelopeds) unequal in size and shape (Figs. 3i, j, k; 4a, d, e, f); major cheliped (broken between carpus and propodus in lectotype) ischium short; merus subrectangular, ventral surface flattened, eight

movable spines and fringe of setae along ventromesial margin; carpus cup-shaped, small subacute tooth protruding from ventromesial margin; major chela subrectangular in outline, laterally compressed, elongate, lacking depressions or grooves, margins sparsely setose, chela length about 3.9 times height, propodus length about 2.9 times length of dactylus, mesial and lateral surface of palm smooth; dactylus sparsely setose, rounded distally. Minor cheliped ischium short; merus subrectangular, ventral surface flattened, six movable spines and fringe of setae along ventromesial margin; carpus stout, cup-shaped; chela slender, long, lacking depressions or grooves, chela length about 5.7 times height, palm smooth, about 1.6 times as long as dactylus, linea impressa inconspicuous, fingers with long marginal setae, tips slightly crossing.

Second pereopod (missing on both sides in lectotype, description based on ULLZ 6207) slender, ischium equal in length to merus; carpus composed of five articles with length ratio 1:1:1:2.3:2 (distal to proximal); chela simple, fingers slightly longer than palm, sparsely setose distally (Fig. 5a). Third pereopod robust, ischium armed with movable spine on ventrolateral surface (Fig. 5b); merus about twice as long as carpus; propodus slightly longer than carpus, five robust movable spines on ventrolateral margin (Fig. 3l) and fringe of setae along distoventral margin; dactylus simple, spatulate, slightly curved. Fourth pereopod similar to third, shorter and more slender (Fig. 5c); propodus with four movable spines along ventrolateral surface (Fig. 3m). Fifth pereopod more slender than third and fourth (Fig. 5d); ischium lacking movable spine; merus and carpus subequal in length; propodus (missing in lectotype, description based on ULLZ 6207) with tufts of thick setae and fringe of comb-like setae along distoventral surface, lacking movable spines; dactylus (missing in lectotype, description based on ULLZ 6207) simple, curved, subtriangular, narrowing to acute tip.

First to fourth abdominal somites in males (based on ULLZ 6208) with posterolateral angle of pleura rounded to weakly angular (Fig. 4a). Male second pleopod with appendix masculina slightly overreaching appendix interna (Fig. 4h). Telson (broken in lectotype (Fig. 3o), description based mainly on ULLZ 3560) slightly tapering, length about twice as long as wide (measured medially); two pairs of dorsal movable spines, anterior pair inserted near 3/10, posterior pair near 6/10 length of telson; posterolateral margin broadly rounded, each posterolateral angle with two small movable spines, mesial larger than lateral (Fig. 4i). Uropodal exopod subequal in length to telson and endopod, lateral margin produced with subacute tooth adjacent to strong movable lateral spine; endopod broadly subovate, subequal in length to telson.

Gill formula typical for genus, including well-developed arthrobranch on third maxilliped, mastigobranchs on coxae of third maxilliped and first to fourth pereopods, and setobranchs on coxae of first to fifth pereopod.

Color pattern (Fig. 1a–h). Abdominal somites strikingly marked by short longitudinal bars of interconnecting chromatophores of varied olive green, brown, maroon, or orange pigmentation; gastric region of carapace with broken median stripe of similar pigment framed one to several pairs of crescents of short diagonal bars to either side; chelae heavily mottled with patches of similar color often arranged into ill-defined “banks” on palm; meri of pereopods 3–5 typically with distal band of reddish-orange to maroon framed by pale yellow to yellow-green proximally and distally; carpi and propodi commonly diffuse pale yellow to yellow green, sometimes with weaker darker bands; overall greenish background color of specimens from shallow grassbeds ranges to lighter chalky colors overlain by orange to pale brown patterns in specimens from calcareous sands and muds; fresh eggs pale to bright yellow.

Size. The largest examined male at cl 11.0 mm, tl 29.0 mm (ULLZ 6203); largest examined female at cl 15.0 mm, tl 40.0 mm (USNM 221845); egg diameter 0.4–0.7 mm.

Habitat. Most specimens were collected with a hand-operated suction or “yabby” pump from burrows in muddy sand of intertidal and shallow subtidal seagrass beds; the lectotype was collected at 16 m depth, while the deepest record of *A. floridanus* based on the present material is a specimen from Campeche Banks dredged from muddy bottom at 55–54 m depth.

Distribution. Western Atlantic: from southeastern (Atlantic) coast of Florida (off Ft. Pierce) to southwestern Gulf of Mexico (off Yucatan Peninsula, Campeche Banks), Brazil, and Caribbean Sea.

Type locality. Eastern Gulf of Mexico, Dry Tortugas, channel north of Fort Jefferson.

Remarks. In addition to its unique and distinctive color pattern, *Alpheus floridanus* can be distinguished from *A. hephaestus* sp. nov., *A. platycheirus*, and *A. floridanus africanus* by the longer antennal scale (distinctly overreaching the third article of the antennular peduncle vs. not or barely overreaching the third article of the antennular peduncle, see taxonomic key), and from *A. roblei* sp. nov. by the shape of the antennal scale (not distinctly sinuous vs. sinuous). Morphologically, *A. floridanus* is most similar to *A. ulalae* sp. nov., but the former species has more numerous and conspicuous movable spines on the propodus of the third and fourth pereopods.

Additional differences between present materials of *A. floridanus* and *A. ulalae* can be seen in the shape of the incisor process on the mandible (Table 1).

After examination of Chace's (1972: fig. 17a–e) material from Guadeloupe we conclude that these specimens represent *A. floridanus*. The length of the antennal scale distinctly exceeds the third article of the antennular peduncle, the propodus of the third pereopod bears multiple large movable spines on the ventrolateral surface, and finally, the dentition of the mandibular incisor process is typical of *A. floridanus*. Other records of *A. floridanus* (Holthuis 1951; Shinn 1968; Zimmer 1913), were published with limited descriptions, illustrations, and no catalog numbers thus making a more precise analysis of those materials impossible.

***Alpheus roblesi* sp. nov.**

(Figures 2a–d; 6a–h, 7a–g, 8a–f)

Alpheus floridanus—Chace 1972: 65, fig. 18a–e (Antigua Island) [not *A. floridanus* Kingsley, 1878].

Alpheus floridanus floridanus—Crosnier and Forest 1966: 267–268, fig. 20 a (part, Gabon)

Type material. Mexico (SW Gulf of Mexico). **Holotype:** male, cl 5.0 mm (USNM 1265091 = tissue ULLZ 9141), Campeche Banks, 20°39.66'N, 91°57.09'W, stn. NSF-II-052, box dredge, R/V Pelican, mud, 33–29 m, 11 June 2005, D. Felder *et al.* **Paratypes:** 1 male, cl 7.8 mm (ULLZ 7197A), 1 ovig. female, cl 7.5 mm (ULLZ 7197B), 1 female, cl 8.0 mm (ULLZ 7197C), Campeche Banks, 20°39.66'N, 91°57.09'W, stn. NSF-II-052, box dredge, R/V Pelican, mud, 33–29 m, 11 June 2005, D. Felder *et al.*; 1 ovig. female, cl 8.0 mm (ULLZ 6623), 21°33.97'N, 91°04.75'W, stn. NSF-II-057, box dredge, R/V Pelican, muddy sand and rubble, 32–33 m, 12 June 2005, D. Felder *et al.*

Additional material. **Florida:** 1 juvenile (ULLZ 12208), Ft. Pierce Inlet, South AIA Causeway Flat, mudflat, 21 July 2010, D. Felder *et al.*; 1 juvenile (ULLZ 12202), Ft. Pierce Inlet, South AIA Causeway Flat, mudflat, yabby pump, 20 July 2010, D. Felder *et al.* **SW Gulf of Mexico:** 1 male (ULLZ 6991), 21°34.18'N, 91°04.71'W, stn. NSF-II-060, box dredge, R/V Pelican, mud, 33 m, 11 June 2005, D. Felder *et al.*; 1 female (ULLZ 7440), 21°34.18'N, 91°04.71'W, stn. NSF-II-060, box dredge, R/V Pelican, mud, 33 m, 11 June 2005, D. Felder *et al.*; 1 ovig. female (ULLZ 6549), 22°05.87'N, 91°22.96'W, stn. NSF-II-086, box dredge, R/V Pelican, mud, 41–42 m, 15 June 2005, D. Felder *et al.*; 1 female (ULLZ 9142), 20°39.66'N, 91°57.09'W, stn. NSF-II-052, box dredge, R/V Pelican, mud, 29–33 m, 11 June 2005, D. Felder *et al.*; 1 female (ULLZ 7471), 21°36.44'N, 91°04.06'W, stn. NSF-II-084, box dredge, R/V Pelican, rubble, 30–20 m, 15 June 2005, D. Felder *et al.* **Caribbean Sea:** 1 male (USNM 135953), Antigua, English Harbor, Tank Bay, Smithsonian-Bredin Expedition, stn. 74–56, 3 April 1956; 1 ovig. female (USNM 135954), Antigua, English Harbor, Freemans Bay, Smithsonian-Bredin Expedition, stn. 79–58, seagrass patch, 19 April 1958; 1 male (MNHN-IU-2013-12176), Guadeloupe, 16°22.57'N, 61°31.74'W, stn. GS19, Expedition: Karubenthos 2012, bouée PCA, 8 m, 15 May 2012; 1 female (MNHN-IU-2013-12174), Guadeloupe, 16°08.07'N, 61°46.71'W, stn. GS12, Expedition: Karubenthos 2012, Baie de Bouillante, 6 m, 10 May 2012; 1 female (MNHN-IU-2013-16134), Guadeloupe, 16°27.34'N, 61°32.07'W, stn. GS20, Expedition: Karubenthos 2012, entrée Grotte aux Barracudas (Port-Louis), 19 m, 16 May 2012. **Eastern Atlantic:** 1 ovig. female (IU-2013-13191), Africa, Gabon, Port Gentil, 0°42'S, 08°47'E, Expedition Calypso, stn. DC58, 10 m, coll. Marche-Marchad 16 June 1956, det. J. Forest.

Description (based on holotype unless otherwise indicated). Carapace with narrow, acute rostrum not exceeding first article of antennular peduncle, shallow median postrostral carina extending onto carapace midlength, flanked anteriorly by adrostral furrows reaching posteriorly to base of eyes (Fig. 6a, b, c); ocular hoods ovate, barely extending beyond eye, unarmed; anterolateral margin of carapace not weakly swollen adjacent to ocular hoods; pterygostomial angle distinct, rounded; cardiac notch deep.

Antennular peduncle first article with large ventromesial carina ending in acute tooth, first article about 2.5 times length of width, second article 2.7 length of width, third article about 1.6 length of width (Fig. 6a, b, c); mesial flagellum narrower than lateral, distal ½ of lateral bearing aesthetascs; stylocerite broad, lamellate, tapering into sharp tip, not over-reaching distal margin of first article. Antenna with stout basicerite bearing strong, sharp, ventrolateral tooth; antennal scale (scaphocerite) broad, lateral margin sinuous, distolateral spine prominent, extending distinctly beyond rounded anterior margin of blade, overreaching antennular peduncle by 1.7 times length of third article, barely overreaching carapacerite (6a, b).

TABLE 1. Comparison of morphological characters among members of the *Alpheus floridanus* Kingsley, 1878 complex treated in this study. * Chace (1972) and Crosnier and Forest (1966) noted the presence of 3 movable spines on P3 in *A. floridanus africanus*, while we never observed more than 2 spines on the P3 propodus in the RMNH material; Crosnier and Forest (1966) noted the absence of spines on the P4 propodus in their material of *A. floridanus africanus* (rare occasions 1-2 spines present), while we consistently observed 1 or 2. Abbreviations used: P = pereopod, AP = antennular peduncle.

Character	<i>A. floridanus</i> Kingsley, 1878	<i>A. hephaestus</i> sp. nov.	<i>A. platycheirus</i> Boone, 1927	<i>A. roblesi</i> sp. nov.	<i>A. floridanus</i> <i>africanus</i> Balss, 1916	<i>A. ulatae</i> sp. nov.	<i>Alpheus</i> sp. cf. <i>platycheirus</i>
1. Color pattern	strong pattern of brown, maroon or orange longitudinal bars on abdominal somites	strong pattern of interconnected rust to dark red chromatophores and patches on abdominal somites, especially on 6th	pattern of ill-defined rose, orange, or rust bars and diffuse patches on abdominal somites, and especially uropodal endopods	diffuse dorsal patch of small reddish orange to rust chromatophores on each translucent abdominal somite	Unknown	diffuse dorsal patch of rose red to reddish orange small chromatophores on each translucent abdominal somite	Unknown
2. P5, ventromesial propodal spines	None	None	None	Yes, 1-3, large, rarely lacking	None	None	(P5 missing)
3. P3, ventrolateral propodal spines	3-5, large	3-4	2-5	5-6, large	1-3*, small, proximal 1/2	1-2, proximal 1/2	3
4. P4, ventrolateral propodal spines	3-5, large	3-4	1-4	4-6, large	0-2*, small, proximal 1/2	1-2, proximal 1/2	3
5. Incisor process of mandible, dentition	Teeth developed across entire margin	Teeth well-developed across 1/2, blunt across 1/2	Teeth well-developed across 1/2, blunt across 1/2	Teeth well-developed across entire margin	Teeth well-developed across 1/2, blunt across 1/2	Teeth well-developed across 1/2, blunt across 1/2	Teeth well-developed across 1/2, blunt across 1/2
6. Length of antennal scale	Distinctly over-reaching 3 rd article of AP	Barely over-reaching or subequal to 3 rd article of AP	Barely over-reaching or subequal to 3 rd article of AP	Subequal to or generally over-reaching 3 rd article of AP	Barely over-reaching or subequal to 3 rd article of AP	Distinctly over-reaching 3 rd article of AP	Barely over-reaching 3 rd article of AP
7. Lateral margin of antennal scale	Slight to distinct concave	Straight to slight concave	Straight to slight concave	Simuous	Straight to slight concave	Slight to distinct concave	Slight concave
8. Adrostral furrows	Shallow to deep	Usually deep	Shallow to deep	Shallow to deep	Deep	Deep	Deep
9. Carapace, dorsal carina	Shallow, extending to mid-length	Generally sharp, extending to mid-length	Shallow or Sharp, extending to posterior 1/2 or 3/4	Generally shallow, extending to mid-length	Sharp, extending to mid-length	Shallow, extending to posterior 1/4	Sharp, extending to mid-length

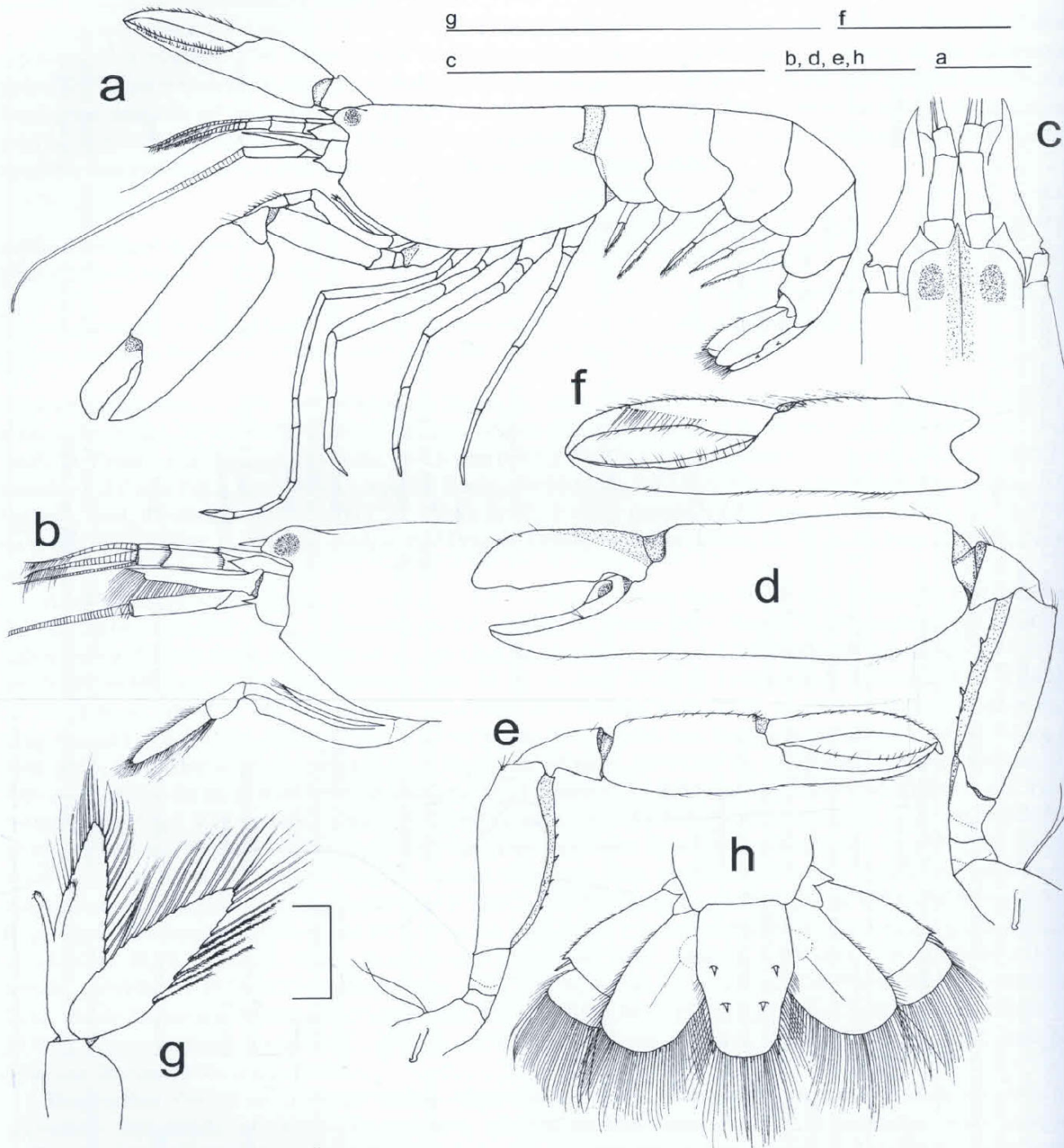


FIGURE 6. *Alpheus roblei* sp. nov.: a–g, holotype male (USNM 1265091 = tissue ULLZ 9141); h, paratype ovigerous female (ULLZ 7197B): a, habitus, lateral; b, anterior carapace, left side, lateral; c, anterior carapace, dorsal; d, left major cheliped, lateral; e, right minor cheliped, lateral; f, right minor cheliped, propodus and dactylus, mesial (balaeniceps setae shown); g, right second pleopod, appendix interna and appendix masculina (serrated setae shown only in bracket); h, sixth abdominal somite, telson and uropods, dorsal. Scale bars = 2.0 mm.

Mandible incisor process with eight teeth distributed along full width of cutting edge, central teeth enlarged (Fig. 7a); molar process rounded, blunt; palp two-segmented. Maxillule, maxilla, first and second maxilliped typical for genus (Figs. 7b–e). Third maxilliped exopod slender, setose, not extending beyond antepenultimate

article of endopod (Fig. 7f); endopod terminal article flattened, spatulate, mesial surface and periphery bearing tufts of thick setae (Fig. 7g), penultimate article subrectangular, broadening distally, bearing fringe of long setae extending from ventrodistal lip, antepenultimate article quadrate, sparsely setose.

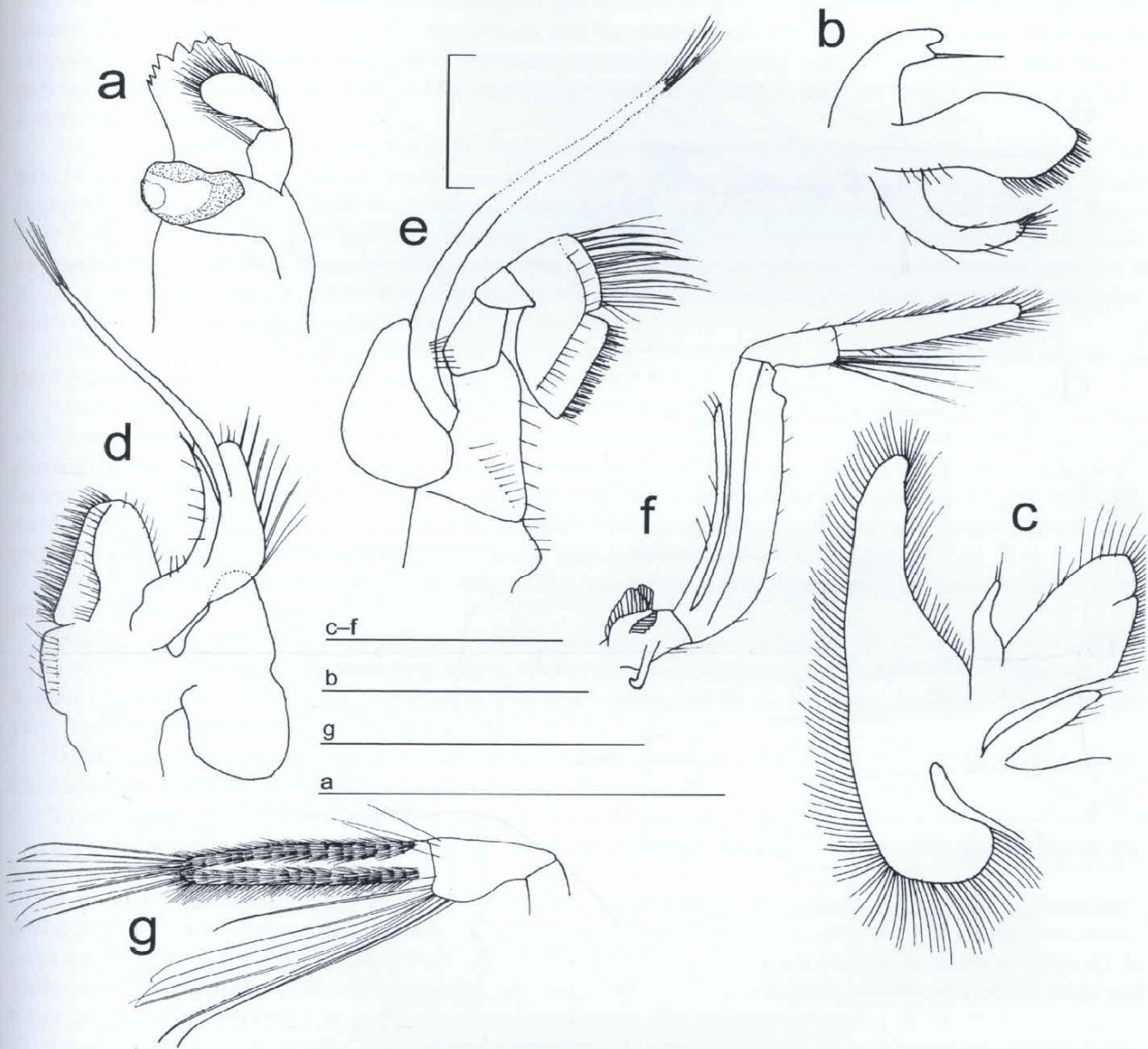


FIGURE 7. *Alpheus roblei* sp. nov.: a–g, holotype male (USNM 1265091 = tissue ULLZ 9141): a, right mandible, mesial; b, right maxillule, lateral; c, right second maxilla, lateral; d, left first maxilliped, lateral; e, right second maxilliped (exopod broken), lateral; f, right third maxilliped, lateral; g, right third maxilliped, terminal and penultimate article, mesial. Scale bars = 1.0 mm (b–e), 2.0 mm (a, f, g).

First pereopods (chelipeds) unequal in size and shape (Fig. 6a, d–f); major cheliped ischium short; merus subrectangular, ventral surface flattened, with three large and one small movable spines along ventromesial margin (others may have broken off; five in paratype ULLZ 7197B); carpus cup-shaped, lacking subacute tooth protruding from ventromesial margin (present as small tubercle in some paratypes); major chela laterally compressed, subcylindrical in lateral view, lacking depressions or grooves, margins sparsely setose, chela length about 3.4 times height (2.9 times in paratype ULLZ 7197B), propodus length about 2.8 times dactylus length (also 2.8 times in paratype ULLZ 7197B), mesial and lateral surface of palm smooth; dactylus lacking obvious setae, rounded

distally. Minor cheliped ischium short; merus subrectangular, ventral surface flattened, six movable spines along ventromesial margin (seven in paratype ULLZ 7197C); carpus stout, cup-shaped; chela slender (weakly balaniceps in holotype and some paratype males), long, lacking depressions or grooves, chela length about 4.8 times height (4 times in paratype ULLZ 7197C), palm smooth, about 2 times as long as dactylus (1.7 times in paratype ULLZ 7197C), linea impressa evident, fingers sparsely setose along margins, tips slightly crossing.

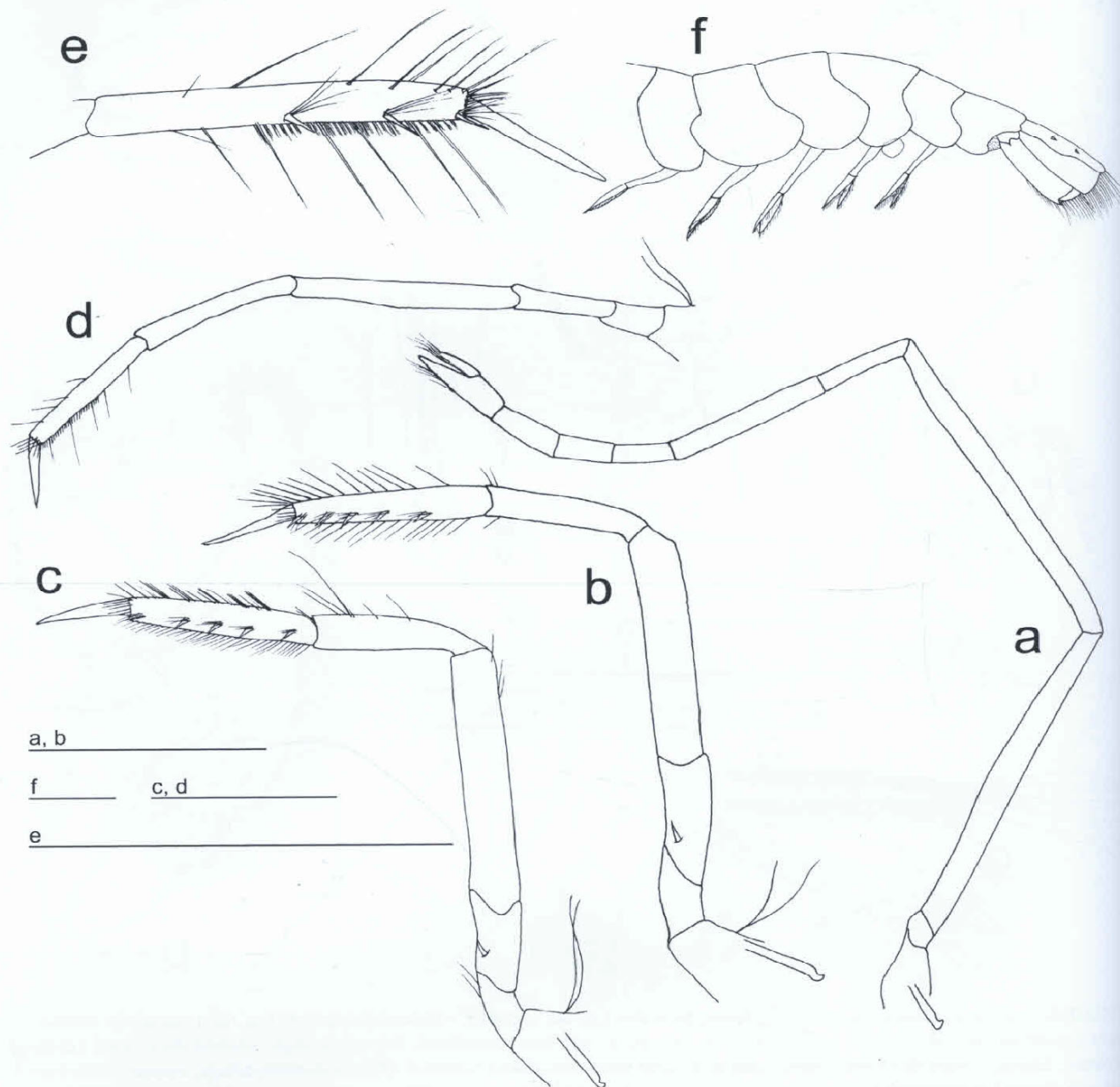


FIGURE 8. *Alpheus roblesi* sp. nov.: a–e, holotype male (USNM 1265091 = tissue ULLZ 9141); f, paratype ovigerous female (ULLZ 7197B): a, left second pereopod, lateral; b, left third pereopod, lateral; c, left fourth pereopod, lateral; d, left fifth pereopod, lateral; e, left fifth pereopod, propodus and dactylus, mesial; f, abdomen, telson, uropods, pleopods, and egg, lateral. Scale bars = 2.0 mm.

Second pereopod slender (Fig. 8 a), much longer than pereopods 3–5, ischium equal in length to merus; carpus composed of five articles with length ratio 1:1:1:3.7:2 (distal to proximal); chela simple, fingers slightly longer than palm, sparsely setose distally. Third pereopod robust (Fig. 8b), ischium armed with movable spine on

ventrolateral surface; merus about 1.8 times as long as carpus; propodus slightly longer than carpus, five conspicuously large movable spines along ventrolateral surface (six in paratype ULLZ 7197C, five in paratype 7197B), thick setae along entire superior and ventral margins, fringe along distal superior and ventral margin; dactylus simple, falciform. Fourth pereopod similar to third, shorter, more slender (Fig. 8c), propodus with five large movable spines (five in paratypes ULLZ 7197C and 7197B) along ventrolateral surface. Fifth pereopod more slender than third and fourth (Fig. 8d, e); ischium lacking movable spine; merus slightly longer than carpus; propodus with tufts of thick setae, three conspicuous movable spines along ventromesial surface (also three in paratype ULLZ 7197B), fringe of comb-like setae along distal mesial surface; dactylus simple, curved, triangular, narrowing to acute tip.

First to fourth abdominal somites in male with posterolateral angle of pleura rounded to weakly angular (Fig. 6a). Male second pleopod with appendix masculina slightly over-reaching appendix interna (Fig. 6g). Telson slightly tapering (Fig. 6h), length about twice as long as width (medially); two pairs of dorsal movable spines, anterior pair inserted near 4/10, posterior pair near 6/10 length of telson; posterolateral margin broadly rounded; each posterolateral angle with two small movable spines, mesial larger than lateral. Uropodal exopod subequal in length to telson and endopod, lateral margin produced with subacute tooth adjacent to strong movable lateral spine; endopod broadly subovate, subequal in length to telson (6h).

Gill formula typical for genus, including arthrobranch on third maxilliped, mastigobranch epipod on coxa of third maxilliped to fourth pereopod, setobranch on coxa of first to fifth pereopod.

Color pattern (Fig. 2a–d). Body translucent with orange and yellow chromatophores, especially on first chelipeds; abdominal somites marked dorsally by broad diffuse bands of small reddish orange to rust brown chromatophores, loosely scattered laterally, inconspicuous in translucent live specimens; carapace anterior margin lateral to orbital hoods marked by distinct vertical slash of reddish orange; chelae with palm and fingers irregularly banded by orange to rust brown; pereopods 3–5 each with weak orange band just beyond mid-length of meri and on proximal propodus, otherwise translucent pale yellow; eggs bright yellow.

Size. Largest examined male at cl 10.0 mm, tl 26.0 mm (USNM 135953); largest examined female at cl 8.0 mm, tl 22.0 mm.

Habitat. Most specimens were collected with vessel-deployed box dredges in 20–42 m depth on muddy or sandy bottoms, sometimes with calcareous rubble. However, some specimens were collected in less than 0.7 m (2 feet) of water (Chace 1972), while our material from southeastern Florida includes two juveniles collected with a yabby pump on a muddy-sandy intertidal grass flat.

Distribution. Western Atlantic: southeastern Florida, southern and southwestern Gulf of Mexico and eastern Caribbean Sea (Antigua, Guadeloupe); Eastern Atlantic: Gabon, Africa.

Type locality. Southwestern Gulf of Mexico, off Yucatan Peninsula, Campeche.

Etymology. This patronym honors our close friend and colleague, Dr. Rafael Robles, who assisted in this and many other studies of decapod phylogenetics.

Remarks. The sinuous shape of the antennal scale lateral margin, translucent color, and the presence of movable spines on the ventromesial surface of the propodus of the fifth pereopod (absent in one juvenile examined) serve to distinguish *A. roblesi* sp. nov. from all other species of the *A. floridanus* complex (see also Table 1). In addition, adult specimens of *A. roblesi* sp. nov. are characterized by the relatively smaller size of the body and major chela when compared to all other other members of the *A. floridanus* complex.

Chace's (1972) material from Antigua was assigned to *A. roblesi* (fig. 18a–e) as it represents all diagnostic features of this species. However, Hendrix's (1971) material from Florida identified as *A. floridanus* may contain representatives of both *A. floridanus* and *A. roblesi* sp. nov. Hendrix described a "row of 4 slender spines" on the propodus of the fifth pereopod, which is an important characteristic feature of *A. roblesi* sp. nov. However, Hendrix's description of the color pattern matches *A. floridanus* and not *A. roblesi* sp. nov.

Morphological evidence suggests that the distribution of *A. roblesi* sp. nov. extends into the eastern Atlantic. Crosnier and Forest (1966) reported two subspecies of *A. floridanus* from western Africa, as *A. floridanus floridanus* and *A. floridanus africanus*. Their illustrations clearly show morphological features of *A. roblesi* sp. nov. for the *A. floridanus floridanus* variant (sinuous antennal scale margin, smaller chelae, large movable spines on the third pereopod). We examined Crosnier and Forest's material of *A. floridanus floridanus* from Gabon, Africa (MNHN-IU-2013-13191) and concluded it clearly falls within the limits of *A. roblesi* sp. nov. (sinuous scaphocerite and presence of at least 1 spine on propodus of the 5th pereopod), suggesting this species has a trans-Atlantic distribution. From the limited African material available to us for examination we have been able to

identify at least two morphotypes in the eastern Atlantic, which exhibits morphological features of *A. roblei* sp. nov. and *A. floridamus africanus* (see discussion).

It is possible (if not probable) that *A. roblei* has been taken previously at varied localities within the western Atlantic (White 1982) and more specifically the type locality, Campeche (Hernandez Aguilera *et al.* 1996; Roman-Contreras 1988), but materials on which those reports are based must be reexamined to confirm which member or members of the complex are represented.

***Alpheus ulalae* sp. nov.**

(Figures 2e, f; 9a–g; 10a–f; 11a–f)

Type material. NE Gulf of Mexico off Florida. **Holotype:** ovig. female, cl 7.5 mm (USNM 1265092 = tissue/sequence ULLZ 6815), 28°10.01'N, 84°94'W, stn. NSF-III-054, box dredge, R/V Pelican, sandy mud, 41.4–41.7 m, 19 July 2006, D. Felder *et al.* **Paratype:** 1 male, cl 11.0 mm (USNM 273137, specimen A of lot), 26°45.52'N, 83°21.26'W, trawl, Continental Shelf Associates, 50.2 m, 2 May 1981, P. McLaughlin.

Additional material. NE Gulf of Mexico off Florida: 3 males, 1 female (USNM 273137, specimen B–E of lot), same collection data as paratype; Caribbean Sea: 1 female (MNHN-IU-2013-12135), Guadeloupe, 16°22.57'N, 61°34.12'W, stn. GD02, Expedition: Karubenthos 2012, 80 m, 04 May 2012.

Description (based on holotype unless otherwise indicated). Carapace with narrow, acute rostrum not exceeding first article of antennular peduncle, median postrostral carina extending onto carapace midlength, flanked anteriorly by adrostral furrows reaching posteriorly to base of eyes (Fig. 9a–c); front projecting fully over eyes, ocular hood ovate, extending well beyond eye, unarmed; anterolateral margin of carapace weakly swollen adjacent to orbital hoods; pterygostomial angle distinct, rounded; cardiac notch deep.

Antennular peduncle (left side broken) first article with large ventromesial carina ending in acute tooth, first article about 3.2 times length of width, second article about 4.9 times length of width, third article about 1.9 length of width (Fig. 9b, c); mesial flagellum narrower than lateral (broken); distal ½ of lateral bearing aesthetascs; stylocerite broad, tapering into sharp tip, not over-reaching distal margin of first article. Antenna with stout basicerite bearing strong, sharp, ventrolateral tooth (Fig. 9b, c); antennal scale (scaphocerite) long, lateral margin distinctly concave, distolateral spine prominent, extending distinctly beyond rounded anterior margin of blade, over-reaching antennular peduncle by at least twice length of third article (2.7 in holotype, USNM 1265092 = tissue/sequence ULLZ 6815), distinctly overreaching carapocerite (9a, b, c).

Mandible (left) incisor process with five well-developed teeth, two enlarged, mostly confined to inferior half of cutting edge, superior margin dentition poorly defined (Fig. 10a); molar process rounded, blunt; palp two-segmented. Maxillule, maxilla, first and second maxilliped typical for genus (10b–e). Third maxilliped exopod slender, setose, not extending beyond antepenultimate article of endopod (Fig. 10f); endopod terminal article flattened, spatulate, densely covered by thick setae, penultimate article subrectangular, broadening distally, bearing fringe of long setae extending from ventrodial lip; antepenultimate article quadrate, sparsely setose.

First pereopods (chelipeds) unequal in size and shape (Fig. 9d–f); major cheliped ischium short; merus subrectangular, ventral surface flattened, with eight conspicuous movable spines (6 in paratype USNM 273137A) along ventromesial margin; carpus cup-shaped, lacking small subacute tooth protruding from ventromesial margin, major chela rectangular in shape, laterally compressed, elongate, lacking depressions or grooves, margins setose, chela length about 4 times height (in paratype USNM 273137A, length 3 times height), propodus length about 3 times dactylus length (in paratype USNM 273137A length 3 times dactylus length), mesial and lateral surface of palm smooth; dactylus setose, truncate distally. Minor cheliped missing in holotype, in paratype (USNM 273137A, Fig. 9g) ischium short; merus subrectangular, ventral surface flattened, with seven movable spines (two broken) and sparse setae along ventromesial margin; carpus stout, distally cup-shaped; chela slender, long, lacking depressions or grooves, chela length about 4.3 times height, palm smooth, about 1.6 times as long as dactylus, linea impressa inconspicuous, fingers with long setae along margins, tips slightly crossing.

Second pereopod slender (Fig. 11a), ischium equal in length to merus; carpus composed of five articles with length ratio 1:1:1:3.6:2.5 (distal to proximal); chela simple, fingers slightly longer than palm, sparsely setose distally. Third pereopod robust (Fig. 11b–d), ischium armed with movable spine on ventrolateral surface; merus about twice as long as carpus; distal superior margin of carpus distinctly overhanging propodus; propodus slightly longer than carpus, single proximal movable spine on ventrolateral surface, long setae along entire superior and

ventral margin, lacking dense tufts; dactylus simple, sub-ovate, slightly curved, narrowing to acute tip. Fourth pereopod (Fig. 11e) similar to third, shorter, more slender, propodus with two movable spines along proximal half of ventrolateral surface. Fifth pereopod more slender than third and fourth (Fig. 11f); ischium lacking movable spine; merus, carpus, and propodus subequal in length; propodus lacking movable spines, with long sparse setae along margins and fringe of comb-like setae along distoventral surface; dactylus simple, curved, triangular, narrowing to acute tip.

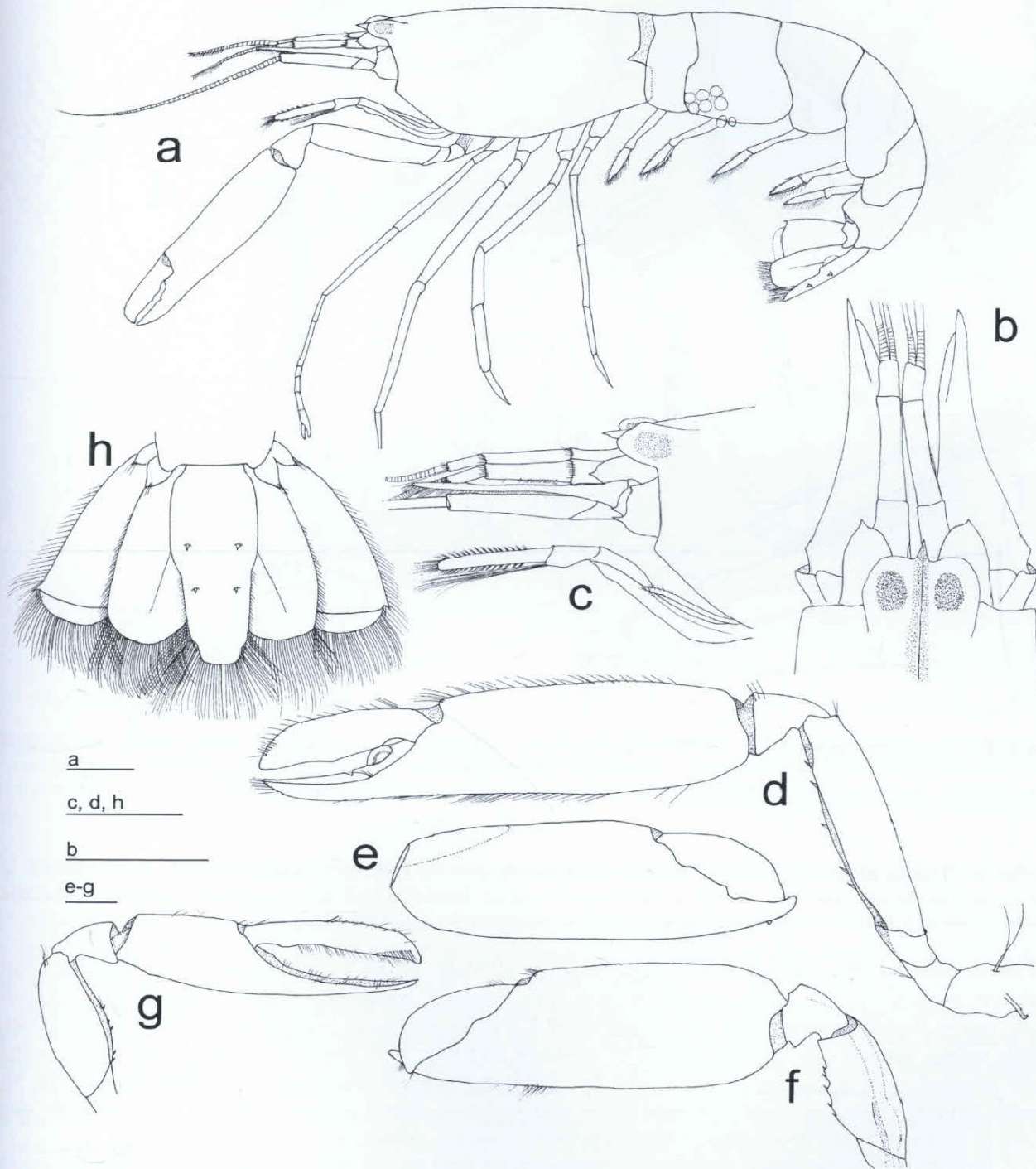


FIGURE 9. *Alpheus ulalae* sp. nov.: a–d, h, holotype ovig. female (USNM 1265092 = tissue/sequence ULLZ 6815); e–g, paratype male (USNM 273137A): a, habitus, lateral (minor chela missing); b, anterior carapace, dorsal; c, anterior carapace, left side, lateral; d, left major cheliped, lateral; e, right major cheliped, lateral; f, left major cheliped, mesial; g, left minor cheliped, lateral; h, abdominal somite six, telson, and uropods, dorsal. Scale bars = 2.0 mm.

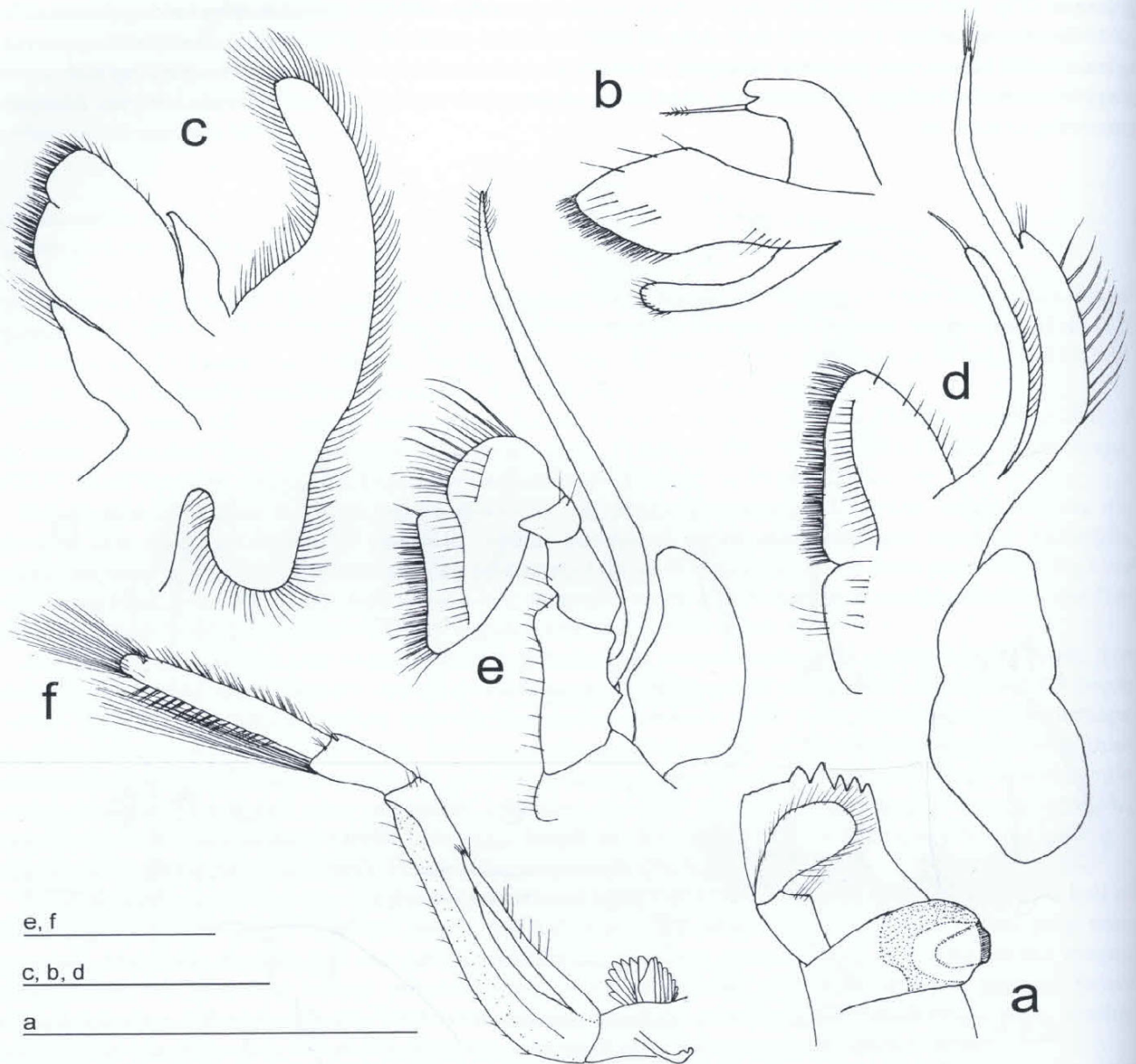


FIGURE 10. *Alpheus ulalae* sp. nov.: a–f, holotype ovig. female (USNM 1265092 = tissue/sequence ULLZ 6815): a, left mandible, mesial; b, left maxillule, lateral; c, left second maxilla, lateral; d, left first maxilliped, lateral; e, left second maxilliped, lateral; f, left third maxilliped, lateral. Scale bars = 1.0 mm (b–e), 2.0 mm (a, f).

First to fourth abdominal somites in male paratype (USNM 273137) with posterolateral angle of pleura rounded to weakly angular. Male second pleopod with appendix masculina, slightly over-reaching appendix interna. Telson slightly tapering (Fig. 9h), length about 2.6 times as long as wide (medially), two pairs of dorsal movable spines, anterior pair inserted near $3/10$, posterior pair near $5/10$ length of telson; posterolateral margin broadly rounded, each posterolateral angle with two small movable spines, mesial larger than lateral (Fig. 9h). Uropodal exopod extending slightly beyond telson and endopod, lateral margin produced with subacute tooth adjacent to strong movable lateral spine; endopod broadly subovate, subequal in length to telson (9h).

Gill formula typical for genus, including arthrobranch on third maxilliped, mastigobranch epipod on coxa of third maxilliped to fourth pereopod, setobranch on coxa of first to fifth pereopod.

Color pattern. (Fig. 2e–f). Abdominal somites marked by diffuse dorsal bands of small rose red to reddish orange chromatophores, densest on posterior of each somite (Fig. 2e, f); carapace anterior margin lateral to orbital

hoods marked by narrow but distinct vertical slash of red color; lateral margin of antennal scale and peduncle with series of 6-7 red dash marks; major cheliped with reddish pigment dorsally on palm, carpus and distal merus, forming diffuse bands fading laterally; eggs bright yellow-green.

Size. Largest examined male at cl 11.0 mm, tl 31.0 mm (USNM 273137A); largest examined female at cl 11.0 mm, tl 24.0 mm (USNM 273137C); egg diameter 0.4 mm (measured in the holotype).

Habitat. Specimens were dredged from sandy mud bottoms, usually with shell fragments, at a depth range of 41–80 m.

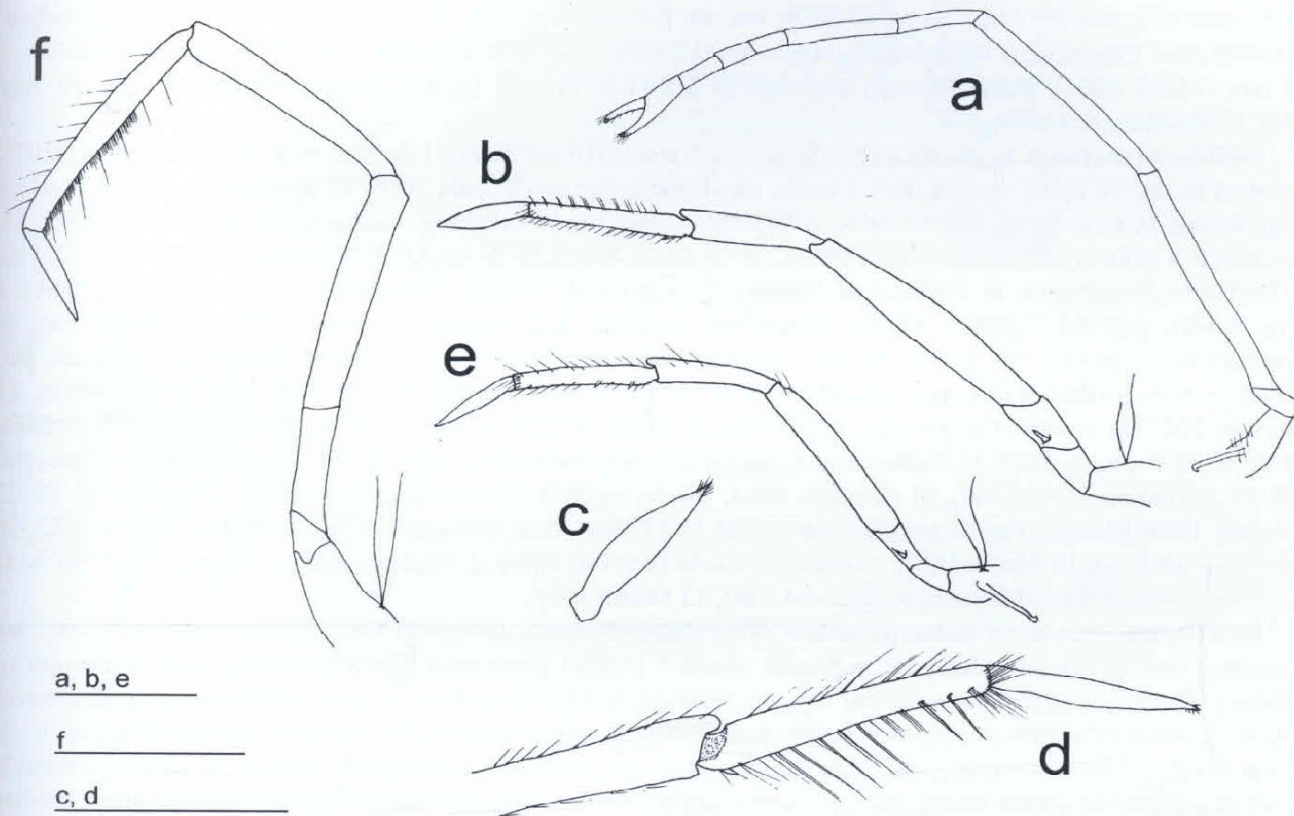


FIGURE 11. *Alpheus ulalae* sp. nov.: a–f, holotype ovig. female (USNM 1265092 = tissue/sequence ULLZ 6815): a, left second pereopod, lateral; b, left third pereopod, lateral (epipod not illustrated); c, dactylus of left third pereopod, dorsal; d, left third pereopod, carpus, propodus, dactylus, mesial; e, left fourth pereopod, lateral; f, left fifth pereopod, lateral. Scale bars = 2.0 mm.

Distribution. Western Atlantic: continental shelf off western Florida, in the northeastern Gulf of Mexico and Caribbean Sea (Guadeloupe).

Type locality. Northeastern Gulf of Mexico, off Tampa Bay, Florida.

Etymology. The specific name “*ulalae*” is a feminine transformation of the abbreviation “ULALA,” a colloquial acronym representing the University of Louisiana at Lafayette.

Remarks. *Alpheus ulalae* sp. nov. is morphologically most similar to *A. floridanus*. In both species, the distal tooth of the antennal scale extends distinctly beyond the third article of the antennal peduncle, separating them from *A. hephaestus* sp. nov. and *A. platycheirus*. The shape of the antennal scale and absence of movable spines on the propodus of the fifth pereopod can be used to distinguish *A. ulalae* sp. nov. and *A. floridanus* from *A. roblei* sp. nov. The position, robustness and number of spines on the propodus of the third and fourth pereopod separate *A. ulalae* sp. nov. from *A. floridanus*. *Alpheus ulalae* has 1–2 movable spines located on the proximal half of the propodus of the third and fourth pereopods. In contrast, *A. floridanus* has 3–5, (rarely more) movable spines along the entire ventrolateral surface of the propodus of the third and fourth pereopods. The two species may also be separated by the shape of the mandible incisor process (Table 1): with strong dentition only on the inferior half of the distal cutting edge in *A. ulalae* sp. nov. vs. with strong dentition along the entire margin in *A. floridanus*.

***Alpheus hephaestus* sp. nov.**

(Figures 2g–i, 12a–g, 13a–f, 14a–g)

Alpheus floridanus—Wicksten 1983: 45; Kim & Abele 1988: 53, fig. 22 a–m (part, Mexico, Panama, Ecuador); Vargas 1999: 901; Wicksten & Hendrickx 2003: 64; McClure 2005: 141 (part, fig. 22 a–m only, from Kim & Abele 1988); Hendrickx 2005: 165.

Alpheus floridanus A (E. Pac.)—Williams *et al.* 2001: 377.

Type material. Costa Rica (Pacific coast). **Holotype:** male, cl 8.8 mm (USNM 1265093 = tissue/sequence ULLZ 6205), west of Loma, 09°24.03'N, 84°29.20'W, stn. 48, R/V Urraca, trawl, 44.5–42.5 m, 17 July 2005, H. Bracken, R. Collin *et al.* **Paratypes:** 1 ovig. female, cl 6.6 mm (ULLZ 6377), same collection data as for holotype; 1 male, cl 9.1 mm (ULLZ 6204), Bahía Naranjo, 10°44.04'N, 85°41.37'W, stn. 13, R/V Urraca, dredge, 40.2 m, 15 July 2005, H. Bracken, R. Collin *et al.*

Additional material. Costa Rica (Pacific coast): 2 males (ULLZ 8004), 1 male, 3 ovig. females (ULLZ 9507), 09°24.03'N, 84°29.20'W, stn. 48, R/V Urraca, trawl, 44.5–42.5 m, 17 July 2005, H. Bracken, R. Collin *et al.*; 1 ovig. female (ULLZ 6206), 10°47.29'N, 85°43.58'W, stn. 19, R/V Urraca, dredge, 39.5 m, 15 July 2005, H. Bracken, R. Collin *et al.*; 1 male (ULLZ 6375), 09°24.03'N, 84°29.20'W, stn. 48, R/V Urraca, dredge, 44.5–42.5 m, 17 July 2005, H. Bracken, R. Collin *et al.* Panama (Pacific coast): 1 male, 2 females (1 ovig.) (USNM 237984), 1 ovig. female, (USNM 237984), Venado Beach Spit, stn. 132–2; 2 females (1 ovig.) (USNM 237988), East of Panama Canal Channel, stn. 150-C, 19 April 1973; 2 males (USNM 237987), Amador Causeway, Isla Naos, stn. 141–B; 3 male, 5 females (3 ovig.) (ULLZ 9508), 07°41.70'N, 81°42.50'W, stn. 1, R/V Urraca, dredge, 100 m, 21 February 2007, D. Felder *et al.*; 1 ovig. female (ULLZ 9509), 0722.47'N, 80°16.19'W, stn. 1, R/V Urraca, dredge, 20–25 m, 22 February 2007, D. Felder *et al.* Ecuador: 2 males, 1 female (USNM 237981), Cape San Francisco, stn. 216–34, 20 fathoms (= 36.5 m), 11 February 1934; 1 male (USNM 237990), Cape San Francisco, stn. 850–38, 23 February 1938. Mexico (Pacific coast): 1 male (USNM 237989), Baja California, Agua Verde Bay, stn. 655–37, 10 fathoms (=18.2 m), 10 March 1937; 2 males, 1 female (USNM 237983), Baja California, Gonzaga Bay, Willards Point, stn. 714–37, 16–30 fathoms (= 29.2–54.8 m), 23 March 1937.

Description (based on holotype unless otherwise indicated). Carapace with narrow, acute rostrum, not exceeding first article of antennular peduncle, shallow median postrostral carina extending onto midlength of carapace, flanked anteriorly by adrostral furrows reaching posteriorly to base of eyes, shallow carapacial grooves extending posteriorly from pterygostomial angle and postorbital hood (not in all material examined) (Fig 12a, b, c); ocular hoods ovate to subtriangular, extending beyond eye, unarmed; anterolateral margin of carapace weakly concave adjacent to orbital hoods; pterygostomial angle distinct, angle acutely produced toward anterior; cardiac notch deep.

Antennular peduncle first article with large ventromesial carina ending in acute tooth, first article about 3.5 times length of width, second article about 4.2 length of width, third article about 1.5 length of width (Fig. 12a, b, c); mesial flagellum narrower than lateral, distal ½ of lateral bearing aesthetascs; stylocerite broad, lamellate, tapering into sharp tip, not over-reaching distal margin of first article. Antenna with stout basicerite bearing strong, sharp, ventrolateral tooth; antennal scale (scaphocerite) broad, lateral margin weakly concave to almost straight, distolateral spine barely over-reaching rounded anterior margin of blade and length of third article, not exceeding carapocerite (12a, c).

Mandible incisor process (right and left) with five or six well-developed teeth, one enlarged, on inferior half of margin (Fig. 13a), dentition of superior half poorly defined; molar process rounded, blunt; palp two-segmented palp. Maxillule, maxilla, first and second maxilliped typical for genus (13b–e). Third maxilliped exopod slender, setose, not extending beyond antepenultimate article of endopod (Fig. 13f); endopod terminal article flattened, spatulate, densely covered in thick setae, penultimate article subrectangular, broadening distally, bearing fringe of long setae extending from ventrodial lip, antepenultimate article quadrate, sparsely setose.

First pereopods (chelipeds) unequal in size and shape (Figs. 12a, d, e; 14 a, b); major cheliped ischium short; merus subrectangular, ventral surface flattened, four movable spines and fringe of setae along ventromesial margin; carpus cup-shaped, small subacute tooth protruding from ventromesial margin; major chela subrectangular, laterally compressed, elongate, lacking depressions or grooves, margins sparsely setose, chela length about 4 times height; propodus length about 2.8 times dactylus length, ventral surface densely setose, mesial and lateral surface of palm smooth; dactylus setose, truncate distally. Minor cheliped ischium short; merus subrectangular, ventral

surface flattened, with possibly four movable spines along ventromesial margin, but some appear broken/damaged (eight in male paratype, ULLZ 6204); carpus stout, cup-shaped; chela slender, long, lacking depressions or grooves, chela length about 5.5 times height, palm smooth, about 1.7 as long as dactylus, linea impressa evident, fingers densely setose.

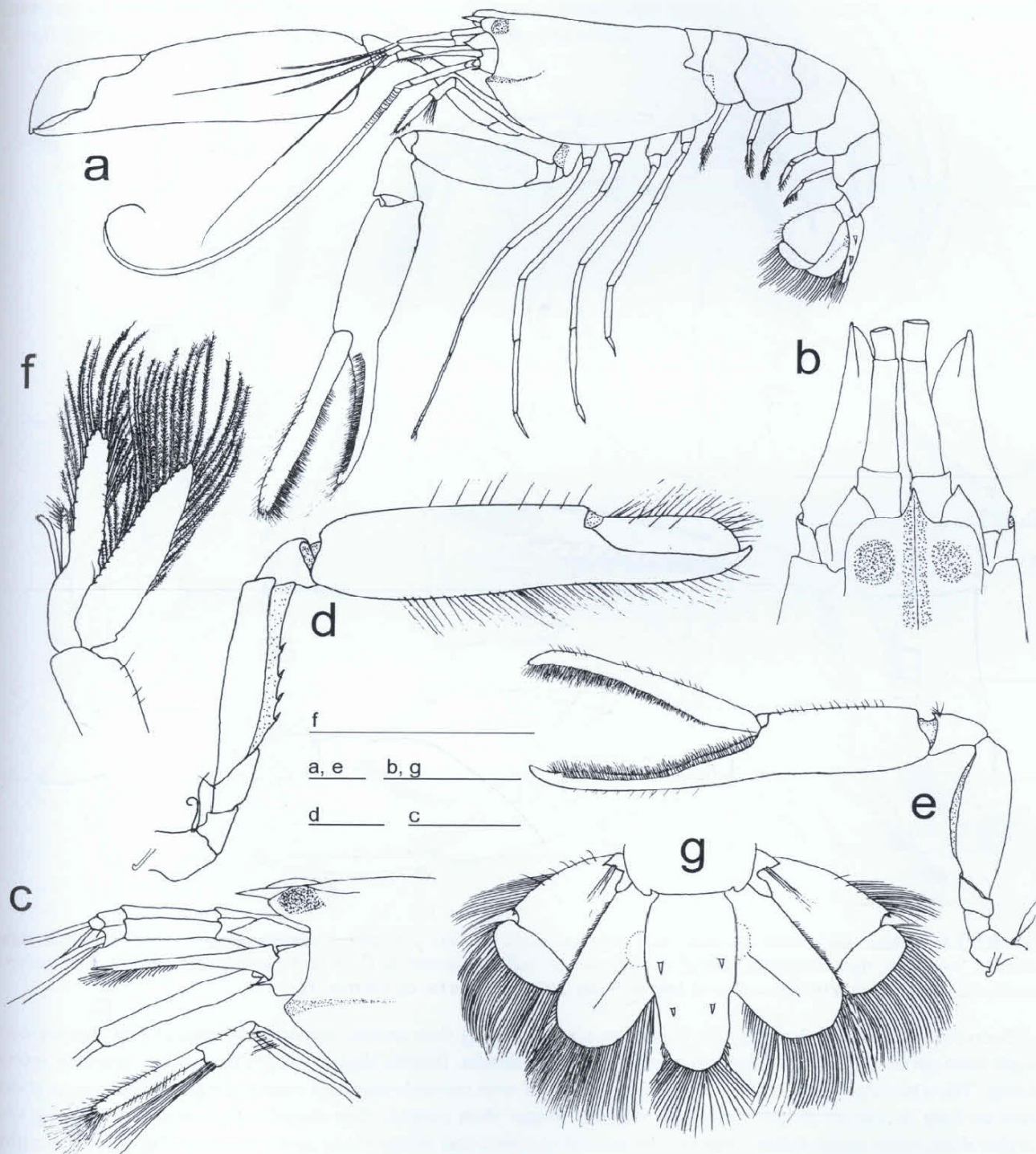


FIGURE 12. *Alpheus hephaestus* sp. nov.: a–c, e–g, holotype male (USNM 1265093 = tissue/sequence ULLZ 6205); d, paratype ovigerous female (ULLZ 6377): a, habitus, lateral; b, anterior carapace, dorsal, setation not shown; c, anterior carapace, left side, lateral; d, right major cheliped, lateral; e, left minor cheliped, lateral; f, right second pleopod, appendix interna, and appendix masculina; g, sixth abdominal somite, telson and uropods, dorsal. Scale bars = 2.0 mm.

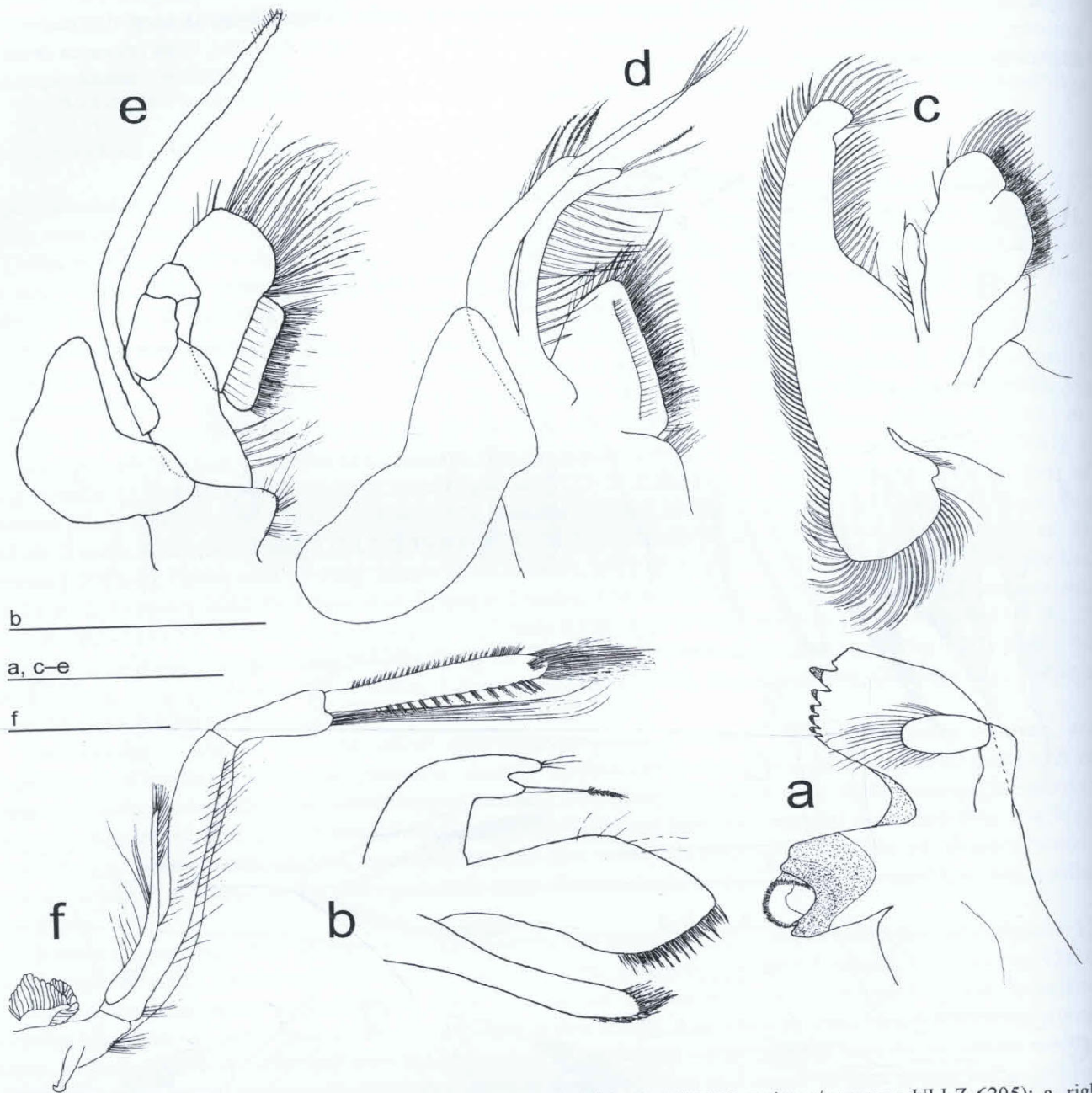


FIGURE 13. *Alpheus hephaestus* sp. nov.: a–f, holotype male (USNM 1265093 = tissue/sequence ULLZ 6205): a, right mandible, mesial; b, right maxillule, lateral; c, right second maxilla, lateral; d, right first maxilliped, lateral; e, right second maxilliped, lateral; f, right third maxilliped, lateral. Scale bars = 1.0 mm (a–e), 2.0 mm (f).

Second pereopod slender (Fig. 14c), ischium slightly longer than merus; carpus composed of five articles with length ratio about 1:1:1:2.6:2 (distal to proximal); chela simple, fingers slightly longer than palm, sparsely setose distally. Third pereopod robust (Fig. 14d), ischium armed with movable spine on ventrolateral surface; merus about twice as long as carpus length; propodus slightly longer than carpus, four movable spines along ventrolateral margin, thick setae along entire superior and ventral margins and fringe along distal superior and ventral margin; dactylus simple, subspatulate, curved. Fourth pereopod similar to third, shorter, more slender (Fig. 14e); propodus with four movable spines (also four in paratypes ULLZ 6204, 6377 and four in USNM 237981) along ventrolateral surface. Fifth pereopod more slender than third and fourth (Fig. 14f), ischium lacking movable spine, merus similar in length to carpus and propodus; propodus with tufts of thick setae, lacking movable spines, setose along distal superior and ventral margins; dactylus simple, curved, narrowing to acute tip.

First to fourth abdominal somites in male with posterolateral angle of pleura rounded to weakly angular (Fig. 12a). Male second pleopod with appendix masculina subequal in length to appendix interna (Fig. 12f). Telson slightly tapering (Fig. 12g), length about 2.5 times as long as wide (medially), two pairs of dorsal movable spines, anterior pair inserted near $3/8$, posterior pair near $5/8$ length of telson; posterolateral margin broadly rounded, each posterolateral angle with two small movable spines, mesial larger than lateral (Fig. 12g). Uropodal exopod subequal in length to telson and endopod, lateral margin produced with subacute tooth adjacent to strong movable lateral spine; endopod broadly subovate, subequal in length to telson.

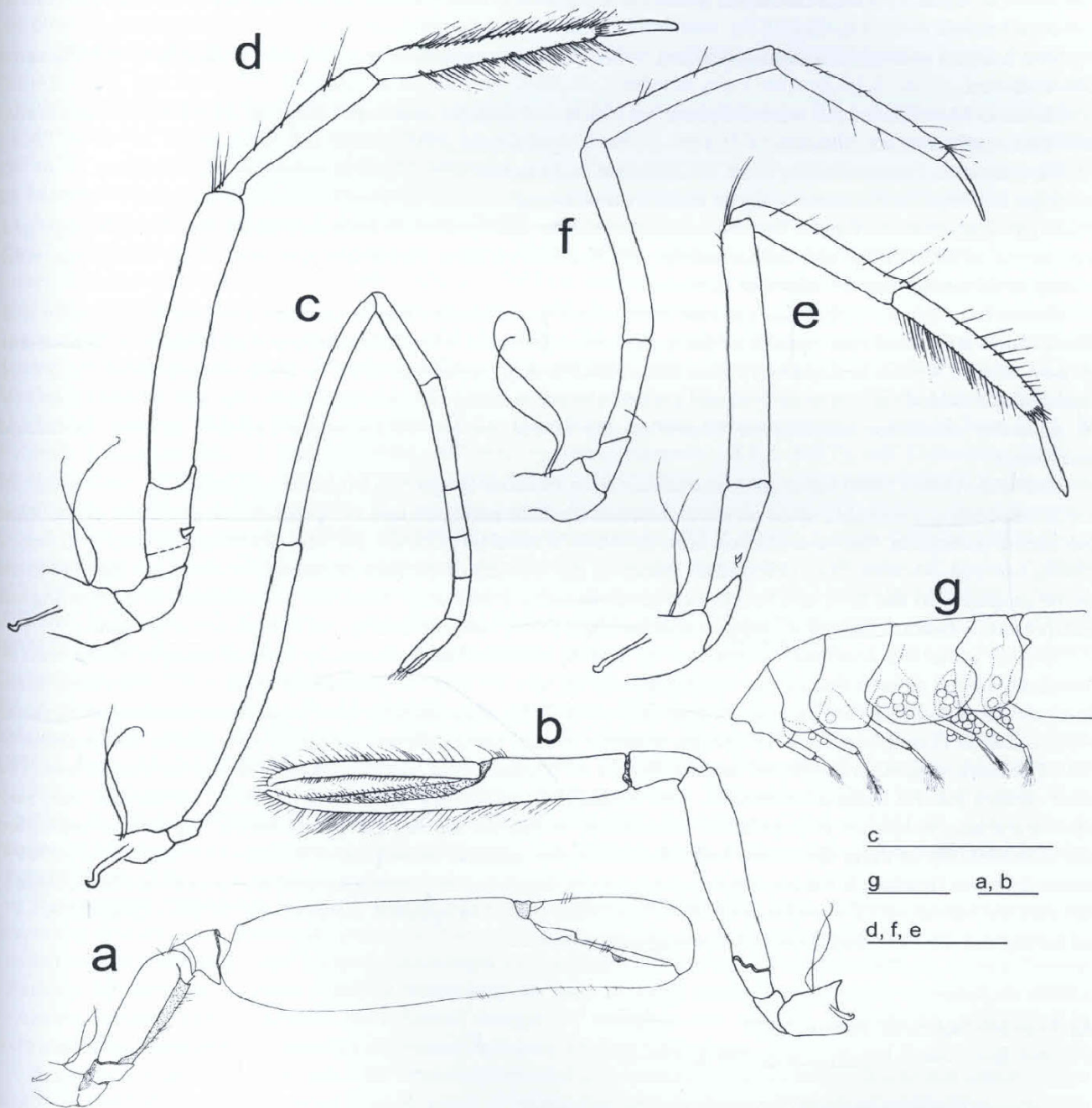


FIGURE 14. *Alpheus hephaestus* sp. nov.: a, c–e, f, holotype male (USNM 1265093 = tissue/sequence ULLZ 6205); b, g, paratype ovigerous female (ULLZ 6377): a, right major cheliped, lateral; b, left minor cheliped, lateral; c, right second pereopod, lateral; d, right third pereopod, lateral; e, right fourth pereopod, lateral; f, right fifth pereopod, lateral; g, abdomen, pleopods, and eggs, right side, lateral. Scale bars = 2.0 mm.

Gill formula typical for genus, including arthrobranch on third maxilliped, mastigobranch epipod on coxa of third maxilliped to fourth pereopod, setobranch on coxa of first to fifth pereopod.

Color (Fig. 2g–i). Carapace and abdominal somites marked by rust to pink-red isolated and interconnected chromatophores and color patches on brownish to whitish ground color; pigment cover especially dense on anterior margin of carapace lateral to orbital hoods, antennular peduncles, area encompassing rostral carina between eyes, and sixth abdominal somite, sometimes forming broad ill-defined dorsolateral bars or crescents on abdominal somites; chelae with broadly distributed patches of orange to rust brown pigment, poorly (if at all) defined into encircling bands; pereopods 3–5 with often diffuse reddish band on distal third of merus, and with broader less defined band of same pigment on carpus where most pigment is concentrated on extensor margin; eggs pale yellow to orange-brown.

Size. Largest examined male at cl 8.8 mm, tl 25.1 mm; largest female at cl 9.0 mm, tl 26.0 mm; egg diameter 0.30–0.45 mm.

Habitat. Most specimens were collected by trawls and dredges at a depth range of 24–100 m, on mud, silt, sand-mud-shell, and sand bottoms.

Distribution. Eastern Pacific: Gulf of California to Ecuador.

Type locality. Pacific coast of Costa Rica, west of Loma.

Etymology. Named for the fire-red color common in this species, in reference to the Greek mythology god Hephaestus, symbol of fire and craftsmanship, who was thrown from Mount Olympus and fell for many days until landing in the ocean near the island of Lemnos.

Remarks. *Alpheus hephaestus* sp. nov. is restricted to the eastern Pacific and has a unique color pattern that distinguishes it from all other species of the *A. floridanus* complex. Morphologically and genetically, *A. hephaestus* sp. nov. is most similar to *A. platycheirus*, from which it may be distinguished by the configuration of the orbital hoods, which extend well past the eyes and are more ovate to triangular in *A. hephaestus* sp. nov. (Table 1), and by the generally shallower longitudinal furrow on the lateral surface of the major cheliped ischium in mature specimens.

Kim and Abele (1988) reported *A. floridanus* from Ecuador (Cape San Francisco, Ecuador, pg. 53–55, fig. 22 a–m), mentioning a movable spine on the ischium of the fifth pereopod and no spines on the propodus of the third and fourth pereopods. We re-examined Kim & Abele's material (USNM 237981, 237990, 237989; 3 males, 1 female, sta. 216–34, 850–38) and found no spines on the ischium of the fifth pereopod; however, we did find them on the propodus of the third and fourth pereopods (usually 4 on each). Thus, the combination of morphological features and collection locality all suggest that the Ecuadorian material belongs to *A. hephaestus* sp. nov.

In their molecular analyses, Williams *et al.* (2001) identified two genetically distinct lineages allied with *A. floridanus* in the eastern Pacific (as "*A. floridanus* sp. A - P" and "*A. floridanus* sp. B - P"). However, these lineages were recovered only by cytochrome oxidase I (COI); other markers used in the analysis (elongation factor 1-alpha and GPI) were not sensitive enough to detect species level differences. Based on a genetic comparison of COI, GenBank sequences AF308987 and AF309901 of Williams *et al.* (2001) represent *A. hephaestus* sp. nov. The other eastern Pacific material (GenBank nos. AF308993, AF309899) also cluster with *A. hephaestus*, and may represent a second species or population substructure within the eastern Pacific. However, the lack of resolution and unavailability of these specimens make definitive placement of these gene sequences (AF308993, AF309899) impossible (see Bracken & Felder, this volume for more details). It is noteworthy that Williams *et al.* (2001, table I) reported the habitat of "*A. floridanus* sp. B - P" as "mud/rocks" as opposed to "mud" for "*A. floridanus* sp. A - P", indicating that the two lineages may be ecologically separated.

Alpheus platycheirus Boone, 1927

(Figures 2j–l, 15a–f, 16a–h, 17a–g, 18a–g, 19a–h)

Alpheus platycheirus—Boone 1927: 131–135, figs. 29, 30 (Cuba).

Alpheus floridanus—Chace 1972: 65 (part, fig. 20a–f, Louisiana); Felder *et al.* 2009: 1057, 1091 (part, Louisiana).

Alpheus floridanus—Christoffersen 1979: 312 (part, Rio de Janeiro).

? *Alpheus floridanus* Kingsley, 1878 (part, mutilated male syntype of *A. floridanus*, MCZ 4987, see text).

? *Alpheus platycheirus*—Boone 1930: 49–51, figs. 9, 9a (Haiti).

Type material. Holotype: 1 male, cl = 11.4 mm (YPM 6628 = tissue/sequence ULLZ 8630) Sigüanea Bay, Isle of Pines, Cuba, R/V "Pawnee I", trawl, 12 fathoms, 1925.

Additional material. USA, N Gulf of Mexico: 1 male (USNM 1265090 = tissue/sequence ULLZ 5855), off Louisiana/Mississippi, 28°20.60'N, 90°46.93'W, stn. Core 1, box core, R/V Pelican, 54 m, 2 July 2001, D. Felder *et al.*; 1 male, (ULLZ 1181), off Louisiana/Mississippi, 28°55.40'N, 89°48.80'W, stn. 14847, R/V Oregon II, 36.5 m, 5 June 1974, T. Shirley; 1 male (ULLZ 11936), off Louisiana, trawl, R/V Pelican, stn. 1294, LA WLF Seemap Cruise, April 2010, S. Pecnik *et al.*; 1 male (ULLZ 11937), off Louisiana, trawl, R/V Pelican, stn. 1214, LA WLF Seemap Cruise, April 2010, S. Pecnik *et al.*; 1 male (ULLZ 11939), off Louisiana, trawl, R/V Pelican, stn. 1188, LA WLF Seemap Cruise, April 2010, S. Pecnik *et al.*; 1 male (ULLZ 10599), off Louisiana, box dredge, R/V Pelican, 58-60 m, 1 August 2002, D. Felder *et al.*; 1 female (ULLZ 8275), Louisiana, off Mississippi River Delta, 90°W, box core, 28 March 1996, 91 m, D. Felder *et al.*; 1 juvenile (ULLZ 6819), off Louisiana, 28°48.09'N, 89°22.89'W, stn. NSF-III-007, box core, R/V Pelican, 86 m, 28 July 2006, D. Felder *et al.*; 1 male (ULLZ 5857), Louisiana, off Mississippi River Delta, stn. MP299, mud, 16 September 2002; 1 ovig. female (ULLZ 6209), off Louisiana, 28°87'N, 90°46'W, stn. C6B R1, March 2004, M. Millman *et al.*; 1 male (ULLZ 6210), off Louisiana, 28°87'N, 90°46'W, stn. C6B R2, December 2003, M. Millman *et al.*; 1 male (ULLZ 6460), off Louisiana, box core, 122 m, 28 March 1996, D. Felder *et al.*; 1 female (GCRL 2496), offshore, NOAA project; 2 males (GCRL 2497), offshore, 13 June 1992, NOAA project; 1 male (GCRL 2498), off Mississippi, south of Dog Keys Pass, 30°812.50'N, 88°47.30'W, 20 March 1998, NOAA project; 1 male (GCRL 2500), offshore, 2 November 1993, NOAA project; 3 males, 4 females (1 ovig.) (GCRL 2495), offshore, NOAA project; 1 ovig. female (ULLZ 5858), off Louisiana, 29°17'N, 88°59.5'W, R/V Oregon II, 12 m, 15 April 1980, R. Bouchon and R. Foreman; 1 male (ULLZ 9583), Texas, Seven and One-half Fathom Reef, 26°51'N, 96°51'W, mud sample between rocks, 26 August 1968, W. Tunnell; 1 female (ULLZ 6421), Mississippi River off South Pass, soft mud, box core, R/V Pelican, 91 m, 25 May 1990, D. Felder *et al.*; 4 males (USNM 103528), off Louisiana, south of Grand Isle, trawl, 37 m. Mexico, SW Gulf of Mexico: 1 male (ULLZ 12269), off Veracruz, Enmedio Reef, in mud from discarded tin pot, 19 June 1978, W. Tunnell. Caribbean Sea: 1 male (USNM 1071493 = tissue/sequence ULLZ 8627), off Colombia, Gulf of Morrosquillo, 09°36.12'N, 75°51.46'W to 09°36.17'N, 75°52.40'W, trawl, CIOH-INVEMAR-Smithsonian Expedition, 38-40 m, 3 August 1995, R. Lemaitre and N. Campos; 1 male (USNM 1071493A = tissue/sequence ULLZ 9258), 1 ovig. female (USNM 1071493B = tissue/sequence ULLZ 9259), 1 male (USNM 1071493C = tissue/sequence ULLZ 9260), same collection data as for previous specimens; 2 females, 2 males (USNM 1071493), same collection data as for previous specimens; 1 male, 3 females (1 ovig.) (USNM 1071509), 1 female (USNM 1071643), off Colombia near Ceycen Island, 09°41.04'N, 75°46.08'W, trawl, expedition CIOH-INVEMAR-Smithsonian, 29 m depth, 6 August 1995, R. Lemaitre *et al.*; 1 female (MNHN-IU-2013-13189) Guadeloupe, transversal en bordure de la microalgune de Rotours, chalutage 5', 11h15, 21 March 1978, coll. Rojas, det. Anker A. Brazil: 1 male (USNM 144013), Rio de Janeiro, Ilha Grande, Sepetiba, stn. 190 Bde A No. 24, 4 February 1971; 1 male (MZUSP 05372), Rio de Janeiro, Ilha Grande, 28 July 1966, det. Christoffersen 05 March 1983; 1 male (MZUSP 24525), Piuma, ES, 28 March 2010, coll. Afonso Jório, det. G. Soledade 13 September 2012; 1 ovig. female, 1 male (MZUSP 31814), Maceió, Ponto 6, 27 June 1989, det. A. Anker and P. Pachele 2013; 2 males, 4 females (MNHN-IU-2013-13192), 23°04'S, 44°14'W, Expedition Calypso 1961-62, Entre Rio de Janeiro et Santos, Navire océanographique "Calypso", stn. DR114, 45 m, 8 December 1961, coll. Métivier, det. Christoffersen 1979.

Description (based on holotype unless otherwise indicated). Carapace with narrow, acute rostrum not exceeding first article of antennular peduncle (Figs. 15a-c, 16a-d, 19a-c), shallow (prominent in some) postrostral median carina extending onto carapace midlength (extending to posterior 1/4 of carapace in some), flanked anteriorly by adrostral furrows reaching posteriorly to base of eyes; ocular hoods ovate (rounded in some), extending beyond eye, unarmed; anterolateral margin of carapace not swollen adjacent to orbital hoods; pterygostomial angle evident, rounded (indistinct in some); cardiac notch deep.

Antennular peduncle first article with large ventromesial carina ending in acute tooth, first article about 2 times length of width, second article about 4 times length of width, third article about 1.5 length of width (Figs. 15b, 16b, d, e; 19b, c); mesial flagellum narrower than lateral, distal 1/2 of lateral bearing aesthetascs; stylocerite broad, lamellate, tapering into sharp tip, not over-reaching distal margin of first article. Antenna with stout basicerite bearing strong, sharp, ventrolateral tooth (Figs. 15c, 16b; 19c); antennal scale (scaphocerite) broad, lateral margin weakly concave to almost straight, distolateral spine slightly over-reaching rounded anterior margin of blade and third article, also reaching about to distal tip of carapocerite (falling just short in some) (Figs. 15a, c, 16a, b, 19a, c).

Mandible (based on ULLZ 1181) incisor process with seven well-developed teeth (Fig. 17a), one enlarged, on inferior half of margin, superior margin with poorly defined dentition; molar process rounded, blunt; palp two-segmented. Maxillule, maxilla, first and second maxilliped typical for genus (17b–e). Third maxilliped exopod long, slender, setose, not extending beyond antepenultimate article of endopod (Fig. 17f); endopod terminal article flattened, spatulate, mesial surface and periphery bearing tufts of thick setae, penultimate article subrectangular, broadening distally, bearing fringe of long setae extending from ventrodiscal lip, antepenultimate article quadrate, sparsely setose.

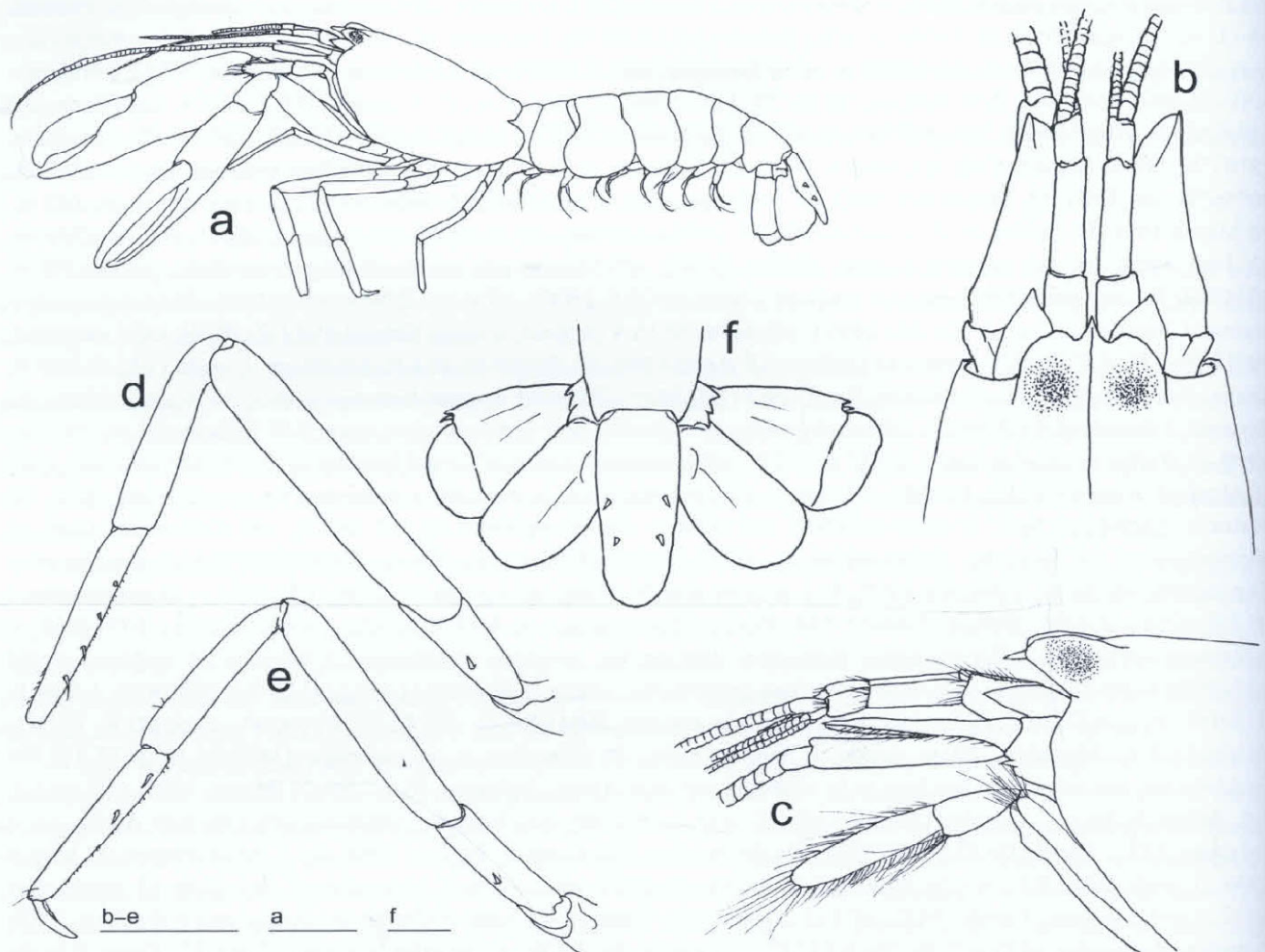


FIGURE 15. *Alpheus platycheirus* Boone, 1927: a–f, holotype male (YPM 6628 = tissue/sequence ULLZ 8630): a, habitus, lateral; b, anterior carapace, dorsal; c, anterior carapace, lateral; d, left third pereopod, lateral (dactylus missing, epipod not shown); e, left fourth pereopod, lateral (epipod not shown). Scale bars = 2.0 mm.

First pereopods (chelipeds) unequal in size and shape (Figs. 15a, 16a, f, g; 18a–c; 19a, d–g; Boone, 1927, figs. 29, 30; Boone, 1930, figs. 9, 9a), often massively large in males (e.g., ULLZ 1181, GCRL 2497, GCRL 2500); major cheliped ischium short; merus subrectangular, ventral surface flattened, six movable spines and fringe of setae along ventromesial margin (only two in ULLZ 1181); carpus cup-shaped, small subacute tooth (rounded tubercle in some) on mesial surface protruding from ventromesial margin; major chela rectangular in outline, laterally compressed, elongate, lacking depressions or grooves, ventral margin setose, chela length about 4 times height (5.3 times in ULLZ 1181, 5 times in GCRL 2497), propodus length about 2.3 times (3–4 times in some males) dactylus length, mesial and lateral surfaces of palm flattened to weakly concave (very weakly convex in some), texture smooth to minutely granular; dactylus setose. Minor cheliped balaeniceps-shaped in male, with short ischium; merus subrectangular, ventral surface flattened, with eight movable spines (six in USNM 1071493 = tissue/sequence ULLZ 8627, four in ULLZ 1181) and fringe of setae along ventromesial margin; carpus stout, cup-

shaped; chela slender, lacking depressions or grooves, chela length about 5.3 times height (often more; 5.5 times in USNM 1071493 = tissue/sequence ULLZ 8627, 9.6 times in ULLZ 1181, 8 times in GCRL 2497), palm smooth, about 1.8 times as long as dactylus, linea impressa evident, fingers densely setose, tips slightly crossing.

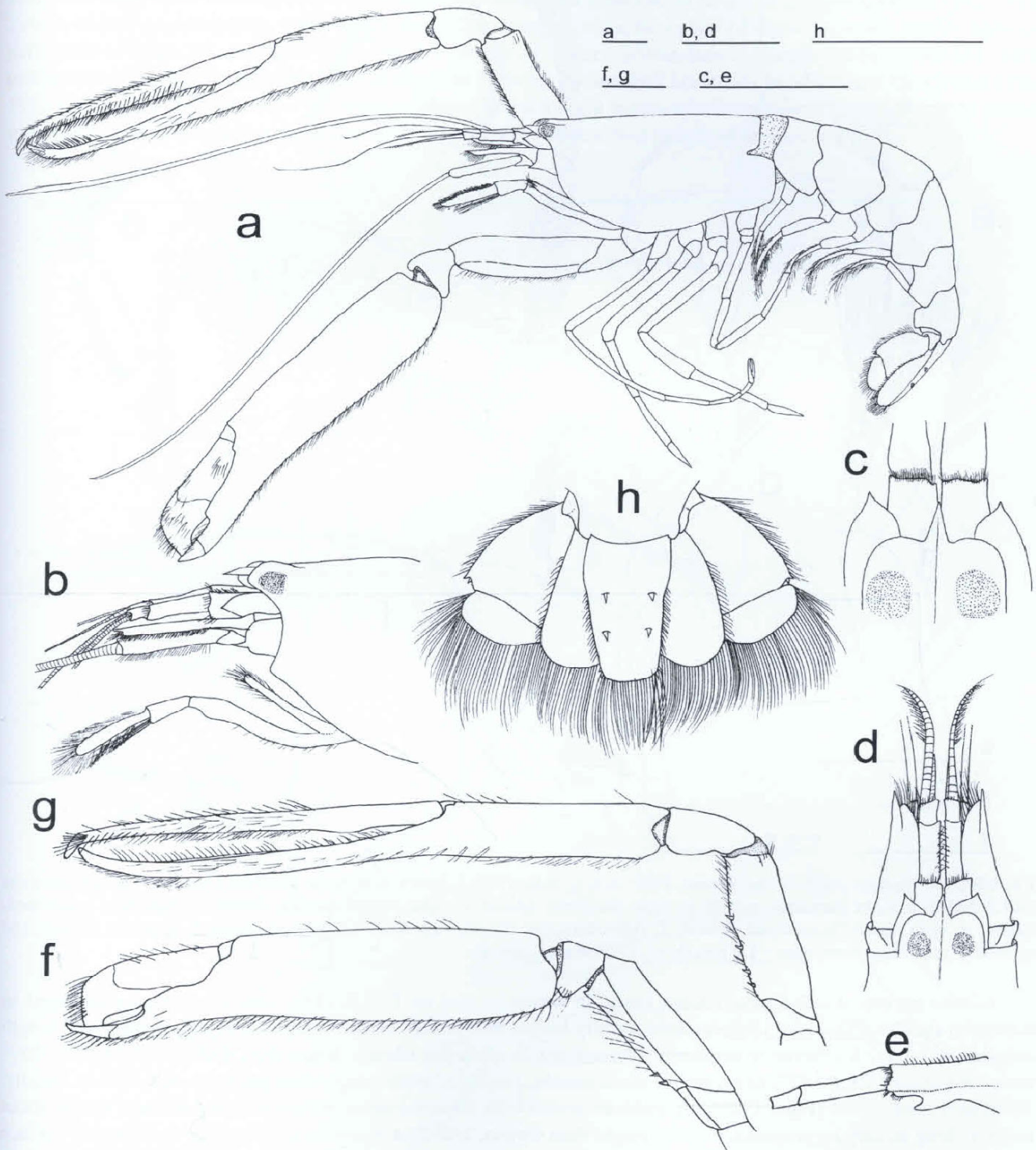


FIGURE 16. *Alpheus platycheirus* Boone, 1927: a, f, g, male (ULLZ 1181); b–e, h, male (USNM 1265090 = tissue/sequence ULLZ 5855): a, habitus, lateral; b, anterior carapace, lateral; c, anterior carapace, dorsal; d, anterior carapace, dorsal; e, antennular peduncle and carinal ridge, lateral; f, left major cheliped, lateral; g, right minor cheliped, mesial; h, sixth abdominal somite, telson, and uropods, dorsal. Scale bars = 2.0 mm.

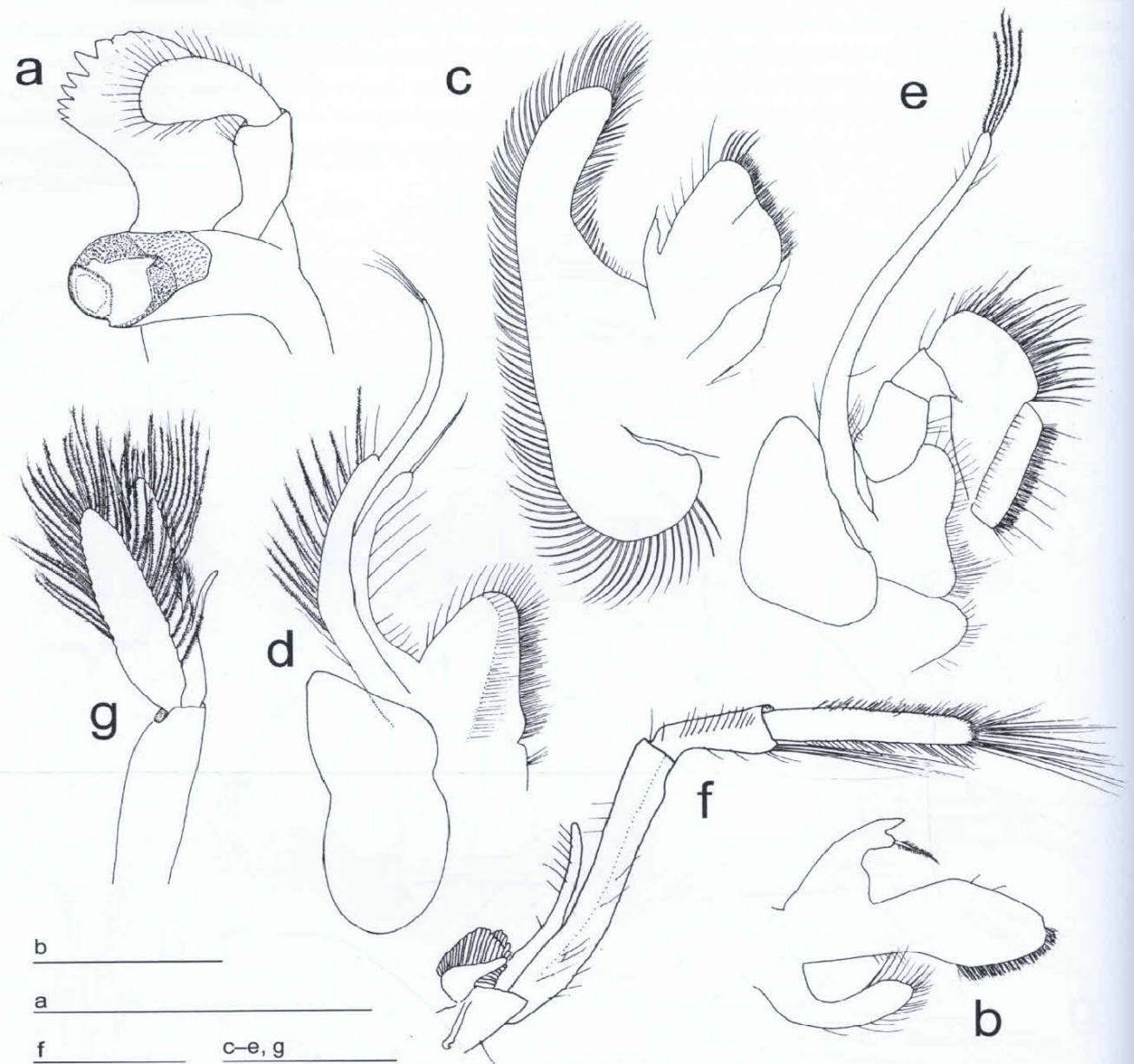


FIGURE 17. *Alpheus platycheirus* Boone, 1927: a, f, g, male (ULLZ 1181); b–e, male, (USNM 1265090 = tissue/sequence ULLZ 5855): a, right mandible, mesial; b, right maxillule, lateral; c, right second maxilla, lateral; d, right first maxilliped, lateral; e, right second maxilliped, lateral; f, right third maxilliped, lateral; g, left second pleopod, appendix interna and appendix masculina. Scale bars = 1.0 mm (b–c), 2.0 mm (a, f, and g).

Second pereopod (P2-5 descriptions based in whole or part on ULLZ 1181, where missing or damaged in holotype) slender (Figs. 15a; 18d), ischium slightly longer than merus; carpus composed of five articles with length ratio about 1:1:1:2.8:2 (distal to proximal) (second article of carpus slightly longer than first in USNM 1071493 = tissue/sequence ULLZ 8627, not typical); chela simple, fingers slightly longer than palm, sparsely setose distally. Third pereopod robust (Figs. 15d; 18e), ischium armed with movable spine on ventrolateral surface; merus about twice as long as carpus; propodus slightly longer than carpus, with four movable spines along ventrolateral surface (two in ULLZ 1181, four in USNM 1071493 = tissue/sequence ULLZ 8627, five in USNM 1265090 = tissue/sequence ULLZ 5855), setae along superior and ventral margins, fringe of setae along distal superior margin; dactylus simple, subspatulate, slightly curved. Fourth pereopod (Figs. 15e; 18f) similar to third, propodus with two movable spines along ventrolateral surface (one in ULLZ 1181, two in USNM 1071493 = tissue/sequence ULLZ 8627 and USNM 1265090 = tissue/sequence ULLZ 5855). Fifth pereopod more slender than third and fourth (Figs.

15a; 18g); ischium lacking movable spine; merus slightly longer than carpus; carpus and propodus similar in length; propodus with tufts of thick setae, lacking movable spines, fringe of comb-like setae along distoventral surface, dactylus simple, curved, narrowing to acute tip.

First to fourth abdominal somites in male with posterolateral angle of pleura rounded to weakly angular (Figs. 15a; 16a; 19a). Male second pleopod with appendix masculina subequal in length to appendix interna (Fig. 17g). Telson slightly tapering (Fig. 19h), length about 2.4 as long as wide, two pairs of dorsal movable spines, anterior pair inserted near 3/7, posterior pair near 4/7 length of telson; posterolateral margin broadly rounded, each posterolateral angle with two small movable spines (missing in damaged holotype), mesial larger than lateral (Fig. 19h). Uropodal exopod subequal in length to telson, lateral margin produced with subacute tooth adjacent to strong movable lateral spine; endopod broadly subovate, slightly overreaching length of exopod and telson.

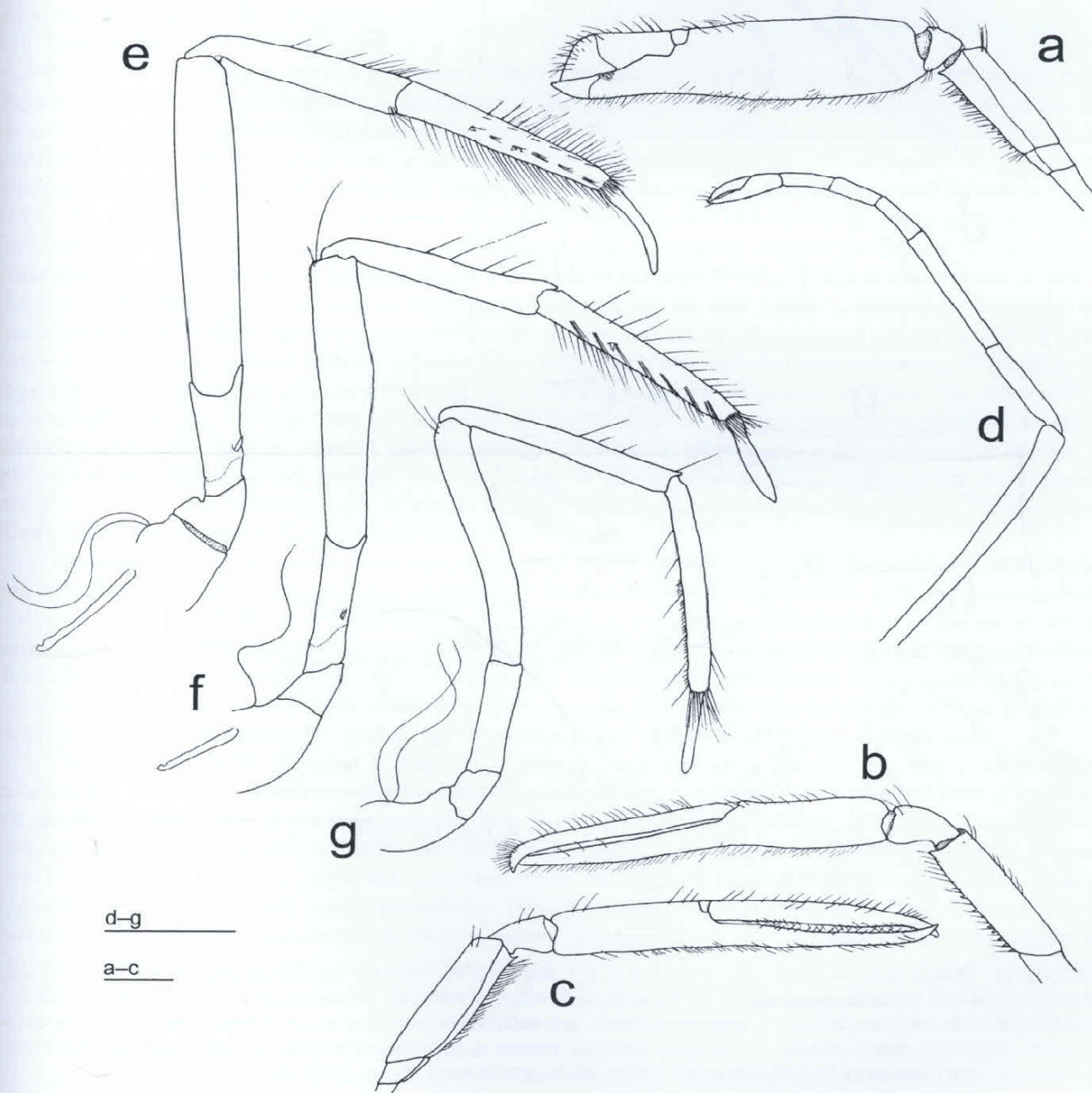


FIGURE 18. *Alpheus platycheirus* Boone, 1927: a–c, male (USNM 1265090 = tissue/sequence ULLZ 5855); d–g, male (ULLZ 1181): a, left major cheliped, lateral; b, right minor cheliped, mesial; c, same, lateral; d, right second pereopod, mesial; e, right third pereopod, lateral; f, right fourth pereopod, lateral; g, right fifth pereopod, lateral. Scale bars = 2.0 mm.

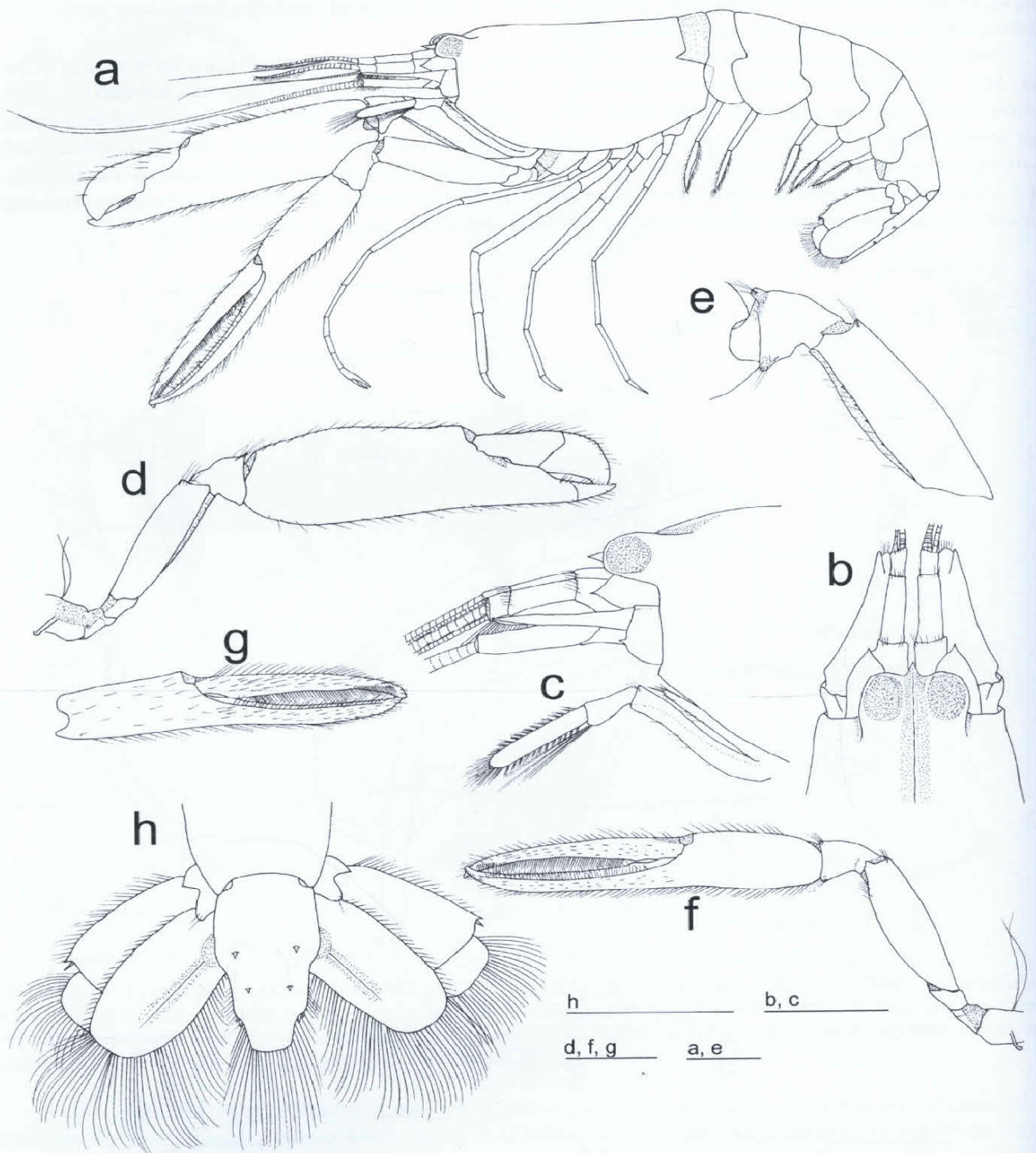


FIGURE 19. *Alpheus platycheirus* Boone, 1927: a, d, g, e, f, male (USNM 1071493 = tissue/sequence ULLZ 8627); h, male (USNM 1071493 = tissue/sequence ULLZ 9259); b, c, male (USNM 1071493 = tissue/sequence ULLZ 9258): a, habitus, lateral; b, anterior carapace, dorsal; c, anterior carapace, left side, lateral; d, right major cheliped, lateral; e, right major cheliped, carpus and merus, mesial; f, left minor cheliped, lateral; g, left minor cheliped, propodus and dactylus, mesial (balaeniceps setae illustrated); h, sixth abdominal somite, telson, and uropods, dorsal. Scale bars = 2.0 mm.

Gill formula typical for genus, including arthrobranch on third maxilliped, mastigobranch epipod on coxa of third maxilliped to fourth pereopod, setobranch on coxa of first to fifth pereopod.

Color pattern (Fig. 2j–l). Carapace and abdominal somites with locally interrupted coverage of pink-red to

rust-brown chromatophores, sometimes in patches; pigment cover especially dense on anterior margin of carapace lateral to orbital hoods, antennular peduncles, rostral carina; dorsolateral surface of abdominal somites and proximal half of uropodal endopods with poorly defined bands; chelae with broad interconnected patches of orange to rust brown pigment, poorly (if at all) defined into encircling bands; pereopods 3-5 with diffuse reddish band on distal third of merus, and broader, less defined reddish band on carpus, more intense on extensor margin.

Size. Largest examined male at cl 13.0 mm, tl = 32.0 mm, length of major chela 23.0 mm, minor 24.5 mm (GCRL 2497); largest female cl = 12.0 mm, tl = 22.0 mm, length of major and minor chelae about 8.0 mm; egg diameter 0.5 mm (USNM 1071493).

Habitat. Muddy bottom, depth range 12–122 m; all specimens were collected by dredges, trawl nets and box cores.

Distribution. Western Atlantic: Gulf of Mexico (off Louisiana, Mississippi, Mexico), Caribbean Sea (off Colombia and Guadeloupe), and Brazil.

Type locality. Isles of Pines, Cuba.

Remarks. The holotype of *A. platycheirus* (YPM 6628), was collected by a dredge at 12 fathoms (22 m) in Siguanea Bay, Isle of Pines (= Isla de la Juventud), Cuba. Boone provided a full description with illustrations of an undamaged specimen in her 1927 publication (Boone 1927), although the holotype was later described as “badly mutilated” (Boone 1930) leaving some questions as to how/when the holotype was damaged. At present, the holotype is lacking both propodi on the fifth pereopods, which is inconsistent with the specimen figured by Boone (1927, fig. 29) showing a complete specimen with intact fifth pereopods. This species was long suspected to be a member of the *A. floridanus* complex (e.g., Chace 1972). Our observations suggest the features of the antennal scale and propodal spines on the third and fourth pereopods of the holotype of *A. platycheirus* are very similar to those of the specimens from the Gulf of Mexico and Colombia that we here regard as conspecific. However, the major chela of the holotype appears to be more broadly elevated and strongly compressed compared to those of the recent materials. Mutilation of Boone’s type material (YPM 6628) also included anterior tearing of the abdomen exposing small amounts of muscle tissue that were recovered for use in genetic analyses. We were able to successfully amplify ~200 bp from 16S fragment of the holotype of *A. platycheirus*. The obtained sequence differed by only one bp from those of the Colombian material assigned to *A. platycheirus*. Since the amount of variation in this region of 16S typically exceeds 10 (up to 18) bp between other species of the *A. floridanus* complex, we feel this provides some molecular evidence that *A. platycheirus* extends from the Caribbean Sea (Cuba, Colombia) to the northern Gulf of Mexico.

The material of *A. platycheirus* from Haiti reported by Boone (1930) could not be located for re-examination and is therefore tentatively assigned to *A. platycheirus*. Two of the Haitian specimens, a male and a female (both complete), were found inside a loggerhead sponge, which is a highly unusual habitat for species of the *A. floridanus* complex. The third mutilated specimen was collected from a fish stomach. Importantly, Boone’s (1930) illustrations of the major and minor cheliped depart from Boone’s (1927) illustrations of the holotype specimen, however these differences seem to be attributed to differences in the illustrator’s artistic rendition (Lee Boone? vs. Helen Ziska). Other characteristics, such as the antennal scale, are in accordance with *A. platycheirus*.

Christoffersen (1979) provided a detailed description (including color pattern) and figures of Brazilian material of *A. floridanus*. In an attempt to locate Christoffersen’s material (much of which lacked catalog numbers) we requested several lots of Brazilian material from MZUSP, USNM, and MNHN. We successfully obtained material from USNM and MNHN, which was confirmed to be *A. platycheirus* (MNHN-IU-2013-13192, USNM 144013). However, when we requested specimens from MZUSP, we learned that catalog numbers used in Christoffersen (1979) did not match present-day catalog numbers in MZUSP (eg. MZUSP 25 was not *A. floridanus*, but rather a non-decapod), making direct comparison of this material impossible. Some of Christoffersen’s material, in addition to alternative lots obtained from MZUSP and molecular evidence (Bracken-Grissom *et al.* this volume), suggests the distribution of *A. platycheirus* extends to Brazil (Rio de Janeiro to Maceió). However, *A. floridanus* was also identified among Brazilian material (USNM 310856, MZUSP 05322, MZUSP 25380) so careful study will be required in separating these populations (see also *A. floridanus*).

Alpheus platycheirus is closely related to the eastern Pacific *A. hephaestus* **sp. nov.**, from which it can be distinguished by the color pattern (Fig. 2j–k, g–i) and a generally deeper longitudinal furrow on the lateral surface of the major cheliped ischium in mature specimens. For genetic differences between *A. platycheirus* and *A. hephaestus* **sp. nov.** see Bracken-Grissom *et al.* (this volume). *Alpheus platycheirus* can be separated from other

members of the *A. floridanus* complex by the length of the antennal scale (not extending distinctly beyond the third article of the antennular peduncle) and lack of movable spines on the fifth pereopod (Table 1).

Some males of *A. platycheirus* have remarkably elongate chelae, up to 6 times as long as high for the major chela and up to 10 times as long as high for the minor chela. Chace (1972) illustrated strikingly elongate chelipeds of two males from Louisiana (as *A. floridanus*), which were re-examined by us and confirmed to be *A. platycheirus*. Elongate chelipeds were also present in some males from other localities in the northern Gulf of Mexico (e.g. ULLZ 1181, GCRL 2497, GCRL 2500) and several individuals from Brazil (e.g. MZUSP 24525, MZUSP 05372).

The second syntype specimen of *A. floridanus* Kingsley, 1878 (MCZ 4987, male) is tentatively assigned to *A. platycheirus*, based on the length of scaphocerite, armature of the propodus of the fourth pereopod (Figs. 20a–g, 21a–e, 22a–e; see also Table 1), mandible characteristics, as well as partial gene sequences (Bracken-Grissom *et al.* this volume).

Discussion

The present revision of the *Alpheus floridanus* complex has targeted American representatives. It is noted that future studies should examine more material from the eastern Atlantic (Balss 1916; Holthuis 1951; Crosnier & Forest 1966), eastern Pacific, and Caribbean Sea (Williams *et al.* 2001). In addition, several species more or less closely related to *A. floridanus* may exist in the Indo-West Pacific (Chace 1972; Hayashi & Nagata 2002) but exhaustive treatment of those populations is beyond presently available material resources and the scope of this study.

Kingsley's type material. Upon thorough investigation of the syntypes, it becomes evident that they represent two separate species. Morphologically, these two individuals can be distinguished by the size and shape of their antennal scale. The female syntype has a long antennal scale with the distal tooth clearly over-reaching the third article of the antennular peduncle. In the male syntype, the antennal scale is less elongate with the tooth barely over-reaching the third article of the antennular peduncle, a feature mentioned by Kingsley in his original description. Additional molecular evidence supports this separation (following paper, this volume).

In the interest of taxonomic stability, we selected the female syntype as the lectotype of *A. floridanus* s.s. This phenotype is clearly the one most commonly reported in a large body of literature under the name *A. floridanus*, the common shallow water species of the tropical western Atlantic. The male syntype is provisionally placed within *A. platycheirus* based on partial gene sequence and morphological evidence (Figs. 20 a–g, 21 a–e, 22 a–e).

Alpheus floridanus africanus Balss, 1916

Balss (1916) recognized a subspecies, *A. floridanus* Kingsley var. *africana*, from the Ivory Coast (Wappu), which Anker and Dworshak (2004) treated as the species *Alpheus africanus* Balss, 1916, though without further comparative analyses of type materials. In his short description, Balss included a few comments on major cheliped and pereopod morphology, which he used to distinguish the African form from the typical western Atlantic form. After reassessment of Balss' material and new specimens collected, Crosnier and Forest (1966) argued that two forms should be recognized off western Africa, herewith called *A. floridanus floridanus* and *A. floridanus africanus*. Characters used to discriminate between *A. floridanus africanus* and *A. floridanus floridanus* included shape of the major chela, presence/absence of movable spines on the propodus of the pereopods, and length of the second cheliped (Crosnier & Forest 1966). Balss (1916), Chace (1972), and Crosnier and Forest (1966) all acknowledged the existence of a unique eastern Atlantic *A. floridanus africanus* but disagreed on a key diagnostic character: the presence/absence of movable spines on the propodus of the pereopods. Balss (1916) noted no movable spines on the propodus for any of the pereopods, but Chace (1972) and Crosnier and Forest (1966) reported as many as three such spines on the propodus of the third pereopod. Crosnier and Forest (1966) also found 1–2 such spines on the propodus of the fourth pereopod, noting that those spines were in some instances absent. While our present cursory examination of eastern Atlantic materials cannot broadly represent populations of the complex from off western Africa, the specimens that we examined (RMNH 9312, RMNH D.21576, RMNH D10208, IU-2013-13191) all bore movable spines on the propodus of the third and fourth pereopod, much as reported by Chace (1972) and Crosnier and Forest (1966). However, these spines were sometimes found to be inconspicuous even at high magnification and easily could be overlooked.

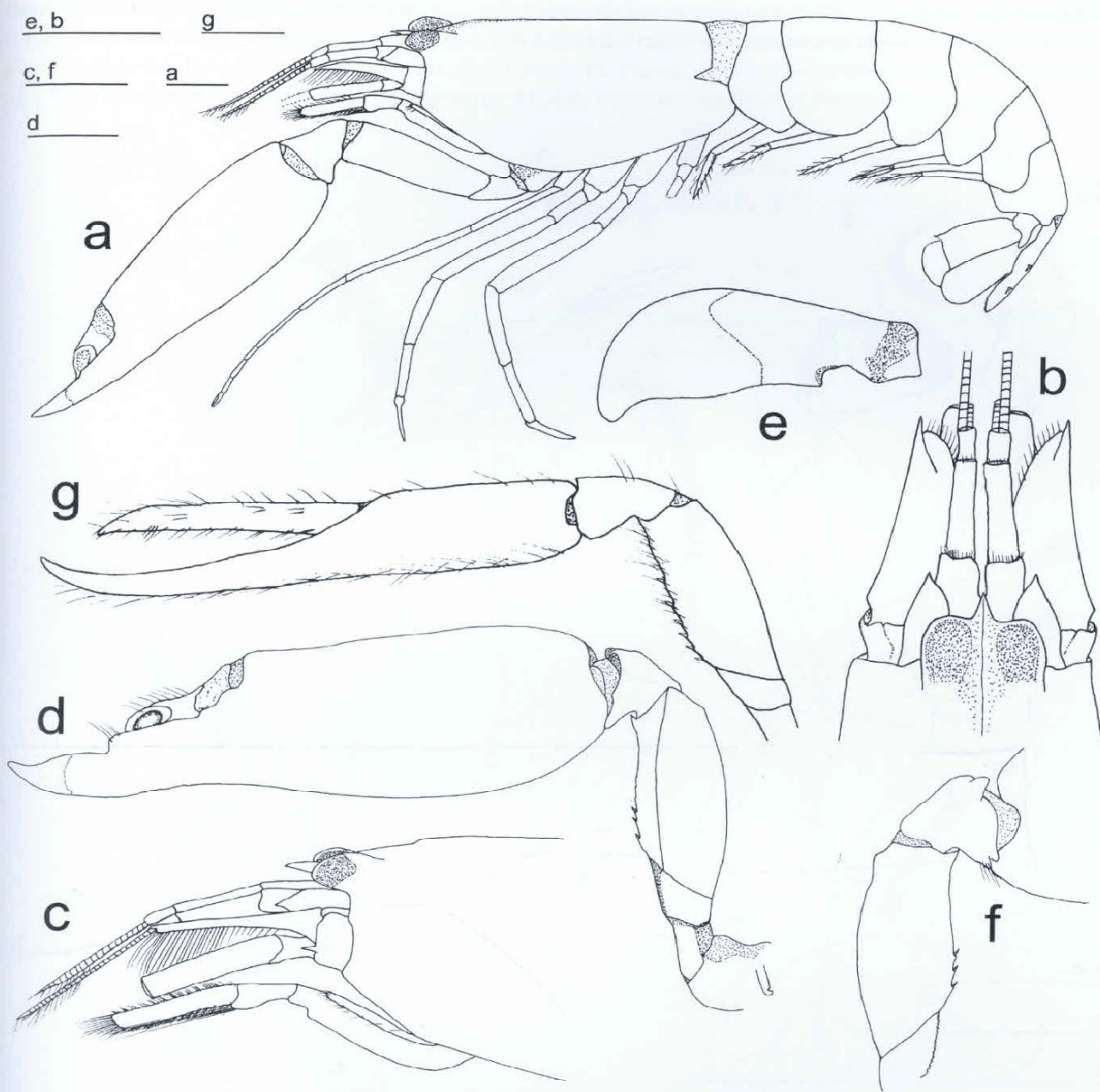


FIGURE 20. *Alpheus* sp., possibly *A. platycheirus* Boone, 1927: a–g, male (MCZ 4987, second syntype of *A. floridanus*): a, habitus, lateral; b, anterior carapace, dorsal; c, anterior carapace, lateral; d, major cheliped (lacking dactylus), lateral (setobranch not shown); e, disarticulated dactylus of major chela, lateral; f, major cheliped, proximal articles, mesial; g, right minor cheliped, mesial (dactylus possibly atypical). Scale bars = 2.0 mm.

Holthuis (1951) also recognized *A. floridanus africanus*, stating the main difference between the two variants to be found in the shape of the first pereopods, as previously noted by Balss (1916). Holthuis' (1951) material from the Gold Coast of Africa contained individuals with slender first chelipeds, deep adrostral furrows and steep dorsal carinas extending postorbitally along the carapace. His description and illustrations match the specimens we examined and appear to accurately characterize *A. floridanus africanus*.

From the limited African material we have examined some exhibit morphological features reminiscent of the "africanus" form described by previous workers, as we herein represent by illustration (RMNH 9312, RMNH D.21576, RMNH D10208, Figs 23a–h, 24a–g, and 25a–f). The second "floridanus" form reported from western Africa is confirmed to be *A. roblesi* sp. nov. (MNHN-IU-2013-13191) after examination of Crosneir and Forest's

(1966) material. Without having yet accessed type materials upon which Balss based his subspecies (*A. floridanus africanus*), some uncertainty must remain as to whether our "africanus" material in fact represents the same form that other workers (Anker & Dworschak 2004) have elevated to the species, *A. africanus*.

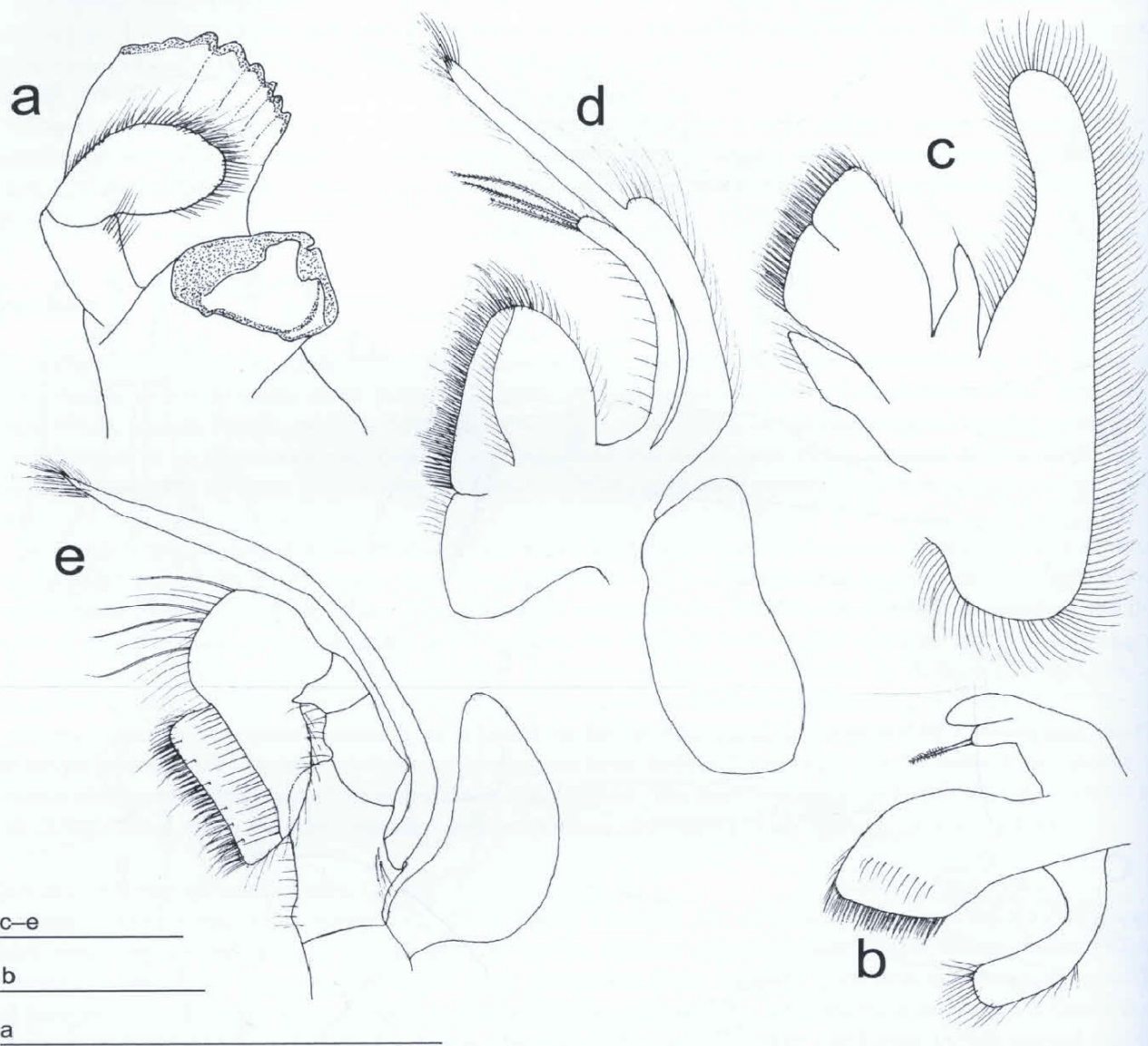


FIGURE 21. *Alpheus* sp., possibly *A. platycheirus* Boone, 1927: a–e, male (MCZ 4987, second syntype of *A. floridanus*): a, left mandible, mesial; b, left maxillule, lateral; c, left second maxilla, lateral; d, left first maxilliped, lateral; e, left second maxilliped, lateral. Scale bars = 2.0 mm (a) and 1.0 mm (b–e).

Molecular evidence excludes our material of "africanus" from the group of American species that we have here reported upon, and supports its distinction at the species level, albeit with close affinity to *A. floridanus* s.s. from the western Atlantic (Bracken-Griessom *et al.* this volume). However, the "africanus" morphological features are in many respects very near those of *A. platycheirus* and *A. hephaestus* **sp. nov.** (Table 1), and a more comprehensive comparative study of African populations is certainly warranted. To date, there is also nothing known of color patterns for the west African materials, which would likely facilitate distinctions such as herein made on the basis of color among other members of this species complex.

Color pattern. Color and pigment pattern can be of great utility for discrimination between closely related species within the genus *Alpheus* (Anker *et al.* 2007a; 2008b; 2008c; Knowlton & Mills 1992), particularly within the *A. floridanus* complex (Figs. 1 and 2). Christoffersen (1979) reported *A. floridanus* s.l. to have a "body

speckled with green and brown chromatophores; traces of blue or black pigmented pleura, uropods and telson; chelae with irregular greenish brown stains, spaces between these sometimes speckled by blue chromatophores; major chela with finger tips between brown and pink.” This description is in general keeping with published color photographs of *A. floridanus* s.s. by one of us (D.L.F) from Ft. Pierce, Florida (McLaughlin *et al.* 2005; Williams *et al.* 1989), though the origins of those photographic subjects were not identified at the time of publication.

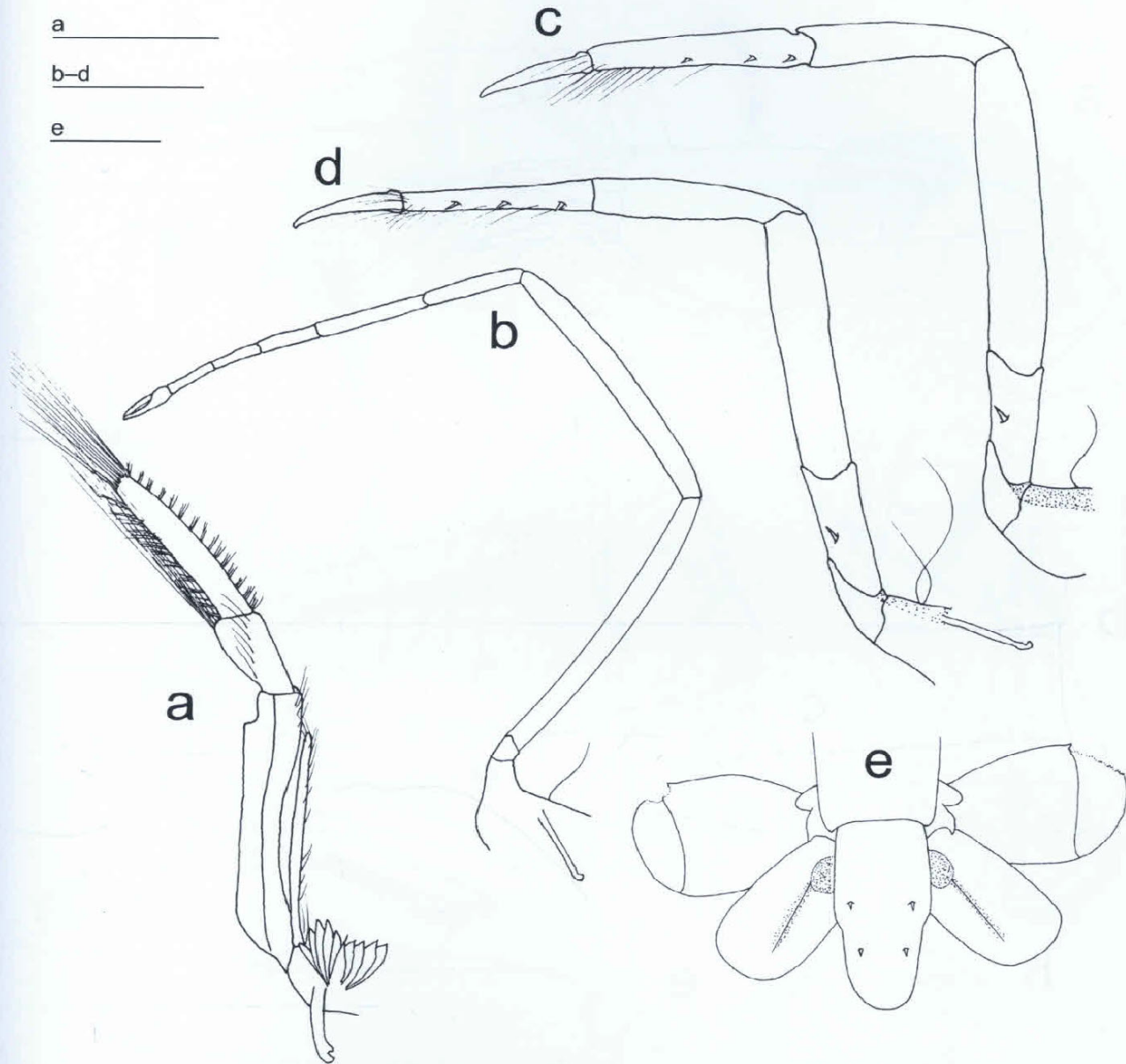


FIGURE 22. *Alpheus* sp., possibly *A. platycheirus* Boone, 1927: a–g, male (MCZ 4987, second syntype of *A. floridanus*): a, left third maxilliped, lateral; b, left second pereopod, lateral; c, left third pereopod (missing epipod), lateral; d, left fourth pereopod, lateral; e, sixth abdominal somite, telson and uropods, dorsal. Scale bars = 2.0 mm.

We herewith document color and pattern for specimens of *A. hephaestus* **sp. nov.**, *A. roblesi* **sp. nov.**, *A. ulalae* **sp. nov.**, *A. platycheirus*, and *A. floridanus* s.s. Striking variations within the *A. floridanus* complex range from patterns of fire-red or brown chromatophores in some species to others with a translucent-opaque appearance (Figs. 1 and 2). However, it is important to note that color varies within yet-to-be-determined ranges for most of these species, as seen when comparing populations *A. floridanus* s.s. from Ft. Pierce, Florida, Belize, and the southwestern Gulf of Mexico (Fig. 1). So far as presently evident (Table 1), *A. platycheirus*, *A. ulalae* **sp. nov.**, and *A. roblesi* **sp. nov.** all have a speckled or patchy orange pattern, especially evident on the major and minor

chelipeds, while none appears to have the striking pattern of longitudinal bars seen on the abdomen of *A. floridanus* s.s. *Alpheus roblei* sp. nov. is largely translucent and ovigerous females carry bright yellow eggs. *Alpheus ulalae* sp. nov. is similarly translucent, and females carry bright greenish eggs. *Alpheus hephaestus* sp. nov. can be most easily distinguished from the other species by its dense pattern of reddish-orange anastomosing chromatophores. Within the *A. floridanus* complex, it is likely that color and pattern can be further developed as powerful tools for identifications in the field, especially with enhanced efforts for proper photodocumentation.

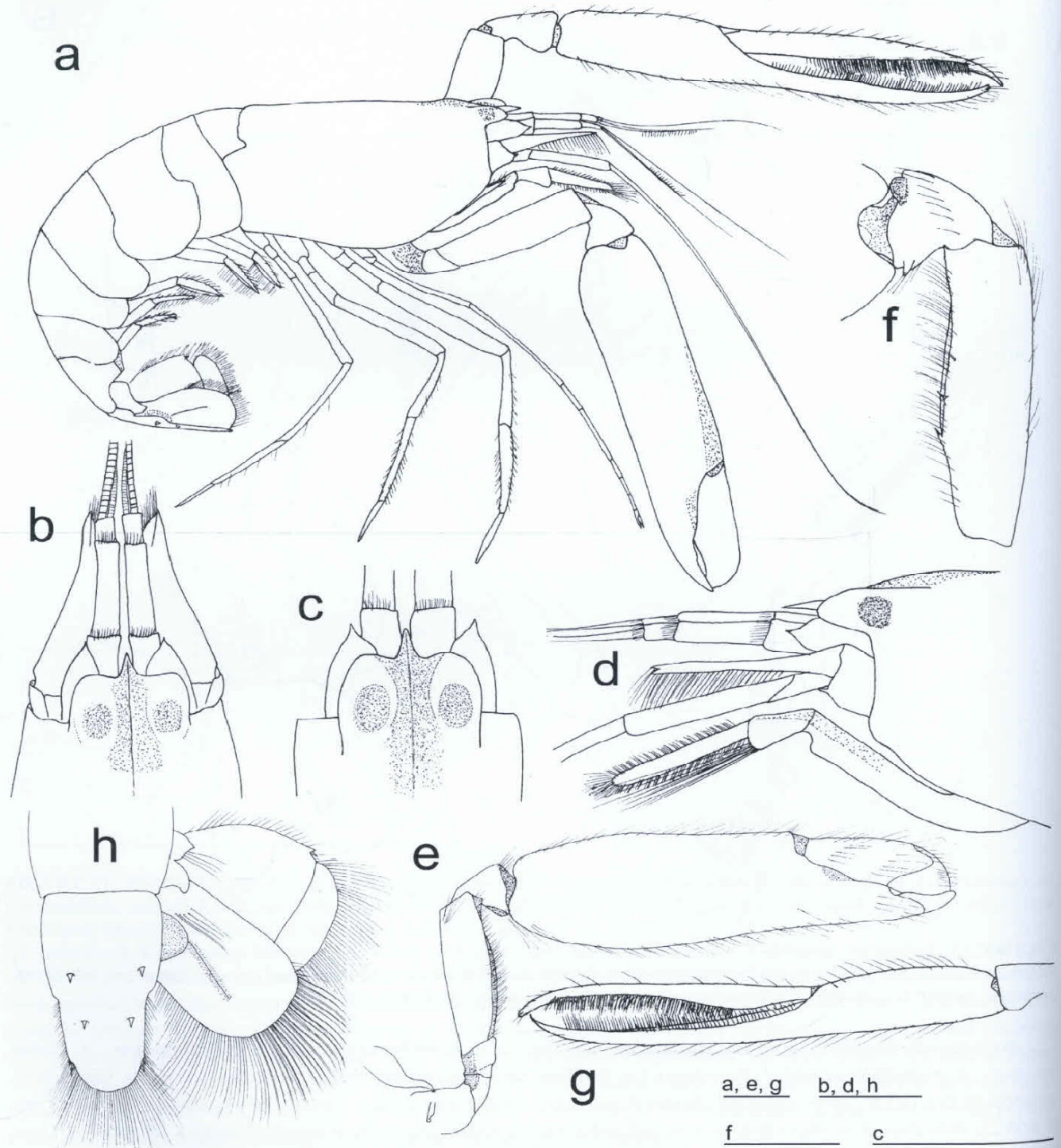


FIGURE 23. *Alpheus floridanus africanus* Balss, 1916: a–h, male (RMNH 9312 = tissue/sequence ULLZ 9122): a, habitus; b, c, anterior carapace, dorsal; d, anterior carapace; e, major right cheliped, lateral; f, right major cheliped carpus and merus, mesial; g, right minor cheliped, lateral; h, sixth abdominal somite, telson and uropods, dorsal. Scale bars = 2.0 mm.

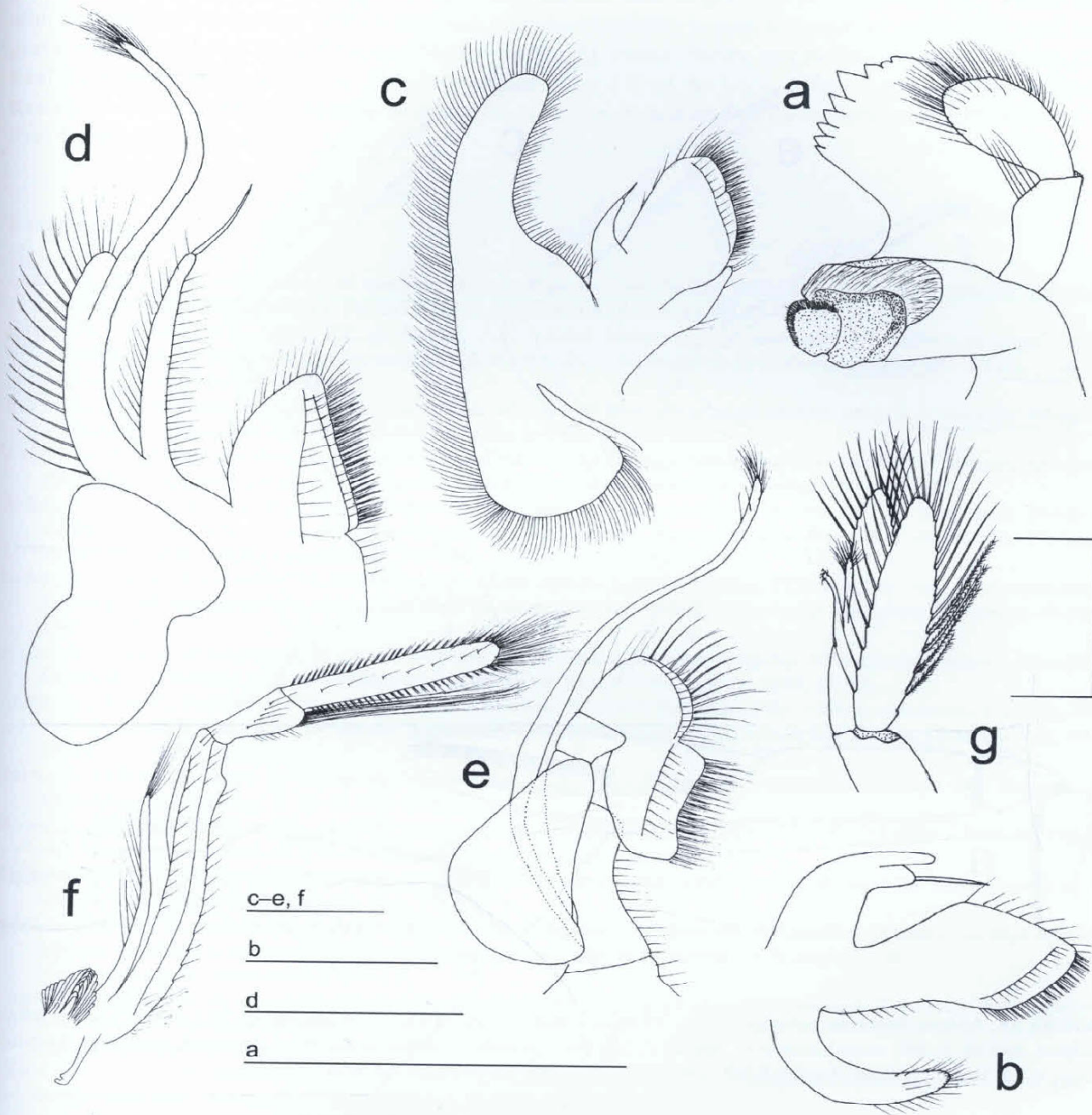


FIGURE 24. *Alpheus floridanus africanus* Balss, 1916: a–g, male (RMNH 9312 = tissue/sequence ULLZ 9122): a, right mandible, mesial; b, right maxillule, lateral; c, right second maxilla, lateral; d, right first maxilliped, lateral; e, right second maxilliped, lateral; f, right third maxilliped, lateral; g, right second pleopod, appendix masculina and appendix interna (serrated setae shown only in bracket). Scale bars = 1.0 mm (b–e), 2.0 mm (a, f, g).

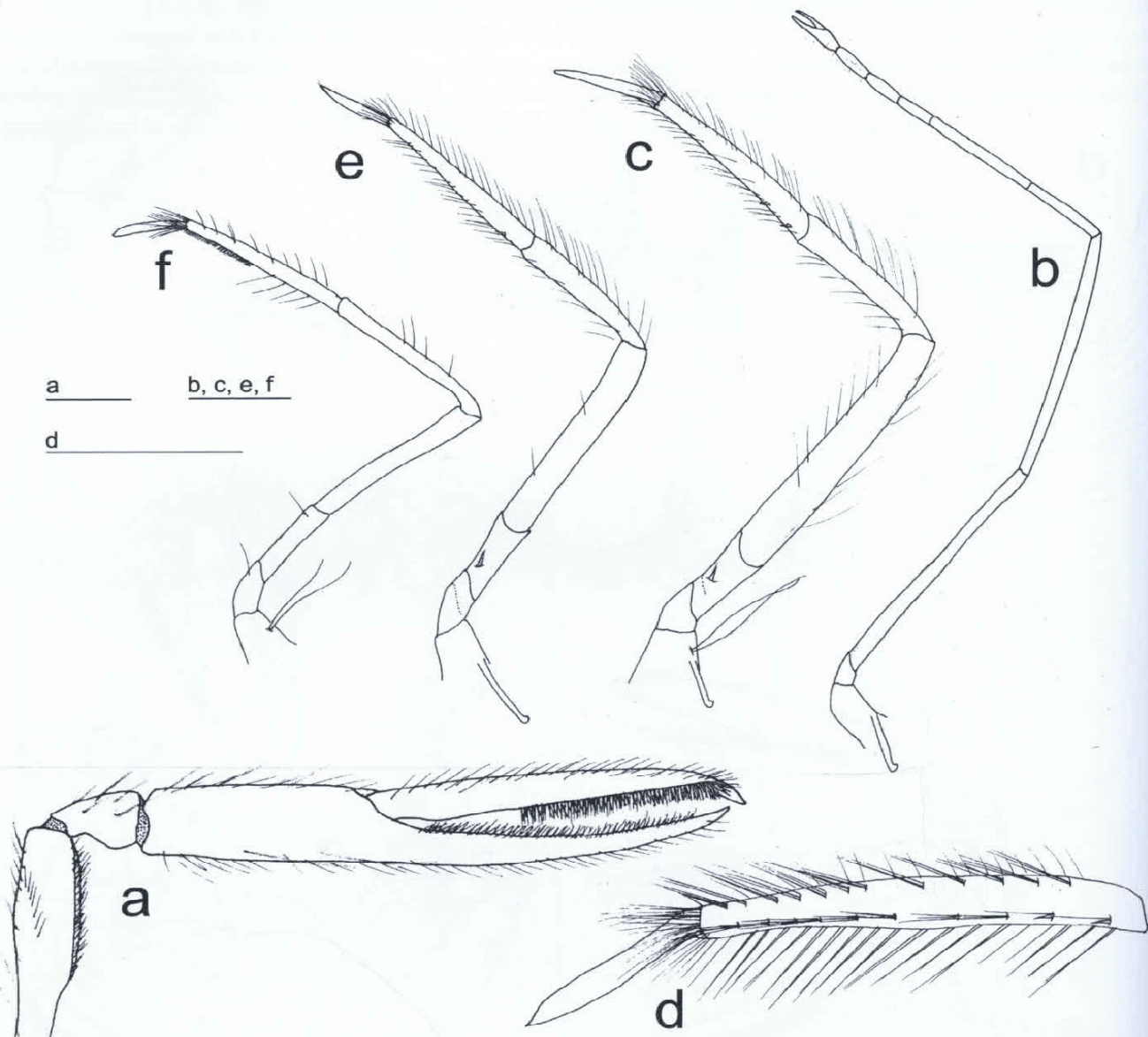


FIGURE 25. *Alpheus floridanus africanus* Balss, 1916: a–f, male (RMNH 9312 = tissue/sequence ULLZ 9122): a, left minor cheliped, mesial; b, left second pereopod, lateral; c, left third pereopod, lateral; d, left third pereopod, propodus, dactylus, lateral; e, left fourth pereopod, lateral; f, left fifth pereopod, lateral. Scale bars = 2.0 mm.

Acknowledgments

We thank F. Alvarez, L. Colbari, R. Collin, S. De Grave, E. Escobar, J. Felder, C. Fransen, S. Fredericq, E. García, G. Giribet, E. Lazo-Wasem, R. Lemaitre, P. Martin-Lefevre, E. Palacios-Theil, V. Paul, S. Rabalais, M. Rice, R. Robles, K. Ruetzler, M. Tavares, B. Thoma, and A. Windsor for providing museum materials and/or helping us to otherwise obtain collections. Staff at the National Museum of Natural History, Smithsonian Institution; Universidad Nacional Autónoma de México; Smithsonian Tropical Research Institute's Bocas del Torro Research Station; Peabody Museum of Natural History at Yale University; Museum of Comparative Zoology, Harvard University; Muséum National d'Histoire Naturelle, Paris; Museum of Zoology of the University of São Paulo; and Oxford University Museum of Natural History kindly assisted with loans, field research, or hosting our visits. We are grateful to A. Anker, R. Bauer, C. Chlan, S. De Grave, S. France, and R. Robles for valuable comments and

advice on this manuscript. This study was supported under funding by U.S. National Science Foundation grants NSF/BS&I DEB-0315995, NSF/AToL EF-0531603, and NSF RAPID grant no. DEB-1045690 to D. Felder, along with support from the Gulf of Mexico Research Initiative (GOMRI) to both investigators. Additional small travel grants were provided by the Smithsonian Marine Station, Ft. Pierce Florida, and the Smithsonian Caribbean Coral Reef Ecosystems Program, Belize. This is contribution no. 170 of the UL Lafayette Laboratory for Crustacean Research, no. 973 for the Smithsonian Marine Station, Ft. Pierce, and no. 969 for the Smithsonian Caribbean Coral Reef Ecosystems Program.

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Key to American species of the *Alpheus floridanus* complex

1. Antennal scale (scaphocerite) lateral margin sinuous (Fig. 6 c), medial bend (toward body midline) originating near midlength; pereopod 5 propodus bearing 1–7 movable spines (rarely lacking, often conspicuous) on ventromesial surface (Fig. 8 e); in life, weakly pigmented except for irregular orange banding on chelae, body translucence overlain by diffuse dorsal aggregations of small orange chromatophores [inner continental shelf, southern Gulf of Mexico, southeastern Florida and Caribbean; eastern Atlantic, Africa] *Alpheus robesli* sp. nov.
- Antennal scale lateral margin concave (Figs. 3 a, 4 b, 9 b, 12 b, 15 d), medial bend (if any) restricted to spine at tip; pereopod 5 propodus lacking movable spines along ventromesial surface; in life, body pigmentation varied, sometimes including strongly contrasting dorsal patterns of red, orange, green, brown, or yellow. 2
2. Antennal scale (scaphocerite) blade and its distolateral tooth distinctly over-reaching distal end of antennular peduncle (Figs. 3 a, 4 b, 9 b), distolateral tooth distinctly over-reaching blade, often by $\geq 1/10$ blade length 3

- Antennal scale blade and its distolateral tooth reaching about to distal end of antennular peduncle, rarely with both slightly over-reaching it, distolateral tooth exceeding blade by $<1/10$ blade length, if at all 4
- 3. Pereopod 3 and 4 propodus bearing 1–2 movable spines on proximal half of ventrolateral margin (Fig. 11 b, d, e); mandible incisor with strong dentition on $\leq 1/2$ of cutting edge (Fig. 10 a); in life, body translucence overlain by diffuse dorsal aggregations of small orange chromatophores, lacking distinct longitudinal bars on carapace and abdomen (Fig. 2 e–f) [inner continental shelf, Gulf of Mexico and Caribbean] *A. ulalae* sp. nov.
- Pereopod 3 and 4 propodus bearing 3 or more movable spines along ventrolateral margin, often extending onto distal half (Figs. 3 l, m; 5 b, c); mandible incisor with strong dentition along entire margin (Fig. 3 c); in life, chromatophores forming strong pattern of brownish-maroon to orange longitudinal bars on off-white to pale green background of carapace and abdomen (Fig. 1 a–g) [nearshore and shallow western Atlantic, southern Gulf of Mexico, Brazil, southeastern Florida and Caribbean] *A. floridanus* s.s.
- 4. In life, chromatophores typically rust-orange to red, loosely distributed into interconnected spots and ill-defined lateral bars or crescents on abdominal somites, sixth somite not dorsally more pigmented than preceding somites or proximal half of uropodal endopods (Fig. 2 j–l); mature specimens with major cheliped ischium lateral longitudinal furrow deeply defined; pereopod 4 propodus bearing 1–4 movable spines on ventrolateral surface [muddy middle and inner continental shelf, northern Gulf of Mexico through Caribbean and Brazil] *Alpheus platycheirus*
- In life, chromatophores typically deep fire-red to reddish brown, densely distributed overall, sixth abdominal somite more densely pigmented than fifth or proximal half of uropodal endopods (Fig. 2 g–i); mature specimens with major cheliped ischium lateral longitudinal furrow broad, shallow; pereopod 4 propodus bearing 3–4 movable spines on ventrolateral surface [muddy middle and inner continental margins, eastern Pacific, Gulf of California to Ecuador] . . . *Alpheus hephaestus* sp. nov.