



## Sponge-dwelling snapping shrimps of Curaçao, with descriptions of three new species\*

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### Abstract

Sixteen species of sponge-dwelling snapping shrimp in the genus *Synalpheus* (*gambarelloides* group) were collected from sites spanning the south coast of Curaçao, including three new to science. *Synalpheus hoetjesi* sp. nov. belongs to a species complex that includes *Synalpheus pandionis*, *S. dardeauui*, *S. yano*, *S. goodei*, *S. longicarpus*, and *S. ul*. *Synalpheus kuadramanus* sp. nov. is a distinctive shrimp characterized by a short, square moveable finger on the major first pereopod and by brilliant turquoise embryos in females. *Synalpheus orapilosus* sp. nov. is a shrimp most morphologically similar to *Synalpheus barahonensis*—both species share the distinctive character of a tuft of setae on the distal end of the third maxilliped, instead of a distal circlet of spines—but can be distinguished from the latter by the number of carpal segments on the second pereopod. Although eusocial *Synalpheus* species (defined here as species that live in large colonies with strong reproductive skew) are often the most numerically abundant *Synalpheus* collected from sponges at other sites, only pair-bonding *Synalpheus* species were recorded from our collections in Curaçao.

**Key words:** *Synalpheus*, *Zuzalpheus*, *gambarelloides* group, Alpheidae, sponge, symbiotic, coral reef, eusociality

### Introduction

Snapping shrimp in the genus *Synalpheus* Bate are some of the most numerically abundant (Felder & Chaney 1979; Reed *et al.* 1982; Snelgrove & Lewis 1989) and taxonomically diverse (Coutière 1909; Banner & Banner 1975; Bruce 1976) cryptic fauna inhabiting coral reefs worldwide. The genus *Synalpheus* contains over 150 species (Chace 1988; Rios & Duffy 2007), and the majority of Caribbean species belong to the “*gambarelloides*” group (formerly known as “*laevimanus*” group, e.g. Coutière 1909), characterized by a dense brush of setae on the dactyl of the minor first chela. *Synalpheus* species in the *gambarelloides* group were placed in a new genus (*Zuzalpheus*) by Rios & Duffy (2007), based on several morphological synapomorphies and strong molecular support for monophyly of this group in the western Atlantic (Morrison *et al.* 2004). However, following the recent argument that designation of this new genus should await a more comprehensive taxonomic revision of *Synalpheus* (Anker & De Grave 2008), here we refer to this group as the *gambarelloides* species group within the genus *Synalpheus*.

Most, if not all, species in the *gambarelloides* group are obligate sponge-dwellers that inhabit the internal canals of their sponge hosts (Duffy 1992; Macdonald *et al.* 2006; Rios & Duffy 2007). In the west Atlantic, >30 described species in the *gambarelloides* group inhabit ~20 different sponge host species (Macdonald *et al.* 2006; Rios & Duffy 2007; Anker & Tóth 2008; Macdonald *et al.* 2009), and distribution of these species is thus closely linked to the distribution and abundance of their sponge hosts. *Gambarelloides* group *Synalpheus* are also unusual in containing the first described cases of eusociality in marine invertebrates (Duffy 1996a): many species of *Synalpheus* live in large, reproductively skewed colonies (often in excess of 100 individuals),

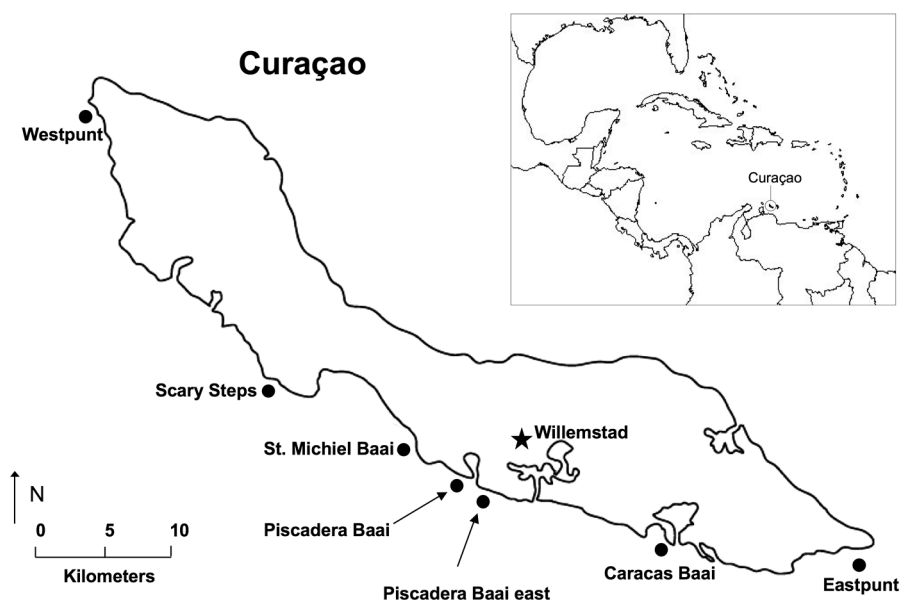
with breeding limited to only one or a few females (Duffy 2007). Eusociality has evolved at least four times in the genus (Duffy *et al.* 2000; Morrison *et al.* 2004; Didderen *et al.* 2006), and eusocial species are often the most numerically abundant *Synalpheus* species living in sponges (in Belize and Jamaica, e.g. Macdonald *et al.*, 2006; Macdonald *et al.* 2009). Eusocial species have been recorded from every Caribbean site surveyed by recent workers in this group, including Florida (Morrison *et al.* 2004), Caribbean Panama (Duffy 1998; Anker & Tóth 2008), Jamaica (Macdonald *et al.* 2009) and Belize (Rios & Duffy 2007). These systematic surveys, conducted over the last decade, have also doubled the number of described species in the group (Duffy 1996b, 1998; Macdonald & Duffy 2006; Rios & Duffy 2007; Anker & Tóth 2008; Macdonald *et al.* 2009). Molecular work has thus far supported the monophyly of these species (Duffy *et al.* 2000; Morrison *et al.* 2004; KMH unpublished data), despite often subtle morphological differences separating many closely related species. However, the majority of these recent surveys have been focused on the northwestern Caribbean (e.g., the Greater Antilles and the Central American coast), and relatively little is known about the *Synalpheus* fauna of the southeastern Caribbean and the Lesser Antilles (but see Westinga & Hoetjes 1981; Snelgrove and Lewis 1989).

Here we report results of a survey of sponge-dwelling *Synalpheus* of the leeward (southern) coast of Curaçao. Sponge distribution and abundance have been relatively well-studied in Curaçao (van Soest 1978, 1980, 1984; Zea & Weil 2003; Hunting 2008). In one of the first systematic surveys of cryptofaunal sponge communities, Westinga & Hoetjes (1981) investigated the fauna living inside the loggerhead sponge *Sphaciospongia vesparium* Lamarck in Curaçao and Bonaire. They reported that *S. vesparium*—at that time common at several sites in Curaçao—hosted a range of taxa, some of the most numerically abundant of which were alpheid shrimp (including *Synalpheus goodei* Coutière, *Synalpheus sanctithomae* Coutière, *Synalpheus pectiniger* Coutière, *Synalpheus brooksi* Coutière, and *Alpheus cylindricus* Kingsley). However, little is known about the diversity and distribution of sponge-associated *Synalpheus* species inhabiting other sponge hosts in Curaçao. In this study, we systematically sampled ten species of shrimp-bearing sponges from sites spanning the southern coast of Curaçao to characterize the distribution and host use of sponge-dwelling shrimp fauna of this region.

## Materials and methods

We sampled sponges and shrimp from seven sites spanning the south coast of Curaçao (Fig. 1) between 17 June and 25 June 2008; all material was collected and identified by the authors. We collected individual shrimp-bearing sponges (or large pieces of coral rubble containing individual sponges) by hand using SCUBA and snorkeling, specifically focusing on sponge species inhabited by *Synalpheus* from other locations (Macdonald *et al.* 2006; Rios & Duffy 2007; Macdonald *et al.* 2009). These sponge species are generally characterized by having large networks of interior canals; however, to ensure that we did not miss any potential shrimp-bearing sponges, we sectioned unfamiliar sponge species in the field (2 or 3 individuals per species), and collected any sponges that possessed interior canals. We also extensively searched cryptic sponge individuals found in the rubble. We attempted to collect at least 3 or 4 individuals of each appropriate sponge host species spanning a wide size range from each site. We removed whole specimens of exposed or semi-exposed sponges (*Agelas* cf. *clathrodes* Schmidt, *Aiolochoxia crassa* Hyatt, *Spongia* sp.); extensively searched live reefs, coral rubble, and large stones for cryptic sponges (*Hymeniacidon caerulea* Pulitzer-Finali); and carefully extracted semi-cryptic sponges (*Hyattella intestinalis* Lamarck, *Xestospongia proxima* Duchassaing and Michelotti, *Xestospongia subtriangularis* Duchassaing) from rubble in the field or whole pieces of rubble transported to the laboratory. Sponges and rubble were transported to the CARMABI field station at Piscadera Baai in mesh bags and retained in circulating seawater until processed. Before dissecting individual sponges for shrimp, we estimated sponge volume using displacement in seawater, subtracting rubble matrix if necessary. Each individual sponge was carefully dissected, and all macrofauna were removed. All fauna removed from individual sponge canals was preserved in 95% EtOH (including echinoderms and non-caridean crustaceans); we sorted alpheid shrimps by species, counted individuals and recorded whether or not they were ovigerous females (i.e., bearing developing ovaries or carrying embryos), recorded embryo

color for all ovigerous females, and photographed a subset of collected individuals alive. We report distribution and abundance of *gambarelloides* group *Synalpheus* only, as non-*gambarelloides* group species constituted only a small portion of our collection and because our methods did not produce quantitative collections of these free-living species. Voucher material and type specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) and in the Virginia Institute of Marine Science, Gloucester Point, VA (VIMS). Specimens were assigned numbers in the field (hereafter VIMS numbers); additional samples from the VIMS collection (e.g., non-type specimens) will eventually also be deposited in the USNM (collections are currently under active study). Size measurements, taken from preserved specimens, represent carapace length (CL) in millimeters, as measured from the base of the rostrum to the posterior edge of the carapace. Specimens were figured using digital photos taken with a Leica EZ4D dissecting microscope and a LAS-EZ imaging system (Leica Microsystems, Ltd.) or an Olympus Camedia C5050 camera attached to an Olympus BH-2 compound microscope, and figured using Adobe Illustrator CS4 (Adobe Systems Inc.). For the majority of specimens, we list specimens as ovigerous (ov.) females or non-ovigerous (non-ov.) individuals, as sexes in *Synalpheus* are difficult to definitively assign without scanning electron microscopy (Tóth & Bauer 2007). However, because non-eusocial *Synalpheus* live in heterosexual pairs, for type specimens we assign large, non-ovigerous individuals found with ovigerous females to be male.



**FIGURE 1.** Map of Curaçao showing sampling sites (black circles). Inset indicates location of Curaçao in the Caribbean.

Selected individuals from the “*pandionis*” species complex (which includes *S. dardeai*, *S. longicarpus*, *S. pandionis*, *S. yano*, and *S. ul*) were sequenced for a portion of the cytochrome *c* oxidase subunit I (COI) gene (specifically, a ~550 bp portion past the 3’ end of the HCO/LCO region). We used extraction protocols, *Synalpheus*-specific primers, and PCR profiles described in an earlier study (Morrison *et al.* 2004) to extract and amplify partial COI sequences from 14 individuals from Curaçao (this study) and seven individuals from Barbados and Caribbean Panama (Table 2). Amplified PCR products were sequenced on an ABI Prism 3730XI sequencer. Forward (5’–3’) and backwards (3’–5’) COI sequences were visually checked and trimmed using the program SEQUENCHER v4.8 (Gene Codes corporation) and aligned with existing GenBank sequences from a subset of related *Synalpheus* species (e.g., Morrison *et al.* 2004) using the program MUSCLE (Edgar 2004). We constructed a Bayesian consensus tree using MrBayes v3.12 (Ronquist & Hulsenbeck 2003) and a nucleotide substitution model calculated using Modeltest v3.7 (Posada & Buckley 2004). We ran Markov Chain Monte Carlo (MCMC) searches with four chains for  $1 \times 10^6$  generations (at which point runs had converged to a stationary distribution) sampled the chain every 100 generations, and discarded the first 25% of the samples as the burn-in (for more details, see Morrison *et al.* 2004).

To determine how completely we sampled the sponge-dwelling *Synalpheus* fauna of Curaçao, we plotted the accumulation of 1) *gambarelloides* group *Synalpheus* species, 2) shrimp-bearing sponge species, and 3) shrimp/sponge associations (any unique pairing between a shrimp species and host sponge species) as a function of number of samples collected to see if values reached an asymptote. Using these sample data, we calculated mean estimates of the true richness of shrimp species, sponge species, and shrimp-sponge associations using the Michaelis-Menten logistic curve-fitting function in the program EstimateS (Colwell 2005). We also estimated true species richness and number of associations using the Chao2 (Chao 1987), second-order jackknife (Burnham & Overton 1978), and bootstrap (Smith & van Belle 1984) functions in EstimateS.

**Collecting sites.** We sampled seven sites in Curaçao (Fig. 1, Table 1) spanning the southern coast, including some sites surveyed in previous studies on sponge-dwelling shrimp (Westinga & Hoetjes 1981). All sites were accessed from the shore, and typically consisted of reefs located 20–100 meters offshore along the edge of a shallow shelf that rims most of the south coast and drops off sharply at 5–8 m depth; we searched from 5 to >15 m depth. We also extensively searched patch reefs that occurred in the shallow sand flats leading to shelf habitats (2–6 m depth). The Piscadera Baai site (12°07'21.36"N, 68°58'17.40"W) is located on the north west side of the channel leading to Piscadera Baai (adjacent to the CARMABI research station), and consists of a dense near-monoculture of live *Madracis* sp., often infilled with sponges, with occasional patch reefs in shallower sand flats. Piscadera Baai east (12°07'15.96"N, 68°58'11.64"W) spans the southeast side of the channel, and consists of *Madracis* sp. patches (with slightly lower live cover) interspersed with industrial debris, both infilled with sponges and extending from 6 to >15 m depth. Sponges were also collected at 65 m depth at this site from a deep, silty reef adjacent to the seawater intake pipe for the CARMABI station. St. Michiel Baai (12°08'48.84"N, 68°59'59.64"W) consists of sparse live and dead *Madracis* sp. growing on and around small boulders (often encrusted by sponges) and boulder corals (*Siderastrea* spp.). Although the shrimp-hosting sponge *Spheciospongia vesparium* was common at this site during earlier surveys (Westinga & Hoetjes 1981), it was not found in our surveys despite intensive searching. The shelf at Caracas Baai (12°04'11.64"N, 68°51'43.56"W) consisted of patchy live and dead *Madracis* spp., *Acropora* spp., and industrial debris infilled with sponges. Large individual sponges (*Agelas* cf. *clathrodes*, *Spongia* sp., *Aiolochoxia crassa*) were also collected at this site from the pilings of a large tanker pier at the south end of the bay. Caracas Baai was surveyed twice, and extensively canvassed for *Spheciospongia vesparium* (e.g., Westinga & Hoetjes 1981). Westpunt (12°22'33.96"N, 69°09'36.36"W) consisted of healthy reef matrix (*Montastraea* spp., *Madracis* spp.) hosting a wide diversity of cryptic and exposed sponges. This site was at the northwest tip of the island, and was noticeably more high-energy than other sites. Scary Steps (12°12'04.68"N, 69°04'54.84"W) consisted of extensive live *Madracis* spp. beds and *Montastraea* spp. patch reefs extending from 6–15 m depth. Eastpunt (12°02'26.22"N, 67°14'54.18"W) was the only site accessed by boat, and was at the far eastern tip of the island. This site had extremely high live coral cover (estimated 70–100%) and diversity of large corals in both shallow areas and extending down the shelf (9–15 m depth). *Madracis* and *Acropora* spp. were much rarer in Eastpunt than at other sites, and the interstices of these coral species hosted little cryptic sponge fauna.

**TABLE 1. Localities sampled in Curaçao.**

Locality Name	Date(s) surveyed	Depth (m)	Geographic Coordinates
Piscadera Baai	17 June 2008	6–11	12°07'21.36"N, 68°58'17.40"W
St. Michiel Baai	18 June 2008	6–11	12°08'48.84"N, 68°59'59.64"W
Caracas Baai	19 & 24 June 2008	6–15	12°04'11.64"N, 68°51'43.56"W
Westpunt	21 June 2008	6–11	12°22'33.96"N, 69°09'36.36"W
Scary Steps	22 June 2008	6–15	12°12'04.68"N, 69°04'54.84"W
Piscadera Baai east	23 June 2008	6–15, 65	12°07'15.96"N, 68°58'11.64"W
Easpunt	25 June 2008	6–18	12°02'26.22"N, 67°14'54.18"W

**TABLE 2.** West Atlantic *Synalpheus* species in the *longicarpus* species complex (viz. Morrison *et al.* 2004) sampled for partial sequences of the cytochrome oxidase *c* subunit I (COI) gene. Asterisks (\*) indicate new sequences for this study.

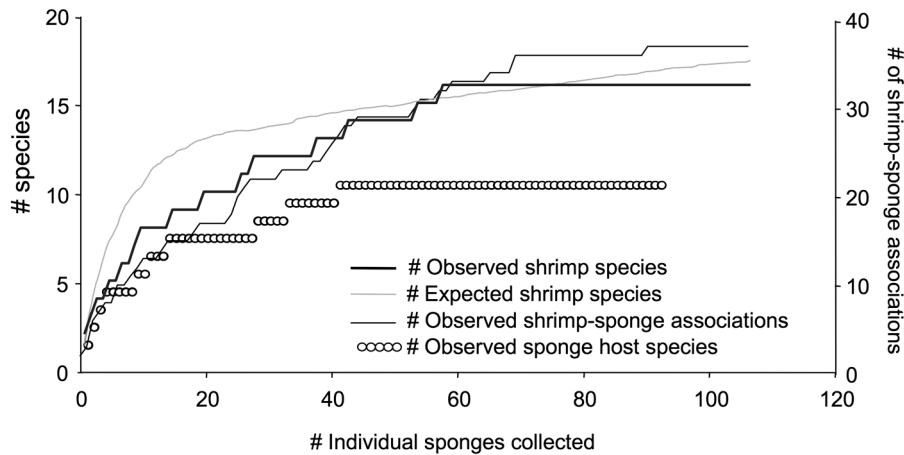
<i>Synalpheus</i> species	Sponge Host	Region	VIMS number or CODE in Morrison <i>et al.</i> (2004)	Genbank Accession #
<i>dardeai</i>	<i>Lissodendoryx colombiensis</i>	Panama	lnpnPA02	AY344704
" <i>pandionis</i> red"	<i>Sphaciospongia vesparium</i>	Panama	panrPA01	AY344707
<i>pandionis</i>	--	Belize	pandBE02	AY344706
<i>pandionis</i>	<i>Lissodendoryx</i> cf. <i>strongylata</i>	Barbados	08BR2706	GQ424443*
<i>pandionis</i>	<i>Lissodendoryx</i> sp. "soft"	Barbados	08BR8602	GQ424444*
<i>ul</i>	<i>Xestospongia subtriangularis</i>	Curaçao	08CU9503	GQ424424*
<i>ul</i>	<i>Xestospongia</i> sp. "soft"	Curaçao	08CU4702	GQ424425*
<i>ul</i>	<i>Agelas</i> cf. <i>clathrodes</i>	Curaçao	08CU1002	GQ424426*
<i>ul</i>	<i>Xestospongia subtriangularis</i>	Curaçao	08CU10003	GQ424427*
<i>ul</i>	<i>Hymeniacion caerulea</i>	Curaçao	08CU3303	GQ424428*
<i>ul</i>	<i>Hymeniacion caerulea</i>	Panama	07P3701-1	GQ424429*
<i>yano</i>	<i>Lissodendoryx colombiensis</i>	Belize	lnpnBE01	AY344718
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Barbados	08BR6701	GQ424431*
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Barbados	08BR6708	GQ424432*
<i>hoetjesi</i> sp. nov.	<i>Agelas</i> cf. <i>clathrodes</i>	Barbados	08BR9603	GQ424433*
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Curaçao	08CU5603	GQ424434*
<i>hoetjesi</i> sp. nov.	<i>Xestospongia subtriangularis</i>	Curaçao	08CU9704	GQ424435*
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Curaçao	08CU4106	GQ424436*
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Curaçao	08CU4101	GQ424437*
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Curaçao	08CU5601	GQ424438*
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Curaçao	08CU4103	GQ424439*
<i>hoetjesi</i> sp. nov.	<i>Xestospongia subtriangularis</i>	Curaçao	08CU2901	GQ424440*
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Curaçao	08CU4102	GQ424441*
<i>hoetjesi</i> sp. nov.	<i>Hyattella intestinalis</i>	Curaçao	08CU9901	GQ424442*
<i>goodei</i>	<i>Calyx podatypa</i>	Belize	goodBE04	AY344698
<i>goodei</i>	<i>Calyx podatypa</i>	Panama	08P9201-2	GQ424430*
<i>longicarpus</i>	<i>Sphaciospongia vesparium</i>	Panama	longPA03	AY344702
<i>agelas</i>	<i>Agelas</i> cf. <i>clathrodes</i>	Florida	agelFL01	AY344681

## Results

In total, we collected 107 individual shrimp-bearing sponges from a total of ten sponge species in Curaçao. We record 16 species of shrimp in the genus *Synalpheus* (*gambarelloides* group), three of which are new to science, and 37 unique sponge-shrimp associations.

Our observed shrimp species richness (16 species) was very close to estimates of "true" species richness calculated by various methods, including the Michaelis-Menten, Chao2, jackknife, and bootstrap functions (which estimated richness at 17, 18, 19, and 17 species, respectively; Fig. 2). Similar calculations demonstrate that we have sampled nearly all of the shrimp-bearing sponges: the same four functions estimate true richness of shrimp-bearing sponges at 11, 11, 12, and 11 sponge species. While we only collected ten sponges, the asymptote of sponge diversity was reached once we had sampled ~50% of the sponges in our collection (Fig.

2), suggesting that new shrimp species found after that were primarily rarer species found in more common sponges or found only in sponges from certain sites. Although we recorded 37 unique shrimp-sponge associations, we may not have sampled all associations (the four functions estimate the number of unique shrimp-sponge associations at 47, 47, 48, and 42). Overall, we estimate that we have sampled approximately 90% of the true shrimp species richness, 89% of the true sponge richness, and 80% of the potential shrimp-sponge associations (percentage of observed relative to estimated richness, averaged over four estimators).



**FIGURE 2.** Observed accumulation of *Synalpheus* species in the *gambarelloides* group (thick black line); expected species accumulation curve (grey line) estimated using the bootstrap function in EstimateS (Colwell 2005); observed unique shrimp-sponge associations (thin black line, right y-axis); and observed accumulation of unique sponge host species (white circles) as a function of collection effort (number of unique sponge samples collected, x-axis).

## Taxonomy

### Alpheidae Rafinesque, 1815

#### *Synalpheus* Bate, 1888

#### *Synalpheus agelas* Pequegnat & Heard, 1979

(Pl. 1A–C)

**Material examined.** Curaçao: 5 ov. females, 12 non-ov. individuals (VIMS 08CU3006–7, 3801–4, 3903), Caracas Baai, in the canals of *Agelas* cf. *clathrodes*. 1 ov. female, 3 non-ov. individuals (VIMS 08CU12701, 13003), Eastpunt, in canals of *A.* cf. *clathrodes*. 3 ov. females, 3 non-ov. individuals (VIMS 08CU703–4, 08CU1401, 08CU1701–2, 08CU1902), Piscadera Baai, in canals of *A.* cf. *clathrodes*. 1 ov. female, 2 non-ov. individuals (VIMS 08CU8702), Piscadera Baai east, in the canals of *A.* cf. *clathrodes*. 8 ov. females, 11 non-ov. individuals (VIMS 08CU7601, 8202, 8205–6, 8215), Scary Steps, in the canals of *A.* cf. *clathrodes*. Largest ov. female, CL 4.6 mm, largest non-ov. individual, CL 3.8 mm.

**Color.** Orange, with orange-tipped major chela, similar to specimens reported from other locations. Ovaries and embryos orange or green in ovigerous females.

**Hosts and ecology.** In Curaçao, as in all other known locations, *S. agelas* was a specialist inhabiting only sponges in the genus *Agelas*, in this case canals of *Agelas* cf. *clathrodes*. In Curaçao, *S. agelas* typically occurs in heterosexual pairs (sometimes with juveniles), often sharing an individual sponge with *Synalpheus carpenteri* Macdonald and Duffy and *Synalpheus mcclendonii* Coutière.

**Distribution.** Florida Keys, USA (Morrison *et al.* 2004), Bahamas (Dardeau 1984), Gulf of Mexico (Pequegnat & Heard 1979; Dardeau 1984), Puerto Rico (Dardeau 1984), Cuba (Martínez Iglesias & García Raso 1999), Belize (Macdonald *et al.* 2006; Rios & Duffy 2007), Jamaica (Macdonald *et al.* 2009), and Curaçao (this study).

**Remarks.** Unlike *S. agelas* collected in other locations, which typically have females with orange embryos and ovaries, most individuals collected in Curaçao had green embryos (sometimes verging on brownish or with an orange tint), and orange or green ovaries (see Plates 1A–C).

### *Synalpheus belizensis* Anker & Tóth, 2008

(Pl. 1D–F)

**Material examined.** Curaçao: 1 individual (VIMS 08CU3602), Caracas Baai, no host found. 2 ov. females, 7 non-ov. individuals (VIMS 08CU11101, 11201–2), Caracas Baai, from the canals of *Xestospongia proxima*. 1 ov. female, 1 non-ov. individual (VIMS 08CU3701–2), Caracas Baai, from the canals of *Xestospongia* sp. “soft”. 1 ov. female, 3 non-ov. individuals (VIMS 08CU2903, 08CU10501, 11502), Caracas Baai, from the canals of *Xestospongia subtriangularis*. 1 non-ov. individual (VIMS 08CU12102), Eastpunt, no host found. 1 non-ov. individual (VIMS 08CU12801), Eastpunt, from the canals of *Xestospongia* sp. “soft”. 1 non-ov. individual (VIMS 08CU9301), Piscadera Baai east, no host found. 7 ov. females, 6 non-ov. individuals (VIMS 08CU9103, 9401, 9501–2, 9701, 10001–2), Piscadera Baai east, from the canals of *Xestospongia subtriangularis*. 1 ov. female, 1 non-ov. individual (VIMS 08CU8001–2), Scary Steps, from the canals of *Xestospongia proxima*. 1 ov. female, 1 non-ov. individual (VIMS 08CU4902–3), Westpunt, from the canals of *Xestospongia proxima*. Largest ov. female, CL 4.9 mm, largest non-ov. individual, CL 4.8 mm.

**Color.** Body translucent, females with bright orange-yellow embryos and ovaries.

**Hosts and ecology.** In Curaçao, *S. belizensis* was most often found in sponges in the genus *Xestospongia*, similar to other locations (Anker & Tóth 2008; Macdonald *et al.* 2009). Non-ovigerous *S. belizensis* individuals that could not be definitively assigned to a sponge host (i.e., no host found) were always found in pieces of rubble that contained *Xestospongia* spp.

**Distribution.** Belize (Anker & Tóth 2008); Jamaica (Macdonald *et al.* 2009); Curaçao (this study).

**Remarks.** *S. belizensis* individuals collected from Curaçao had particularly distinctive scaphocerite blades, extending from 50% to 80% the length of the scaphocerite lateral spine. This distinctive character easily distinguished *S. belizensis* from the closely related species *Synalpheus bocas* (which always lacks a blade) also found in our surveys in Curaçao.

### *Synalpheus bocas* Anker & Tóth, 2008

(Pl. 2A–B)

**Material examined.** Curaçao: 1 ov. female, 2 non-ov. individuals (VIMS 08CU7501–2, 7702), Scary Steps, from the canals of *Xestospongia* sp. “soft”. Largest ov. female, CL 4.1 mm, largest non-ov. individual, CL 4.2 mm.

**Color.** The single ovigerous female collected had greenish-yellow embryos.

**Hosts and ecology.** In Curaçao, *S. bocas* was relatively rare in comparison to closely related species *S. belizensis*, despite frequent collection of the host sponge it was found in (*Xestospongia* sp. “soft”, 6 individual sponges collected) and other *Xestospongia* species (*X. subtriangularis* and *X. proxima*, 27 individual sponges collected).

**Distribution.** Caribbean Panama (Anker & Tóth 2008), Jamaica (Macdonald *et al.* 2009); Curaçao (this study).

**Remarks.** *Synalpheus bocas* from Curaçao closely resemble original descriptions of this species from Caribbean Panama (Anker & Tóth 2008). They can be easily distinguished from *S. belizensis* by the lack of a blade in *S. bocas*.

***Synalpheus bousfieldi* Chace, 1972**

(Pls. 2C–F, 3A–B)

**Material examined.** Curaçao: 9 ov. females, 15 non-ov. individuals (VIMS 08CU4107–11, 4115–6, 10102, 10402, 11903), Caracas Baai, from the canals of *Hyattella intestinalis*. 1 individual (VIMS 08CU12302), Eastpunt, from the canals of *Agelas* cf. *clathrodes*. 4 ov. females, 5 non-ov. individuals (VIMS 08CU12201–2), Eastpunt, from the canals of *H. intestinalis*. 2 ov. females, 2 non-ov. individuals (VIMS 08CU701–2, 1901), Piscadera Baai, from the canals of *A.* cf. *clathrodes*. 1 ov. female, 1 non-ov. individual (VIMS 08CU402–3), Piscadera Baai, from the canals of an unidentified crumbly white sponge. 8 ov. females, 8 non-ov. individuals (VIMS 08CU301–2, 501–3, 601–2, 801–2, 1301–2, 1801–3), Piscadera Baai, from the canals of *H. intestinalis*. 3 individuals (VIMS 08CU1103, 1201), Piscadera Baai, no host found (in coral rubble with sponges). 17 ov. females, 11 non-ov. individuals (VIMS 08CU103–4, 111–132), Piscadera Baai, from the canals of *Aiolochoxia crassa*. 1 individual (VIMS 08CU8704), Piscadera Baai east, from the canals of *A.* cf. *clathrodes*. 23 ov. females, 44 non-ov. individuals (VIMS 08CU8901, 9302, 9903), Piscadera Baai east, from the canals of *H. intestinalis*. 9 ov. females, 13 non-ov. individuals (VIMS 08CU9806–11), Piscadera Baai east, from the canals of *A. crassa*. 3 ov. females, 2 non-ov. individuals (VIMS 08CU9003, 9101–2, 10005), Piscadera Baai east, from the canals of *Xestospongia subtriangularis*. 3 ov. females, 4 non-ov. individuals (VIMS 08CU8602), Scary Steps, from the canals of *H. intestinalis*. 1 ov. female, 1 non-ov. individual (VIMS 08CU8401–2), Scary Steps, no host recorded (in coral rubble with sponges). 12 ov. females, 15 non-ov. individuals (VIMS 08CU8302–13), Scary Steps, from the canals of *Xestospongia proxima*. 1 individual (VIMS 08CU5002), Westpunt, in coral rubble, possibly associated with a webby white and purple sponge. 8 ov. females, 8 non-ov. individuals (VIMS 08CU5605–7, 5611, 5801–2, 5807, 5901–2, 7001), Westpunt, from the canals of *H. intestinalis*. 1 individual (VIMS 08CU6802), Westpunt, no host recorded (in coral rubble with sponges). 4 individuals (VIMS 08CU6503), Westpunt, from the canals of *A. crassa*. 2 ov. females, 2 non-ov. individuals (VIMS 08CU4802, 4804, 6701, 6703) and newly released swimming larvae (VIMS 08CU4803 and 08CU6702, released from 08CU4802 and 08CU6701, respectively), Westpunt, from the canals of *X. proxima*. 1 individual (VIMS 08CU6102), Westpunt, no definitive host recorded, possibly associated with a yellow-purplish webby sponge in coral rubble. Largest ov. female, CL 7.3 mm, largest non-ov. individual, CL 4.7 mm.

**Color.** *Synalpheus bousfieldi* from different sponges differed in size (see Remarks) and embryo or body color. Ovigerous females from *Aiolochoxia crassa* had embryos varying from a deep dark red to an orange or chestnut-brown, and some individuals had a somber purplish tinge (see plate 2f). Several *S. bousfieldi* individuals from *A. crassa* (both ovigerous and non-ovigerous) had distinctive, black-tipped major chelae, specifically a ring of black pigment around the distal dactyl with the very tip of the dactyl lacking pigment (Plates 2d–e). Individuals from *Agelas* cf. *clathrodes*, *Hyattella intestinalis*, and *Xestospongia proxima* were drab with orange-tipped chelae, with embryo and ovary color ranging from brownish-olive, to light chestnut, to orange-red (Plates 2f, 3a–b).

**Hosts and ecology.** In Curaçao, *S. bousfieldi* was the most commonly encountered *Synalpheus* species and occurred across a wide range of hosts, primarily *Hyattella intestinalis* but also *Xestospongia proxima*, *Xestospongia subtriangularis*, *Agelas* cf. *clathrodes*, and *Aiolochoxia crassa*. In Belize, *S. bousfieldi* is primarily found in *H. intestinalis* (Macdonald *et al.* 2006).

**Distribution.** Bahamas (Dardeau 1984); Cuba (Martínez Iglesias & García Raso 1999); Gulf of Mexico (Dardeau 1984); Yucatan Peninsula, Mexico (Chace 1972); Belize (Macdonald & Duffy 2006; Rios & Duffy 2007); possibly Brazil (Christofferson 1979); Curaçao (this study).

**Remarks.** Despite variation in size, and in some cases color patterns, careful examination of morphological characters and genetic sequencing (KMH unpublished data) support classification of these specimens as *Synalpheus bousfieldi*. All specimens of *S. bousfieldi* possessed a combination of characters that clearly distinguish this species from others in the *S. brooksi* species complex, including an acute major chela projection (directed downwards towards the dactyl) with a small secondary projection, a minor chela with a thick tuft of setae on the moveable finger, scaphocerite and basicerite spines exceeding the second antennal



segment, and a stout stylocerite (see Macdonald *et al.* 2009 for a table summarizing the characters differentiating members of the *S. bousfieldi* complex). However, specimens of *S. bousfieldi* from *Agelas* cf. *clathrodes* were smaller (mean CL 2.9 mm) than individuals from *Hyattella intestinalis* and *X. proxima* (pooled mean CL 4.1 mm), and individuals from *Aiolochoxia crassa*—a sponge with large canals—were the largest (mean CL 4.9 mm). *S. bousfieldi* can be distinguished most readily from *Synalpheus carpenteri* co-occurring in *A.* cf. *clathrodes* by the length of the basicerite (clearly exceeding the second antennal segment in *S. bousfieldi*, rarely exceeding the first antennal segment in *S. carpenteri*). In the sponge *A. crassa*, *S. bousfieldi* can be distinguished from *Synalpheus herricki* by the stylocerite (long and thin in *S. herricki*, stout in *S. bousfieldi*) and the dactyl of the major chela (strongly hooked in *S. herricki*).

***Synalpheus carpenteri* Macdonald & Duffy, 2006**  
(Pl. 3C)

**Material examined.** Curaçao: 25 ov. females, 46 non-ov. individuals (VIMS 08CU3012–5, 3805–6, 3901–2), Caracas Baai, from the canals of the sponge *Agelas* cf. *clathrodes*. 2 ov. females, 6 non-ov. individuals (VIMS 08CU13001), Eastpunt, from the canals of *A.* cf. *clathrodes*. 1 ov. female, 1 non-ov. individual (VIMS 08CU1601–2), Piscadera Baai, from the canals of *A.* cf. *clathrodes*. 4 ov. females, 3 non-ov. individuals (VIMS 08CU8701), Piscadera Baai east, from the canals of *A.* cf. *clathrodes*. 23 ov. females, 22 non-ov. individuals (VIMS 08CU8201, 7–14), Scary Steps, from the canals of *A.* cf. *clathrodes*. Largest ov. female, CL 3.8 mm, largest non-ov. individual, CL 3.2 mm.

**Color.** Body color transparent to orange-tinged, ovigerous females with orange or reddish-orange ovaries and embryo color ranging from orange to dull pinkish red.

**Hosts and ecology.** As in all other known locations, *S. carpenteri* in Curaçao is a host specialist on sponges in the genus *Agelas* (*Agelas* cf. *clathrodes* in Curaçao), which it often occupied along with *Synalpheus agelas* and less frequently with *Synalpheus sanctithomae* and *Synalpheus mcclendoni*. *S. carpenteri* occurred as a single pair in smaller sponges or in larger groups of approximately equal sex ratios in larger sponges.

**Distribution.** Bahamas (as *S. bousfieldi* in part, Dardeau 1984; see Macdonald & Duffy 2006); Caribbean Panama (Macdonald & Duffy 2006); Belize (Macdonald & Duffy 2006; Macdonald *et al.* 2006; Rios & Duffy 2007); Jamaica (Macdonald *et al.* 2009); Curaçao (this study).

**Remarks:** *Synalpheus carpenteri* was one of the most widespread species in Curaçao (though not the most abundant), occurring in most locations where *Agelas* cf. *clathrodes* was usually collected. In life, *S. carpenteri* in Curaçao can be easily distinguished from other species occupying *Agelas* cf. *clathrodes* by the distinctive, brilliant orange coloring of the body and developing ovaries. *S. carpenteri* can also be distinguished from *S. agelas* (the most common co-inhabitant in *A.* cf. *clathrodes*) by the number of segments on the carpus of the second pereopod (4 in *S. agelas*, 5 in *S. carpenteri*).

***Synalpheus dardeau* (Rios & Duffy, 2007)**

**Material examined.** Curaçao: 1 non-ov. individual (VIMS 08CU4305), Piscadera Baai east (65 m depth), from the canals of *Spongia* sp., CL 4.2 mm.

**Color.** Non-descript and drab.

**Hosts and ecology.** The single individual of *S. dardeau* collected in Curaçao inhabited a *Spongia* sp. collected at ~65 m depth that also hosted several individuals of *Synalpheus idios*.

**Distribution.** Belize (Macdonald *et al.* 2006; Rios & Duffy 2007), Caribbean Panama (Morrison *et al.* 2004, as “*pandionis giant*”), Curaçao (this study).

**Remarks.** *S. dardeau* is the largest species in the sponge-dwelling *Synalpheus gambarelloides* group (Rios & Duffy 2007) and as such tends to inhabit sponges with larger canals such as *Sphaciospongia*

*vesparium* and *Lissodendoryx colombiensis* Zea & van Soest (Macdonald *et al.* 2006, Rios & Duffy 2007). These sponge species were absent from our surveys in Curaçao, and *S. dardeau* occurred only in *Spongia* sp. from deep water, which had some of the largest canal sizes of any of the sponges sampled in our survey. Previous surveys of *Sphaciospongia vesparium* from Curaçao (Westinga & Hoetjes 1981) did not report *Synalpheus longicarpus* Herrick or *Synalpheus pandionis* Coutière, (the closest described morphological relatives of *S. dardeau*; *S. dardeau* was not described until 2007), suggesting that this species may not have been common in *S. vesparium* when it was abundant in shallower areas in Curaçao.

### ***Synalpheus goodei* Coutière, 1909**

(Pl. 3D)

**Material examined.** Curaçao: 1 ov. female (VIMS 08CU5101), Westpunt, from the canals of *Xestospongia proxima*, CL 4.3 mm. Panama: 1 ov. female (VIMS08CU9201–2), Isla San Cristobal (09° 18' 02.04" N, 82° 16' 28.74" W), from the canals of *Calyx podatypa* de Laubenfels.

**Color.** Body drab and colorless, with pinkish-brown embryos.

**Hosts and ecology.** The single individual of *Synalpheus goodei* collected in Curaçao was found in the sponge *Xestospongia proxima*. *S. goodei* occurs in the related sponges *Xestospongia wiedenmayeri* and *Calyx podatypa* in Belize (Macdonald *et al.* 2006; Rios & Duffy 2007) and Panama (this study).

**Distribution.** Florida (Coutière 1909); Gulf of Mexico (Coutière 1909; Dardeau 1984); Cuba (Martínez Iglesias & García Raso 1999); Dominica, Tobago (Chace 1972); Belize (Macdonald *et al.* 2006; Rios & Duffy 2007), Curaçao (this study; Westinga & Hoetjes, 1981), Caribbean Panama (this study).

**Remarks.** The specimen found here was similar in morphology to described species of *S. goodei* elsewhere, but was exceedingly rare despite frequent sampling of the host sponge it was found in (*Xestospongia proxima*, 15 individual sponges from four different locations). Westinga and Hoetjes (1981) recorded *S. goodei* from the canals of *Sphaciospongia vesparium* (which was never collected in our study, despite intensive searching), suggesting that this species may have been more common in Curaçao in the recent past.

### ***Synalpheus herricki* Coutière, 1909**

(Pls. 3E–F, 4A)

**Material examined.** Curaçao: 32 ov. females, 42 non-ov. individuals (VIMS 08CU3201–6, 4001–3, 10701–3, 10801–3), Caracas Baai, from the canals of *Aiolochoxia crassa*. 4 ov. females, 5 non-ov. individuals (VIMS 08CU101–2, 105–11), Piscadera Baai, from the canals of *A. crassa*. 6 ov. females, 5 non-ov. individuals (VIMS 08CU8902–3), from the canals of *Hyattella intestinalis*, Piscadera Baai east. 7 ov. females, 6 non-ov. individuals (VIMS 08CU9802–5), Piscadera Baai east, from the canals of *A. crassa*. 2 individuals (VIMS 08CU8603), Scary Steps, from the canals of *H. intestinalis*. 31 ov. females, 40 non-ov. individuals (VIMS 08CU2601–10, 2701–9, 2802–7), St Michiel Baai, from the canals of *A. crassa*. 2 ov. females, 4 non-ov. individuals (VIMS 08CU6501–2), Westpunt, from the canals of *A. crassa*. Largest ov. female, CL 7.6 mm, largest non-ov. individual, CL 7.0 mm.

**Color.** Drab non-descript body, developing ovaries grey to olive-green, embryos either 1) olive green to pale grass green, or 2) dark red wine-colored.

**Hosts and ecology.** *S. herricki* occurs in approximately equal sex ratios in the common sponges *Aiolochoxia crassa* and less commonly in *Hyattella intestinalis*. Some individuals had bopyrid parasites in branchial regions (Plate 4A).

**Distribution.** Florida (Coutière 1909); Gulf of Mexico (Coutière 1909; Dardeau 1984); Belize (Rios & Duffy 2007), Curaçao (this study).

**Remarks.** Female *Synalpheus herricki* collected in Curaçao occurred in two distinct color morphs: with olive- to grass-green embryos (Plate 3E; as described from other localities), or with dark red wine-colored

embryos (Plate 3F). These two morphs sometimes (but not always) co-occurred in individual sponges, and males in these species were indistinguishable. Careful examination of females with two different colored embryos revealed no distinct morphological differences except that females with wine-colored embryos were slightly larger (mean CL 6.87 mm  $\pm$  0.16 SE) than females with green embryos (mean CL 6.03 mm  $\pm$  0.34 SE), and had slightly longer stylocerites (75–100% of the length of the first antennal peduncle) than females with green embryos (50–75% of length of peduncle). These data suggest larger, more mature individuals may be more likely to have wine-colored embryos and longer stylocerites.

***Synalpheus hoetjesi* sp. nov.**

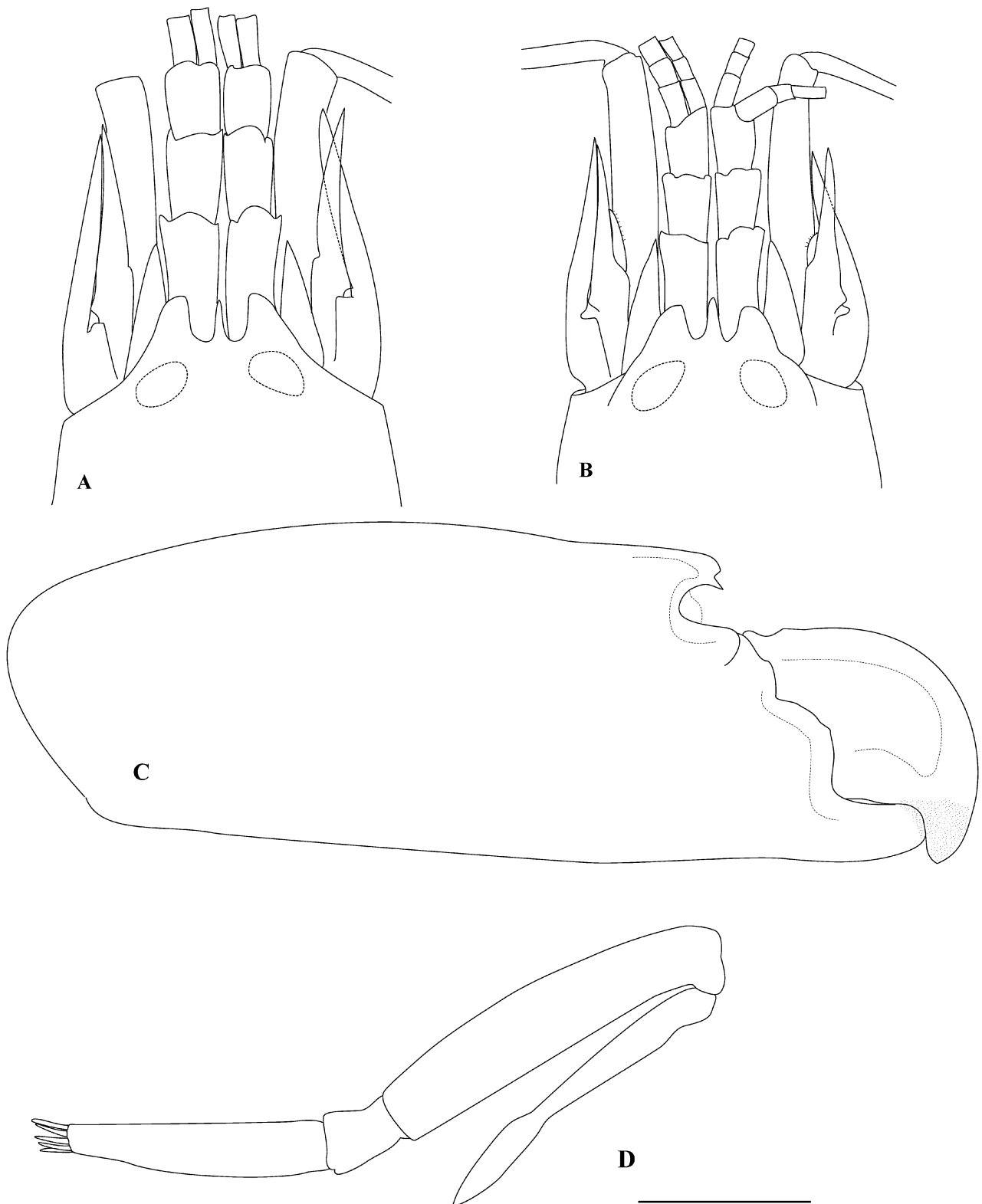
(Figs. 3–9, Pl. 4B–D)

**Type material.** *Holotype*: Male, CL 4.80 mm (USNM 1128421, original VIMS 08CU4104), Caracas Baai, Curaçao (12°04'11.64"N, 68°51'43.59"W), from the canals of *Hyattella intestinalis*, 19.VI.2008. *Allotype*: Ov. female, CL 4.50 mm (USNM 1128422, original VIMS 08CU4101), same data as holotype. *Paratypes*: 3 non-ov. individuals, CL 3.4–4.27 mm (USNM 1128423, 1128424, 1128425, original VIMS 08CU4103, 5, 12), 1 ov. female, CL 3.5 mm (USNM 1128426), original VIMS 08CU4106), same data as holotype.

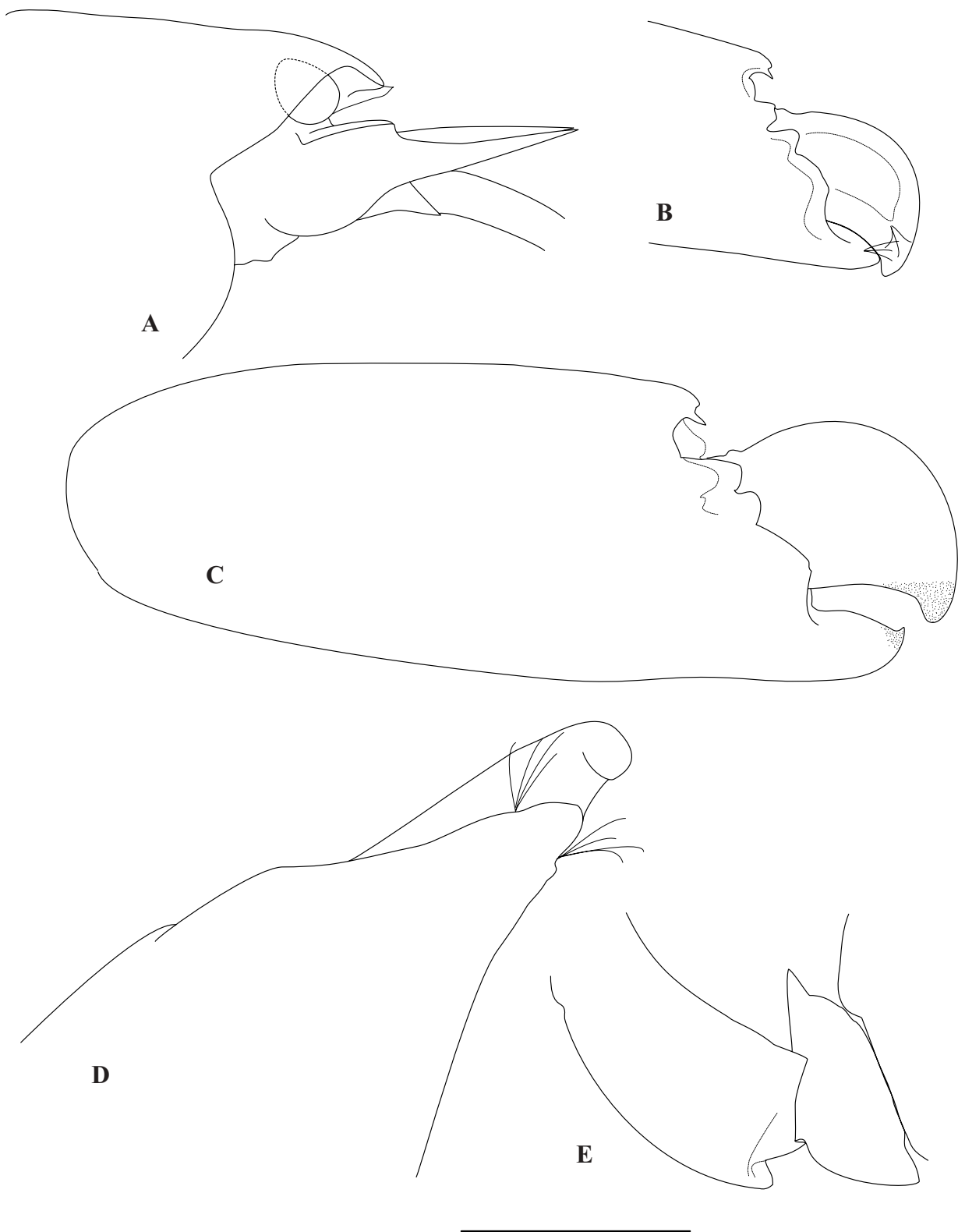
**Additional material examined.** Curaçao: 3 ov. females, 5 non-ov. individuals (VIMS 08CU10101, 10401, 11901–2), Caracas Baai, from the canals of *Hyattella intestinalis*. 2 ov. females, 3 non-ov. individuals (VIMS 08CU2901–2, 11501), Caracas Baai, from the canals of *Xestospongia subtriangularis*. 1 ov. female, 2 non-ov. individuals (VIMS 08CU11203–4), Caracas Baai, from the canals of *Xestospongia proxima*. 2 ov. females, 2 non-ov. individuals (VIMS 08CU303–3, 1804), Piscadera Baai, from the canals of *H. intestinalis*. 2 ov. females, 4 non-ov. individuals (VIMS 08CU9702–4), Piscadera Baai, from the canals of *X. subtriangularis*. 6 ov. females, 9 non-ov. individuals (VIMS 08CU8904, 9901–2), Piscadera Baai east, from the canals of *H. intestinalis*. 2 ov. females, 2 non-ov. individuals (VIMS 08CU8601), Scary Steps, from the canals of *H. intestinalis*. 2 ov. females, 2 non-ov. individuals (VIMS 08CU5601–4) and swimming larvae released from female 5603 (VIMS 08CU5612), Westpunt, from the canals of *H. intestinalis*. Largest ov. female in Curaçao, CL 6.2 mm, largest non-ov. individual, CL 5.3 mm. Barbados: 1 ov. female, 1 non-ov. individual (VIMS 08BR6701, 6708–1), Cement Factory (13°17'21.84"N, 59°39'27.72"W, 6–10 m depth), from the canals of *H. intestinalis*. 1 ov. female (VIMS 08BR9603), Thunder Bay (13°13'11.16"N, 59°38'29.58"W, 2–4 m depth), from the canals of *Agelas* cf. *clathrodes*.

**Description.** Subcylindrical; carapace smooth, sparsely setose, posterior margin with distinct cardiac notch. Frontal margin (Figs. 3A–B, 4A): rostrum clearly narrower than ocular hoods, approximately as long as ocular hoods. Ocular hoods hoof-shaped to triangular, separated from rostrum by deep sinus. Stylocerite broadly slender, tip bluntly acute, length equal or subequal to distal margin of first segment of antennular peduncle. Basicerite without sharp spine-like tooth on dorsolateral corner, and with longer ventrolateral spine clearly overreaching 2<sup>nd</sup> antennular peduncle. Scaphocerite acute lateral spine also clearly overreaching 2<sup>nd</sup> antennular peduncle, typically similar in length as basicerite lateral spine (often slightly shorter or longer); blade variable, often absent on larger individuals and ovigerous females, occasionally present or vestigial on one side (<25% length of acute lateral spine). Maxilliped 3 (Fig. 3D) with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment.

Major pereopod 1 (Figs. 3C, 4B–E) massive, fingers shorter than half-length of palm; in ventral view, outer face of fixed finger without pronounced protuberance. Palm of chela with distal superior margin produced into pronounced tubercle that bulges over downwardly directed acute spine on its ventral face. Merus, extensor margin convex, with distal angular projection. Minor pereopod 1 (Fig. 5A–B) with palm about 2 times longer than high; fingers shorter than palm; dactyl with flexor margin straight, blade-like, with subdistal accessory tooth parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl conspicuous, with plumose setae. Fixed finger with flexor margin straight, bladelike, and with subdistal accessory protuberance.



**FIGURE 3.** *Synalpheus hoetjesi* sp. nov. Holotype (A, D), male (USNM 1128421, original VIMS 08CU4104) from *Hyattella intestinalis*, Caracas Baai, Curaçao; Allotype (B, C) ov. female (USNM 1128422, original VIMS 08CU4101) from *Hyattella intestinalis*, Caracas Baai, Curaçao. A, carapace, anterior region, and cephalic appendages, dorsal view; B, carapace, anterior region, and cephalic appendages, dorsal view; C, chela of major first pereopod, dorsal view; D, third maxilliped. Scale bar = 1 mm.



**FIGURE 4.** *Synalpheus hoetjesi* sp. nov. Paratype (A), non-ov. individual (USNM 1128423, original VIMS 08CU4103) from *Hyattella intestinalis*, Caracas Baai, Curaçao; allotype (B, C) ov. female (USNM 1128422, original VIMS 08CU4101) from *Hyattella intestinalis*, Caracas Baai, Curaçao; holotype (D, E) male (USNM 1128421, original VIMS 08CU4104) from *Hyattella intestinalis*, Caracas Baai, Curaçao. A, carapace, anterior region, lateral view; B, detail of distal end of chela of major first pereopod, dorsal view; C, chela of major first pereopod, dorsal view; D, chela of major first pereopod, mesial view; E, merus and carpus of major first pereopod. Scale bar = 1 mm (A, D); 2 mm (B, C, E).

2<sup>nd</sup> pereopod (Fig. 5C) with carpus 5-segmented, slightly longer than merus.

3<sup>rd</sup> pereopod (Fig. 6A–B) stout; dactyl biunguiculate, with clearly unequal teeth; and flexor tooth wider at base than extensor tooth; propodus with 8 mobile spines on flexor margin and 1 pair on distal end; carpus with 1 mobile distal spine; merus without any spine on flexor margin. 4<sup>th</sup> pereopod (Fig. 6C–D) similar to 3<sup>rd</sup>, but with 7 mobile spines on flexor margin. 5<sup>th</sup> pereopod (Fig. 6E–F) similar to 4<sup>th</sup>, but without distal spine on carpus, and with 7 transverse combs of stout setae on ventral face of propodus.

Pleura 1 of male (Fig. 7B) with posterior corner produced ventrally and anteriorly, hook-like; 2<sup>nd</sup> pleura of male with posterior corner broadly rounded; 3<sup>rd</sup> to 5<sup>th</sup> pleura with posterior margin forming blunt acute angle. Telson (Fig. 7C), mesial pair of distal telson spines distinctly stouter than lateral pair, relative length of mesial vs. lateral distal telson spines ranges from subequal to strongly unequal (mesial spines longer than lateral).

Uropods with 4–6 fixed teeth on outer margin of exopod anterior to moveable spine.

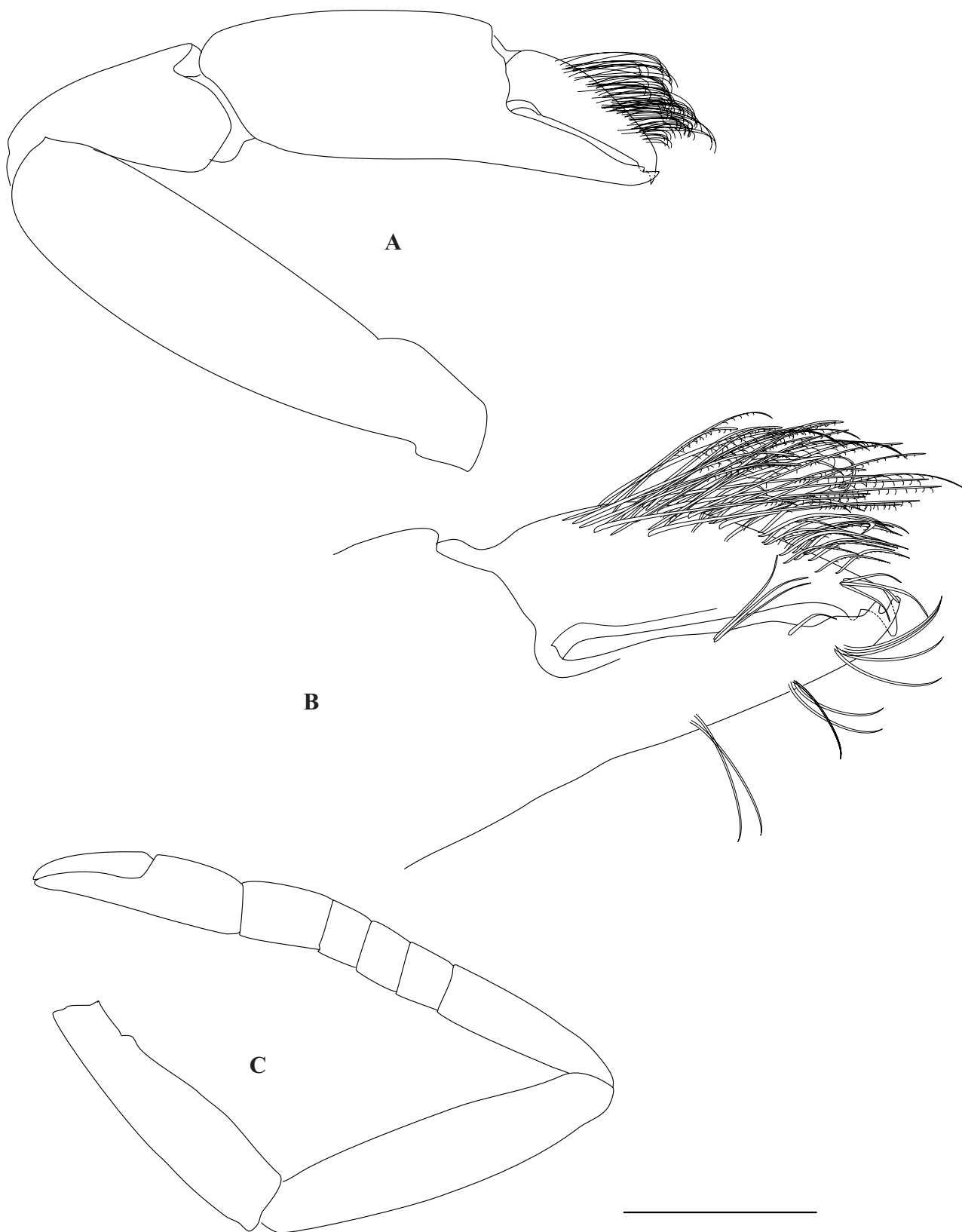
**Color.** Live specimens range from drab to orange-tinged; ovigerous females have brilliant orange ovaries, embryo color ranges from reddish-brown to chestnut-colored.

**Etymology.** We are honored to name this species after Dr. Paul Hoetjes, who was one of the first to examine cryptofaunal sponge communities in Curaçao (Westinga & Hoetjes 1981) and who provided invaluable assistance to us during this expedition.

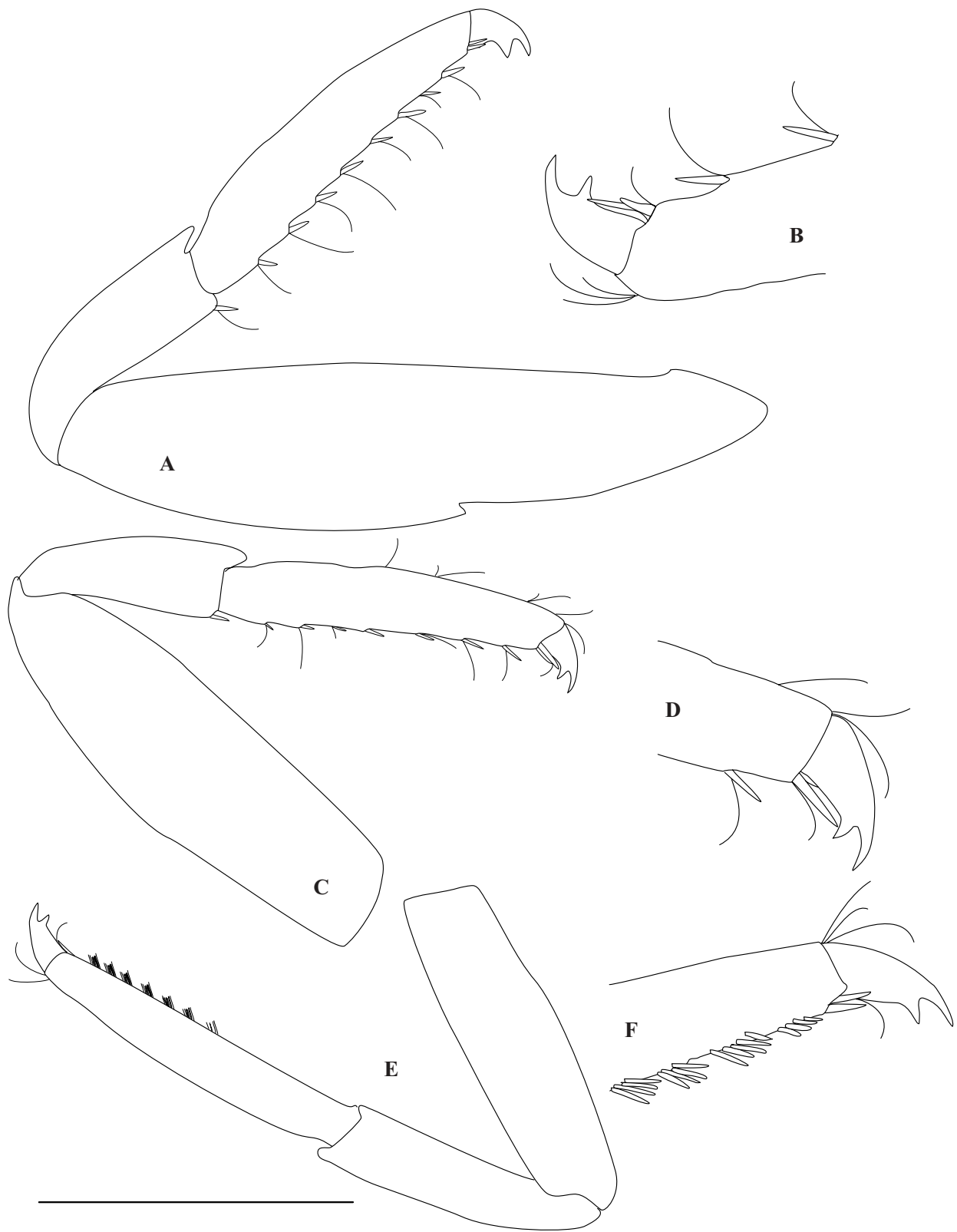
**Hosts and ecology.** *Synalpheus hoetjesi* was found most frequently in the sponge *Hyattella intestinalis* and (less frequently) in *Xestospongia proxima* and *Xestospongia subtriangularis* (see notes above). *S. hoetjesi* has also been recorded from the sponges *Hyattella intestinalis* and *Agelas* cf. *clathrodes* in Barbados (Table 2).

**Distribution.** Curaçao (this study), Barbados (this study).

**Remarks.** This species is morphologically and phylogenetically most closely related to *Synalpheus ul* and *Synalpheus yano*, but is distinguishable from them by host use, size, and several morphological characteristics. *S. hoetjesi* can be distinguished from *S. yano* by the posterior corner of the male 2<sup>nd</sup> pleura (which forms an obtuse angle in *S. yano* and is broadly rounded in *S. hoetjesi*) and by the relative thickness of the distal telson spines (medial spines clearly thicker and stouter than lateral spines in *S. hoetjesi*, but equal or subequal in thickness in *S. yano*). In Curaçao, where *S. hoetjesi* co-occurs with *S. ul*, *S. hoetjesi* was most often found in *Hyattella intestinalis*, and was very easy to differentiate from *S. ul* living in *Hymeniacion caerulea* and *Agelas* cf. *clathrodes*. In the latter hosts, *S. hoetjesi* is easily distinguishable from *S. ul* by body size (*S. hoetjesi* mean CL 4.70 mm, *S. ul* mean CL 3.36 mm), scaphocerite blade (absent or vestigial in *S. hoetjesi*, present and ~20–75% the length of the scaphocerite in *S. ul*), shape of the distal superior margin in the major chela (bulging over the accessory spine in *S. hoetjesi*, gently sloping in *S. ul*), and thickness of distal telson spines (mesial > lateral in *S. hoetjesi*, mesial  $\approx$  lateral in *S. ul*). Additionally, specimens identified as *S. ul* based on the COI gene tree were never found in *H. intestinalis*, and specimens identified as *S. hoetjesi* based on COI were never found in *Hymeniacion* or *Agelas*, suggesting (along with aforementioned differences in morphology) that these species are clearly delineated in these hosts. However, although *S. hoetjesi* formed a distinct clade in the mitochondrial COI gene tree (Fig. 8), individuals of *S. hoetjesi* from hosts other than *Hyattella intestinalis* were more difficult to distinguish morphologically from *Synalpheus ul* (Fig. 9). In particular, sponges in the genus *Xestospongia* (*Xestospongia* sp. “soft”, *X. proxima*, and *X. subtriangularis*) hosted both *S. ul* and *S. hoetjesi* as identified using the COI gene tree (Fig. 8), but these individuals sometimes exhibited ambiguous characters (Fig. 9). *S. hoetjesi* from *X. subtriangularis* usually possessed the bulging major chela protuberance typical of *S. hoetjesi* from *H. intestinalis*, but often had distal telson spines that were nearly equal in thickness, which is otherwise typical of *S. ul*. Likewise, *S. ul* from *X. subtriangularis* and *Xestospongia* sp. “soft”, often had distal telson spines equal in thickness, but sometimes had major chela protuberances that approached the “bulge” characteristic of *S. hoetjesi*. Close phylogenetic relationships between *S. hoetjesi* and *S. ul*, along with convergence of morphological characters in sponge hosts in which these two species co-occurred, suggests these species may be hybridizing in these hosts, although additional genetic analyses with nuclear markers are necessary to confirm this hypothesis.

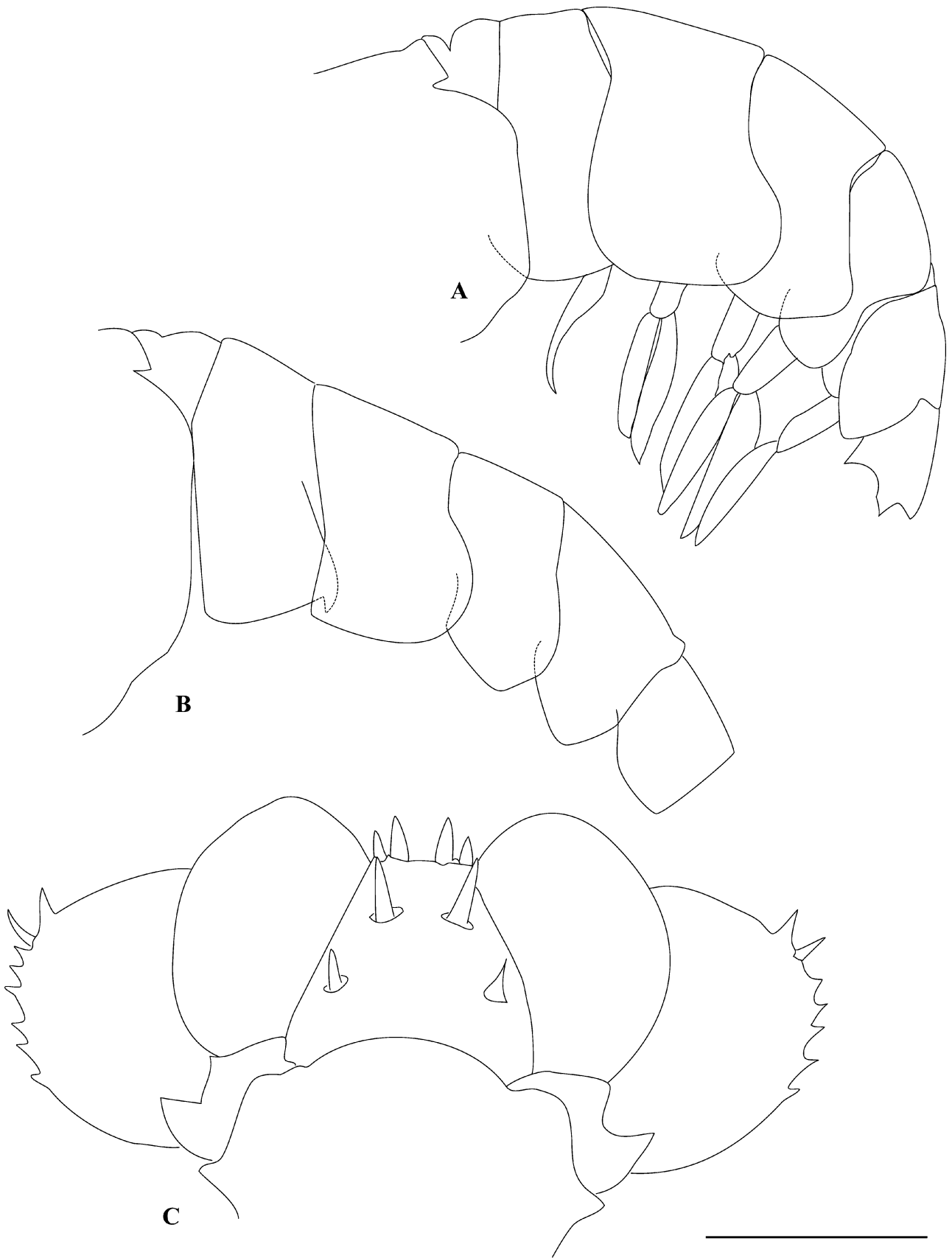


**FIGURE 5.** *Synalpheus hoetjesi* sp. nov. Holotype male (USNM 1128421, original VIMS 08CU4104) from *Hyattella intestinalis*, Caracas Baai, Curaçao: A, minor first pereopod, dorsal view; B, minor first pereopod, detail of distal end; C, left second pereopod. Scale bar = 1 mm (A, C); 0.5 mm (B).

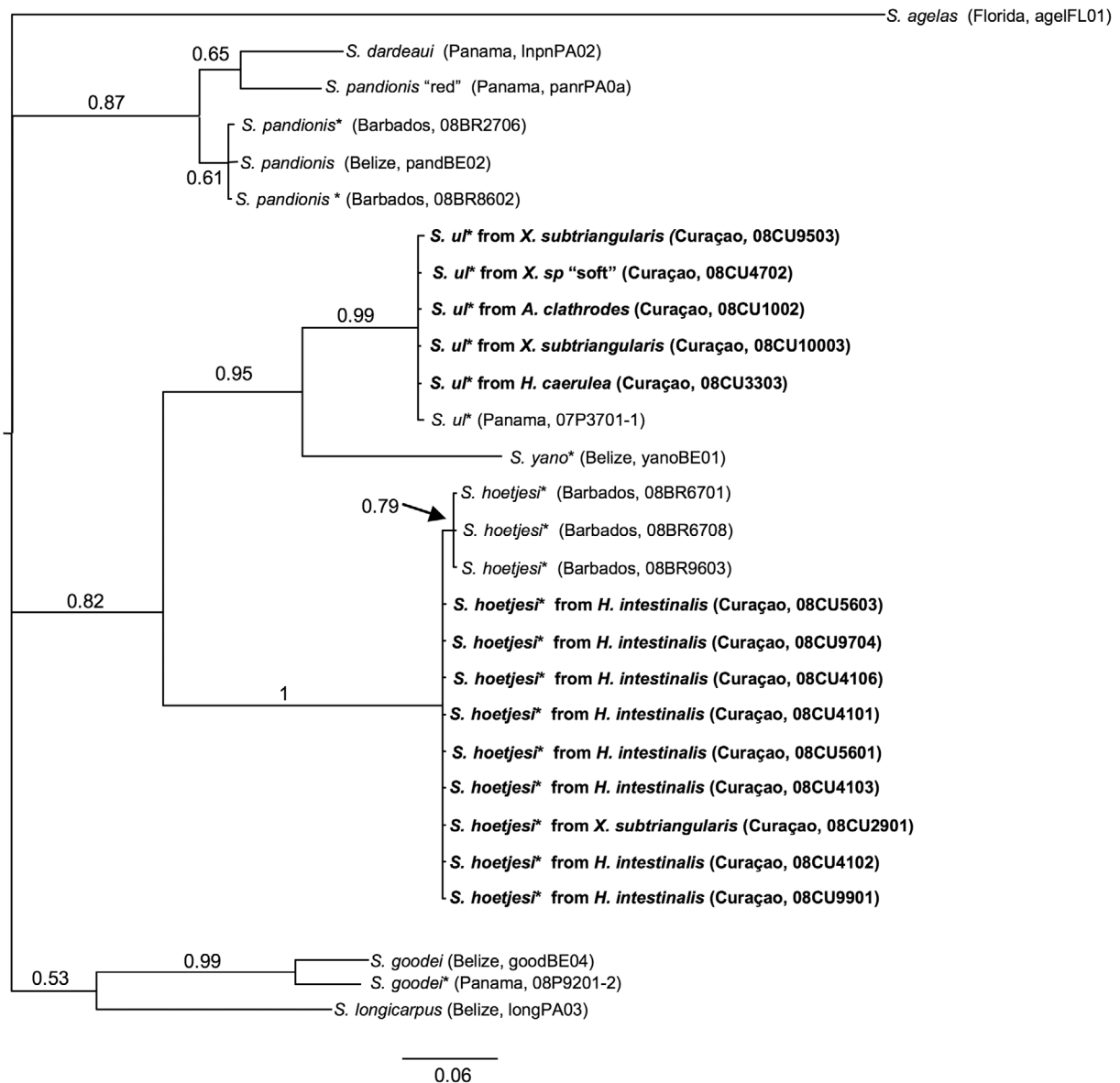


**FIGURE 6.** *Synalpheus hoetjesi* sp. nov. Holotype male (USNM 1128421, original VIMS 08CU4104) from *Hyattella intestinalis*, Caracas Baai, Curaçao: A, third pereopod; B, same, detail of distal region; C, fourth pereopod; D, same, detail of distal region; E, fifth pereopod; F, same, detail of distal region. Scale bar = 1 mm (A, C, E); 0.5 mm (B, D, F).



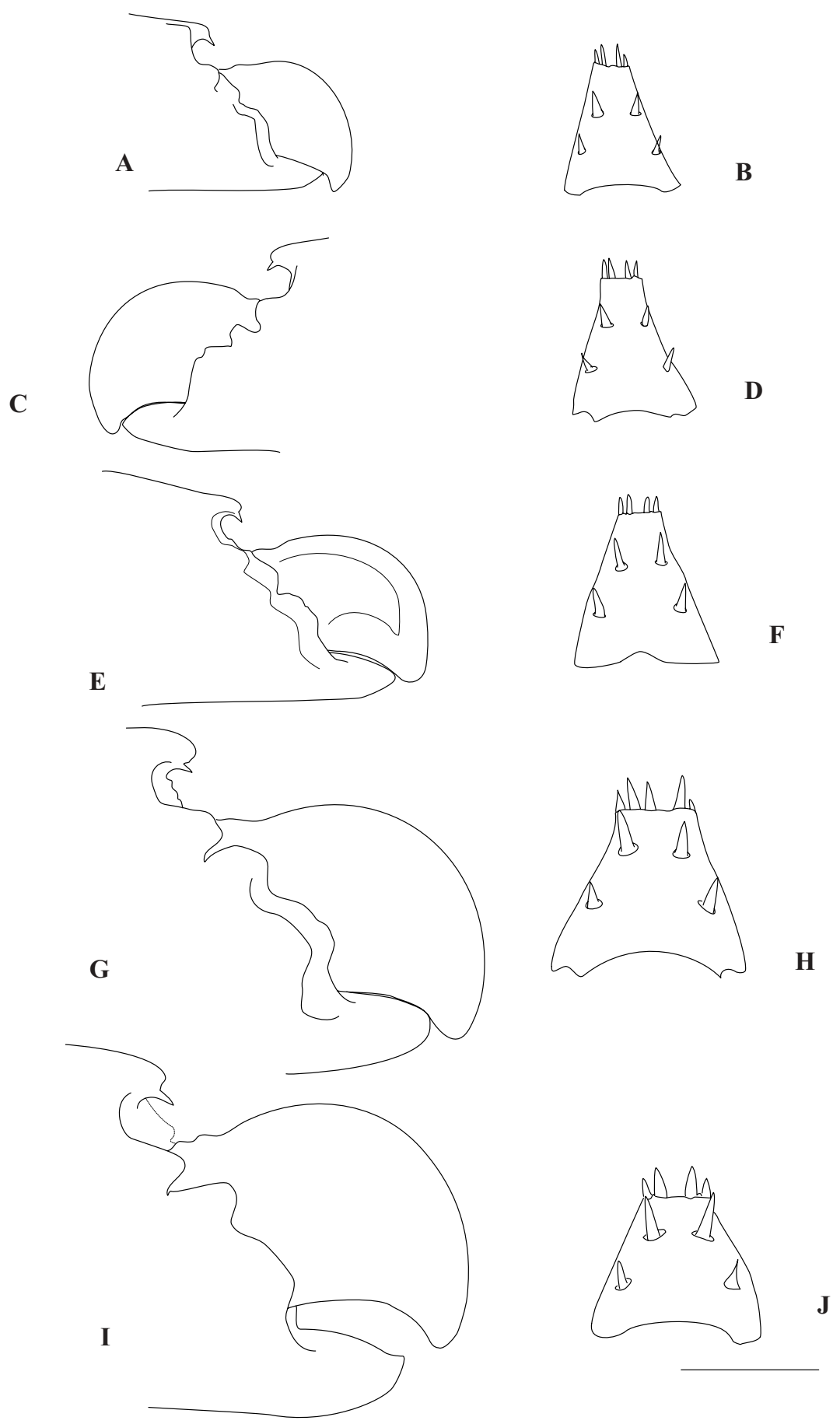


**FIGURE 7.** *Synalpheus hoetjesi* sp. nov. Allotype (A) ov. female (USNM 1128422, original VIMS 08CU4101) from *Hyattella intestinalis*, Caracas Baai, Curaçao, holotype (B–C) male (USNM 1128421, original VIMS 08CU4104) from *Hyattella intestinalis*, Caracas Baai, Curaçao. A, abdomen, lateral view; B, abdomen, lateral view; C, telson and uropods, dorsal view. Scale bar = 2 mm (A–B); 1 mm (C).



**FIGURE 8.** Gene tree of partial cytochrome *c* oxidase subunit I (COI) sequences from taxa in the *pandionis* species complex of *Synalpheus* from Curaçao and their closest phylogenetic relatives based on Bayesian analysis. Numbers on branches indicate posterior probability values. Species marked with an asterisk (\*) represent new sequences, all other sequences are from a previous study (Morrison *et al.* 2004). Species from Curaçao are in bold, and noted with their sponge host and VIMS collection number (e.g., "08CU10003"); species from other locations are noted with their VIMS collection number only. Scale bar indicates number of substitutions per site. See Table 2 for GenBank accession numbers.

**FIGURE 9.** *Synalpheus ul* (A–F) and *Synalpheus hoetjesi* sp. nov. (G–J) from different sponge hosts. A–B, from *Hymeniacidon caerulea* (original VIMS number 08CU3303). C–D, from *Xestospongia* sp. "soft" (VIMS 08CU4702). E–F, from *Xestospongia subtriangularis* (VIMS 08CU2501). G–H from *Xestospongia subtriangularis* (VIMS 08CU2902). I–J, from *Hyattella intestinalis* (VIMS 08CU4104). A, C, E, G, I, major first pereopod, detail of distal end, dorsal view; B, D, F, H, J, telson, dorsal view. Scale bar = 1 mm.



***Synalpheus idios* (Rios & Duffy, 2007)**

(Pl. 4E–F)

**Material examined.** Curaçao: 5 ov. females, 11 non-ov. individuals (VIMS 08CU10301, 10901–2), Caracas Baai, from the canals of *Spongia* sp. 21 ov. females, 27 non-ov. individuals (VIMS 08CU901–16, 918–9), Piscadera Baai, from the canals of *Spongia* sp. 19 ov. females, 36 non-ov. individuals (VIMS 08CU4306–11, 8801–4), Piscadera Baai east, from the canals of *Spongia* sp. Largest ov. female, CL 5.6 mm, largest non-ov. individual, CL 5.7 mm.

**Color.** Non-descript, sometimes with a pale milky tinge, with developing embryos and ovaries deep scarlet to brick red.

**Hosts and ecology.** In Curaçao, *Synalpheus idios* was found in groups of several individuals (with numerous ovigerous females present) in *Spongia* sp.

**Distribution.** Belize (Macdonald *et al.* 2006; Rios & Duffy 2007), Curaçao (this study).

**Remarks.** *Synalpheus idios* collected in Curaçao strongly resemble the type series described from Belize. In Curaçao, live specimens of *S. idios* can be easily distinguished by coloration of embryos in ovigerous females (dark brick to scarlet red) and host association (*S. idios* appears to be limited to *Spongia* sp. in this locality). *S. idios* can be distinguished from the related species *S. bousfieldi* in Curaçao by the shape of the distal projection on the major chela, which forms a blunt tubercle in *S. idios* and nearly always has a small secondary projection in *S. bousfieldi*.

***Synalpheus kuadramanus* sp. nov.**

(Figs. 10–13 Pl. 5A)

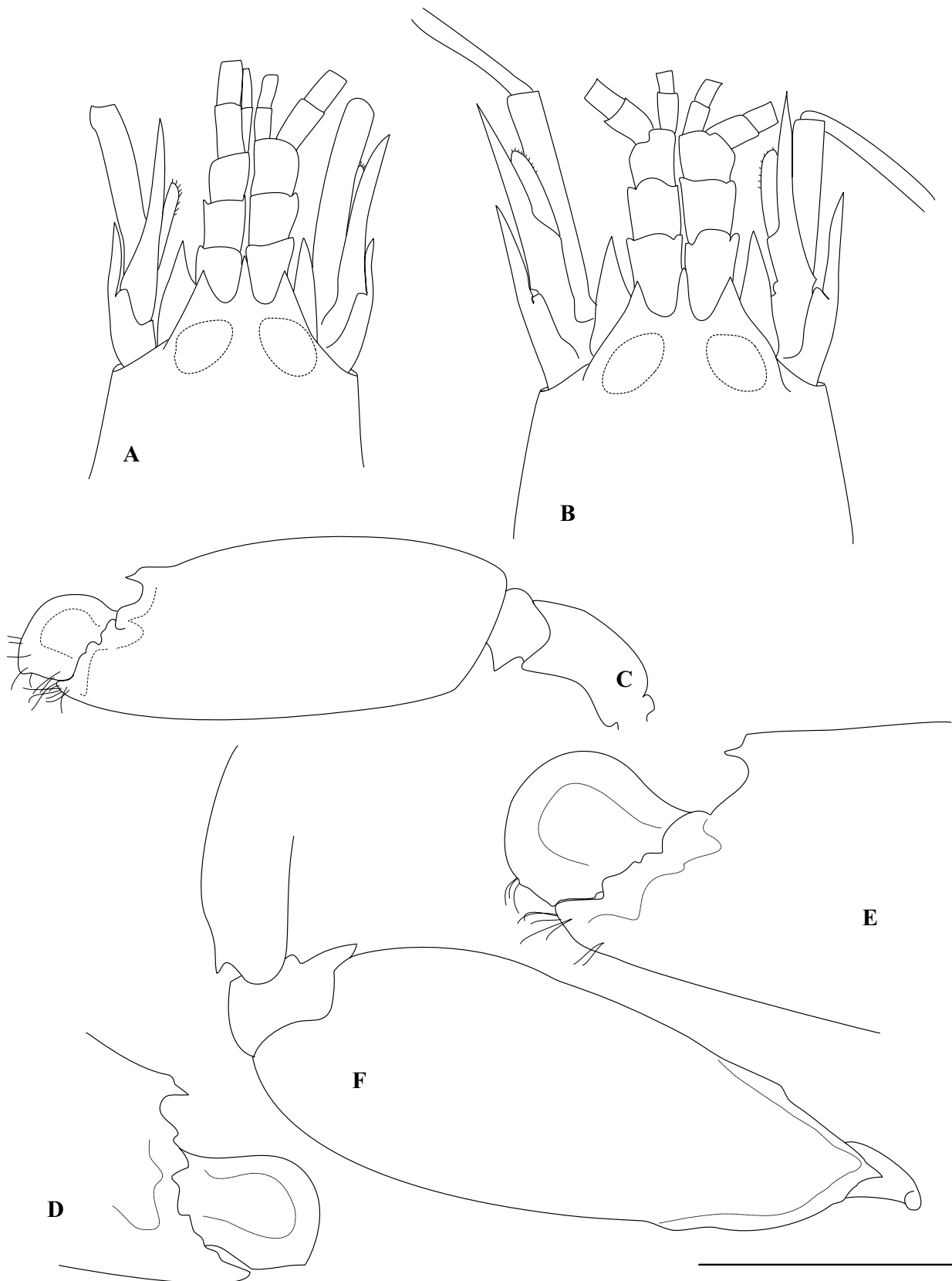
**Type material.** *Holotype*: Ov. female, CL 2.09 mm (USNM 1128430, original VIMS 08CU9001) Piscadera Baai east (12° 07' 15.96" N, 68° 58' 11.64" W), in *Xestospongia subtriangularis*, 23.VI.2008. *Allotype*: Male, CL 2.41 mm (USNM 1128429, original VIMS 08CU9002), same data as holotype.

**Additional material examined.** 1 ov. female, CL 2.85 mm, missing major chela (VIMS 08CU6601), Westpunt, Curaçao, from the canals of *Xestospongia proxima*.

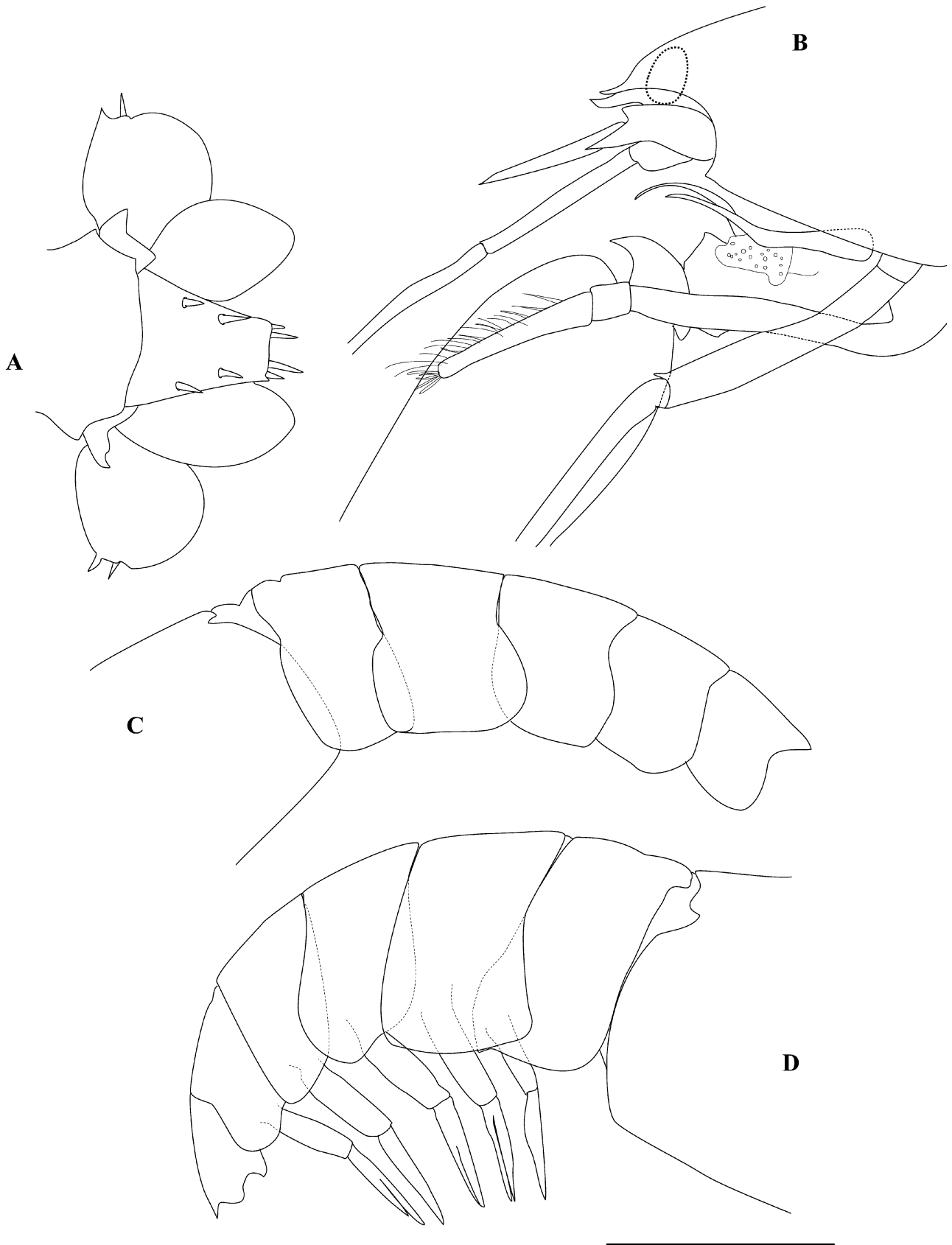
**Description.** Body subcylindrical; carapace smooth, sparsely setose, posterior margin with distinct cardiac notch. Frontal margin (Fig. 10A, B, 11B): rostrum clearly narrower than ocular hoods, slightly longer than ocular hoods, and distally upturned. Ocular hoods triangular, separated from rostrum by deep adrostral sinus. Stylocerite tip acute, not sharp, equivalent in length (or slightly longer than) distal margin of first segment of antennular peduncle. Basicerite without sharp spine-like tooth on dorsolateral corner, and with longer ventrolateral spine not reaching beyond 2<sup>nd</sup> antennal peduncle. Scaphocerite twice as long as basicerite, with large blade extending 50%–75% the length of the acute lateral spine, latter robust and far overreaching 3<sup>rd</sup> antennal peduncle. Maxilliped 3 (Fig. 12D) with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment.

Major pereopod 1 (Fig. 10C–F) massive, fingers shorter than 1/3 length of palm, fixed finger reduced, noticeably shorter than moveable finger; in ventral view, outer face of fixed finger without pronounced basal protuberance. Moveable finger short, with flexor margin distinctly squared-off (approaching concave), giving finger a square appearance from lateral view. Palm of chela with distal superior margin produced into prominent, square tubercle with acute spine directed forward. Merus, extensor margin convex, with distal angular projection. Minor pereopod 1 (Fig. 12A, C) with palm about 2 times longer than high, fingers shorter than palm, dactyl with flexor margin straight, blade-like, with slightly unequal bidentate tips, sparse dorsal setal combs on distal half of extensor surface of dactyl, setae plumose; fixed finger with flexor margin straight, bladelike, and subdistal accessory bump. Extensor margin of merus convex, ending in acute angle.

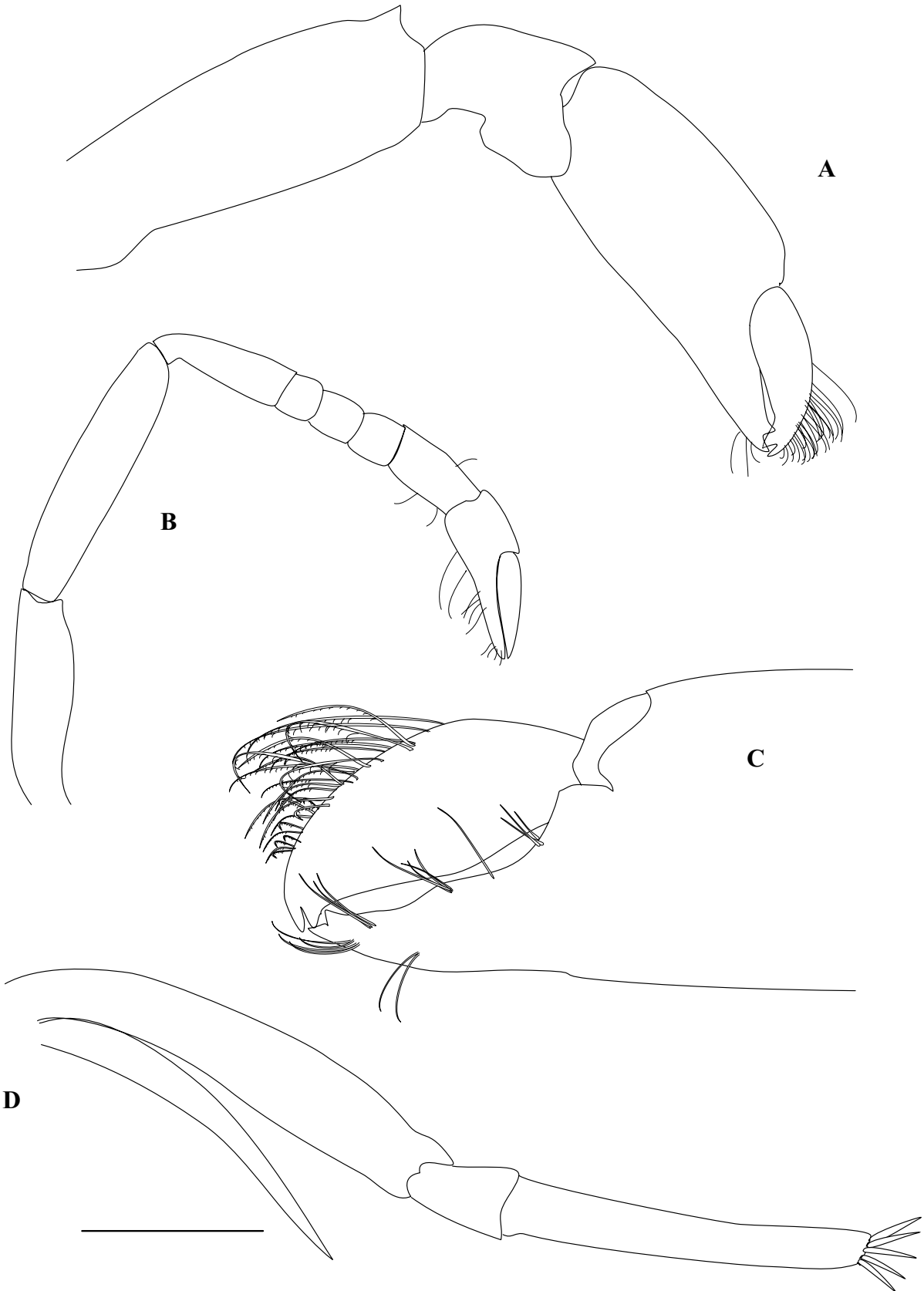
2<sup>nd</sup> pereopod (Fig. 12B) with carpus 5-segmented, slightly longer than merus.



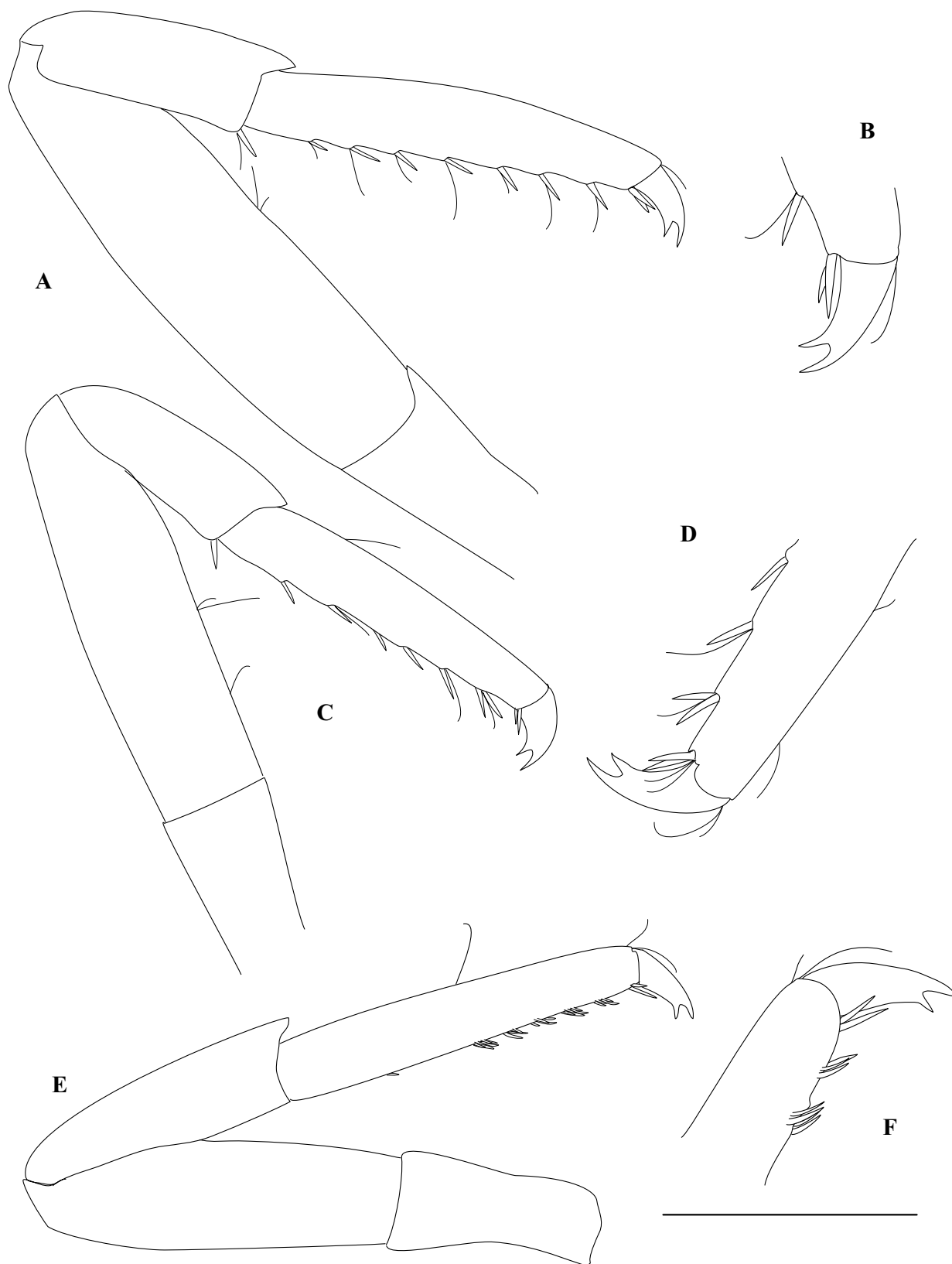
**FIGURE 10.** *Synalpheus kuadramanus* sp. nov. Holotype (A, C–D, F), ov. female (USNM 1128430, original VIMS 08CU9001) from *Xestospongia subtriangularis*, Piscadera Baai east, Curaçao. Allotype (B, E), male (USNM 1128429, original VIMS 08CU9002) from *X. subtriangularis*, Piscadera Baai east, Curaçao. A, carapace, anterior region, and cephalic appendages, dorsal view; B, carapace, anterior region, and cephalic appendages, dorsal view; C, chela of major first pereopod, dorsal view; D, chela of major first pereopod, detail of distal end, ventral view; E, chela of major first pereopod, dorsal view; F, chela of major first pereopod, mesial view. Scale bar = 1 mm.



**FIGURE 11.** *Synalpheus kuadramanus* sp. nov., allotype (A, D) male (USNM 1128429, original VIMS 08CU9002) from *X. subtriangularis*, Piscadera Baai east, Curaçao. Holotype (B, C) ov. female (USNM 1128430, original VIMS 08CU9001) from *Xestospongia subtriangularis*, Piscadera Baai east, Curaçao. A, telson and uropods, lateral view; B, anterior region of carapace, lateral view; C, D, abdomen, lateral view. Scale bar = 1 mm.



**FIGURE 12.** *Synalpheus kuadramanus* sp. nov., allotype (A, C) male (USNM 1128429, original VIMS 08CU9002) from *X. subtriangularis*, Piscadera Baai east, Curaçao. Holotype (B, D) ov. female (USNM 1128430, original VIMS 08CU9001) from *Xestospongia subtriangularis*, Piscadera Baai east, Curaçao. A, minor first pereopod, dorsal view; B, second pereopod; C, minor first pereopod, detail of distal end, mesial view; D, left third maxilliped. Scale bar = 0.5 mm (A, B, D); 0.25 mm (C).



**FIGURE 13.** *Synalpheus kuadramanus* sp. nov. Allotype male (USNM 1128429, original VIMS 08CU9002) from *X. subtriangularis*, Piscadera Baai east, Curaçao: A, third pereopod; B, same, detail of distal region; C, fourth pereopod; D, same, detail of distal region; E, fifth pereopod; F, same, detail of distal region. Scale bar = 0.5 mm (A, C, E); 0.3 mm (B, D, F).



3<sup>rd</sup> pereopod (Fig. 13A, B) stout; dactyl biunguiculate, with clearly unequal teeth; and flexor tooth wider at base than extensor tooth; propodus with 7 mobile spines on flexor margin and 1 pair on distal end; carpus with 1 mobile distal spine; merus without any spine on flexor margin. 4<sup>th</sup> pereopod (Fig. 13C, D) with 6 single mobile spines on flexor margin and 2 pairs of spines on distal end. 5<sup>th</sup> pereopod (Fig. 13E, F) similar to fourth, but without distal spine on carpus, and with 5 rows of setal combs on ventral face of propodus.

Pleura 1 of male (Fig. 11D) with posterior corner produced ventrally and anteriorly, subtly hook-like; 2<sup>nd</sup> pleura with posterior corner broadly rounded; 3<sup>rd</sup> to 5<sup>th</sup> pleura with posterior margin forming broadly rounded corner.

Telson (Fig. 11A), space between distal spines about 1/3 of distal margin. Uropods with single fixed tooth on outer margin of exopod anterior to moveable spine.

**Color.** Drab body, females with turquoise embryos and ovaries.

**Etymology.** This species is named in honor of the country in which it was found. “Kuadramanus” is a word derived from the indigenous Papiamentu terms for square (kuadrá) and hand (man).

**Hosts and ecology.** *S. kuadramanus* is found in the sponges *Xestospongia subtriangularis* and *Xestospongia proxima* in Curaçao.

**Distribution.** Curaçao (this study).

**Remarks.** This species is morphologically most similar to *S. sanctithomae* and *S. mcclendoni*, but can be easily distinguished from these species by a number of characters. Like *S. sanctithomae* and *S. mcclendoni*, *S. kuadramanus* sp. nov. has a single uropod tooth, a scaphocerite twice the length of the basicerite, and a large scaphocerite blade. *S. kuadramanus* can easily be distinguished from these species by the distinctively squared-off distal tip of the moveable finger of the major chela after which it is named (versus a moveable finger with a bluntly pointed distal tip). *S. kuadramanus* can also be differentiated by the bright turquoise color of developing embryos in ovigerous females (versus yellowish-green or orange eggs in *S. sanctithomae* and *S. mcclendoni*). *S. kuadramanus* also shares some similarities to species in the *S. paraneptunus* species complex, notably the broadly rounded abdominal pleura of non-ovigerous individuals and relatively sparse setae on the minor chela. However, setae on the minor chela of *S. kuadramanus* are organized into transverse rows, as opposed to a scattered field of setae in species in the *S. paraneptunus* complex. Two individuals of *S. kuadramanus* were preserved with pieces of their host sponge in their mouths (Fig. 11B).

### ***Synalpheus mcclendoni* Coutière, 1910**

(Pls. 5B–C)

**Material examined.** Curaçao: 2 non-ov. individuals (VIMS 08CU3002–3), Caracas Baai, from the canals of *Agelas* cf. *clathrodes*. 2 ov. females, 2 non-ov. individuals (VIMS 08CU12401, 13002), Eastpunt, from the canals of *A.* cf. *clathrodes*. 1 individual (VIMS 08CU12203), Eastpunt, from the canals of *Hyattella intestinalis*. 1 ov. female, 1 non-ov. individual (VIMS 08CU504–5), Piscadera Baai, from the canals of *H. intestinalis*. 1 ov. female, 2 non-ov. individuals (VIMS 08CU9801), Piscadera Baai east, from the canals of *Aiolochoxia crassa*. 1 individual (VIMS 08CU8203), Scary Steps, from the canals of *A.* cf. *clathrodes*. 1 individual (VIMS 08CU2801), St. Michiel Baai, from the canals of *A. crassa*. 1 ov. female (VIMS 08CU5608), 1 non-ov. individual (VIMS 08CU5609), Westpunt, from the canals of *H. intestinalis*. Largest ov. female, CL 3.1, largest non-ov. individual, CL 3.9 mm.

**Color.** Individuals found in Curaçao typically had a brightly colored major chela, with distal red tips, a white crescent, and the rest of the chela proximal to the white crescent blue (Plate 5B). This “red white and blue” color morph has also been described from specimens collected from Belize and Caribbean Panama (Rios & Duffy 2007). Ovigerous females tended to have more drab coloration on the major chela, and had yellowish-green embryos.

**Hosts and ecology.** In Curaçao, *S. mcclendoni* was typically found in equal sex ratios and occurred in low frequencies across three different sponge hosts (*Agelas* cf. *clathrodes*, *Hyattella intestinalis*, and *Aiolochoxia crassa*).

**Distribution.** Florida (Coutière 1910); Bahamas (Dardeau 1984); Cuba (Martínez Iglesias & García Raso 1999); Yucatan peninsula of Mexico (Chace 1972); Caribbean Panamá (Duffy 1992), Belize (Rios & Duffy 2007), Jamaica (Macdonald *et al.* 2009); Curaçao (this study).

**Remarks.** *S. mcclendoni* can be distinguished from its morphologically closest relative (*S. sanctithomae*) on the basis of its curved major chela fingers (not curved in *S. sanctithomae*) and the broad fan of plumose setae on the distal margin of the telson (typically containing <6 setae in *S. sanctithomae*).

***Synalpheus orapilosus* sp. nov.**

(Figs. 14–17, Pls. 5D–E)

**Type material.** *Holotype:* Male, CL 3.17 mm (USMN 1128427, original VIMS 08CU3102) Caracas Baai, Curaçao (12° 04' 11.64" N, 68° 51' 43.56" W), in an unidentified white web-like sponge embedded in *Madracis* sp. rubble, 19.VI.2008. *Allotype:* Ov. female, CL 3.23 mm (USNM 1128428, original VIMS 08CU3101.), same data as holotype.

**Description.** Body subcylindrical; carapace smooth, sparsely setose, posterior margin with distinct cardiac notch. Frontal margin shallow (Fig. 14A–C): rostrum clearly narrower than ocular hoods, approximately same length as ocular hoods, distally upturned. Ocular hoods in dorsal view bluntly triangular, separated from rostrum by shallow adrostral sinus; in lateral view distally down turned. Stylocerite with acute tip, very short, length falling well short of distal end of first antennular peduncle. Basicerite without sharp spine-like tooth on dorsolateral corner, and with longer ventrolateral spine extending approximately to distal end of 2<sup>nd</sup> peduncle. Scaphocerite blade absent, acute lateral spine robust, approximately equivalent in length to (or slightly longer) than lateral spine of basicerite. Maxilliped 3 (Fig. 14E, 15E) with distal segment terminating in cluster of plumose setae, lacking distal circlet of spines (present on all other described West Atlantic *gambarelloides* group species in the genus *Synalpheus* with the exception of *Synalpheus barahonensis* Armstrong); without ventrodistal spine on antepenultimate segment.

Major pereopod 1 (Fig. 15A–C) massive, fingers shorter than half length of palm; in ventral view, outer face of fixed finger without subtle obtuse protuberance. Palm of chela with distal superior margin produced into blunt forward-facing conical tubercle with subtle secondary projection. Merus, extensor margin convex, without distal angular projection.

Minor pereopod 1 (Fig. 15D) with palm about 2 times longer than high, fingers shorter than palm; dactyl with flexor margin straight, blade-like, with subdistal accessory protuberance parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl conspicuous. Fixed finger with flexor margin straight, bladelike, and with subdistal accessory bump. Extensor margin of merus convex.

Second pereopod (Fig. 14D) with carpus 5-segmented, slightly longer than merus.

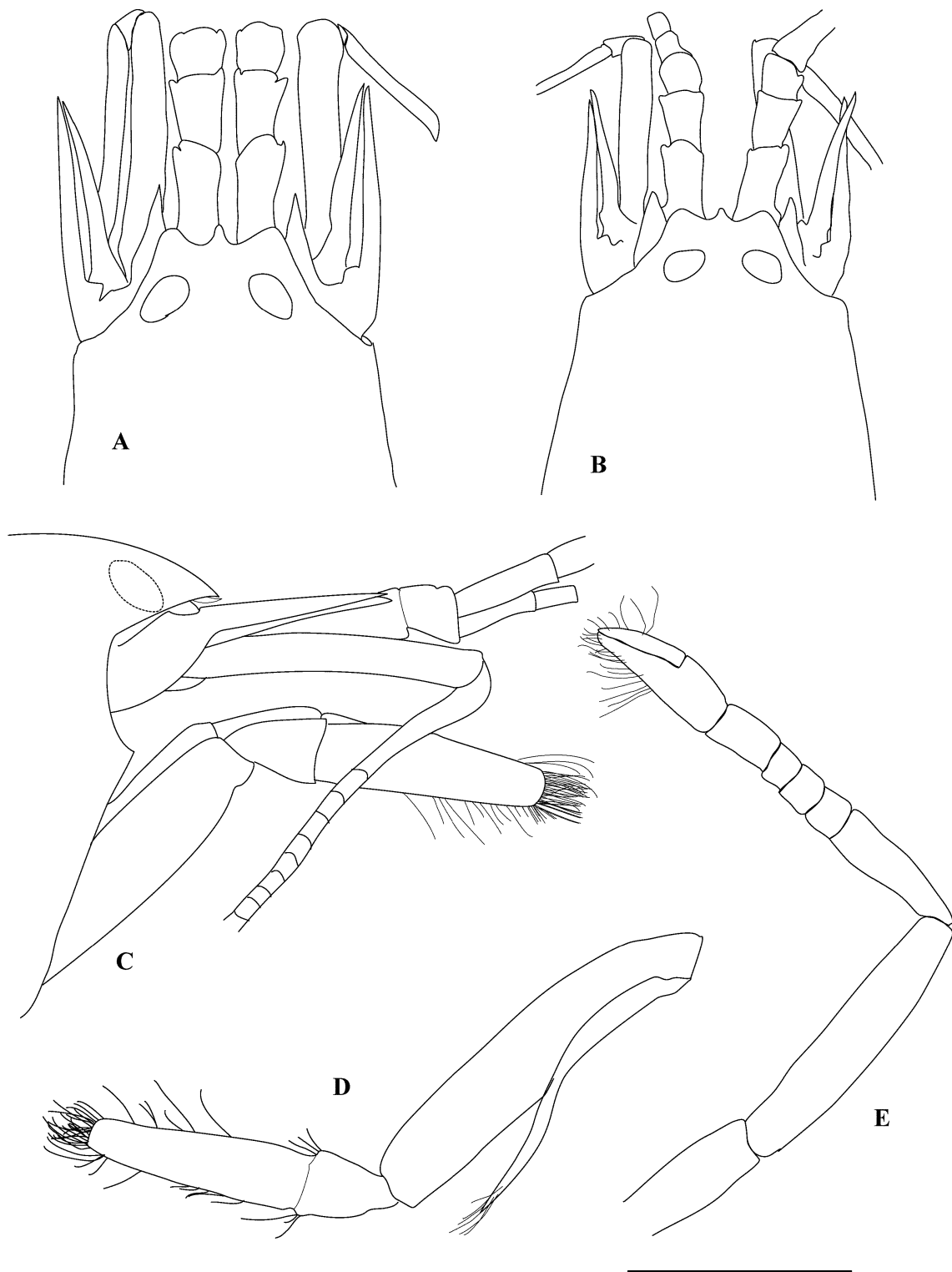
Third pereopod (Fig. 16A, B) dactyl biunguiculate, with clearly unequal teeth; flexor tooth wider at base than extensor tooth; propodus with 5 mobile spines on flexor margin and 1 pair on distal end; carpus with 1 mobile distal spine on flexor margin; merus without any spine on flexor margin. Fourth pereopod (Fig. 16C, D) similar to third, but with 4 mobile spines on flexor margin. Fifth pereopod (Fig. 16E, F) similar to fourth, but with 2 long rows of transverse setae on flexor margin.

Pleura 1 of male (Fig. 17B), ventral margin strongly concave, with posterior corner distinctly produced ventrally and anteriorly, strongly hook-like; anterior corner produced ventrally into a rounded acute corner. Second pleura of male with lower margin sloping posteriorly to a rounded acute posterior corner. Third to fifth pleura similar to second, with posterior margin of each forming a rounded acute corner.

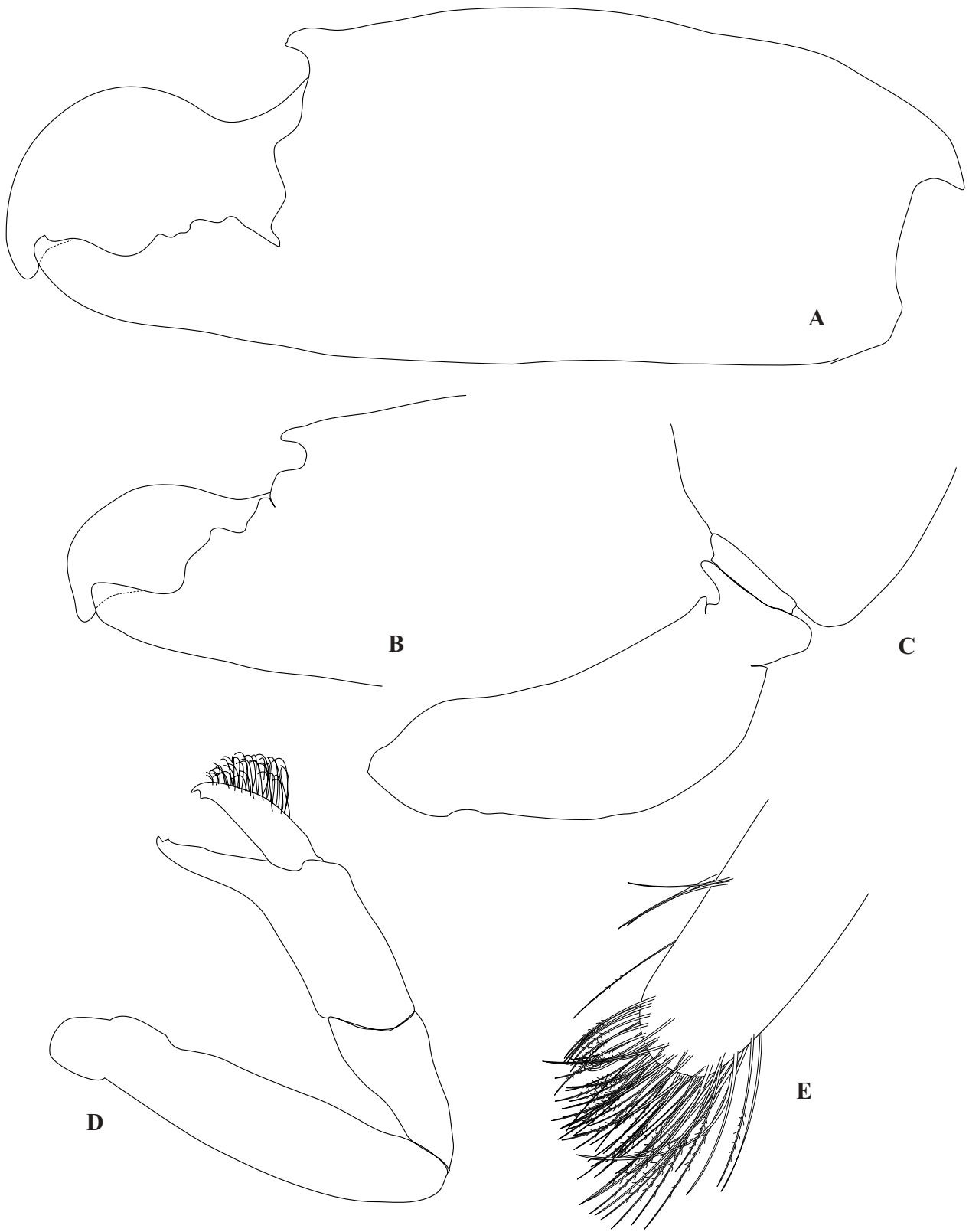
Telson (Fig. 17D), dorsal spines stout, uropods with single fixed tooth on outer margin of exopod anterior to moveable spine (Fig. 17C).

**Color.** Live specimens are drab; ovigerous females have dull green embryos and ovaries.

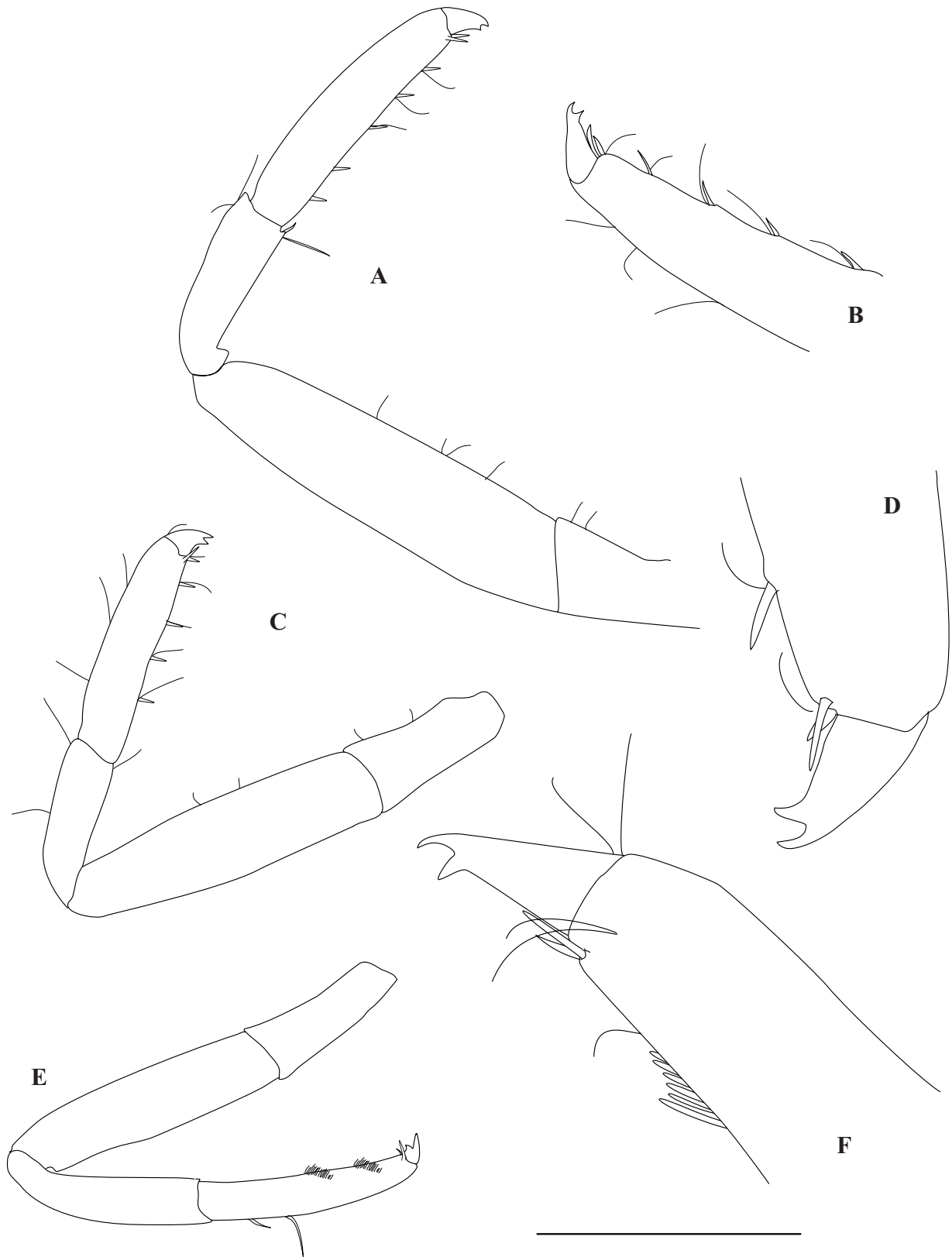
**Etymology.** This species name is derived from the Latin terms “hairy” (*pilosus*) and “mouth” (*ora*) to denote the distinctive character—a third maxilliped with a distal tuft of setae instead of a distal circlet of spines—that distinguishes this species from all other known West Atlantic species of *Synalpheus* with the exception of *S. barahonensis*, (see Remarks).



**FIGURE 14.** *Synalpheus orapilosus* sp. nov. Holotype (A, C–E), male, (USMN 1128427, original VIMS 08CU3102), from an unidentified white webby sponge, Caracas Baai, Curaçao; allotype (B), ov. female, (USNM 1128428, original VIMS 08CU3101), from an unidentified white webby sponge, Caracas Baai, Curaçao. A, carapace, anterior region, and cephalic appendages, dorsal view; B, carapace, anterior region, and cephalic appendages, dorsal view; C, carapace, anterior region, and cephalic appendages, lateral view; D, right third maxilliped; E, left second pereopod. Scale bar = 1.2 mm (A, B); 1 mm (C–E).



**FIGURE 15.** *Synalpheus orapilosus* sp. nov. Holotype (A, C–E) male, (USMN 1128427, original VIMS 08CU3102), from an unidentified white webby sponge, Caracas Baai, Curaçao. Allotype (B) ov. female, (USNM 1128428, original VIMS 08CU3101), from an unidentified white webby sponge, Caracas Baai, Curaçao. A, chela of major first pereopod, lateral view; B, chela of major first pereopod, dorsal view; C, merus and carpus of major first pereopod; D, minor first pereopod, dorsal view; E, right third maxilliped, detail of distal end. Scale bar = 1 mm (A–D); 0.3 mm (E).



**FIGURE 16.** *Synalpheus orapilosus* sp. nov. Holotype male, (USMN 1128427, original VIMS 08CU3102), from an unidentified white webby sponge, Caracas Baai, Curaçao: A, third pereopod; B, same, detail of distal region; C, fourth pereopod; D, same, detail of distal region; E, fifth pereopod; F, same, detail of distal region. Scale bar = 1 mm (A, C, E); 0.3 mm (B); 0.5 mm (D, F).



**FIGURE 17.** *Synalpheus orapilosus* sp. nov. Allotype (A) ov. female, (USNM 1128428, original VIMS 08CU3101), from an unidentified white webby sponge, Caracas Baai, Curaçao. Holotype (B–D) male, (USMN 1128427, original VIMS 08CU3102), from an unidentified white webby sponge, Caracas Baai, Curaçao. A, B, abdomen, lateral view; C, detail of right uropod, dorsal view; D, telson and uropods, dorsal view. Scale bar = 1 mm (A, B, D); 0.5 mm (C).

**Hosts and ecology.** The single pair of *S. orapilosus* was found in an unidentified white webby sponge in Caracas Baai, one of the most species-rich sites we surveyed. This sponge was rare elsewhere despite intensive searching.

**Distribution.** Curaçao (this study).

**Remarks.** *Synalpheus orapilosus* is morphologically most similar to *Synalpheus barahonensis*, originally described from the Bahamas and the only other *gambarelloides* group *Synalpheus* distinguished by a tuft of setae on the distal end of the third maxilliped (instead of a distal circlet of spines). *S. orapilosus* differs from *S. barahonensis* in the number of segments on the 2<sup>nd</sup> minor pereopod (5 in *S. orapilosus*, 4 in *S. barahonensis*).

### ***Synalpheus sanctithomae* Coutière, 1909**

(Pl. 5F)

**Material examined.** Curaçao: 1 ov. female, 1 non-ov. individual (VIMS 08CU11401), Caracas Baai, from the canals of *Agelas* cf. *clathrodes*. 1 ov. female (VIMS 08CU3304), Caracas Baai, from the canals of *Hymeniacidon caerulea*. 2 ov. females, 3 non-ov. individuals (VIMS 08CU12101, 12702), Eastpunt, from the canals of *A. cf. clathrodes*. 1 individual (VIMS 08CU12601), Eastpunt, from the canals of *Xestospongia* sp. “soft”. 1 ov. female (VIMS 08CU201), Piscadera Baai, from the canals of *A. cf. clathrodes*. 1 individual (VIMS 08CU305), Piscadera Baai, from the canals of *Hyattella intestinalis*. 1 ov. female, 1 non-ov. individual (VIMS 08CU1501–2), Piscadera Baai, from the canals of *Xestospongia subtriangularis*. 3 individuals (VIMS 08CU8703), Piscadera Baai east, from the canals of *A. cf. clathrodes*. 1 individual (VIMS 08CU7401), Scary Steps, from the canals of *H. caerulea*. 2 ov. females (VIMS 08CU7701), Scary Steps, from the canals of *X. sp.* “soft”. 1 ov. female, 1 non-ov. individual (VIMS 08CU7801), Scary Steps, from the canals of *X. subtriangularis*. 1 individual (VIMS 08CU5003), Westpunt, near or in a webby white and purple sponge in coral rubble. 1 ov. female, 2 non-ov. individuals (VIMS 08CU5803, 5903–4), Westpunt, in the canals of *H. intestinalis*. 1 ov. female, 1 non-ov. individual (VIMS 08CU5401–2), Westpunt, from the canals of *H. intestinalis*. Largest ov. female, CL 3.9 mm, largest non-ov. individual, CL 3.2 mm.

**Color.** Body typically orange, sometimes with orange-tipped chelae; females with ovaries ranging from green to greenish-brown and embryo color ranging from orange, to green, to olive-brown.

**Hosts and ecology.** In Curaçao, *Synalpheus sanctithomae* is found in a range of different sponges, most commonly in *Agelas* cf. *clathrodes*, *Hyattella intestinalis*, *Hymeniacidon caerulea*, and *Xestospongia subtriangularis*, typically in heterosexual pairs. In Belize, *S. sanctithomae* is found in *A. cf. clathrodes*, *H. intestinalis*, and *H. caerulea* (Macdonald *et al.* 2006).

**Distribution.** Florida (Gore 1981); Virgin Islands (Coutière 1909); Belize (Macdonald *et al.* 2006; Rios & Duffy 2007); Jamaica (Macdonald *et al.* 2009); Curaçao (this study); Brazil (Christofferson 1979).

**Remarks.** Although *Synalpheus sanctithomae* has been distinguished from the closely related species *Synalpheus mcclendoni* by the number of distal telson setae (10 or more in *S. mcclendoni*, <6 in *S. sanctithomae*; Rios & Duffy 2007), this character varied slightly in *S. sanctithomae* collected in Curaçao (2–7 distal telson setae), sometimes among individuals inhabiting the same individual sponge. In addition, some individuals had a row of setae on the dactyl of their major chela.

### ***Synalpheus ul* (Rios & Duffy, 2007)**

(Pl. 6A–D)

**Material examined.** Curaçao: 2 ov. females, 1 non-ov. individual (VIMS 08CU3301–3), Caracas Baai, from the canals of *Hymeniacidon caerulea*. 4 ov. females, 7 non-ov. individuals (VIMS 08CU10601, 11301–2, 11701, 12002), Caracas Baai, from the canals of *Xestospongia subtriangularis*. 1 ov. female, 1 non-ov. individual (VIMS 08CU1001–2), Piscadera Baai, from the canals of *Agelas* cf. *clathrodes*. 1 ov. female, 1 non-ov. individual (VIMS 08CU1101–2), Piscadera Baai, from the canals of *H. caerulea*. 4 ov. females, 4

non-ov. individuals (VIMS 08CU9201, 9503, 10003–4), Piscadera Baai east, from the canals of *X. subtriangularis*. 2 ov. females, 2 non-ov. individuals (VIMS 08CU2101, 2501–2), St. Michiel Baai, from the canals of *X. subtriangularis*. 1 ov. female, 1 non-ov. individual (VIMS 08CU4701–2), Westpunt, from the canals of *Xestospongia* sp. “soft.” Largest ov. female from Curaçao, CL 4.6 mm, largest non-ov. individual, CL 3.6 mm. Panama: 1 ov. female (VIMS 07P3701–1), Hospital Point (09° 20' 0.24"N, 82°13'6.84"W), from the canals of *H. caerulea*.

**Color.** Body transparent to orange-tinged, females with orange or pinkish-orange ovaries and embryos.

**Hosts and ecology.** In Curaçao, *Synalpheus ul* occurred in roughly equal sex ratios, most often as a single pair, and occupied *Hymeniacidon caerulea*, *Xestospongia subtriangularis*, *Agelas* cf. *clathrodes*, and *Xestospongia* sp “soft”. Individuals found in *Xestospongia* sp. were often morphologically ambiguous (often resembling *Synalpheus hoetjesi*) and host records from sponges other than *H. caerulea* and *A. cf. clathrodes* in Curaçao should be treated with caution (see description for *S. hoetjesi* for more details). In Panama, *S. ul* is primarily found in *H. caerulea*.

**Distribution.** Belize (Rios & Duffy 2007); Jamaica (Macdonald *et al.* 2009); Curaçao (this study); Barbados (this study); Panama (this study).

**Remarks.** In Curaçao, *Synalpheus ul* from sponge hosts *Hymeniacidon caerulea* and *Agelas* cf. *clathrodes* strongly resembled the original type series described (from *H. caerulea*) from Belize (Rios & Duffy 2007). Conversely, *S. ul* living in sponges in the genus *Xestospongia* were relatively difficult to distinguish from the closely related (and morphologically similar) *S. hoetjesi* sp. nov., which also inhabited *Xestospongia* spp., due to occasional convergence of the morphological characters used to separate the species (see *S. hoetjesi* description for further detail). Here we tentatively assign specimens from these hosts to either *S. ul* or *S. hoetjesi* based on a mitochondrial DNA COI gene tree (Fig. 8), i.e., using the maternally-inherited cytochrome *c* oxidase subunit I locus. Further study is needed, preferably employing a number of different molecular markers, to determine whether similarity of morphological characters in these hosts is caused by species hybridization or by host-related morphological convergence.

### ***Synalpheus williamsi* Rios & Duffy, 2007**

(Pl. 6E–F)

**Material examined.** Curaçao: 3 ov. females, 9 non-ov. individuals (VIMS 08CU3305, 3401, 3501, 10201, 11001, 11601, 11801), Caracas Baai, from the canals of *Hymeniacidon caerulea*. 1 ov. female (VIMS 08CU3601), Caracas Baai, no host found. 1 ov. female, 1 non-ov. individual (VIMS 08CU7901–2), Scary Steps, from the canals of *H. caerulea*. 1 ov. female, 2 non-ov. individuals (VIMS 08CU2301, 2401), St. Michiel Baai, from the canals of *H. caerulea*. 1 individual (VIMS 08CU2001), St. Michiel Baai, no host found. 3 ov. females, 4 non-ov. individuals (VIMS 08CU4601–2, 5301, 5501–2, 6401–2), Westpunt, from the canals of *H. caerulea*. 1 individual (VIMS 08CU6801), Westpunt, no host found. Largest ov. female, CL 5.5 mm, largest non-ov. individual, CL 3.8 mm.

**Color.** Bodies drab to bright orange, with brown to orange-tipped major chelae; embryos and ovaries orange.

**Hosts and ecology.** In Curaçao, as in other locations where it has been reported, *S. williamsi* was primarily found in the canals of *Hymeniacidon caerulea*, typically in heterosexual pairs. In Curaçao, juvenile individuals were often found accompanying adult pairs.

**Distribution.** Belize (Macdonald *et al.* 2006; Rios & Duffy 2007); Jamaica (Macdonald *et al.* 2009); Curaçao (this study).

**Remarks.** *S. williamsi* in Curaçao often had traces of their dark blue host sponge (*Hymeniacidon caerulea*) visible in their gut (see Plates 6E–F), as noted in other locations.



## Discussion

We found 16 *gambarelloides* group *Synalpheus* species in Curaçao, three of them new to science (*Synalpheus hoetjesi* sp. nov., *S. kuadramanus* sp. nov., and *S. orapilosus* sp. nov.). Although *Synalpheus* species richness in Curaçao appears to be substantially lower than observed or estimated elsewhere in the Caribbean (Macdonald *et al.* 2006; Rios & Duffy 2007; Macdonald *et al.* 2009), our observed species richness (16 species) falls very close to calculated estimates using several curve-fitting methods (17–19 species), suggesting we have sampled the vast majority of *gambarelloides*-group *Synalpheus* in this region. Surprisingly, we found only pair-dwelling *Synalpheus* species in Curaçao; all shrimp species were found in equal ratios of ovigerous and non-ovigerous individuals (Table 3). Despite their abundance (and even dominance) in collections made elsewhere in the Caribbean (Duffy 1992; Macdonald *et al.* 2006; Rios & Duffy 2007; Macdonald *et al.* 2009; Duffy & Macdonald 2010), we found no eusocial or semi-social *Synalpheus* species in Curaçao.

**TABLE 3.** Mean ratio of ovigerous to non-ovigerous individuals (number of ovigerous females divided by number of non-ovigerous individuals of a species co-occurring in an individual sponge). Only sponges inhabited by >1 individual of a species were counted.

<i>Synalpheus</i> species	#sponges sampled	Mean Ratio (ovigerous/non-ovigerous)	Standard Error
<i>agelas</i>	10	0.95	0.19
<i>belizensis</i>	10	1.00	0.00
<i>bousfieldi</i>	28	1.30	0.12
<i>carpenteri</i>	7	1.21	0.15
<i>herricki</i>	11	1.41	0.19
<i>hoetjesi</i> sp. nov.	12	0.94	0.04
<i>idios</i>	5	1.43	0.27
<i>kuadramanus</i> sp. nov.	1	1.00	
<i>mcclendoni</i> group	5	1.00	0.00
<i>orapilosus</i> sp. nov.	1	1.00	
<i>sanctithomae</i>	10	1.00	0.00
<i>ul</i>	13	1.13	0.17
<i>williamsi</i>	6	1.00	0.00

Since Caribbean *gambarelloides* group *Synalpheus* are obligate sponge dwellers, and often specialized on one or a few host sponge species, diversity of this group in a region is strongly driven by regional sponge host distribution and abundance. As such, we attempted to sample both the full range of shrimp-bearing sponge species in Curaçao and the full extent of variation within individual sponges (e.g., collecting different-sized individual sponges from as many different sites as possible). Of the shrimp-hosting sponges collected in this study, *Aiolochoia crassa* and *Hyattella intestinalis* have been previously reported from Curaçao (van Soest 1978, 1980), and we found sponge diversity in rubble communities to be extremely high, as noted by other studies (Meesters *et al.* 1991). We failed to locate two shrimp-bearing sponge species previously reported from the region: *Lissodendoryx strongylata* van Soest, and *Spheciospongia vesparium*, the latter reported from the area by Westinga and Hoetjes (1981). *S. vesparium* appears to be absent from all of the regions where it was formerly abundant, despite our extensive search of the sites with one of the original authors (P. Hoetjes). Of the four *gambarelloides* group *Synalpheus* previously recorded from *S. vesparium* (*Synalpheus goodei*, *S. sanctithomae*, *S. pectiniger*, and *S. brooksi*), we found only two (*S. goodei* and *S. sanctithomae*) occupying alternate hosts in our survey. *S. goodei* is represented from a single individual recorded from a

sponge collected from our deepest site (65 m depth), suggesting it may be outcompeted by other large *Synalpheus* in *Spongia* sp. and other appropriate host sponges collected from shallower areas. Two species—*Synalpheus brooksi* and *Synalpheus pectiniger*—now appear to be locally extinct from shallow areas in Curaçao due to disappearance of *S. vesparium* from this region. *S. pectiniger* in particular is a strict specialist on *S. vesparium* from all areas in the Caribbean from which it has been reported (Duffy 1992; Macdonald *et al.* 2006; Rios & Duffy 2007; Macdonald *et al.* 2009). This finding underlies the importance of conserving long-lived sponge hosts such as *S. vesparium* to maintain the diversity of not only sponge-dwelling *Synalpheus*, but other more poorly described faunal associates of such sponges.

Despite exhaustive sampling of the south side of the island, we found no eusocial *Synalpheus* in Curaçao. Unlike the case of shrimp associated with the sponge *Sphaciospongia vesparium*, absence of eusocial species does not appear to be due to missing sponge species hosts, as we collected the majority of sponge species that host eusocial species in other Caribbean locations. This includes 19 individuals of *Agelas* cf. *clathroides* (which hosts *S. chacei* in Belize; Macdonald *et al.* 2006; Rios & Duffy 2007), 19 individuals of *Hyattella intestinalis* (which hosts *S. chacei*, *S. regalis*, and *S. elizabethae* in Jamaica and Belize; Macdonald *et al.*, 2009; Macdonald *et al.* 2006; Rios & Duffy 2007), 18 individuals of *Hymeniacidon caerulea* (which occasionally hosts *S. elizabethae* in Belize, and the Florida Keys; Macdonald *et al.* 2006; Rios & Duffy 2007), 9 individuals of *Xestospongia proxima* (which hosts *S. chacei*, *S. filidigitus*, and *S. regalis* in Belize; Macdonald *et al.* 2006; Rios & Duffy 2007), and 18 individuals of *Xestospongia subtriangularis* (which hosts *S. filidigitus* and *S. regalis* in Belize and *S. duffyi* in Jamaica; Macdonald *et al.* 2009; Macdonald *et al.*, 2006; Rios & Duffy, 2007). In Belize, these 5 sponge species account for approximately 64% of the occurrences and 74% of the abundance of social species (Macdonald *et al.* 2006). Individual sponges in Curaçao spanned a similar size range (volume = 5–2000 ml) as sponges collected in regions dominated by social species (KMH unpublished data), suggesting sponge size did not inhibit formation of eusocial colonies. Nor does absence of eusocial species appear to be due to absence of certain shrimp lineages from the region. Curaçao has pair-forming species closely related to at least two of the three independent origins of eusocial species in *Synalpheus*: *S. bousfieldi* is closely related to *S. chacei*; *S. belizensis* and *S. bocas* are sister species to *paraneptunus* “small” (Morrison *et al.* 2004; Duffy 2007; Anker & Toth 2008; KMH unpublished data); all members of the third origin (the *S. rathbunae* species group) are social. It is possible that ocean currents and/or biogeography may limit dispersal of eusocial species to this region. Unlike pair-living species—which have swimming larvae capable of long-distance dispersal—all eusocial *Synalpheus* possess crawl-away larvae with more limited dispersal (Duffy 2007; Duffy & Macdonald 2010). Careful surveying of other sites in this region (including Aruba, Bonaire, and the coast of Venezuela) is necessary to examine this (and alternate) hypotheses explaining this perplexing pattern.

Regardless of the mechanisms driving this pattern, absence of eusocial species in Curaçao appears to have some consequences for host range of pair-dwelling species in the region. Based on 14 years of collections in Belize, Macdonald *et al.* (2006) reported significantly higher host breadth of eusocial species (mean = 4.0 hosts) relative to pair-dwelling species (mean = 1.5 hosts). Although our Curaçao collection is necessarily more limited in terms of sampling (107 sponges sampled, versus 623 sampled over 14 years in Belize), we have some evidence to suggest that pair-dwelling species may have slightly higher host breadth in Curaçao. Applying the strict criteria of Macdonald *et al.* (2006), in which a shrimp-sponge association was tabulated only if a particular *Synalpheus* species occurred in  $\geq 3$  individual sponge specimens, the average number of hosts used by *Synalpheus* species in Curaçao specimens is slightly higher (mean  $\pm 1$  SE =  $1.81 \pm 0.38$ ). Relaxing the association criteria slightly to include hosts in which  $\geq 2$  occurrences were recorded, the average number of different hosts used rises to  $2.25 \pm 0.43$  (mean  $\pm 1$  SE). In particular, one of the most abundant species recorded from Curaçao—*Synalpheus bousfieldi*—occurred reliably in 5 different sponge hosts (tabulated across occurrences in 32 individual sponges), although it was only recorded from a single host in Belize (occurrences recorded from 45 individual *Hyattella intestinalis*). In locations where eusocial species occur, they often dominate individual sponges (Macdonald *et al.* 2006), and absence of these dominant species may release pair-dwelling species from competition and allow them to use a greater range of hosts. Similarly, since pair-dwelling species typically coexist in smaller numbers in individual sponges (often in a

single pair, although up to 60 *S. bousfieldi* individuals occurred in a large sponge host in Curaçao), absence of large eusocial colonies in sponges may facilitate coexistence of multiple pair-dwelling species in the available niche space in a sponge.

*Synalpheus* community diversity and distribution in Curaçao differs strongly from other sites surveyed in the last ~12 years (Duffy 1992; Macdonald *et al.* 2006; Rios & Duffy 2007; Macdonald *et al.* 2009), primarily in the absence of eusocial species. This community shift occurs despite strong similarity in abundance and distribution of appropriate host sponges, suggesting other biotic or abiotic factors may limit geographic distribution of eusocial *Synalpheus* throughout the Caribbean. These findings emphasize the importance of sampling geographically peripheral locations such as Curaçao (and other areas in the Lesser Antilles) in advancing our understanding of the evolutionary diversification of this hyper diverse cryptofaunal group.

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**PLATE 1.** A, *Synalpheus agelas* ov. female (VIMS 08CU8205) from *Agelas* cf. *clathrodes*, Scary Steps, Curaçao; B, *Synalpheus agelas* ov. female (VIMS 08CU1701) from *Agelas* cf. *clathrodes*, Piscadera Baai, Curaçao; C, *Synalpheus agelas* non-ov. individual (VIMS 08CU3803) from *Agelas* cf. *clathrodes*, Caracas Baai, Curaçao; D, *Synalpheus belizensis* ov. female (VIMS 08CU11202) from *Xestospongia proxima*, Caracas Baai, Curaçao; E, *Synalpheus belizensis* ov. female (VIMS 08CU4902), *Xestospongia proxima*, Westpunt, Curaçao; F, *Synalpheus belizensis* non-ov. individual (VIMS 08CU3702) from *Xestospongia* sp. “soft”, Caracas Baai, Curaçao.



**A**



**B**



**C**



**D**



**E**



**F**

**PLATE 2.** A, *Synalpheus bocas* ov. female (VIMS 08CU7501), from *Xestospongia* sp. “soft”, Scary Steps, Curaçao; B, *Synalpheus bocas* non-ov. individual (VIMS 08CU7502), from *Xestospongia* sp. “soft”, Scary Steps, Curaçao; C, *Synalpheus bousfieldi* ov. female (VIMS 08CU701), from *Agelas* cf. *clathrodes*, Piscadera Baai, Curaçao; D, *Synalpheus bousfieldi* ov. female (VIMS 08CU127), from *Aiolochoiria crassa*, Piscadera Baai, Curaçao; E, *Synalpheus bousfieldi* non-ov. individual (VIMS 08CU128), from *Aiolochoiria crassa*, Piscadera Baai, Curaçao; F, *Synalpheus bousfieldi* ov. female (VIMS 08CU1301), from *Hyattella intestinalis*, Piscadera Baai, Curaçao.



**PLATE 3.** A, *Synalpheus bousfieldi* ov. female (VIMS 08CU5605), from *Hyattella intestinalis*, Westpunt, Curaçao; B, *Synalpheus bousfieldi* ov. female (VIMS 08CU8306), from *Xestospongia proxima*, Scary Steps, Curaçao; C, *Synalpheus carpenteri* ov. female (VIMS 08CU8209), from *Agelas* cf. *clathrodes*, Scary Steps, Curaçao; D, *Synalpheus goodei* ov. female (VIMS 08CU5101), from *Xestospongia proxima*, Westpunt, Curaçao; E, *Synalpheus herricki* ov. female (VIMS 08CU9802), from *Aiolochoiria crassa*, Piscadera Baai, Curaçao; F, *Synalpheus herricki* ov. female (VIMS 08CU2704), from *Aiolochoiria crassa*, St. Michiel Baai, Curaçao.



**A**



**B**



**C**



**D**



**E**



**F**

**PLATE 4.** A, *Synalpheus herricki* non-ov. individual (VIMS 08CU2606) with thoracic parasite, from *Aiolochoiria crassa*, St. Michiel Baai, Curaçao; B, *Synalpheus hoetjesi* ov. female (VIMS 08CU2901) from *Xestospongia subtriangularis*, Caracas Baai, Curaçao; C, *Synalpheus hoetjesi* ov. female (VIMS 08CU303) from *Hyattella intestinalis*, Caracas Baai, Curaçao; D, *Synalpheus hoetjesi* non-ov. individual (VIMS 08CU10401) from *Hyattella intestinalis*, Caracas Baai, Curaçao; E, *Synalpheus idios* ov. female (VIMS 08CU909) from *Spongia* sp., Piscadera Baai, Curaçao; F, *Synalpheus idios* non-ov. individual (VIMS 08CU914) from *Spongia* sp., Piscadera Baai, Curaçao.





**PLATE 5.** A, *Synalpheus kuadramanus* ov. female (VIMS 08CU6601) missing major first pereopod, from *Xestospongia proxima*, Westpunt, Curaçao; B, *Synalpheus mcclendoni* non-ov. individual (VIMS 08CU504), from *Hyattella intestinalis*, Piscadera Baai, Curaçao; C, *Synalpheus mcclendoni* ov. female (VIMS 08CU505) from *Hyattella intestinalis*, Piscadera Baai, Curaçao; D, *Synalpheus orapilosus* non-ov. individual (VIMS 08CU3102, USNM 1128427) from a white web-like sponge, Caracas Baai, Curaçao; E, *Synalpheus orapilosus* ov. female (VIMS 08CU3101, USNM 1128428) from a white web-like sponge, Caracas Baai, Curaçao; F, *Synalpheus sanctithomae* ov. female (VIMS 08CU5401) from *Hymeniacidon caerulea*, Westpunt, Curaçao.



**PLATE 6.** A, *Synalpheus ul* non-ov. individual (VIMS 08CU2502) from *Xestospongia subtriangularis*, St. Michiel Baai, Curaçao; B, *Synalpheus ul* non-ov. individual (VIMS 08CU3302), from *Hymeniacion caerulea*, Caracas Baai, Curaçao; C, *Synalpheus ul* ov. female (VIMS 08CU3303) from *Hymeniacion caerulea*, Caracas Baai, Curaçao; D, *Synalpheus ul* ov. female (VIMS 08CU11301) from *Xestospongia subtriangularis*, Caracas Baai, Curaçao; E, *Synalpheus williamsi* non-ov. individual (VIMS 08CU4601) from *Hymeniacion caerulea*, Westpunt, Curaçao; F, *Synalpheus williamsi* ov. female (VIMS 08CU4602) from *Hymeniacion caerulea*, Westpunt, Curaçao.