



Revision of the *Alpheus cylindricus* Kingsley, 1878 species complex (Crustacea: Decapoda: Alpheidae), with revalidation of *A. vanderbilti* Boone, 1930

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Abstract

Alpheus cylindricus Kingsley, 1878, previously believed to be widely distributed in the tropical eastern Pacific and western and eastern Atlantic, is revised. Two species are recognized based on morphology, color pattern and genetics. *Alpheus cylindricus* is restricted to the tropical eastern Pacific, from the Gulf of California to the Galapagos. A neotype of *A. cylindricus* from the type locality, Las Perlas Islands, is designated. On the Pacific coast of Panama, this species commonly inhabits purple sponges growing among or under large intertidal rocks. *Alpheus vanderbilti* Boone, 1930 is formally resurrected from the synonymy of *A. cylindricus*; it occurs in the tropical western Atlantic, from Bermuda to Brazil, and in the tropical eastern Atlantic, around the islands of the Gulf of Guinea. In the Caribbean, *A. vanderbilti* is most often encountered in large loggerhead sponges, *Spheciospongia vesparia* (Lamarck, 1814), while in the Gulf of Guinea it inhabits sponge-lined tunnels in coral rocks. Complete synonymies and GenBank barcodes (COI) are provided. Phylogeography of the *A. cylindricus* complex is discussed based on molecular data.

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

Introduction

Alpheus cylindricus Kingsley, 1878 is characterized by a uniquely shaped, cylindrical major chela, making it one of the most distinctive and unmistakable species of the genus *Alpheus* Fabricius, 1798. This hyper-diverse genus (the largest in the Decapoda) is traditionally subdivided into seven informal species groups. *Alpheus cylindricus* was initially placed in the *A. crinitus* Dana, 1852 group (Coutière 1899; Crosnier & Forest 1966; Kim & Abele 1988) based on its reduced rostrum and orbital teeth, swollen and largely smooth major chela, and distoventrally unarmed basicerite. However, the twisted dactylus and the presence of a deep longitudinal groove and subacute distal teeth on the palm of the major chela—remnants of reduced crests (see Kim & Abele 1988: fig. 19)—suggest affinities with species of the *A. macrocheles* (Hailstone, 1835) group (Anker 2001b). Molecular studies (Williams *et al.* 2001) support this hypothesis, as *A. cylindricus* was found to be close to *A. peasei* (Armstrong, 1940), a typical member of the *A. macrocheles* group. The highly modified morphology of *A. cylindricus* may reflect the fact that it typically lives in the enclosed spaces of sponges or sponge-lined rock cavities. The reduction of chela sculpture and blunting of acute structures such as the rostrum, orbital teeth and the basicerite tooth appear to have evolved independently in a number of sponge- and

cavity-dwellers, e.g., some members of the *Alpheus crinitus* group, *A. simus* Guérin-Méneville, 1856 and *A. saxidomus* Holthuis, 1980, and many sponge-dwelling species of *Synalpheus* Bate, 1888 (A. Anker, pers. obs.).

Alpheus cylindricus was originally described from Las Perlas Islands on the Pacific coast of Panama (Kingsley 1878a). Its range previously encompassed the tropical eastern Pacific and western and eastern Atlantic (Chace 1937, 1972; Crosnier & Forest 1966; Christoffersen 1979, 1998; Wicksten 1983; Kim & Abele 1988). The western Atlantic form was originally described as *A. vanderbilti* Boone, 1930 from a female specimen dredged south of Key West, Florida. Boone (1930) provided a few figures and listed two differences between *A. vanderbilti* and the eastern Pacific *A. cylindricus*, referring to Kingsley's (1878a) brief description of the latter species. Chace (1937) compared specimens of *A. cylindricus* from the Gulf of California with those of *A. vanderbilti* from Bermuda and found "no apparent difference between the two". Since some of Kingsley's statements in the original description of *A. cylindricus* appear to be "ambiguous", Chace decided to place *A. vanderbilti* in synonymy with *A. cylindricus*. Crosnier & Forest (1966) extended the range of *A. cylindricus* to the tropical eastern Atlantic, providing a detailed description and good illustrations. These authors stated that they could not find any differences between the eastern Atlantic, western Atlantic and eastern Pacific specimens. Christoffersen (1979) reported *A. cylindricus* from Brazil and noted some differences between his Brazilian and Crosnier & Forest's (1966) material. Finally, Kim & Abele (1988) provided a detailed description and excellent illustrations of *A. cylindricus* based on specimens from the Pacific coast of Mexico.

On the other hand, several workers expressed doubts about the conspecific status of Atlantic and Pacific populations of *A. cylindricus*. Knowlton *et al.* (1993) showed genetic divergence and reproductive incompatibility between the transisthmian populations of *A. cylindricus*; Williams *et al.* (2001) provided additional genetic data pointing to their distinctiveness; finally, Anker (2001a) listed *A. cylindricus* as a possible species complex on morphological grounds.

The present study is the first revision of the *A. cylindricus* complex, based on study of specimens from the eastern Pacific (Panama), western Atlantic (Panama) and eastern Atlantic (São Tomé). We show that based on morphology, color patterns, ecology and genetics, *A. cylindricus sensu lato* is a complex of three genetically distinct populations. Two of them—the eastern Atlantic and the western Atlantic populations—have not diverged sufficiently to be considered distinct species, although subspecific status might be warranted with additional data. On the other hand, the eastern Pacific and Atlantic populations exhibit substantial divergence in genetics and color pattern (as well as reproductive compatibility), although they are not clearly distinguishable in morphology. Therefore, we recognize two distinct species: *A. cylindricus* (*sensu* Kingsley 1878a; Kim & Abele 1988) in the eastern Pacific and *A. vanderbilti* (*A. cylindricus sensu* Crosnier & Forest 1966; Chace 1972; Christoffersen 1979) in the western and eastern Atlantic.

Since Kingsley's type of *A. cylindricus* appears to be lost (Hendrix 1971), a recently collected, complete male specimen from Las Perlas is designated as a neotype to fix the identity of this species. Boone's types, including that of *A. vanderbilti*, could not be located at the American Museum of Natural History, New York (AMNH) (C. Boyko, pers. comm.); however, as we did not have a specimen from Florida, a similarly desirable neotype of *A. vanderbilti* could not be selected. An updated synonymy, GenBank barcodes (COI) and color photographs are provided for *A. cylindricus* and *A. vanderbilti* (both eastern and western Atlantic forms).

Material and methods

Specimens were collected under rocks at low tide or from crevices of coral rocks at depths of 2–5 m; most were photographed alive before being preserved in 70% or 95% ethanol. Specimens selected for RNA/DNA extractions were preserved in RNAlater (Ambion) or frozen; in some cases, a leg was detached from a speci-

men and preserved in RNAlater, while the body of the specimen was preserved in ethanol.

The material is deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM), Muséum national d'Histoire naturelle, Paris, France (MNHN), Oxford University Museum of Natural History, Oxford, UK (OUMNH), and Colección de Referencia, Departamento de Biología Marina, Universidad de Panamá, Panama City, Panama (UP). Carapace length (CL) and total length (TL) were measured in mm along the mid-dorsal line from the tip of the rostrum to the posterior margin of the carapace and telson, respectively. Other abbreviations used in the text: BAMZ—Bermuda Aquarium, Natural History Museum and Zoo, Bermuda; fcn—field collection number; EP—eastern Pacific; EA—eastern Atlantic; WA—western Atlantic.

COI sequencing and PCR amplifications were carried out as described in Anker *et al.* (2007). Genetic distances were calculated using the Kimura 2-Parameter (K2P) distance method as implemented in Mega v3.1 in order to facilitate comparisons with alpheid distances obtained previously (Knowlton *et al.* 1993; Knowlton & Weigt 1998). A rate of 1.5 % sequence divergence per million years was used to estimate the timing of divergence of sister taxa. This rate was estimated by averaging the K2P genetic distances for both 5' and 3' COI sequences obtained from the transisthmian sister species pair *Alpheus antepaenultimus* Kim & Abele, 1988 / *A. chacei* Carvacho, 1979 (GenBank accession numbers AF309875, AF309876, AF309884, AF308989, AF308983, EF532616–EF532619). This geminate species pair has the smallest observed genetic distance of all transisthmian comparisons, and its divergence is likely to correspond to the final closing of the Panamanian isthmus (approximately three million years ago) (Knowlton & Weigt 1998). This rate differs slightly from the published rate of 1.4% (Knowlton & Weigt 1998), obtained from comparisons of COI sequences from the 3' end only.

Taxonomy

Alpheus Fabricius, 1798

Alpheus cylindricus Kingsley, 1878

(Figs. 1; 3A, D; 4A–D, I)

Alpheus cylindricus Kingsley 1878a: 196; Kingsley 1878b: 58; Lockington 1878: 478; Kingsley 1883: 120; Coutière 1899 (for page numbers see Chace & Forest 1970); Rodríguez de la Cruz 1977: 28; Carvacho & Ríos 1982: 282; Wicksten 1983: 43 (part.); Kim & Abele 1988: 47, fig. 19; Villalobos-Hiriart *et al.* 1989: 18; Flores-Hernandez 1991: 96; Alvarez del Castillo *et al.* 1992: 5; Wicksten & Hendrickx 1992: 4 (part.); Hendrickx 1992: 8; Hendrickx 1993a: 306; Hendrickx 1993b: 6; Hendrickx 1995: 432; Lemaitre & Alvarez-Leon 1992: 42; Knowlton *et al.* 1993: 1630 (part.); Camacho 1996: 67; Villalobos 2000: 47, fig. 23; Williams *et al.* 2001: 377 (part.); Wicksten & Hendrickx 2003: 63 (part.).

Crangon cylindricus—Chace 1937: 121; Schmitt 1939: 24.

Alpheus cylindrius (lap. cal.)—Vargas & Cortés 1999: 899.

Not *Alpheus cylindricus*—Zimmer 1913: 394; Crosnier & Forest 1965: 606; Crosnier & Forest 1966: 257, fig. 16; Hendrix 1971: 71; Coelho & Ramos 1972: 149; Chace 1972: 65; Pequegnat & Ray 1974: 246, fig. 49d; Ray 1974: 92, figs. 72–78; Christoffersen 1979: 310; Christoffersen 1980: 50; Coelho & Ramos-Porto 1980: 135; Coelho *et al.* 1980: 48; Abele & Kim 1986: 196, 206–207, fig. a–c; Sterrer 1986: 326, text. pl. 105, pl. 9, fig. 7; Rodríguez 1986: 138, fig. 33; Martínez-Iglesias *et al.* 1993: 11; Knowlton *et al.* 1993: 1630 (part.); Martínez-Iglesias *et al.* 1996: 33; Martínez-Iglesias *et al.* 1997: 404, fig. 9; Williams *et al.* 2001: 377 (part.); McClure 2005: 138, fig. 11 (reproduced from Kim & Abele 1988); Coelho *et al.* 2006: 51 (= *A. vanderbilti* Boone, 1930).

Not *Crangon cylindricus* – Schmitt 1924: 74; Pearse 1950: 150 (= *A. vanderbilti* Boone, 1930).

Type material. Panama (Pacific coast). Neotype: male (CL 9.4), USNM 1109158, Las Perlas Islands, off Contadora, extreme low tide, rocky intertidal, from rock crevices, coll. J. Jara, C. Hurt, A. Anker, E. Tóth and E. Gómez, 31 Mar 2006 [fcn 06-373A].

Additional material. Panama (Pacific coast). 1 ovig. female (CL 11.0), USNM 1109159, same collection data as for neotype [fcn 06-373B]; 1 male (CL 9.7), 1 ovig. female (CL 11.3), USNM 1109160, same collection data as for neotype [fcn 06-367]; 3 males (CL 6.7–8.8), 1 ovig. female (CL 9.6), USNM 1109161, Taboga, off Taboguilla, dredged from less than 30 m, coll. P. Barber *et al.*, 30 Sep 2005 [fcn 05-134]; 1 male (CL 8.3), OUMNH-ZC 2007-13-036, Amador causeway, Punta Culebra, rocky intertidal, extreme low tide, from sponges among mud-covered boulders, coll. A. Anker and C. Hurt, 2 Mar 2006 [06-276, with host sponge]; 1 male (CL 6.9), 1 female (CL 7.7), USNM 1109162, same collection data as for previous specimen [fcn 06-278, with host sponge]; 1 male (CL 9.3), USNM 1109163, same collection data as for previous specimen [fcn 06-274]; 1 ovig. female (CL 8.9), USNM 1109164, same collection data as for previous specimen [fcn 06-275]; 1 male (CL 7.5), 1 ovig. female (CL 10.0), MNHN-Na 16706, same collection data as for previous specimen [fcn 06-272, 06-273]; 1 male (CL not determined), UP, Amador Causeway, Isla Naos, Punta Culebra, under rocks in purple sponge, low tide, coll. A. Anker and I. Marin, 17 Apr 2007 [fcn 07-124].

Diagnosis. Species of *Alpheus macrocheles* group. Frontal margin of carapace with very short rostrum, without or with blunt orbital teeth; orbital hoods moderately inflated. Antennule with second peduncular segment about three times as long as wide; stylocerite with blunt tip, not reaching distal margin of first segment. Antenna with basicerite lacking sharp distoventral tooth; scaphocerite with strong distolateral tooth and reduced blade; carpocerite overreaching scaphocerite, reaching or slightly overreaching end of antennular peduncle, distomesial margin with small tooth. Third maxilliped not particularly broadened, antepenultimate and penultimate segments with rows of spines on ventral margin. Major cheliped with merus lacking sharp distomesial tooth; chela subcylindrical, without notches or constrictions; mesial face smooth; lateral face with shallow groove bordered by subacute tooth distally; adhesive disks well developed; dactylus reaching far beyond pollex, compressed, twisted laterally, with greatly reduced plunger; pollex reduced to short subacute protuberance. Minor cheliped with merus lacking sharp distomesial tooth; chela smooth; fingers slightly longer than palm, slender and strongly curved laterally, without balaeniceps setae. Second pereopod with first carpal segment about twice as long as second; chela with groups of thickened setae. Third pereopod with unarmed ischium; merus and carpus without spines on ventral margin, distoventral angle not projecting as tooth; propodus with row of spines; dactylus stout, biunguiculate. Male second pleopod with typical appendices masculina and interna. Uropod with protopod bearing acute lateral tooth; exopod with distolateral spine bordered laterally by sharp distolateral tooth and mesially by triangular tooth of transverse suture; endopod with row of spines on distomesial margin. Telson tapering distally, with two pairs of strong dorsal spines; posterior margin slightly convex, with two pairs of spines at each posterolateral angle.

Description. For detailed description and illustrations see Kim & Abele (1988).

Color pattern. Background color pale grey, semitransparent; carapace with broadly X-shaped patch of red chromatophores on gastric region, patches of red chromatophores also on rostral and post-rostral region; red transverse band present along posterior margin of carapace and articulation between carapace and abdomen; abdomen with broad longitudinal band of red chromatophores running along lateral surface of pleurae and dorsomedially protruding into colorless mediodorsal area, latter usually “spruce-shaped” (Fig. 3A) and interrupted by narrow pale red band on sixth somite; walking legs colorless; second pereopod with orange-red chromatophores; antennular peduncles bright red; antennal peduncles including scaphocerite partly transparent and orange, carpocerite distally reddish; antennular and antennal flagella pale yellow; cheliped meri and carpi mostly colorless mesially, pale orange laterally; palm of major chela pale orange becoming orange-brown distally; linea impressa delimiting pale grey to whitish oval proximolaterally; dactylus purple-brown with white tip; minor chela pale orange, darker distally and on fingers (Fig. 1, 3A); eggs in females bright yellow-orange (Fig. 3D).

Size. The largest examined specimen is an ovigerous female from Las Perlas with CL 11.3 mm and TL 31.3 mm. Kim & Abele (1988) gave the size range of their specimens as following: CL 6.1–9.5 mm for males, 4.8–7.6 mm for females and 5.6–9.3 mm for ovigerous females.

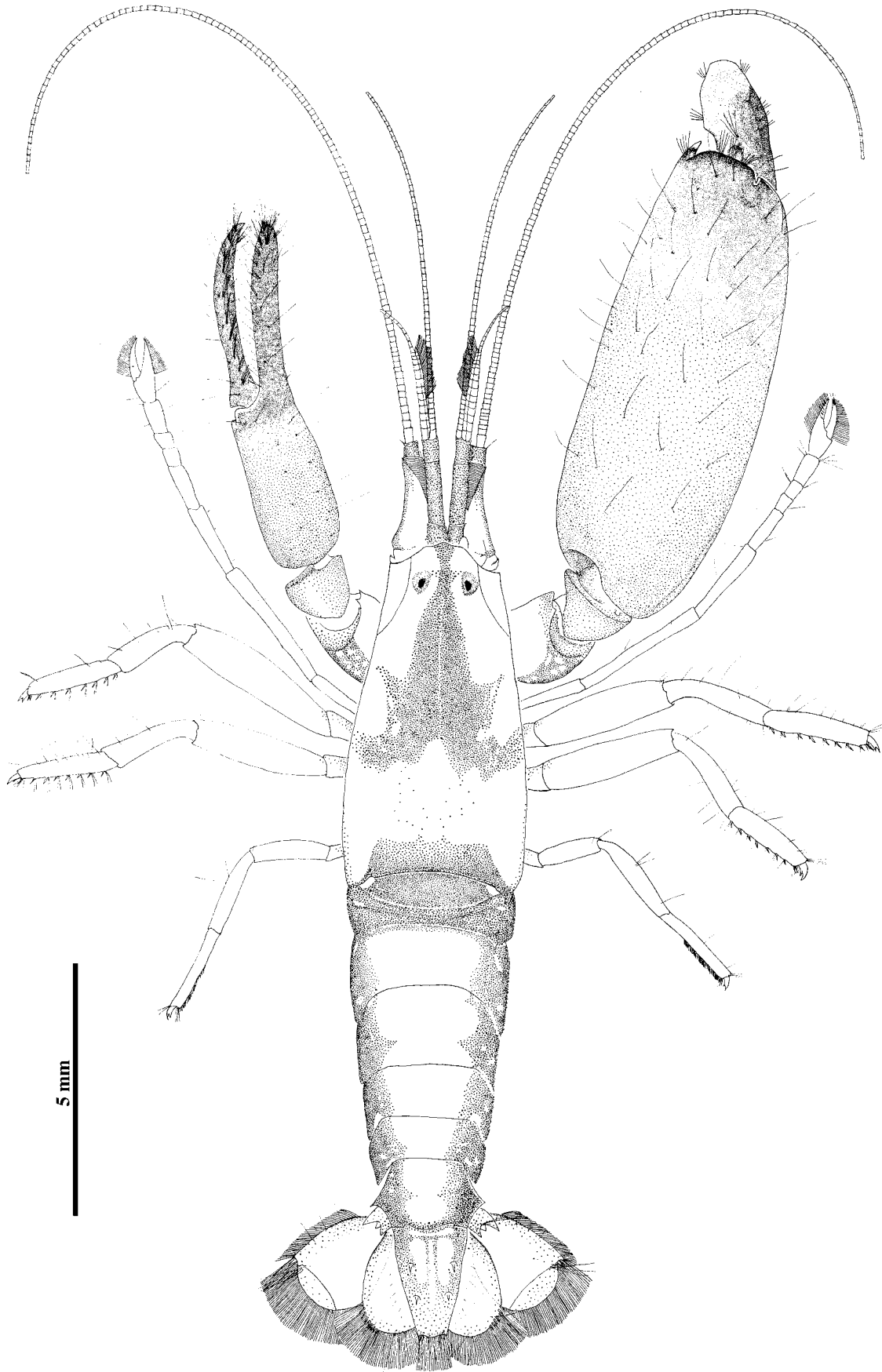


FIGURE 1. Color pattern of *Alpheus cylindricus* Kingsley, 1878, male from Isla Bartolomé, Pacific coast of Panama.

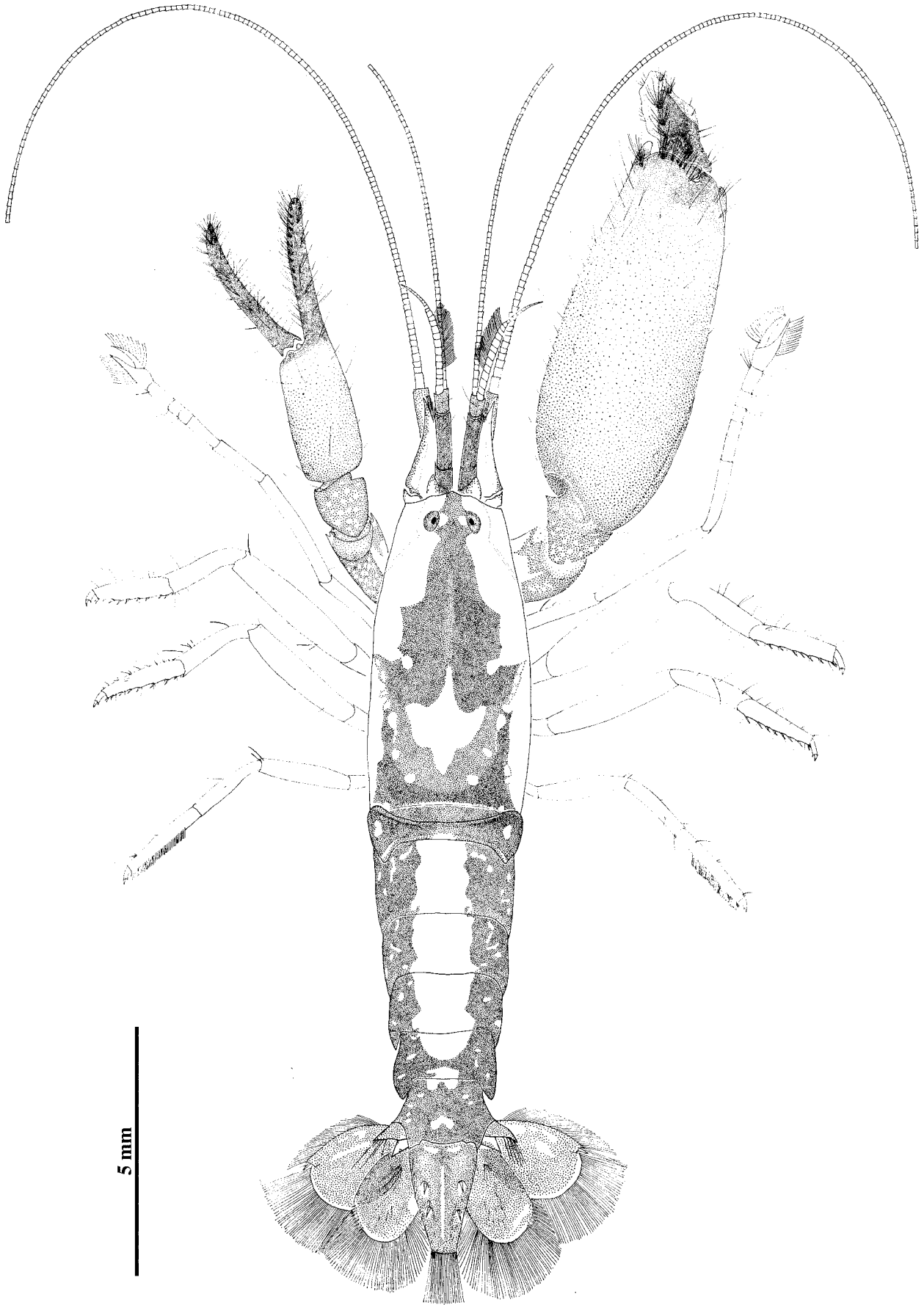


FIGURE 2. Color pattern of *Alpheus vanderbilti* Boone, 1930, male from San Blas Islands, Caribbean coast of Panama.

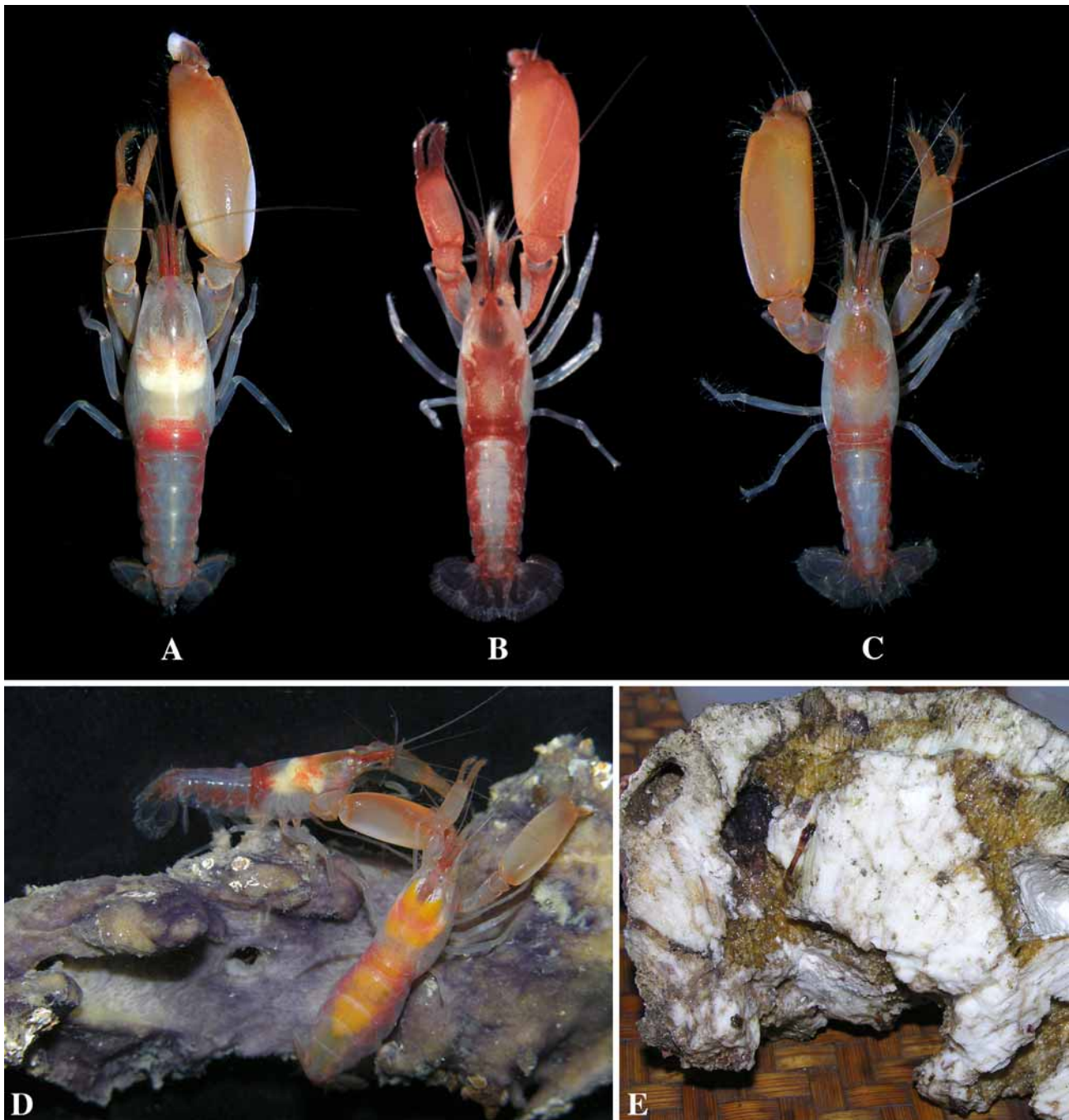


FIGURE 3. Color patterns and microhabitats of *Alpheus cylindricus* Kingsley, 1878 (A, D), *Alpheus vanderbilti* Boone, 1930, western Atlantic (B), and *Alpheus vanderbilti*, eastern Atlantic (C): A—male from Las Perlas Islands, Pacific coast of Panama (USNM 1109160); B—male from Bermuda (specimen in BAMZ, photograph courtesy of W. Sterrer); C—male from São Tomé (USNM 1109176), D—male and ovigerous female from Punta Culebra, Pacific coast of Panama, in their host sponge; E—coral rock with sponge-lined tunnels and bore-holes from where many São Tomé specimens of *A. vanderbilti* were extracted.

Ecology. Largely in intertidal and shallow subtidal to about 37 m (Kim & Abele 1988) or deeper: 64–82 m (Chace 1937); on mud and rock-mud bottoms; also in rocky intertidal, often in pairs in unidentified grey-purple sponges (Fig. 3D) growing among or under large rocks; usually in male-female pairs (Fig. 3D).

Type locality. Las Perlas Islands, Bay of Panama (Pacific coast).

Distribution. Eastern Pacific from central Gulf of California to Galapagos (Kim & Abele 1988). Specific localities include: Mexico: Cerralvo Island, central Gulf of California (Villalobos-Hiriart *et al.* 1989; Villalo-

bos 2000); southern Baja California (Wicksten 1983); Guayamas, Sonora (Rodríguez de la Cruz 1977); Nayarit (Camacho 1996); southern Sinaloa (Kim & Abele 1988; Hendrickx 1993b); Jalisco (Alvarez del Castillo *et al.* 1992); Costa Rica: Puerto Culebra and Parker Bay (Kim & Abele 1988); Panama: vicinity of Panama City, Taboga and Las Perlas Islands, Honda Bay, Secas Islands (Kingsley 1878a; Kim & Abele 1988; present study); Colombia: Utria Sound and Gorgona Island (Wicksten 1983; Kim & Abele 1988); Galapagos (Schmitt 1939).

Variation. *Alpheus cylindricus* appears to be extremely variable in the shape of the orbital teeth and rostrum (Fig. 4A-D). Kim & Abele (1988) noted that the “ocular hood [is] not inflated dorsally, with anterior margin sinuous”. The illustrated specimen from Baja California had no distinct orbital teeth (cf. Kim & Abele 1988: fig. 19b). However, some of our specimens from Panama bear large, subtriangular teeth on the orbital hoods (Fig. 4D), while others have less marked, rounded teeth (Fig. 4B, C) or no teeth at all (Fig. 4A). The shape of the strong tooth on the mesioventral carina of the first segment of the antennular peduncle is also somewhat variable (A. Anker, pers. obs.).

Remarks. *Alpheus cylindricus* is morphologically indistinguishable from *A. vanderbilti*, but may be separated from the latter species by the absence of red chromatophores on the posterior dorsal half of the carapace and the colorless mediodorsal band being laterally fringed by triangles (more or less “spruce-shaped”) and running without interruption from the first to the sixth abdominal somite, although there might be a few scarce chromatophores near the posterior margin of the fifth and on the sixth somites (compare Figs. 1, 3A and Figs. 2, 3B, C). Despite their morphological similarity, comparison of COI gene sequences confirm that *A. cylindricus* and *A. vanderbilti* are distinct species (see below).

GenBank accession number. EU652331, EU652332, EU652333 (specimens will be deposited in USNM).

***Alpheus vanderbilti* Boone, 1930**

(Figs. 2; 3B, C; 4E–H, J, K)

Alpheus vanderbilti Boone 1930: 163, fig. 5, pl. 58.

Alpheus cylindricus (not *sensu* Kingsley 1878) – Zimmer 1913: 394; Crosnier & Forest 1965: 606; Crosnier & Forest 1966: 257, fig. 16; Hendrix 1971: 71; Coelho & Ramos 1972: 149; Chace 1972: 65; Pequegnat & Ray 1974: 246, fig. 49d; Ray 1974: 92, figs. 72–78; Christoffersen 1979: 310; Christoffersen 1980: 50; Coelho & Ramos-Porto 1980: 135; Coelho *et al.* 1980: 48; Abele & Kim 1986: 196, 206–207, fig. a–c; Sterrer 1986: 326, text. pl. 105, pl. 9, fig. 7; Rodríguez 1986: 138, fig. 33; Martínez-Iglesias *et al.* 1993: 11; Knowlton *et al.* 1993: 1630 (part.); Martínez-Iglesias *et al.* 1996: 33; Martínez-Iglesias *et al.* 1997: 404, fig. 9; Williams *et al.* 2001: 377 (part.); McClure 2005: 136, not fig. 11; Coelho *et al.* 2006: 51.

Crangon cylindricus (not *sensu* Kingsley 1878) – Schmitt 1924: 74; Pearse 1950: 150.

Material examined. Panama (Caribbean coast). 1 male (CL 5.9), USNM 1109165, San Blas Islands, Tiantupo, in loggerhead sponge, *Sphaciospongia vesparia*, coll. N. Knowlton *et al.*, 22 Feb 1993 [fcn C-761]; 1 male (CL 4.3), USNM 1109166, San Blas Islands, Tiantupo, in loggerhead sponge, *Sphaciospongia vesparia*, coll. N. Knowlton *et al.*, 22 Feb 1994 [fcn C-763]; 1 male (CL 6.7), USNM 1109167, San Blas Islands, coll. N. Knowlton *et al.*, 4 Apr 1992 [fcn C-435]; 1 male (CL 5.3), USNM 1109168, San Blas Islands, in sponge, coll. N. Knowlton *et al.*, 3 Apr 1992 [fcn C-415]; 1 female (CL 5.3), USNM 1109169, San Blas Islands, Tiantupo, in loggerhead sponge, coll. N. Knowlton *et al.*, 23 Feb 1994 [fcn C-764]; 1 male (CL 6.5), USNM 1109170, same collection data as previous specimen [fcn C-762]; 1 male (CL 5.4), USNM 1109171, San Blas Islands, in green sponge, coll. N. Knowlton *et al.*, 4 Apr 1992 [fcn C-416]; 1 male (CL 5.2), 1 ovig. female (CL 4.4), USNM 1109172, San Blas Islands, “old yellow” (in yellow sponge ?), coll. N. Knowlton *et al.*, 4 Apr 1992 [fcn C-417, C-418]; 1 female (CL 5.1), USNM 1109173, San Blas Islands, Tiantupo, in loggerhead sponge, *Sphaciospongia vesparia*, coll. N. Knowlton *et al.*, 23 Feb 1994 [fcn C-765]. São Tomé. 1 male (CL

9.7), USNM 1109174, ST 12: Ilha Santana, from crevices of rocks, depth 15–20 m, coll. N. Knowlton and F. Nunes 9 Feb 2006 [fcn 06-202]; 1 female (CL 10.0), OUMNH-ZC 2007-13-035, same collection data as for previous specimen [fcn 06-201]; 1 male (CL 7.5), USNM 1109175, same collection data as for previous specimen [fcn 06-200, cephalothorax and tail fan only]; 1 male (CL 7.8), USNM 1109176, ST 4: 2 km west of Lagoa Azul, near ship wreck, off rocky shore with crusts of coralline algae, from crevices of massive rock, depth at low tide about 4 m, coll. A. Anker and N. Knowlton, 1 Feb 2006 [fcn 06-104]; 1 ovig. female (CL 7.5), USNM 1109177, same collection data as for previous specimen [fcn 06-101]; 1 ovig. female (CL 7.9), USNM 1109178, same collection data as for previous specimen [fcn 06-102]; 1 male (CL 7.1), USNM 1109179, same collection data as for previous specimen [fcn 06-105]; 1 male (CL 8.5), USNM 1109180, same collection data as for previous specimen [fcn 06-106].

Diagnosis. See under *A. cylindricus*, from which *A. vanderbilti* is morphologically virtually undistinguishable, whilst differing in color and DNA sequences (see below).

Description. For detailed description and some figures see Boone (1930); for additional illustrations see Zimmer (1913), Crosnier & Forest (1966), Pequegnat & Ray (1974), Rodríguez (1986) and Martínez-Iglesias *et al.* (1997).

Color pattern. Western Atlantic specimens: background color pale grey, semitransparent; carapace with large complexly shaped patch of red chromatophores on gastric region, central area of this patch colorless, patches of red chromatophores also on rostral and post-rostral region; deep red transverse band also present along posterior margin of carapace and articulation between carapace and abdomen; abdomen with broad longitudinal band of red chromatophores running along lateral surface of pleurae; mediadorsal area of first to fourth somites colorless, that of fifth and sixth somites with red chromatophores; walking legs colorless; second pereopod mostly colorless with some reddish chromatophores; antennular peduncles bright red; antennal peduncles including scaphocerite mostly transparent, margins of scaphocerite and basicerite orange-red, carapocerite distally reddish; antennular and antennal flagella pale yellow; cheliped meri and carpi mostly colorless mesially, reddish laterally; palm of major chela red-orange, darker distally; linea impressa delimiting paler, grey-pink oval proximolaterally; dactylus purple-red with whitish tip; minor chela pale red-orange, purple-red distally and on fingers (Fig. 2, 3B). Eastern Atlantic specimens: very similar to western Atlantic specimens; gastric region of carapace with more regular and less contrasting oval patch, with slightly larger colorless central area (Fig. 3C); developing embryos (“eggs”) in females bright yellow-orange.

Size. The CL and TL of the San Blas specimens ranged from 4.4 to 6.7 mm, and 10.8 mm to 17.0 mm, respectively. The largest specimen from São Tomé is a female with CL 10.0 mm and TL 28.7 mm.

Ecology. Western Atlantic: lower intertidal (rare) and subtidal to about 36–45 m (Boone 1930; Christoffersen 1979); more common in shallow subtidal (3–10 m); lives in male-female pairs in loggerhead sponges, *Sphaciospongia vesparia* (Lamarck, 1816) (Pearse 1950; Chace 1972); also in algal crusts and crevices of dead corals (Christoffersen 1979; Rodríguez 1986). Eastern Atlantic: lower intertidal (rare) and shallow subtidal to about 73 m; in crevices of coral rocks and crusts of red algae on basaltic rocks (Crosnier & Forest 1966); all our specimens were extracted from crevices and tunnels thinly lined with purple or yellow sponges in coral rocks (Fig. 3E).

Type locality. Sand Key, Key West, Florida.

Distribution. Western Atlantic: from Florida and Bermuda to Caribbean, Gulf of Mexico and northwestern Brazil (Chace 1972; Sterrer 1986; Christoffersen 1998). Specific localities include: Bermuda (Sterrer 1986); Florida: southern Florida and Florida Keys (Boone 1930; Hendrix 1971); Texas: West Flower Garden Bank (Pequegnat & Ray 1974); Bahamas: Bimini (Pearse 1950); Grenadines (Chace 1972); Barbados (Zimmer 1913; Schmitt 1924); Cuba: Gulf of Batabano (Martínez-Iglesias *et al.* 1997); Panama: San Blas Islands (present study); Venezuela: Los Roques (Rodríguez 1986); Brazil: Maranhao, Paraiba and Bahia (Coelho & Ramos 1972; Christoffersen 1979, 1998). Eastern Atlantic: São Tomé, Príncipe and Annobon in the Gulf of Guinea (Crosnier & Forest 1966; present study).

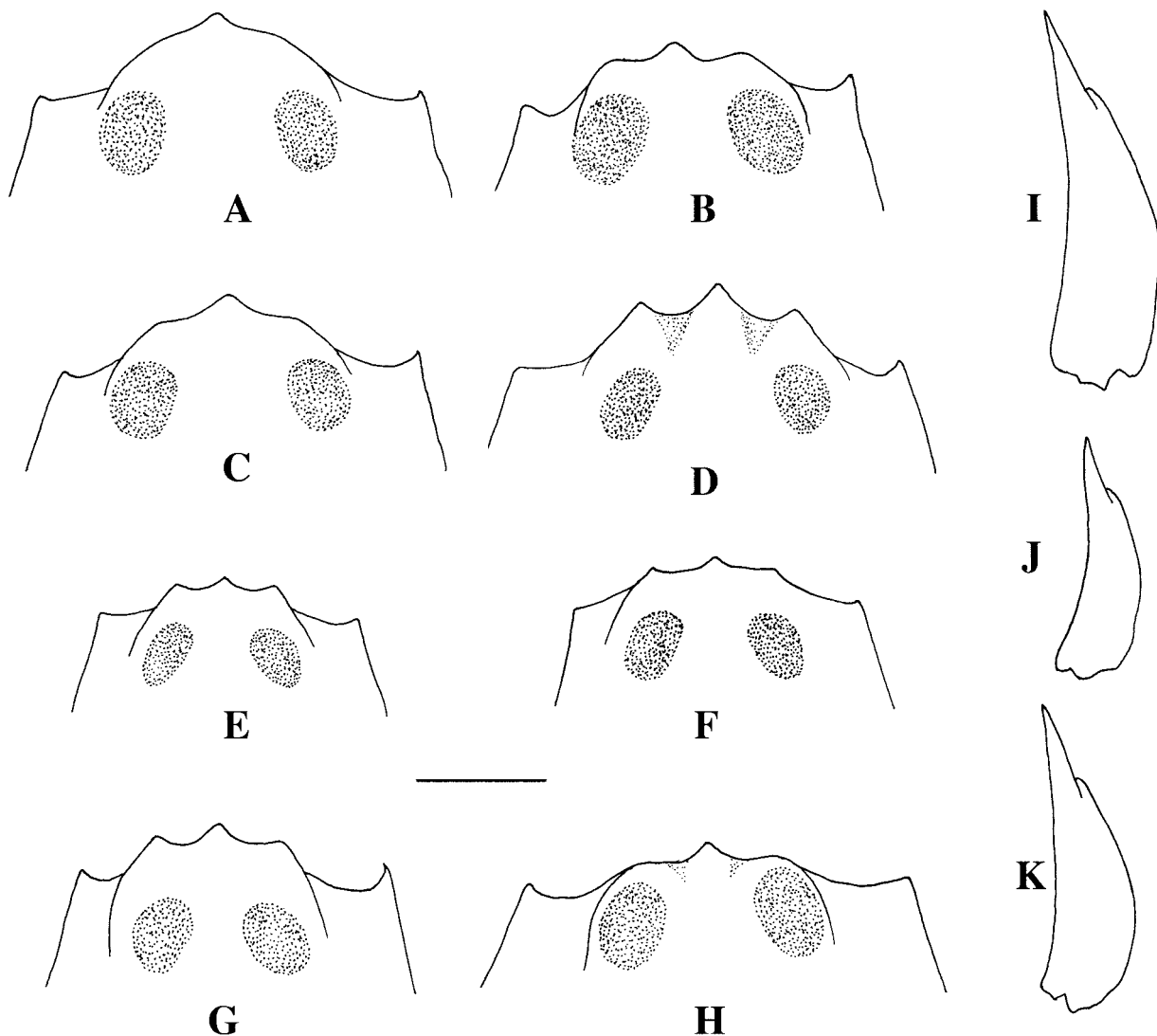


FIGURE 4. Variation in the shape of the frontal margin of the carapace (A–H) and outline of the scaphocerite (I–K) in *Alpheus cylindricus* Kingsley, 1878 (A–D, I), *Alpheus vanderbilti* Boone, 1930, western Atlantic (E, F, J) and *Alpheus vanderbilti*, eastern Atlantic (G, H, K): A, I—male from Taboga, Pacific coast of Panama (USNM 1109161); B—male from Punta Culebra, Pacific coast of Panama (USNM 1109162); C—female from Punta Culebra (USNM 1109162); D—male from Punta Culebra (OUMNH-ZC 2007-13-036); E, J—male from San Blas Islands, Caribbean coast of Panama (USNM 1109165); F—another male from San Blas Islands (USNM 1109167); G, K—male from São Tomé (USNM 1109179); H—ovigerous female from São Tomé (USNM 1109178). Scale bar = 1 mm.

Variation. Like the previous species, *A. vanderbilti* is variable in the configuration of the orbital teeth and rostrum (Christoffersen 1979; see also Fig. 4E–H) and in the shape of the antennal scaphocerite (Fig. 4J, K, compare with Fig. 4I).

Remarks. *Alpheus vanderbilti* may be separated from *A. cylindricus* by the presence of a patch of red chromatophores on the posterior dorsal half of the carapace and the colorless mediodorsal band laterally without distinct triangles (not “spruce-shaped”) and being interrupted on the fifth segment by a transverse red band, while the sixth somite is almost entirely red (compare Figs. 2, 3B, C and Figs. 1, 3A).

The eastern Atlantic specimens of *A. vanderbilti* differ from the western Atlantic specimens and from *A. cylindricus* only by some minor details in the color pattern, e.g., by the less contrasting red patch on the gastric region of the carapace, with a larger colorless central area (cf. Fig. 3C). These differences are too subtle

and probably inconsistent (red chromatophores may fade away completely or become more intense in stressed specimens) to be considered as taxonomically important.

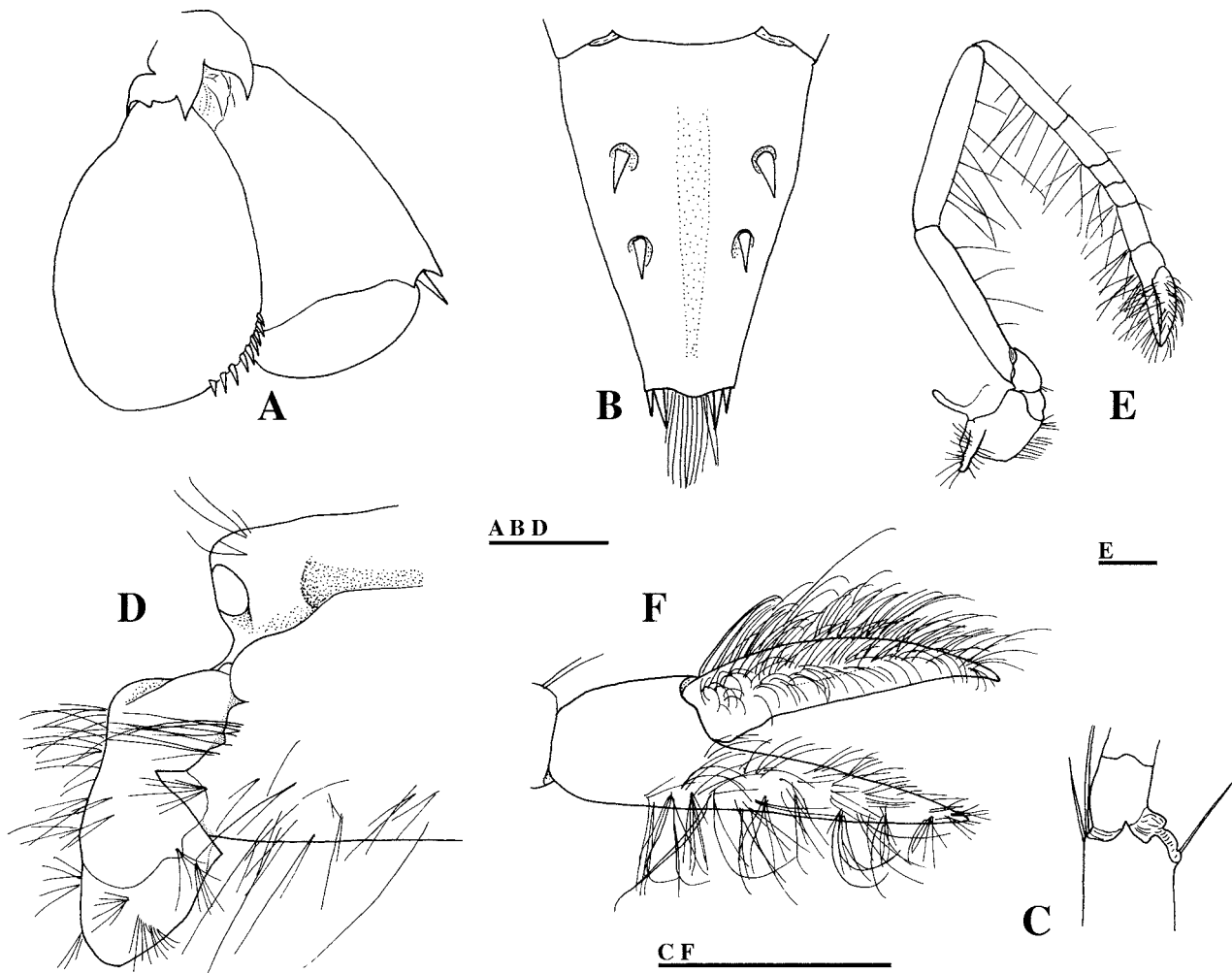


FIGURE 5. Some characteristic features of the *Alpheus cylindrical* Kingsley, 1878 complex, illustrated on *Alpheus vanderbilti* Boone, 1930 — eastern Atlantic, ovigerous female from São Tomé (USNM 1109178): A—right uropod, dorsal view, showing row of spines on endopod; B—telson, dorsal view, showing median groove; C—distomesial margin of antennal carapocerite, note acute tooth; D—fingers of major chela, note triangular tooth on dactylus and pointed pollex tip; E—second pereopod, lateral view; F—same, detail of setation pattern on chela. Scale bars = 1 mm.

In all examined specimens from São Tomé, the uropodal endopod is furnished with a row of strong spines (usually 9–11) on the distolateral margin (Fig. 5A); these spines are also present in the western Atlantic specimens (Ray 1974: fig. 74; Christoffersen 1979) and in *A. cylindrical* (Kim & Abele 1988: fig. 191). They were apparently overlooked by Crosnier & Forest (1966) and not illustrated on the figure of the tail fan (fig. 16h). Furthermore, this figure does not show a deep mediodorsal groove on the telson, which is conspicuous in all of our specimens (Fig. 5B), and which is also present in *A. cylindrical* (cf. Kim & Abele 1988: fig. 191).

Other subtle but diagnostic features of both *A. vanderbilti* and *A. cylindrical* are the presence of a small acute tooth on the distomesial margin of the antennal carapocerite (Fig. 5C); the presence of an acute tooth on both the dactylus and pollex of the major chela (Fig. 5D); and especially the setation pattern on the chela of the second pereopod (P2, Fig. 5E), consisting of particularly dense rows of setae (Fig. 5F). This setation pattern is unusual and perhaps unique among *Alpheus* species (A. Anker, pers. obs.). Dense setal brushes are also present on the P2 of most *Synalpheus* species, but these patterns are different from those of *A. cylindrical* and *A. vanderbilti* (A. Anker, pers. obs.).

GenBank accession number. EU652329, EU652330 (*A. vanderbilti* WA); EU652327, EU652328 (*A. vanderbilti* EA) (specimens will be deposited in USNM).

Discussion

Alpheus cylindricus demonstrates particularly well the necessity of combining detailed studies of morphology, color patterns and ecology with genetics. The available data suggest that the eastern Pacific *A. cylindricus* and the amphi-Atlantic *A. vanderbilti* are a pair of transisthmian sibling species thus corroborating previous results (Knowlton *et al.* 1993; Williams *et al.* 2001). The average K2P genetic distance (COI) between *A. cylindricus* and *A. vanderbilti*-WA (for western Atlantic) and *A. vanderbilti*-EA (for eastern Atlantic) is 10.2% (COI 5' region only). This value is intermediate with respect to other *Alpheus* transisthmian species pairs, which range from 6.4 to 20.1 % and averaged 10.6% (C. Hurt, pers. obs.). The estimated separation time between *A. cylindricus* and *A. vanderbilti*, based on the adjusted molecular clock of Knowlton & Weigt (1998) [see Methods] would be approximately 7 mya.

Like previous authors (Crosnier & Forest 1966; Christoffersen 1979), we were unable to find clear-cut morphological differences between *A. cylindricus* and *A. vanderbilti*, and within the latter species, between *A. vanderbilti*-WA and *A. vanderbilti*-EA. The discrimination between them is further complicated by a remarkably variable frontal margin within *A. cylindricus*, as well as within *A. vanderbilti*-WA and *A. vanderbilti*-EA (Fig. 4). Differences in color between *A. cylindricus* and *A. vanderbilti* are also relatively subtle (Figs. 1, 2, 3A–C). Furthermore, due to changes in color intensity influenced by shrimp's physiology (e.g., stress), color characters may not always be used for species distinction. However, genetic data (Fig. 6), reproductive incompatibility (Knowlton *et al.* 1993), and color characters, in combination with geographical isolation, leave no doubt that *A. cylindricus* and *A. vanderbilti* are separate species.

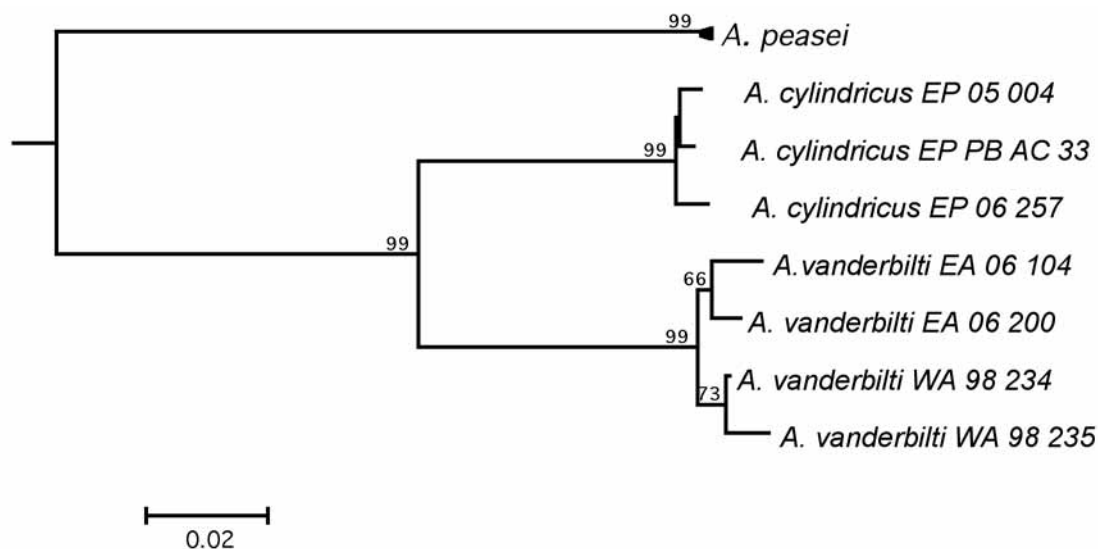


FIGURE 6. A neighbor-joining tree of unique mitochondrial COI haplotypes for the *Alpheus cylindricus* Kingley, 1878 complex. Field collection numbers (numbers associated with each terminal) correspond to specimens from following localities: *A. cylindricus*-EP: 05-004—Punta Culebra, Panama; PB AC 33—Taboga, Panama; 06-257—Río Mar, Panama; *A. vanderbilti*-EA: 06 104 and 06 200—São Tomé; *A. vanderbilti*-WA: 98 234 and 98 235—San Blas, Panama. The tree is rooted with *Alpheus peasei* (Armstrong, 1940), a western Atlantic species of the *Alpheus macrocheles* group.

Present results suggest that *A. vanderbilti* is an amphi-Atlantic (WA/EA) species. The Atlantic populations appear to be geographically separated into three populations: Florida-Caribbean (FC), Brazil (BR) and Gulf of Guinea in the eastern Atlantic (EA). Intensive samplings of decapods around Ascension and St. Hel-

ena islands did not yield specimens of *A. vanderbilti* (cf. Chace 1966; Manning & Chace 1990), which means that *A. vanderbilti* is most likely absent from the central Atlantic. Also, *A. vanderbilti*-FC, *A. vanderbilti*-BR and *A. vanderbilti*-EA differ somewhat in ecology: *A. vanderbilti*-FC was collected from large loggerhead sponges (*Spherospongia vesparia*) and dead corals (Pearse 1950; Rodríguez 1986; present study), *A. vanderbilti*-BR from rocks and calcareous algae (Christoffersen 1979) and *A. vanderbilti*-EA from sponge-lined galleries in coral rocks and rock crevices (Crosnier & Forest 1966; present study). It may be the case that *A. cylindricus* and *A. vanderbilti* are always associated in some way with sponges; for example, the rock cavities from which collected *A. vanderbilti* in São Tomé were so thinly lined by sponges that this kind of association might have been missed by other workers. However, association with large, free-living sponges appears to be limited to the FC populations, making *A. vanderbilti*-BR and *A. vanderbilti*-EA ecologically more similar to the eastern Pacific *A. cylindricus*.

The average KP2 genetic distance between *A. vanderbilti*-FC and *A. vanderbilti*-EA is only 1.8 %, which is significantly below the lowest values of distances observed in transisthmian species pairs (around 6%, C. Hurt, pers. obs.). There are, however, based on our limited samples, five fixed nucleotide differences between the FC and EA populations (compared to 54 separating *A. cylindricus* from all samples of *A. vanderbilti*). We did not have *A. vanderbilti*-BR for comparative DNA analysis, but expect comparably minor genetic distances between Brazilian and Caribbean populations, as was shown in several other (although not all) *Alpheus* species (Williams *et al.* 2001). The level of genetic divergence between the EA and BR populations is also likely to be small and may even be smaller than that observed between the EA and FC populations given oceanographic connections between the Gulf of Guinea and Brazil and the apparent ecological similarity of *A. vanderbilti* in these regions. Nevertheless, the observed genetic and ecological differences between the FC (type locality) and EA populations of *A. vanderbilti* suggests limited gene flow. The decision as to regard the EA populations as a separate species depends on the species concept used (e.g., see Knowlton & Weigt 1997 for *Alpheus*). We have no evidence that reproductive isolation is likely for allopatric populations with this modest level of genetic distinctiveness, but the existence of multiple fixed diagnostic genetic differences may be upheld with further sampling. Subspecific status may be warranted for the various Atlantic groups, but more information (particularly for the Brazilian *A. vanderbilti*) would be desirable before taking this step.

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