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**A review of the sponge-dwelling snapping shrimp from Carrie Bow Cay, Belize,
with description of *Zuzalpheus*, new genus, and six new species
(Crustacea: Decapoda: Alpheidae)**

RUBÉN RÍOS and J. EMMETT DUFFY



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Abstract

We review the taxonomy of sponge-dwelling shrimp in the “Gambarelloides species group” within the genus *Synalpheus* Bate 1888, an informal but widely recognized group that is largely endemic to the western Atlantic and contains the majority of *Synalpheus* species in that region. The validity of most species described from the western Atlantic is reevaluated based on extensive new material from Carrie Bow Cay, Belize, and on examination of types of most described species. Twenty-eight species, including all those historically considered as part of the Gambarelloides group, are herein removed from *Synalpheus* and transferred to *Zuzalpheus*, n. gen., which is diagnosed by two synapomorphies: the dense brush of curved setae on the minor first pereopod, and the mesial lamellae on the coxae of the 3rd pereopods. Six new species are described (*Zuzalpheus dardeaui*, *Z. elizabethae*, *Z. idios*, *Z. kensleyi*, *Z. ul*, *Z. yano*) and *Z. osburni* (Schmitt 1933) n. comb. is removed from synonymy with *Synalpheus goodei*. An identification key to all 34 species of West Atlantic *Zuzalpheus* is presented, as are known host associations, and color plates of most species.

Key words: Decapoda, Alpheidae, Belize, Caribbean, sponge, symbiotic, reef, *Zuzalpheus*, *Zuzalpheus dardeaui*, *Z. elizabethae*, *Z. idios*, *Z. kensleyi*, *Z. ul*, *Z. yano* n. spp.

Introduction

Snapping shrimp in the genus *Synalpheus* Bate, 1888 are abundant and diverse components of the cryptic fauna of coral reefs and other tropical marine ecosystems worldwide (Felder and Chaney 1979, Reed *et al.* 1982). The genus includes more than 150 species (Chace 1988; R. Ríos, pers. obs.) that inhabit the interstices of coral rubble, the internal spaces of sponges, and in the Indo-Pacific, the arms of crinoid echinoderms (Beebe 1928; Pearse 1932; Bruce 1976; Duffy 1992). These shrimp are small (usually <2 cm in length) and reclusive, and are often among the most abundant cryptofaunal macroinvertebrates in reef environments (Pearse 1932; Rützler 1976). Despite their abundance and diversity, the systematic relationships and taxonomy of *Synalpheus* remain poorly resolved.

In a pioneering effort to impose some order on the large and unwieldy genus *Synalpheus*, Coutière (1908, 1909) divided the genus into six informal groups of species based on morphological characters, namely the Comatularum, Brevicarpus, Laevimanus (later called Gambarelloides), Neomeris, Biunguiculatus (later called Coutièrei), and Paulsoni groups. Banner and Banner (1975) reassessed the definitions of these groups, and concluded that only the first three listed “may be coherent enough to continue to be recognized”. In the western Atlantic, the *Synalpheus* fauna is dominated by species in the Gambarelloides group (Coutière 1909; Dardeau 1984), which is largely endemic to that region, and currently includes most of the described species from the western Atlantic. The Gambarelloides group is characterized by a distinctive brush of long, thickly packed setae arranged in transverse parallel rows on the extensor surface of the dactyl of the smaller first chela (Coutière 1908, 1909). All known species in the Gambarelloides group are obligate inhabitants of living sponges, and their distinctive setal brush is used to collect food from the surfaces of the sponge canals in which they live (Duffy 2003).

Over the last 15 years we have obtained abundant new material collected primarily from the vicinity of Carrie Bow Cay, Belize, representing most of the known species in the Gambarelloides group and several previously unknown species. Examination of this material, together with molecular phylogenetic analyses (Morrison *et al.* 2004), led us to the conclusion, foreseen by previous workers (Banner and Banner 1975; Chace 1988), that it is necessary to separate the previously known Gambarelloides group of species as a distinct genus. Thus, we here erect *Zuzalpheus* n. gen., for this group of species, on the basis of morphological, ecological, and molecular evidence. The new genus contains six new species herein described, together with 28 species transferred from *Synalpheus*. We present diagnoses for most of the previously known species found at Carrie Bow Cay, an updated identification key to all 34 species of West Atlantic *Zuzalpheus* n. gen., and color plates of most species recorded from the Carrie Bow Cay region.

Abbreviations used:

CL carapace length.

CNCR Colección Nacional de Crustáceos from the Instituto de Biología UNAM, México.

MNHN Museum National d'Histoire Naturelle, Paris, France.

USNM United States National Museum of Natural History, Smithsonian Institution, Washington, USA.

VIMS Virginia Institute of Marine Science, Gloucester Point, USA.

Historical review of *Synalpheus*

The history of the genus *Synalpheus* has been plagued by confusion from the beginning. Paulson (1875) first noticed that among what was then known as “*Alpheus*”, a distinct group of species lacked epipods on the pereopods. In *Alpheus* as it is currently recognized, epipods are present on the third maxilliped and the first four pairs of pereopods (Banner and Banner 1975) as hooked processes inserted laterally on the coxae. Unfortunately, Paulson (1875) used the name “*Alpheus*” for the group lacking epipods while erecting the new genus *Alpheoides* to include the true *Alpheus*. Meanwhile, De Man (1911), apparently unaware of Paulson’s publication, had also created in 1888 a “group spinifrons” within the genus *Alpheus* for the species corresponding to the present *Synalpheus*. Finally, Bate (1888) formally erected the genus *Synalpheus*. Adding further to the confusion, however, the first species Bate included in his new genus—which became the type species—was *Synalpheus falcatus* (= *S. comatularum*), which had been previously described as *Alpheus comatularum* by Haswell (1882).

Henri Coutière (1897a) provided the first extensive diagnosis that established unequivocally the identity of *Synalpheus* Bate. In his treatise on the Alpheidae, Coutière (1899) gave accurate diagnoses of the 16 genera included in that family at that time. The name *Synalpheus* Bate, 1888 was included on the Official List of Generic Names in Zoology in opinion 470 in 1957 (Holthuis 1993). Nevertheless, a sound definition for the genus is still not readily available (see Verrill 1922; Banner and Banner 1975; and Chace 1988).

Coutière’s (1909) enduring monograph was the first thorough revision of *Synalpheus* from the Americas. Remarkably, of more than 45 species and varieties included therein, Coutière (1909) retained only three species with their previous names, *i. e.* *Synalpheus brevicarpus* Herrick, 1891, *S. longicarpus* Herrick, 1891, and *S. minus* Say, 1818. Two of his new species were given names that had been previously published: *S. hemp-hilli* Coutière, 1908 and *S. pectiniger* Coutière, 1907. Coutière (1909) also included some material from other parts of the world; from this extralimital material he erected 11 new species, two new subspecies, and gave full specific status to *S. laevimanus parfaiti*. With regard to the material from the Americas, Coutière (1909) assigned a new name to *S. lockingtoni*, and erected 20 new species and 20 subspecies.

Methods

This account is based primarily on material collected between 1990 and 2005 from sponges in the vicinity of Carrie Bow Cay on the Belize Barrier Reef tract, Central America (16° 48’ N, 88° 05’ W). Some additional material was collected from the San Blas Islands on the Caribbean coast of Panamá (9° 34’ N, 78° 58’ W). Most shrimp were collected alive via scuba or skin diving by J.E. Duffy and various colleagues from their host sponges, which were identified whenever possible, and most species were photographed digitally. Lists of material examined are not comprehensive; for most species, additional specimens in the VIMS collection were also examined. Type specimens and voucher material are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); the Colección Nacional de Crustáceos

from the Instituto de Biología UNAM, México (CNCR); the Museum National d'Histoire Naturelle, Paris (MNHN); and in the Virginia Institute of Marine Science (VIMS). Measurements correspond to carapace length (CL) in millimeters, taken from the most posterior edge of the carapace on the dorsal midline to the tip of the rostrum, unless otherwise indicated. Fig. 1 illustrates some of the specific morphological characters commonly used in taxonomy of *Synalpheus*. Synonymies included are abbreviated.

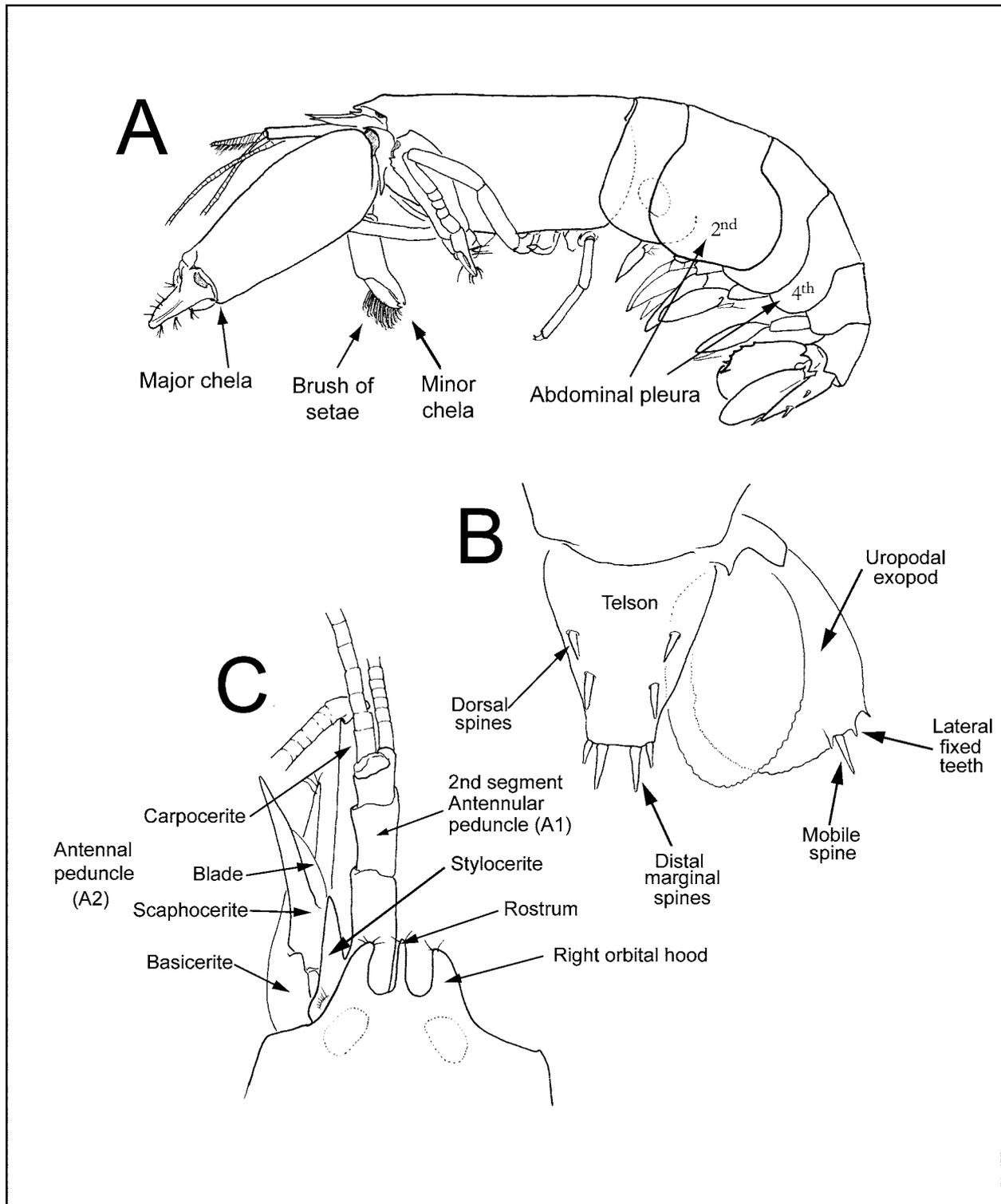


FIGURE 1. Schematic drawings of a *Zuzalpheus* shrimp showing important structures used in taxonomy: a, ovigerous female, lateral view; b, tail fan with left uropod omitted, dorsal view; c, anterior region of carapace with left antennal (A2) and antennular (A1) peduncles, dorsal view.

Systematics

Subphylum Crustacea

Order Decapoda Latreille, 1802

Family Alpheidae Rafinesque, 1815

Genus *Zuzalpheus* n. gen.

Synalpheus, Coutière 1908 and 1909 (in part, only species included in his Group *Laevimanus*)

Type species. *Zuzalpheus kensleyi*, n. sp., here designated.

Diagnosis. Carapace smooth, projected into ocular hoods covering eyes; anterior edge usually with a trispinose appearance due to acute rostrum; cardiac notch present. Rostrum, generally equal to or slightly overreaching ocular hoods. Scaphocerite with or without blade; when present, always shorter than adjacent lateral spine. Basal segment of antennular peduncle usually without tooth on mesioventral edge. Sixth abdominal somite without articulated plate. Telson lacking anal tubercles; distal margin broadly convex or reduced to narrow space between distal marginal spines. Third maxilliped slender, not forming operculum covering remaining mouthparts. First pair of pereopods unequal; major first pereopod, smooth, usually with superodistal edge of palm forming protuberance overhanging base of dactyl, this latter with massive molar-like tooth accommodated in cavity on internal edge of base of fixed finger. Minor first pereopod with distinct brush of dense distally curved setae on extensor surface of dactyl. Second pereopod with carpus 4 or 5-segmented. Third pereopods, with merus usually lacking spines on ventral margin; always with distinct mesial lamella on coxa. Third to fifth pereopods with dactyl biunguiculate. Epipods absent from all pereopods. Second to fifth pleopods in both sexes with only appendix interna. Lateral margin of uropodal exopods with one to several fixed teeth.

Etymology. From the Mayan 'Zuz' (brush), alluding to the synapomorphic brush of setae on the dactyl of the minor first chela, and the ending 'alpheus' common in the names of genera in the family Alpheidae. Gender, masculine.

Zuzalpheus agelas (Pequegnat and Heard, 1979) n. comb.

(Plate 1)

Synalpheus agelas Pequegnat and Heard, 1979:110–116, figs. 1–4; Dardeau 1984:12–18, Figs. 3–6.

Material examined. (1) **Holotype** ♂ (USNM 171424), CL 4.6 mm, West Flower Garden Bank, Gulf of Mexico, 25 m.

(2) **Allotype** ovigerous ♀ (USNM 171425), CL 4.6 mm, Florida Middle Ground, Gulf of Mexico, 30–34 m.

(3) 3 ♀ (at least one ovigerous), 3.8, 3.9, and 4.3 mm (VIMS 93CBC7501), 5 ♂, 3.2 – 3.8 mm (VIMS 93CBC7502), Carrie Bow Cay, Belize, 5 April 1993, in demosponge *Agelas clathrodes* (Schmidt 1870), 20 m.

(4) 1 male, 4.8 mm; 1 ovigerous ♀, missing carapace, slightly larger than ♂ (VIMS 90CBC0101), Carrie Bow Cay, Belize, 26 April 2001, in *Agelas dispar* Duchassaing and Michelotti 1864, 17 m.

(5) 1 ovigerous ♀, 4.9 mm (VIMS 90CBC2902), Carrie Bow Cay, Belize, 11 December 1990, in *Agelas dispar*, 6 m.

(6) 1 ovigerous ♀, 4.4 mm (VIMS 93CBC8201), 2 ♂, 3.8 and 3.5 mm (VIMS 93CBC8203, 93CBC8205), spur and groove reef, Carrie Bow Cay, Belize, 6 April 1993, in *Agelas dispar*, 10 m.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, posterior margin with cardiac notch distinct. Rostrum clearly narrower than, and falling slightly short of, ocular hoods. Orbitorostral process absent. Ocular hoods dorsally convex, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process broad. Ocellary beak in lateral view broad at base, not rod-like. *Stylocerite* with mesial margin slightly concave and lateral margin strongly convex; tip acute, not sharp, falling distinctly short of distal margin of first segment of antennular peduncle; latter without ventromesial tooth, with 2 basal ventral processes. *Basicerite* with dorso-lateral corner forming right angle; longer ventrolateral spine clearly overreaching distal margin of first segment of antennular peduncle. *Scaphocerite* blade reduced, acute lateral spine robust, with lateral margin slightly concave, almost reaching distal margin of second segment of antennular peduncle; mesial projection at base of scaphocerite present. *Third maxilliped* with distal circlet of spines on distal segment and without ventrodorsal spine on antepenultimate segment.

Major pereopod 1 massive, fingers shorter than half length of palm; fixed finger reduced, much shorter than dactyl; in ventral view, outer face of fixed finger without distinct lateral protuberance. Palm of chela with distal superior margin produced into prominent bluntly acute tubercle, downwardly oriented. Merus, extensor margin strongly convex, with distal flat, angular projection.

Minor pereopod 1 with palm less than 2 times longer than high; fingers shorter than palm; dactyl straight, blade-like, with short distinct subdistal teeth, perpendicular to dactyl axis; extensor margin of dactyl with conspicuous transverse dorsal setal combs; fixed finger straight, blade-like, with subdistal bump. Merus extensor margin convex, ending distally in obtuse angle.

Pereopod 2 with carpus 4-segmented, shorter than merus.

Pereopod 3 dactyl biunguiculate, with proximal tooth on flexor margin thicker than distal one; merus rather thick, usually less than 3.5 times longer than wide, without movable spines on flexor margin; coxa with mesial lamella. *Pereopods 4 and 5* normal.

Pleura 1 of male with lower edge sinuous, posteroventral corner produced into thick hook; remaining pleura broadly obtuse. *Pleopod 1* of male with about 3 terminal setae on endopod; pleopod 2 with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods present. *Telson* posterior margin with space between spines more than one-third width of posterior margin; latter with medial convex lobe. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with 1 fixed tooth, occasionally 2, on lateral margin of exopod anterior to, and distinctly removed from, slightly longer mobile spine, latter closely adjacent to internal fixed tooth.

Color (Plate 1). Bright orange with distal palm and fingers of major chela brighter orange. Ovaries and eggs yellow-orange. The black stomach is prominent in freshly collected specimens.

Hosts and ecology. As indicated by its name, *Zuzalpheus agelas* was described from specimens living inside an orange sponge identified by Pequegnat and Heard (1979) as "*Agelas dispar*". At Carrie Bow Cay, we have collected this shrimp exclusively from two species of *Agelas*, *A. dispar*, which is brown (Zea 1987) rather than orange, and *A. clathrodes*, which is orange. Our collections support the suggestion in the original description that *Z. agelas* is a specialist associate of sponges in the genus *Agelas*.

Variations. In some specimens the rostrum is lanceolate rather than triangular. Sometimes the merus of the third pereopod is elongated, almost four times longer than wide. The most frequent number of lateral fixed teeth on the uropodal exopod is one, but sometimes there are two.

Distribution. Western Atlantic: Florida Keys, USA (J.E. Duffy unpublished); Bahamas (Dardeau 1984; J.E. Duffy unpublished); Gulf of Mexico (Pequegnat and Heard 1979; Dardeau 1984); Puerto Rico (Dardeau 1984); Cuba (Martínez Iglesias and García Raso 1999); Belize Barrier Reef (this study); San Blas Islands, Panama (J.E. Duffy unpublished).

Remarks. This species can be diagnosed relatively easily by the combination of four carpal segments on the 2nd pereopod, absence of a spine on dorsal margin of basicerite, and the circlet of stout spines on the third

maxilliped. In life, the combination of bright orange body color with dark black stomach distinguishes *Z. agelas* from its congeners inhabiting *Agelas* spp.

***Zuzalpheus androsi* (Coutière, 1909) n. comb.**

(Plate 1)

Synalpheus androsi Coutière, 1909: 82, fig. 50; Dardeau 1984:18; Ríos 2003: 45.

Material examined. (1) **Holotype** ♀ (USNM 38409), 4.8 mm, Andros Island, Bahamas.

(2) 1 ♂, 2.1 mm (VIMS 93CBC4004), outer ridge of Carrie Bow Cay, Belize, 24 March 1993 in demosponge *Pseudoceratina crassa* (Hyatt 1875).

(3) 1 ♂, 3.2 mm (VIMS 93CBC5201), 1 ovigerous ♀, 3.5 mm (VIMS 93CBC5202), outer ridge of Carrie Bow Cay, Belize, 27 March 1993 in demosponge *Hyattella intestinalis* (Lamarck 1814a), 14 m.

(4) 2 ♀, 4.0 mm (VIMS 99CBC3801) and 3.8 mm (ovigerous, VIMS 99CBC3802), 1 ♂, 3.6 mm (VIMS 99CBC3803), outer ridge of Carrie Bow Cay, Belize, 7 December 1999 in *Hyattella intestinalis*, 14 m.

(5) 1 ovigerous ♀, 4.6 mm (VIMS 03CBC0501), 1 ♂, 4.0 mm (VIMS 03CBC0502), outer ridge of Carrie Bow Cay, Belize, 17 April 2003 in *Hyattella intestinalis*, 15 m.

Diagnosis. Body subcylindrical; carapace smooth, with pterygostomian corner produced into bluntly acute angle, posterior margin with cardiac notch distinct. Frontal region somewhat protruding over first segment of antennular peduncle, beyond commissure of stylocerite. Rostrum triangular, tip beveled, about as wide as ocular hoods, but slightly longer, and distally upturned. Orbitorostral process absent. Ocular hoods dorsally convex, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process nipple-shaped in lateral view, flanged posteriorly under eye. Ocellary beak in lateral view kidney-shaped. *Stylocerite* stout, mesial margin slightly concave, outer margin strongly convex; tip acute, not sharp, falling short of distal margin of first antennular peduncle; latter segment without ventromesial tooth, and with 2 basal ventral processes. *Basicerite* with obtuse dorsolateral corner, lateral spine clearly overreaching midlength of second segment of antennular peduncle. *Scaphocerite* blade absent; lateral spine acute, lateral margin slightly concave, usually overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circlet of spines on distal segment and without ventrodorsal spine on antepenultimate segment.

Major pereopod 1 massive, with ovoid profile; fingers shorter than half length of palm; fixed finger shorter than dactyl; in ventral view, fixed finger lacking conspicuous lateral protuberance. Palm of chela with distal superior margin produced into prominent bluntly acute tubercle. Merus extensor margin convex, with flat distal angular projection.

Minor pereopod 1 with palm less than two times longer than high; fingers shorter than palm; dactyl with flexor margin straight, blade-like, with obtuse emargination at midlength, and small subdistal bump parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor surface obliquely concave, and strongly convex keel behind apex. Carpus with conspicuous narrow ridge on interior margin. Extensor margin of merus almost straight, ending in obtuse angle.

Pereopod 2 with carpus 5-segmented, about as long as merus.

Pereopod 3 unique, dactyl biunguiculate, with flexor tooth thicker than extensor; propodus with distinctly concave flexor surface, defined by thin longitudinal crest or flange on posterior edge; carpus also with concave flexor surface between strong crest or flange on posterior edge and conspicuous longitudinal ridge on anterior edge; merus also with concave flexor surface and crest and ridge on distal half, matching those on carpus; coxa with mesial lamella. *Pereopods 4 and 5* not modified.

Pleura 1 of male with ventroposterior corner acutely produced; pleura 2–5 broadly rounded to obtuse. *Pleopod 1* of male with 3 terminal setae on endopod; pleopod 2 with marginal setae on exopod originating

near midpoint; appendix interna present on male pleopods 2–5. *Telson*, space between posterior marginal spines greater than one-third width of posterior margin; margin with convex lobe; posterior corners adjacent to spines acute. Anal flaps, perianal setae, and postanal setal brush, absent. *Uropods* with single fixed tooth on outer margin of exopod anterior to, and slightly offset from, longer mobile spine, latter adjacent to internal tooth; diaeresis well developed across whole exopod.

Color (Plate 1). Transparent with a faint hue of violet, most apparent on edges of abdomen. Edges of the distal portion of the major chela are translucent brown-green. The digestive gland and the ovaries are orange-brown. Mature embryos are brown, more intensely towards the center.

First larva. Hatching larvae (VIMS 99CBC4102), obtained in the laboratory, were large and exhibited the following characters: eyes not covered by carapace; antennule with three distinct segments and two flagella; antenna with fully developed blade on scaphocerite. First pair of pereopods with chelae; minor chela without the characteristic comb of setae on extensor surface. First to fourth pereopods with exopod. Pleopods biramous.

Hosts and ecology. *Zuzalpheus androsi* lives in heterosexual pairs, almost exclusively inside the demosponge *Hyattella intestinalis* at Carrie Bow Cay. On a few occasions we have collected single males inside *Pseudoceratina crassa*, *Hymeniacidon caerulea* Pulitzer-Finali 1986, and probably also *Agelas clathrodes*. Such occasional records of single individuals are suspect because they may involve movement within clumps of rubble after collection. The eggs are large, fewer than 10 filling the brood chamber of a large ovigerous female.

Distribution. Western Atlantic: Andros Island, Bahamas (Coutière 1909); Lee Stocking Island, Bahamas (K.S. Macdonald, pers. comm.); Belize Barrier Reef (this study).

Remarks. This species is remarkable in the unique structure of the carpus and merus of the third pereopod. It was previously known only from the female holotype, collected at Andros Island, Bahamas (Armstrong 1949). We have found it to be common in the sponge *Hyattella intestinalis* on the outer ridge of the Belize Barrier Reef. In a male specimen from Carrie Bow Cay, there is a mobile spine in the cavity of the merus on the third pereopod. The description of the holotype (Coutière 1909) mentions additional spines on the carpus, besides the distal one, which is present in our specimens, but our specimens do not have additional spines, only thick setae.

***Zuzalpheus bousfieldi* (Chace, 1972) n. comb.**

(Plate 1)

Synalpheus bousfieldi Chace, 1972 (in part):86, Figs. 29–30; Dardeau 1984 (in part):19–25, Figs. 7–10 (and synonymy).

Material examined. (1) **Holotype** ♀ (USNM 135369), 3.2 mm (rostrum excluded), Bahía del Espíritu Santo, Mexico.

(2) 1 ♀ (VIMS 03CBC2401), 4.1 mm, 1 ♂ (VIMS 03CBC2402), 3.4 mm, outer ridge of Long Reef (S of Carrie Bow Cay), Belize, 20 April 2003, from *Hyattella intestinalis*, 13 m.

(3) 2 ♀ (VIMS 04CBC2601, 04CBC2602), 3.0 mm, 3.1 mm, 2 ♂ (VIMS 04CBC2403, 04CBC2603), 2.6 mm, 2.7 mm, outer ridge at Curlew Key, Belize, 14 March 2004, in *Hyattella intestinalis*, 18 m.

(4) 1 ♀ (VIMS 03CBC1901), 3.5 mm, 1 ♂ (VIMS 03CBC1902), 2.9 mm, outer ridge at Carrie Bow Cay, Belize, 19 April 2003, in *Hymeniacidon caerulea*, 15 m.

(5) 1 ♀ (VIMS 04CBC3001), 3.9 mm, 1 ♂ (VIMS 04CBC3002), 3.2 mm, The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize, 14 March 2004, in unidentified white encrusting sponge, 2 m.

Diagnosis. Body subcylindrical; carapace smooth, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Rostrum clearly narrower and longer than ocu-

lar hoods, distally upturned; margins in dorsal view concave. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly triangular, margins straight or convex, separated from rostrum by deep adrostral sinus. Ocular processes present, not elongated. Ocellary beak in lateral view not rodlike. *Stylocerite* slender; mesial margin slightly concave; tip acute; reaching about as far as distal margin of first segment of antennular peduncle; latter without mesio-ventral tooth, and with two basal ventral processes. *Basicerite* without spine on dorso-lateral corner, and with longer lateral spine clearly overreaching tip of stylocerite. *Scaphocerite* with blade absent, acute lateral spine with lateral margin straight, not overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circlet of spines on distal segment, without ventro-distal spine on antepenultimate segment

Major pereopod 1 massive, fingers clearly not longer than half length of palm; fixed finger about as long as dactyl; in ventral view, outer face of fixed finger without distinct protuberance. Palm of chela with distal superior margin produced into tapering acute spine. Merus, extensor margin strongly convex, ending in obtuse angle.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with two distinct distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on extensor margin of dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, with two distinct teeth subequal in length. Extensor margin of merus convex, ending in obtuse angle.

Pereopod 2 carpus with five segments; equal or shorter than merus.

Pereopod 3 slender; dactyl biunguiculate, with subequal ungues; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pleura 1 of male with posteroventral corner acutely produced; *pleura 2* of male rounded to obtuse. *Pleopod 1* of male with many terminal setae on endopod; *pleopod 2* of male with marginal setae on exopod originating near midpoint; appendix interna on male pleopods 2–5 present. *Telson* with space between posterior marginal spines equal or less than one third width of posterior margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush all absent. *Uropods* with a single fixed tooth on outer margin of exopod anterior to movable spine.

Color (Plate 1). A non-descript shrimp: translucent with dull gold tinge to thickened parts of cuticle; distal palm and fingers of major chela brownish; ovaries and eggs olive green to chestnut brown.

Hosts and ecology. *Zuzalpheus bousfieldi* is a common species at Carrie Bow Cay, occurring within sponges in heterosexual pairs or groups of several adults with approximately equal sex ratio. We have collected this species regularly from the demosponge *Hyattella intestinalis* at depths of 12–20 m on the outer ridge of the Belize Barrier Reef, but we have also recorded occasional specimens from several other sponges in this deep environment, including *Hymeniacidon caerulea*, *Hymeniacidon amphilecta*, *Lissodendoryx* sp., *Pseudoceratina crassa*, and a cryptic, unidentified white sponge growing among coral rubble.

Distribution. Western Atlantic: Grand Bahama Island (Dardeau 1984); Cuba (Martínez Iglesias and García Raso 1999); Gulf of Mexico (Dardeau 1984); Yucatan peninsula, Mexico (Chace 1972); Belize Barrier Reef (this study); possibly Brazil (Christoffersen 1979).

Remarks. *Zuzalpheus bousfieldi* is one of a complex of common and morphologically similar species, including the frequently reported *Z. brooksi*, and *Z. idios* n. sp. described herein, which are difficult to distinguish on the basis of preserved specimens. Indeed, a series of specimens tentatively assigned to *Synalpheus bousfieldi* in Chace's (1972) original description were later separated out as *S. chacei* by Duffy (1998). Dardeau (1984) provided a comprehensive synonymy for *S. bousfieldi* and discussed the wide geographic variation among specimens assigned to the species. We suspect that the specimens from *Agelas* spp. that he assigned to *S. bousfieldi* are in fact *Z. carpenteri* (Macdonald and Duffy, 2006). Given its wide variation in morphology and host associations, it seems likely that *Z. bousfieldi*, as currently recognized, includes additional undescribed species. Chace (1972) used the position of the anterior dorsal telson spines arising from

the lateral margin of the telson to distinguish *S. bousfieldi* from *S. brooksi* in his key. We have found this character to be unreliable; instead, we find the most reliable (albeit subtle) distinction to be the shape of the distal tubercle on the palm of the major first chela, which is sharp and curved downward toward the dactyl in *Z. bousfieldi*, but conical, straight, and directed slightly upward away from the dactyl in *Z. brooksi*.

***Zuzalpheus brevifrons* (Chace, 1972) n. comb.**

(Fig. 2, Plate 1)

Synalpheus brevifrons Chace, 1972: 89, Figs. 31–32; Dardeau 1984: 26; Ríos 2003: 49, Fig. 2–1, Plate III.

Material examined. (1) **Holotype** ♀ (USNM 135371), 2.8 mm (rostrum excluded), Dominica, shallow water.

(2) 1 ♂, 3.2 mm (VIMS 95CBC3501), outer ridge of Carrie Bow Cay, Belize, 2 July 1995, in soft gray demosponge lining internal canals of *Pseudoceratina crassa*, 15 m.

(3) 1 ovigerous ♀, 2.9 mm (VIMS 02CBC3602), 1 ♂, 2.6 mm (VIMS 02CBC3603), The Pinnacles (i.e., Sand Bores, 16°44'54.0"N, 88°04'21.8"W), Belize, 28 June 2002, in soft purple-gray sponge, 1 m.

(4) 1 ovigerous ♀, 3.0 mm (VIMS 03CBC2608), 1 ♂, 2.9 mm (VIMS 03CBC2609), The Pinnacles (Sand Bores), Belize, 21 April 2003, no host recorded, 1 m.

(5) 2 ovigerous ♀ (04CBC4501, 04CBC4502), 2.9 mm, 2.7 mm, 1 ♂ (VIMS 04CBC4504), 2.3 mm, spur and groove of Long Reef (S of Carrie Bow Cay), Belize, 16 March 2004, in soft grey sponge, 610 m.

Diagnosis. Body form subcylindrical; carapace smooth, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Rostrum triangular, not upturned, with shallow ventral keel at base; about as long as ocular hoods, but narrower. Orbitorostral process absent. Ocular hoods dorsally convex, very obtuse, margins convex, separated from rostrum by very shallow adrostral sinus. Ocular process broadly obtuse. Ocellary beak in lateral view not rod-like. *Stylocerite* slender; mesial margin straight; tip acute, clearly not reaching distal margin of first segment of antennular peduncle; latter segment without mesio-ventral tooth, with 2 basal ventral processes. *Basicerite* with dorso-lateral corner obtuse, and with longer lateral spine clearly overreaching distal margin of first segment of antennular peduncle. *Scaphocerite* blade absent, lateral spine acute, with lateral margin slightly concave, clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present. Carapocerite overreaching tip of scaphocerite. *Maxilliped 3* with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment.

Major pereopod 1 massive, fingers shorter than half length of palm; fixed finger about as long as dactyl; in ventral view, outer face of fixed finger without protuberance. Palm of chela with distal superior margin produced into prominent blunt tubercle. Merus extensor margin strongly convex, ending distally in obtuse angle.

Minor pereopod 1 with palm clearly less than 2 times longer than high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with 2 strong subequal distal teeth, parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl conspicuous but not dense; fixed finger with flexor margin straight, blade-like, ending distally in 2 strong subequal teeth, parallel to dactyl axis. Extensor margin of merus convex, ending in obtuse angle.

Pereopod 2 with carpus 5-segmented, longer than merus.

Pereopod 3 slender; dactyl biunguiculate, with subequal ungues (teeth); merus without movable spines on flexor margin; mesial lamella on coxa present. Pereopods 4 and 5 normal.

Abdomen of male distinctly flattened dorsoventrally. *Pleura 1* of male with posteroventral corner distinctly produced into a hook; *pleura 2* with posteroventral corner sharply acuminate; *pleura 3* and *4* each with two posteriorly oriented hooks; *5* and *6* with single hook also posteriorly oriented. *Pleopod 1* of male with 2

or 3 terminal setae on endopod; pleopod 2 of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. *Telson*, space between posterior marginal spines greater than one-third width of posterior margin; marginal convex lobe present; posterior corners adjacent to spines obtuse; mesial pair of spines distally upturned. Anal flaps, perianal setae, and postanal setal brush, all absent. *Uropods* with a single fixed tooth on outer margin of exopod anterior to, and distinctly removed from, much longer movable spine, latter adjacent to internal fixed tooth.

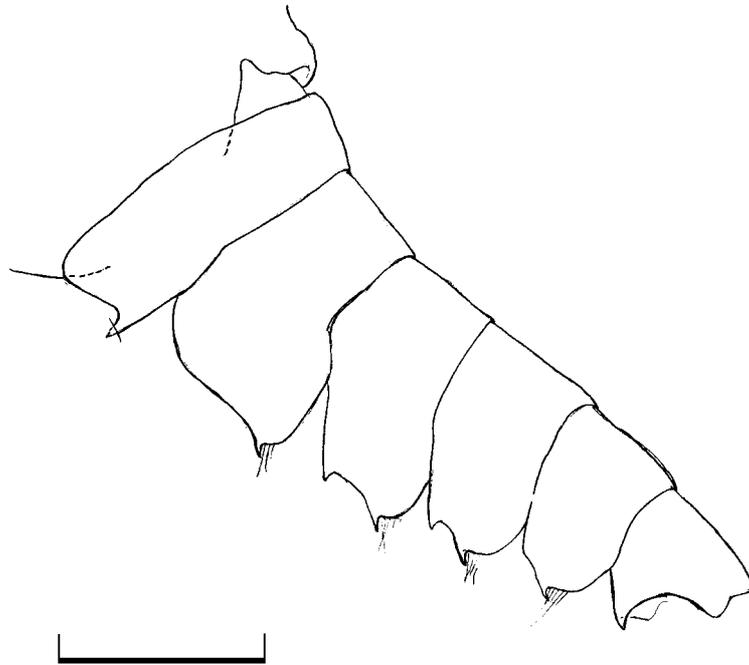


FIGURE 2. *Zuzalpheus brevifrons* (Chace 1972). Male 3.2 mm (VIMS 95CBC3501): lateral view of abdomen. Scale bar = 1 mm.

Color (Plate 1). Translucent to milky white with traces of bright gold on distal edges of chelae; digestive gland faint yellow; ovaries and embryos bright green.

Hosts and ecology. We have collected *Zuzalpheus brevifrons* only from inside the canals of a soft, smooth gray to brown demosponge that grows as a film lining rock cavities or the internal canals of the sponge *Pseudoceratina crassa*.

Distribution. Western Atlantic: Dominica (Chace 1972); Belize Barrier Reef (this study), possibly also San Blas Islands, Panama.

Remarks. This distinctive species was previously known only from the female holotype; in the original figures by Chace (1972), the antennule appears thicker than in our specimens from Belize. The male of the species, figured here for the first time (Fig. 2), bears a striking character, unique among West Atlantic species of *Zuzalpheus*; namely the hooks on the ventral margin of the male abdominal pleura. One male examined had 2 hooks on one of the second pleurae. An ovigerous female from San Blas Islands, Panama, is very similar to *Z. brevifrons*, but has a small blade on the scaphocerite and the spines on the dorsal surface of the telson are distinctly removed from the edge. Because this specimen came from a pink unidentified sponge, it seems likely that this may represent yet another undescribed species.

***Zuzalpheus brooksi* (Coutière, 1909) n. comb.**

(Plate 1)

Synalpheus brooksi Coutière, 1909: Dardeau 1984: pp 26–38, Figs. 11–14 (and synonymy); Morrison *et al.* 2004; Macdonald *et al.* 2006; Macdonald and Duffy 2006: Fig. 16.

Material examined. (1) **Syntype** ♂ and ♀ (USNM 24782), 3.2 and 3.3 mm (rostrum excluded), respectively, off St. Thomas, Virgin Islands.

(2) 1 ♀ (VIMS 93CBC2502), 4.0 mm, 3 ♂ (VIMS 93CBC2503, 93CBC2505, 93CBC2506), 3.5–3.7 mm, from larger colony, Twin Cays, Belize, 21 March 1993, in *Lissodendoryx colombiensis*, 1.5 m.

(3) 1 ♀, 8 ♂ (VIMS 98CBC0802-10), Sand Bores, Belize, 4 December 1998, in *Hyatella intestinalis*, 2 m.

(4) 2 ♂ (VIMS 05CBC0220-21), Blue Ground Range, Belize, 9 July 2005, in *L. colombiensis*, 1–2m.

(4) 1 ovigerous ♀ (VIMS 93P2104), 4.4 mm, 2 ♂ (VIMS 93P2105, 93P2106), both 3.4 mm, from larger colony, Cayos Limones, San Blas Islands, Panama, 26 September 1993, in *Sphēciospongia vesparium*, 2 m.

(5) 2 ovigerous ♀ (VIMS 93P1407), both 2.3 mm, from larger colony, Tiantupo reef, San Blas Islands, Panama, 22 September 1993, in *Agelas clathrodes*, 9 m.

Diagnosis. Body form subcylindrical; carapace smooth, with pterygostomian corner very obtusely angular, and posterior margin with cardiac notch distinct. Rostrum clearly narrower than, and about as long as, ocular hoods, distally upturned; margins in dorsal view concave or convex. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, acute, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes absent. Ocellary beak in lateral view rodlike. *Stylocerite* stocky; mesial margin slightly concave; tip blunt; distinctly shorter than first segment of antennular peduncle; this latter segment without mesio-ventral tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorso-lateral corner, with longer lateral spine clearly overreaching tip of stylocerite but usually falling slightly short of scaphocerite spine. *Scaphocerite* with blade absent, acute lateral spine with lateral margin straight, not overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circlet of spines on distal segment, and without ventro-distal spine on antepenultimate segment

Major pereopod 1 massive, fingers clearly not longer than half length of palm; fixed finger about as long as dactyl; in ventral view, outer face of fixed finger without distinct protuberance. Palm of chela with distal superior margin produced into tapering acute spine. Merus extensor margin strongly convex, ending in obtuse angle.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, terminating in two distinct distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, and terminating in two distinct teeth subequal in length. Extensor margin of merus convex, ending in right angle.

Pereopod 2 carpus with five segments; and equal to or shorter than merus.

Pereopod 3 slender; dactyl biunguiculate, with clearly unequal ungues (teeth); proximal tooth wider at base than distal one; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pleura 1 of male with posteroventral corner distinctly produced, hook-like; *pleura 2* of male rounded to obtuse. *Pleopod 1* of male with few terminal setae on endopod; *pleopod 2* of male with marginal setae on exopod originating near midpoint; appendix interna on male *pleopods 2–5* present. *Telson*, space between posterior marginal spines equal to or less than one third width of posterior margin; marginal convex lobe present; posterior corners adjacent to spines rectangular. Anal flaps, perianal setae, and postanal setal brush all absent. *Uropods* with a single fixed tooth on outer margin of exopod anterior to movable spine.

Color (Plate 1). Non-descript, transparent body, with distal palm and fingers of major chela orange. Ovaries and embryos variable in color, from pale green to gray to pale pink.

Hosts and ecology. *Zuzalpheus brooksi* occurs within several species of sponges, usually in dense groups of 10s to 100s, or even 1000s in a single sponge (Pearse 1932, 1950). These groups often have a paucity of ovigerous females (Duffy 1996b), and thereby appear intermediate in social structure between the apparently ancestral condition of heterosexual pairs common among alpheids, and the several eusocial species that live in large colonies with a single breeding female (Duffy *et al.* 2000). In Belize *Z. brooksi* is reliably found in the loggerhead sponge *Spheciospongia vesparium* (Duffy 1993) and in *Lissodendoryx colombiensis*, usually in shallow depths (less than 5 m).

Distribution. Western Atlantic: Bahamas (Coutière 1909; Pearse 1950; Lemaitre 1984); Biscayne Bay, Florida (Dobkin 1965); Florida Keys (Coutière 1909; Heard and Perlmutter 1977, Duffy 1993); Dry Tortugas (Coutière 1910; McClendon 1911; Pearse 1932); Gulf of Mexico (Coutière 1909; Lyons *et al.* 1971; Dardeau 1984; Erdmann and Blake 1987); Yucatan peninsula (Coutière 1909; Chace 1972); Cuba (Martínez Iglesias and García Raso 1999); Puerto Rico (Rathbun 1901; Coutière 1909); St. Thomas, US Virgin Islands (Coutière 1909); Leeward Islands, Windward Islands, and Tobago (Chace 1972); Netherlands Antilles (Westinga and Hoetjes 1981); Panama (Duffy 1992, 1993, 1996b); Surinam (Holthuis 1959); Belize Barrier Reef (Duffy 1993; this study); Brazil (Coutière 1909; Coelho and Ramos 1972).

Remarks. *Z. brooksi* is among the most widely reported species of *Zuzalpheus*, owing to its wide geographic distribution, and often extremely high densities in conspicuous, shallow-water sponges. Yet the discovery of several related species that are morphologically very similar to this species, including *Z. bousfieldi* (Chace 1972) and *Z. idios* new species, suggests that previous records of *Z. brooksi* from habitats other than its common host *Spheciospongia vesparium* should be treated with some caution.

***Zuzalpheus carpenteri* (Macdonald and Duffy, 2006) n. comb.**
(Plate 2)

Synalpheus bousfieldi (in part), in Dardeau 1984: USNM 189150, fig. 10.
Synalpheus "bousfieldi A": Morrison *et al.* 2004; Macdonald *et al.* 2006.

Material examined. (1) Holotype: ♂, (USNM 1092295, original VIMS 04CBC4201), 3.32 mm, Long Reef, Belize, 16 March 2004, in *Agelas clathrodes* Schmidt, 1870, 5 m.

(2) Allotype: ♀, (USNM 1092296, original VIMS 04CBC4202), 3.86 mm, Long Reef, Belize, in same individual *A. clathrodes* as holotype.

(3) Paratypes: 1 ♀, (AMNH 18492, original VIMS 04CBC4203), 3.01 mm, Long Reef, Belize, in same individual *A. clathrodes* as holotype. 1 ♂ (AMNH 18493, original VIMS 04CBC4305), 2.74 mm, Long Reef, Belize, 16 March 2004, in *A. clathrodes*, 5 m.

(4) 2 ♀ (VIMS 90CBC2002, 90CBC2003), 2.4 mm, 2.9 mm, 2 ♂ (VIMS 90CBC2004, 90CBC2010), 2.2 mm, 2.3 mm, outer ridge at Carrie Bow Cay, Belize, 9 December 1990, in *Agelas dispar*, 16 m.

(5) 1 ♀ (VIMS 96CBC1801), 3.0 mm, 1 ♂ (VIMS 96CBC1802), 2.6 mm, spur and groove reef at Carrie Bow Cay, Belize, 14 June 1996, in *Agelas dispar*, 4 m.

(6) 2 ♀ (VIMS 93CBC3701, 93CBC3704), 3.3 mm, 3.7 mm, 2 ♂ (VIMS 93CBC3702, 93CBC3705), 3.5 mm, 3.1 mm, fore-reef at Carrie Bow Cay, Belize, 23 March 1993, in *Agelas clathrodes*, 5–8 m.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, posterior margin with cardiac notch distinct. *Rostrum* longer than orbital hood, distinctly narrower, distally upturned; margins in dorsal view, straight. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process triangular, flanged posteriorly onto lower side of eye. Ocellary beak in lateral view not rod-like, broader at base. Stylocerite acute, with blunt tip; mesial margin concave; reaching midpoint of first segment of antennular peduncle. First antennular segment without ventromesial tooth, and with two basal ventral pro-

cesses. Basicerite without spine on dorsomesial corner, with longer ventrolateral spine, not reaching third segment of antennular peduncle. Scaphocerite blade absent, acute lateral spine robust, with lateral margin slightly concave, slightly surpassing basicerite spine, not reaching third segment of antennular peduncle; mesial projection at base of scaphocerite present. Third maxilliped with distal cirlet of spines on distal segment, without ventrodiscal spine on antepenultimate segment.

Major pereopod 1 massive, fingers clearly shorter than half length of palm; fixed finger slightly shorter than dactyl. Palm of chela with distal superior margin protuberance, which is secondarily produced distally, directed slightly downward, toward dactyl.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor margin concave, blade-like, terminating in two distinct distal teeth, subequal in length; transverse dorsal setal combs on dactyl, very conspicuous; fixed finger with flexor margin straight, blade-like, terminating in two distinct teeth subequal in length.

Pereopod 2 with carpus 5-segmented, subequal in length to merus. Both fingers terminating in a narrow, curved tooth.

Pereopod 3 slender; dactyl biunguiculate, with flexor tooth clearly thicker than extensor, mesial margin of flexor tooth strongly convex; propodus with row of 6 movable spines on flexor margin and one pair of distal movable spines flanking base of dactylus; carpus with distal movable spine on flexor margin; merus almost 4 times longer than wide, without movable spines on flexor margin; mesial lamella on coxa present. *Pereopod 4* similar to third, slightly weaker. *Pereopod 5* weaker than fourth; propodus with only 3 spines on flexor margin, and 4 transverse combs of stout setae on ventral face; carpus without distal spine.

Pleura 1 of male with posterior corner distinctly produced ventrally into small, anteriorly directed hook; second pleura of male broadly rounded; third to fifth pleura of male progressively acute, but not pointed. *Pleopod 1* of male, with 2 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating in distal 2/3; appendix interna present on second to fifth male pleopods. *Pleopod 2* of female, with marginal setae on exopod originating in distal 1/3; appendix interna present on second to fifth male pleopods. *Telson* length 3/4 width of proximal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with a single fixed tooth on outer margin of exopod distinctly removed from the movable one, the latter slightly longer and more slender than adjacent inner fixed tooth.

Color (Plate 2). Faint to bright orange in overall appearance, distal palm and fingers of major chela more intensely orange. Ovaries and embryos brilliant orange.

Hosts and ecology. Like *Zuzalpheus agelas*, *Z. carpenteri* is evidently a specialist on sponges of the genus *Agelas*, usually occurring as one or a few heterosexual pairs within an individual sponge. In Belize we have collected it from both *Agelas clathrodes* and *Agelas dispar*, at depths ranging from 1.5–20 m.

Distribution. Western Atlantic: Bahamas (as *S. bousfieldi*, Dardeau 1984); San Blas Islands, Panama (J.E. Duffy, unpublished); Belize Barrier Reef (this study).

Remarks. *Z. carpenteri* is one of a complex of several closely related and morphologically quite similar species that includes *Z. brooksi*, *Z. idios* n. sp., *Z. bousfieldi*, *Z. chacei*, and likely other undescribed taxa (e.g., Morrison *et al.* 2004). Based on his figures 7–10 and description, Dardeau's (1984) specimens of *S. "bousfieldi"* from *Agelas* in the Bahamas and possibly in the Florida Middle Ground (Gulf of Mexico) are probably assignable to *Z. carpenteri*.

***Zuzalpheus chacei* (Duffy, 1998) n. comb.**
(Plate 2)

Synalpheus chacei Duffy, 1998:389, Figs. 1–5 (and synonymy); Ríos 2003:53, plate II.

Material examined. (1) **Holotype** ♂ (USNM 282773, VIMS 90CBC3602), 2.4 mm, Carrie Bow Cay, Belize, in *Agelas dispar*, 3 m.

(2) 1 ♀ (?), 2.4 mm (VIMS 96CBC1805), 27 ♂, 1.7–2.4 mm (VIMS 96CBC1806), spur and groove of Carrie Bow Cay, Belize, 14 June 1996, in *Agelas dispar*, 4 m.

(3) 2 ♀ (VIMS 90CBC0203, 90CBC0207), 2.5 mm, 2.4 mm, 6 ♂ (VIMS 90CBC0206, 90CBC0217, 90CBC0218, 90CBC0219, 90CBC0220, 90CBC0222), 1.6–2.2 mm, from larger colony, outer ridge at Carrie Bow Cay, Belize, 12 December 1990, in *Hymeniacidon amphilecta*, 16 m.

(4) 1 ♀ (VIMS 94CBC7803), 2.2 mm, 13 ♂ (VIMS 94CBC7804 – 94CBC7816), 1.5–2.3 mm, Blue Ground Range, W of Carrie Bow Cay, Belize, 28 August 1994, in *Hyattella intestinalis*, 3 m.

(5) 1 ♀ (VIMS 96CBC3702), 2.7 mm, 32 ♂ (VIMS 96CBC3706 – 96CBC3735), 2.3–2.7 mm, outer ridge at Carrie Bow Cay, Belize, 17 June 1996, in *Lissodendoryx* cf. *strongylata*, ~15 m.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner very obtusely angular, and posterior margin with cardiac notch distinct. Rostrum triangular, about as long as, but narrower than, ocular hoods, with slightly upturned tip. Orbitorostral process absent, but convex keel present under rostrum base. Ocular hoods dorsally convex; in dorsal view, bluntly triangular, separated from rostrum by deep adrostral sinus. Ocular process broad and shallow. Ocellary beak triangular in lateral view. Stylocerite stocky; mesial margin slightly concave, occasionally convex; tip blunt; barely reaching midpoint of first segment of antennular peduncle; this latter segment without mesio-ventral tooth, and with 2 basal ventral processes. *Basicerite* with dorso-lateral corner straight to rounded, longer lateral spine surpassing midpoint of 2nd segment of antennular peduncle. *Scaphocerite* blade absent, lateral spine acute, with lateral margin slightly concave, overreaching distal margin of 2nd segment of antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped* 3 with distal circlet of spines on distal segment and without ventrodistal spine on antepenultimate segment.

Major pereopod 1 massive, fingers shorter than half length of palm; fixed finger about as long as dactyl; in ventral view, outer face of fixed finger without protuberance. Palm of chela with distal superior margin produced into prominent but short, blunt tubercle; merus with extensor margin strongly convex, ending in obtuse angle.

Minor pereopod 1 with palm less than 2 times longer than high; fingers shorter than palm; dactyl with flexor margin straight, blade-like, terminating in two strong distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous, uniquely arranged in 2 longitudinal sets separated by a strip lacking setae; fixed finger with flexor margin straight, blade-like, and terminating in two strong teeth subequal in length; extensor margin of merus slightly convex, ending in a right angle.

Pereopod 2 with carpus 5-segmented, about as long as merus.

Pereopod 3 slender; dactyl biunguiculate, with proximal tooth slightly thicker and straighter than distal one; merus without movable spines on flexor margin; mesial lamella on coxa present. Pereopods 4 and 5 normal.

Pleura 1 of male with posteroventral corner acutely produced into wide hook; pleura 2 of male broadly rounded, occasionally with posterior corner obtuse. Remaining pleura increasingly acute, but still obtuse. *Pleopod* 1 of male with 3 or 4 terminal setae on endopod; pleopod 2 of male with marginal setae on exopod originating near midpoint; appendix interna present on male pleopods 2–5. *Telson*, space between posterior marginal spines about one-third width of posterior margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush all absent. *Uropods* with a single fixed tooth on outer margin of exopod anterior to, and distinctly removed from, thicker and longer movable spine, latter adjacent to smaller internal fixed tooth.

Color (Plate 2). Translucent with a milky wash on the major chela and body; legs and tail fan transparent; distal edges of both of first pair of chelae with a gold to brownish tinge. Sometimes, several red chromato-

phores are apparent on the carapace between the eyes. The eggs are yellowish to creamy opaque.

Hosts and ecology. Like *Z. regalis* and *Z. filidigitus*, *Z. chacei* is eusocial and is consistently found in aggregations of tens of individuals, usually with a single reproductive female (Duffy 1998; Duffy *et al.* 2000). This species has among the wider host ranges of West Atlantic *Zuzalpheus* species, inhabiting the internal canals of several species of demosponges; in Belize, we have collected it from *Agelas dispar*, *A. clathrodes*, *Hyattella intestinalis*, *Hymeniacion amphilecta* (de Laubenfels, 1936), and *Lissodendoryx strongylata* van Soest 1984. In Caribbean Panama, it has been collected from *Agelas dispar*, *A. clathrodes*, *Niphates amorpha* Wiedenmayer 1977, and *Lissodendoryx colombiensis* Zea and van Soest 1986 (J.E. Duffy, unpublished).

Distribution. Western Atlantic: British Virgin Islands (Chace 1972); San Blas Islands, Panama (as *S. bousfieldi*, see J.E. Duffy 1992); Belize Barrier Reef (this study).

***Zuzalpheus dardeau*, n. sp.**

(Figs. 3–6, Plate 2)

Synalpheus sp. 1, new species Ríos 2003: 55, figures 2–2 through 2–5, plate I.

Synalpheus “*pandionis* giant”: Morrison *et al.* 2004; Macdonald *et al.* 2006.

Material examined. (1) **Holotype** ♂, 8.5 mm (USNM 1019038, VIMS 01CBC7406), **allotype** ovigerous ♀, 9.9 mm (USNM 1019039, VIMS 01CBC7407), Twin Cays, Belize 26 April 2001 in *Lissodendoryx colombiensis*, 1 m.

(2) **Paratypes:** 1 ♂, 7.6 mm, 1 ♀, 9.2 mm (USNM 1019040, VIMS 99CBC0103, VIMS 99CBC0102); 1 ♂, 7.6 mm, 1 ovigerous ♀, 9.1 mm (USNM 1019041, VIMS 99CBC0201, VIMS 99CBC0401), Twin Cays, Belize, 2 December 1999 in *Lissodendoryx colombiensis*, 2 m.

(3) 2 ovigerous ♀ (VIMS 93CBC2006, 93CBC2007), 6.5 and 6.8 mm, 1 ♂ (VIMS 93CBC2011), 5.1 mm, Blue Ground Range, W of Carrie Bow Cay, Belize, 19 March 1993, in *Sphaciospongia vesparium*, 1.5 m.

(4) 1 ovigerous ♀ (VIMS 93CBC2110), 7.2 mm, 1 ♂ (VIMS 93CBC2106), 5.1 mm, Blue Ground Range, W of Carrie Bow Cay, Belize, 19 March 1993, in *Sphaciospongia vesparium*, 1.5 m.

Description of holotype. Body subcylindrical; carapace smooth, with pterygostomial corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. *Rostrum* lanceolate, distally upturned, slightly longer, but clearly narrower, than ocular hoods. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, hoof-shaped, laterally convex, mesially concave, separated from rostrum by deep adrostral sinus. Ocular process produced into elongated fingerlike structure. Ocellary beak with superior margin straight and inferior margin strongly convex. Stylocerite slender; tip acute; mesial margin convex; distinctly shorter than first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorsolateral corner, longer lateral spine clearly overreaching tip of stylocerite. *Scaphocerite* blade reduced, lateral spine acute, with lateral margin slightly concave, not overreaching antennular peduncle, slightly surpassing basicerite lateral spine; mesial corner at base of scaphocerite right-angled. *Carpocerite* overreaching antennular peduncle. *Maxilliped 3* with distal cirlet of spines on distal segment and without ventrodistal spine on antepenultimate segment. Remaining mouthparts as figured.

Major pereopod 1 massive, fingers about half length of palm; fixed finger shorter than dactyl; in ventral view, outer face of fixed finger with obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle overhanging an acute, forwardly directed spine. Merus with extensor margin strongly convex, with distal flat angular projection on mesial face.

Minor pereopod 1 with palm more than twice as long as high; fingers clearly shorter than palm; dactyl with flexor surface straight, with 2 strong distal teeth, subequal in length, and parallel to dactyl axis; trans-

verse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor surface straight, ending in one strong tooth and one slightly shorter, subdistal tooth. Extensor margin of merus slightly convex, ending in obtuse angle.

Pereopod 2 with carpus 5-segmented, distinctly longer than merus.

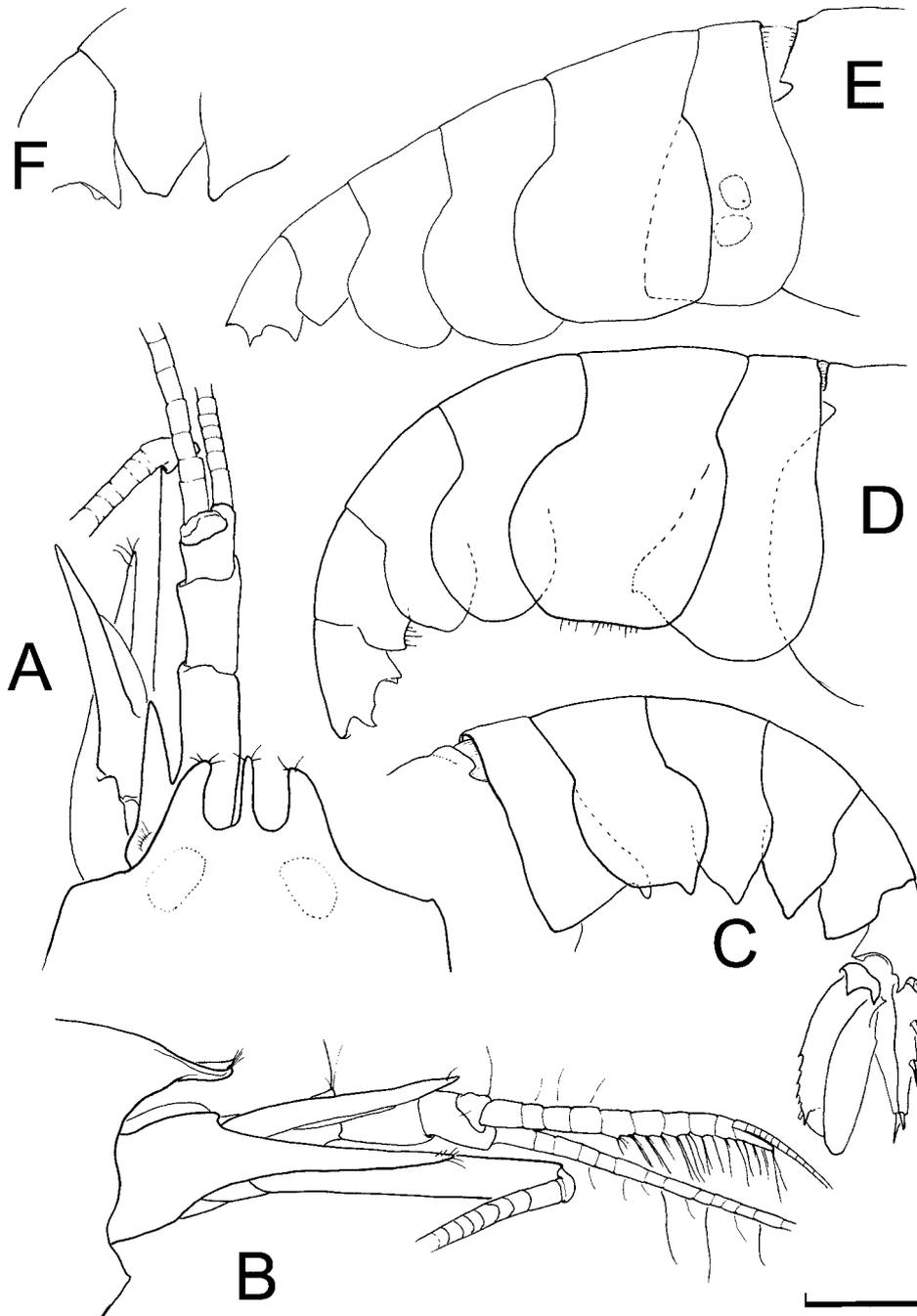


FIGURE 3. *Zuzalpheus dardeauui*, n. sp. Paratype female 9.1 mm (USNM 1019041): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view. Paratype male 7.6 mm (USNM 1019040): c, abdomen, lateral view. Paratype ovigerous female 9.2 mm (USNM 1019040): d, abdomen, lateral view. Allotype ovigerous female 9.9 mm (USNM 1019039): e, abdomen, lateral view. Paratype male 8.2 mm (VIMS 01CBC7408): f, detail of 4th–6th abdominal pleurae, lateral view. Scale bar = 1 mm for a, b; 2 mm for c, d; 2.5 mm for e; and 1.2 mm for f.

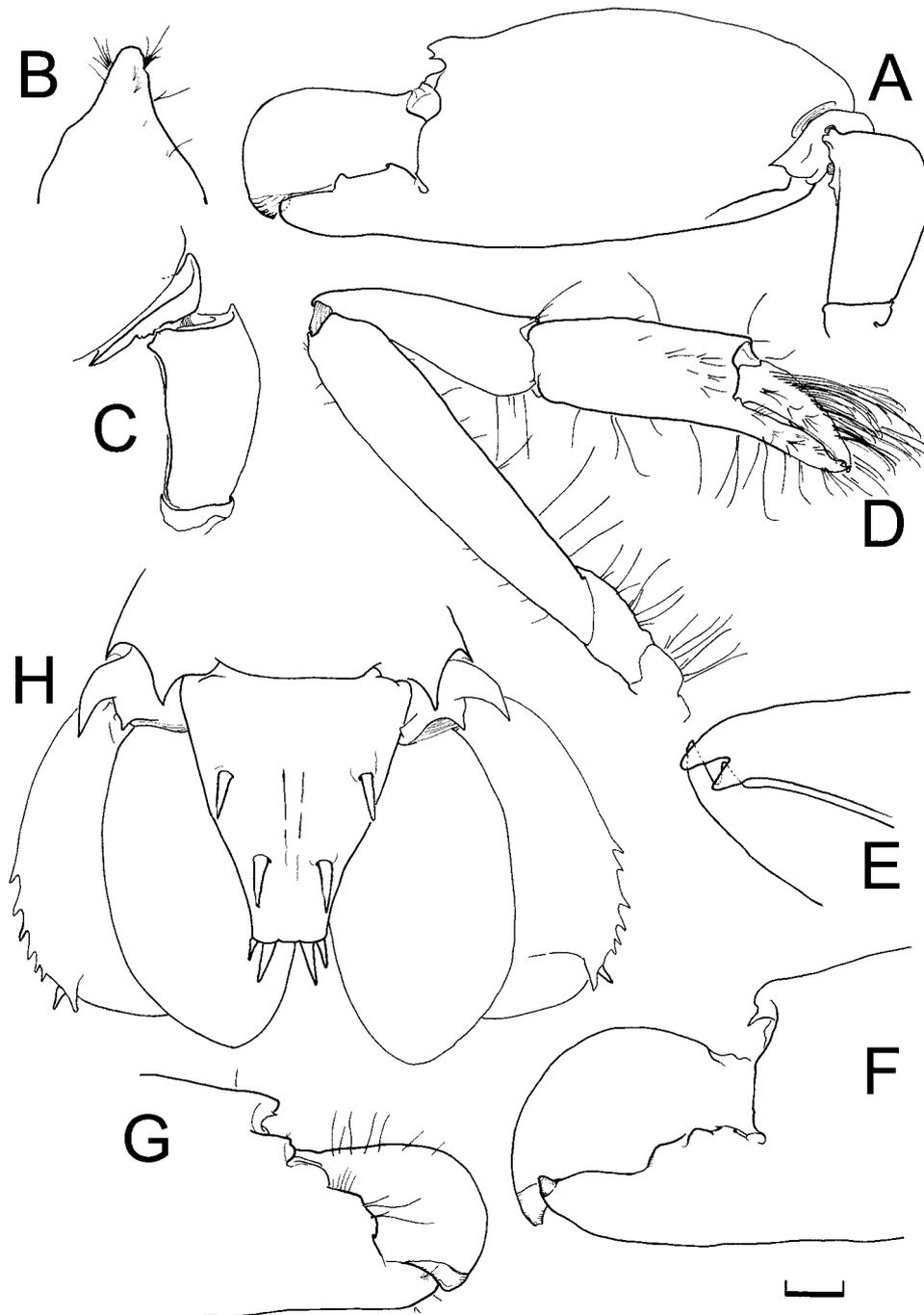


FIGURE 4. *Zuzalpheus dardeai*, n. sp. Paratype male 7.6 mm (USNM 1019040): a, major first pereopod, lateral view; b, same, tip of fixed finger, ventral view; c, same, merus, lateral view; d, minor first pereopod, lateral view; e, distal portion of same, alternate lateral view. Paratype ovigerous female 9.2 mm (USNM 1019040): f, distal portion of chela of major first pereopod, lateral view. Paratype female 9.1 mm (USNM 1019041): g, distal portion of chela of major first pereopod, lateral view; h, telson and uropods, dorsal view. Scale bar = 1 mm for a, c, g; 0.66 mm for b; 0.5 mm for d, f, h; and 0.12 mm for e.

Pereopod 3 dactyl biunguiculate, with proximal tooth clearly thicker than distal one; propodus with a row of 11 (right leg) or 10 (left leg) mobile spines on flexor margin, and 2 paired subdistal spines; carpus slightly longer than half the propodus, with strong mobile spine on distal flexor corner; merus longer than twice carpus length, about 4 times longer than wide, without movable spines on flexor margin; ischium subtrapezoidal, shorter than carpus, devoid of spines; basis shorter than ischium, lower margin strongly convex; coxa with mesial lamella. *Pereopod 4* similar to 3rd, but weaker. *Pereopod 5* similar to 3rd, but more slender, propodus

with 11 transverse parallel rows of thick setae on posterior face, and 5 (right leg) or 4 (left leg) mobile spines on ventral margin; carpus almost 3/4 as long as propodus, without distal spine; merus about as long as propodus, without spines.

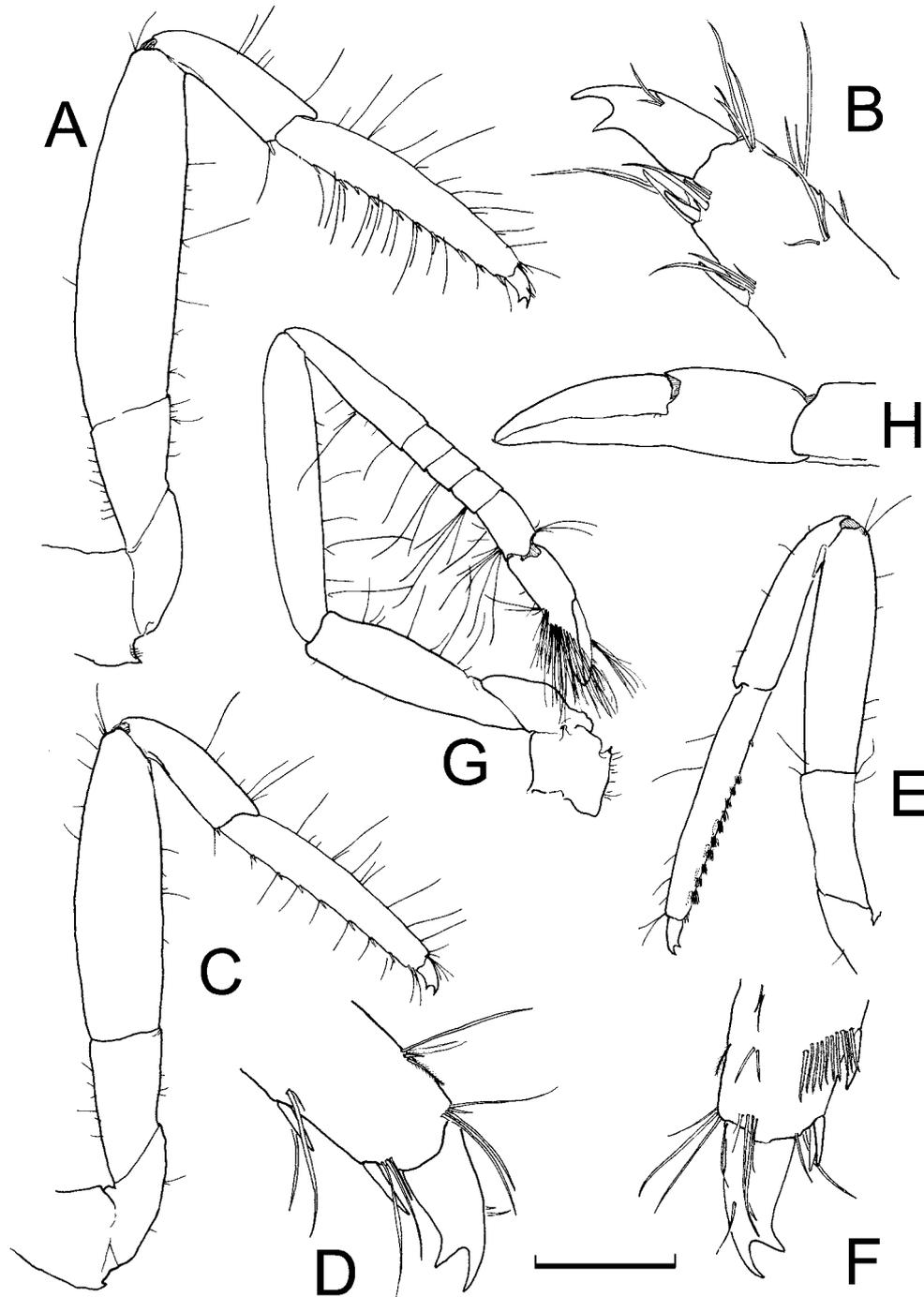


FIGURE 5. *Zuzalpheus dardeauui*, n. sp. Paratype male 7.6 mm (USNM 1019040): a, left third pereopod; b, same, detail of distal portion; c, left fourth pereopod; d, same, detail of distal portion; e, left fifth pereopod; f, same, detail of distal portion; g, left second pereopod; h, same, detail of distal portion. Scale bar = 1 mm for a, c, e, g; 0.25 mm for b, d, f; and 0.5 mm for h.

Pleura 1 of male with anterior ventral corner almost forming right angle, posteroventral corner distinctly produced, hook-like; *pleura 2–5* of male produced posteroventrally into acute angle; abdominal segment 6 with acute projection on posteroventral corner, shallow inferior concavity, acutely produced triangular lateral lobe, shallow obtuse upper emargination, and convex dorsal margin slightly overhanging telson. Female allo-

type with pleura 1 inferior margin slightly concave, 2nd to 4th broadly rounded, 5th acutely produced ventrally. *Pleopod* 1 of male with 6 terminal setae on endopod; *pleopod* 2 of male with marginal setae on exopod originating close to base. *Appendix interna* on *pleopods* 2–5 present in both sexes. *Telson* with space between posterior marginal spines about one-third width of posterior margin; marginal convex lobe present; posterior corners adjacent to spines rectangular. Anal flaps present. Perianal setae absent. Postanal setal brush present. *Uropod* with 5 (right side) or 4 (left side) fixed teeth on outer margin of exopod anterior to, and distinctly removed from, mobile spine, latter closely adjacent to subequally long but wider fixed tooth on mesial side, diaresis well defined; left uropod with supernumerary mobile spine.

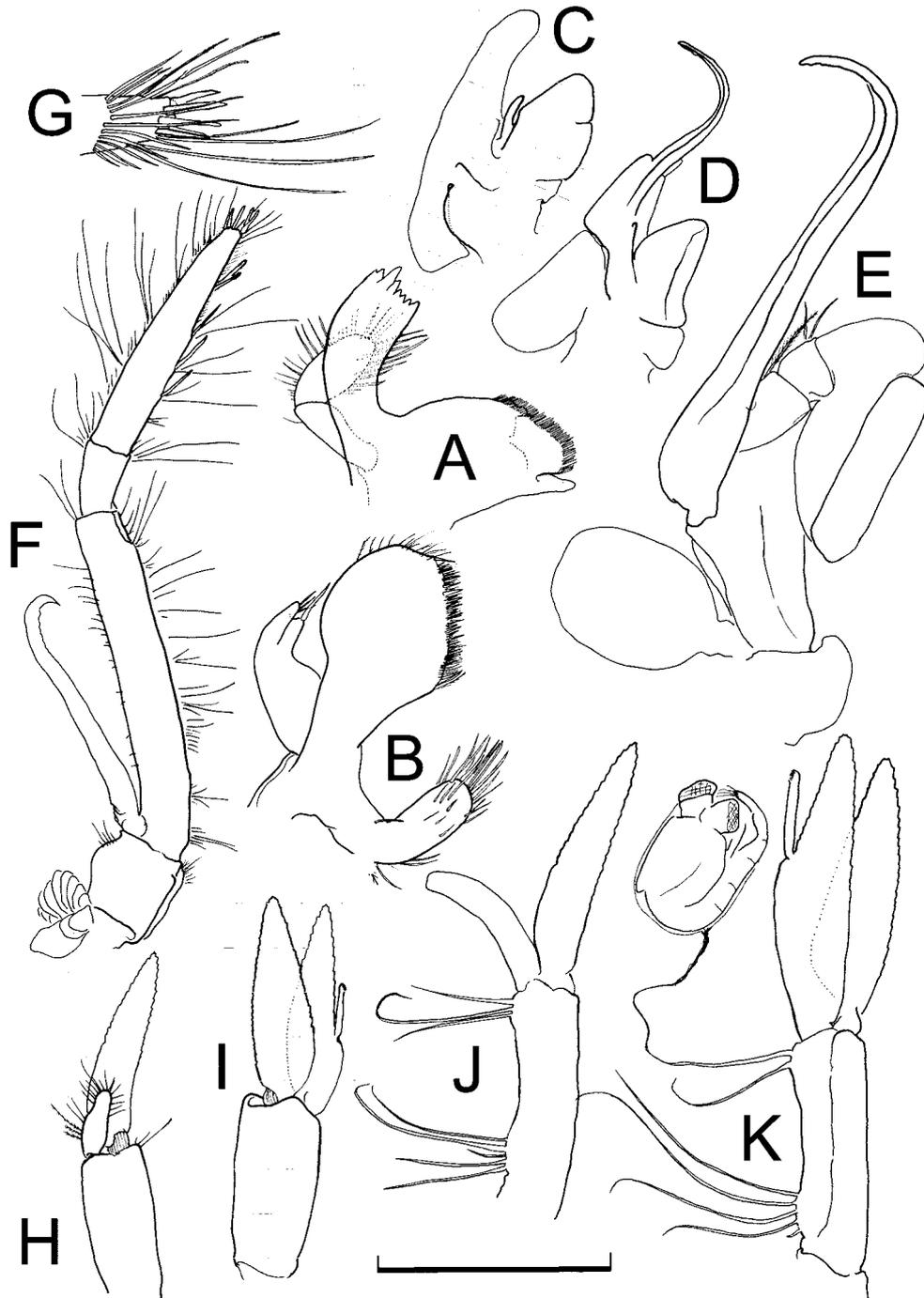


FIGURE 6. *Zuzalpheus dardeai*, n. sp. Paratype male 7.6 mm (USNM 1019040): a, right mandible; b, right first maxilla; c, right second maxilla; d, right first maxilliped; e, right second maxilliped; f, right third maxilliped; g, same, detail of tip; h, left first pleopod; i, left second pleopod. Paratype ovigerous female 9.2 mm (USNM 1019040): j, first pleopod; k, left second pleopod with egg. Scale bar = 1 mm for a, b, e, g; and 2 mm for c, d, f, h, i, j, k.

Color (Plate 2). *Z. dardeai* varies in color, more or less continuously, between two extremes, at one end a translucent dull gold-tan color with brown-black fingers and distal palm of major first chela, at the other extreme an intense red-orange with darker orange tips on the major chela. Ovaries and embryos are orange.

Etymology. The specific name is in honor of Michael R. Dardeau, Dauphin Island Sea Lab, Alabama, in recognition of his important work on *Zuzalpheus* from the Gulf of Mexico and Caribbean.

Hosts and ecology. In Belize we have found *Zuzalpheus dardeai*, n. sp., regularly in the orange demo-sponge *Lissodendoryx colombiensis* and in the loggerhead sponge *Sphaciospongia vesparium* (Lamarck, 1814b). On rare occasions it has been collected inside other, unidentified sponges. An infested sponge usually houses a few heterosexual pairs along with other congeneric species.

Distribution. Offshore reefs of North Carolina, USA (J.E. Duffy unpublished), Belize Barrier Reef (this study).

Remarks. This species belongs in a group of closely related and morphologically similar species that includes *Z. longicarpus* and *Z. pandionis* (Table 1). The combination of hoof-shaped ocular hoods, strong dorsal spines on the telson, strong teeth on the minor chela, and a well defined cardiac notch on the carapace provide the most useful characters in identifying *Zuzalpheus dardeai*, n. sp. Like *Z. longicarpus*, *Z. dardeai*, n. sp., is among the largest species in the genus from the western Atlantic, and also like that species, *Z. dardeai*, n. sp. occurs in *Sphaciospongia vesparium*, making the identification of specimens from this common sponge quite challenging. Careful study has convinced us, however, that the two taxa are indeed separate species, as evidenced by assortative mating among individuals exhibiting the two suites of morphological characters, and by the rarity of intermediates between them.

TABLE 1. Morphological characters useful in distinguishing five species related to *Zuzalpheus longicarpus* (Herrick, 1891).

	<i>Z. dardeai</i>	<i>Z. longicarpus</i>	<i>Z. pandionis</i>	<i>Z. ul</i>	<i>Z. yano</i>
Orbital hoods	hoof	slender	broad	broad	broad
Orbitorostral process	absent	absent	absent	simple	absent
Cardiac notch	normal	reduced ¹	normal	normal	normal
Ocular process	long	broad	double	broad	broad
Stylocerite	slender	slender	slender	thick	slender
Scaphocerite blade	reduced	reduced	reduced	reduced	absent
Minor Pereopod 1 dactyl, terminal teeth	subequal	subequal	unequal	unequal	unequal
2nd pleura, posterior corner	acute	acute	acute	obtuse	obtuse
Uropodal exopod, inner submesial fixed tooth	on edge	on edge	in-set	on edge	on edge
Telson, distal spines	unequal	unequal	subequal	unequal	subequal
Telson, dorsal spines	strong	feeble	strong	strong	strong
Major Pereopod 1 fixed finger, basal protuberance	obtuse	obtuse	acute	absent	absent

¹ Upper angle of notch distinctly obtuse

Zuzalpheus elizabethae, n. sp.

(Figs. 7–10, Plate 2)

Synalpheus “*rathbunae* A”: Duffy 1996c; Morrison *et al.* 2004; Macdonald *et al.* 2006.

Synalpheus sp. 2, new species Ríos 2003: 67, figures 2–6 through 2–9, plate III.

Material examined. (1) **Holotype** ♂, 3.0 mm (USNM 1019042, VIMS 01CBC6602), **allotype** ovigerous ♀, 3.6 mm (USNM 1019043, VIMS 01CBC6601), The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize,

2 May 2001 in demosponge *Hymeniacidon caerulea*, 2 m. **Paratypes:** 1 ♂, 2.7 mm (USNM 1019044, VIMS 01CBC6602), 1 ♂, 2.9 mm (USNM 1019045, VIMS 01CBC6602), from same sponge specimen as holotype.

(2) 1 ♂, 3.1 mm (USNM 1019046, VIMS 99CBC2803), outer ridge (16°48'N, 88°05'W) Carrie Bow Cay, Belize, 6 Dec 1999, in *Lissodendoryx* sp., 18 m.

(3) 1 ovigerous ♀ (VIMS 99CBC5101), 4.0 mm, 5 ♂ (VIMS 99CBC5105–99CBC5109), 3.0–3.3 mm, from colony of 101 individuals, outer ridge at Carrie Bow Cay, Belize, 9 December 1999, in *Lissodendoryx* sp., ~15 m.

(4) 1 ovigerous ♀ (VIMS 04CBC1702), 3.4 mm, 26 ♂ (VIMS 04CBC1701), 2.5–3.0 mm, from a colony of 30 individuals, The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize, 13 March 2004, in *Hymeniacidon caerulea*, 2 m.

(5) 1 ovigerous ♀ (VIMS 99CBC2901), 3.9 mm, 14 ♂ (VIMS 99CBC2903–99CBC2916), 2.9–3.5 mm, from a colony of 122 individuals, outer ridge at Carrie Bow Cay, Belize, 6 December 1999, in *Lissodendoryx* sp., ~15 m.

Description of holotype. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into broad acute angle, posterior margin with cardiac notch distinct. *Rostrum* lanceolate, about as long as, but clearly narrower than, ocular hoods, distally upturned. Ventral surface of carapace behind rostrum flat. Ocular hoods dorsally convex; in dorsal view, broad, bluntly triangular, margins slightly convex, separated from rostrum by deep adrostral sinus. Ocular process like a swollen thick surface. Ocellary beak in lateral view rod-like. Stylocerite thick; mesial margin slightly concave; tip acute; distinctly shorter than 1st segment of antennular peduncle; latter segment without ventromesial tooth, and with 2 basal ventral processes. *Basicerite* with strong sharp spine on dorsal margin, reaching about as far as tip of stylocerite, and with longer lateral spine almost reaching distal margin of 2nd segment of antennular peduncle. *Scaphocerite* blade absent, lateral spine robust, with lateral margin straight, clearly overreaching antennular peduncle, but not reaching as far as distal margin of carapocerite; mesial corner at base of scaphocerite obtuse. *Maxilliped 3* with distal circle of spines on distal segment and without ventrodorsal spine on antepenultimate segment.

Major pereopod 1 massive, somewhat inflated proximally, fingers clearly not longer than half length of palm; fixed finger reduced, clearly shorter than dactyl; in ventral view, outer face of fixed finger with an obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute ventrally directed spine. Merus with extensor margin strongly convex, with distal angular projection.

Minor pereopod 1 with palm less than 2 times longer than high; fingers clearly shorter than palm; dactyl with flexor surface obliquely concave, with no hint of subdistal tooth; transverse dorsal setal combs on extensor surface of dactyl very conspicuous, arranged in two distinct sets, the mesial one shorter; fixed finger with flexor surface obliquely concave, and no hint of second (subdistal) tooth. Extensor margin of merus convex, ending in obtuse angle.

Pereopod 2 with carpus 4-segmented, about as long as merus.

Pereopod 3 slender; dactyl biunguiculate, with proximal tooth clearly thicker than distal one; propodus with a row of 5 mobile spines on the flexor margin, and two paired subdistal spines; carpus about half as long as propodus, with a delicate mobile spine on distal flexor corner; merus longer than propodus, slightly more than 3 times as long as wide, without movable spines on flexor margin; ischium subtrapezoidal, about as long as carpus, devoid of spines; basis shorter than ischium, lower margin strongly convex; coxa with mesial lamella present. Pereopods 4 and 5 similar to 3rd, but 5th with 4 transverse rows of setae on flexor margin of propodus, and carpus without distal spine.

Pleura 1 of male with posteroventral corner strongly produced into tooth, with posterior margin convex, anterior corner slightly produced into acute angle; pleura 2–5 of male produced into acute angle ventroposteriorly. *Pleopod 1* of male with 3 or 4 terminal setae on endopod; pleopod 2 of male with marginal setae on exopod originating near midpoint; appendix interna on male pleopods 2–5 present. *Telson* with space between posterior marginal spines equal to one-third width of posterior margin, and without convex lobe; posterior cor-

ners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush all absent. *Uropods* with 2 fixed teeth on outer margin of right exopod and one on left anterior to, and distinctly removed inwards from, movable spine, mesial fixed tooth slightly superimposed over mobile spine on left side; both of these abnormally duplicated on right exopod.

Color (Plate 2). Translucent gold-orange with sparse chromatophores; the fingers and distal margin of palm of major chela are more intense orange. Digestive gland is olive-green to brown. Ovaries and eggs bright yellow-orange to red-orange.

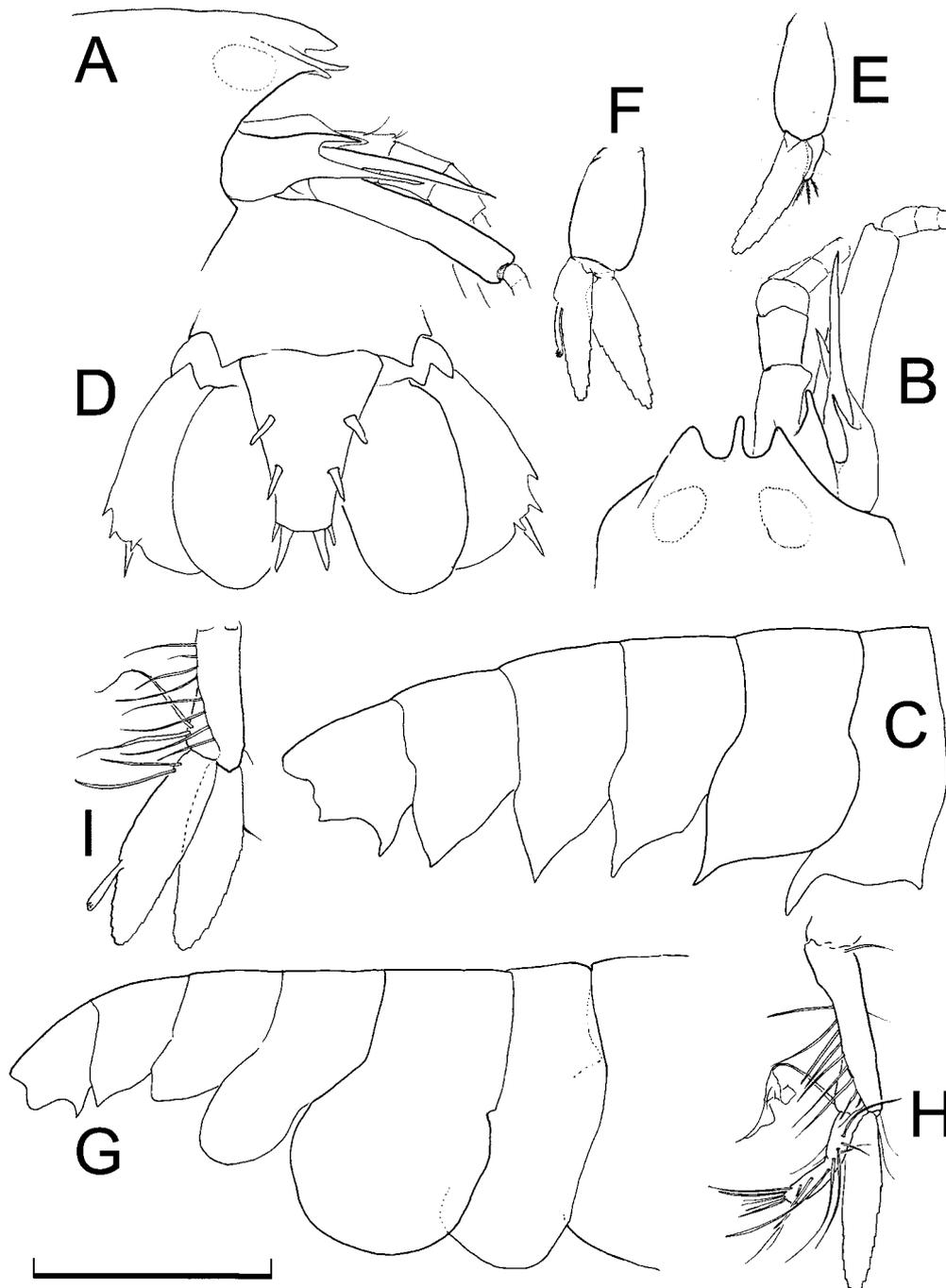


FIGURE 7. *Zuzalpheus elizabethae*, n. sp. Holotype male 3.0 mm (USNM 1019042): a, anterior region of carapace and cephalic appendages, lateral view; b, same, dorsal view; c, abdomen, lateral view. Paratype male 2.9 mm (USNM 1019045): d, telson and uropods, dorsal view. Paratype male 2.7 mm (USNM 1019044): e, first pleopod; f, second pleopod. Allotype ovigerous female 3.6 mm (USNM 1019043): g, abdomen, lateral view; h, first pleopod; i, second pleopod. Scale bar = 1 mm for a, b, c, d; 1.1 mm for e, f, h, i; and 1.5 mm for g.

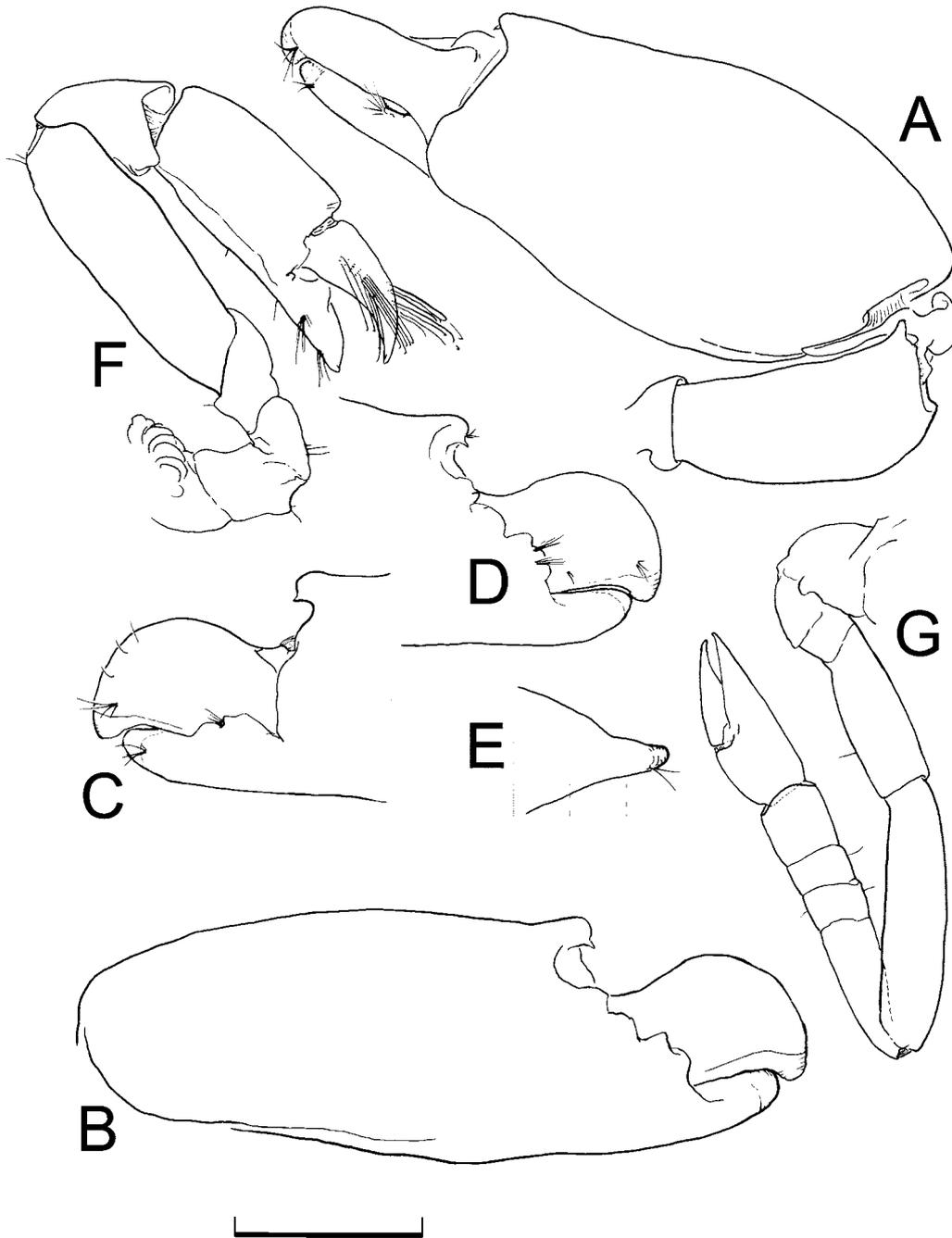


FIGURE 8. *Zuzalpheus elizabethae*, n. sp. Paratype male 2.7 mm (USNM 1019044): a, major first pereopod, dorsal view; b, same, lateral view; c, same, distal portion, lateral view; d, same, alternate view; e, same, tip of fixed finger, ventral view; f, minor first pereopod, lateral view; g, right second pereopod. Scale bar = 1 mm for a, b, c, d, e; and 0.7 mm for f, g.

First larva. Eight newly hatched larvae were obtained in the laboratory from a wild-caught ovigerous female (VIMS 93P3705). These first larvae are crawling megalopae similar to those described from *Z. brooksi* (Dobkin 1965). They have the front of the carapace trispinose, covering the eyes; both pairs of chelae are functional and not dimorphic; the carpus of the second pair has 3 segments; the pleopods and the uropods are both biramous. The first larva of *Z. elizabethae*, n. sp., differs from that of *Z. brooksi* in the following details: the fingers of the first pair of chelae are simple, not bifid; the telson has only one pair of spines on the distal margin; the scaphocerite is more slender, without any suggestion of a blade.

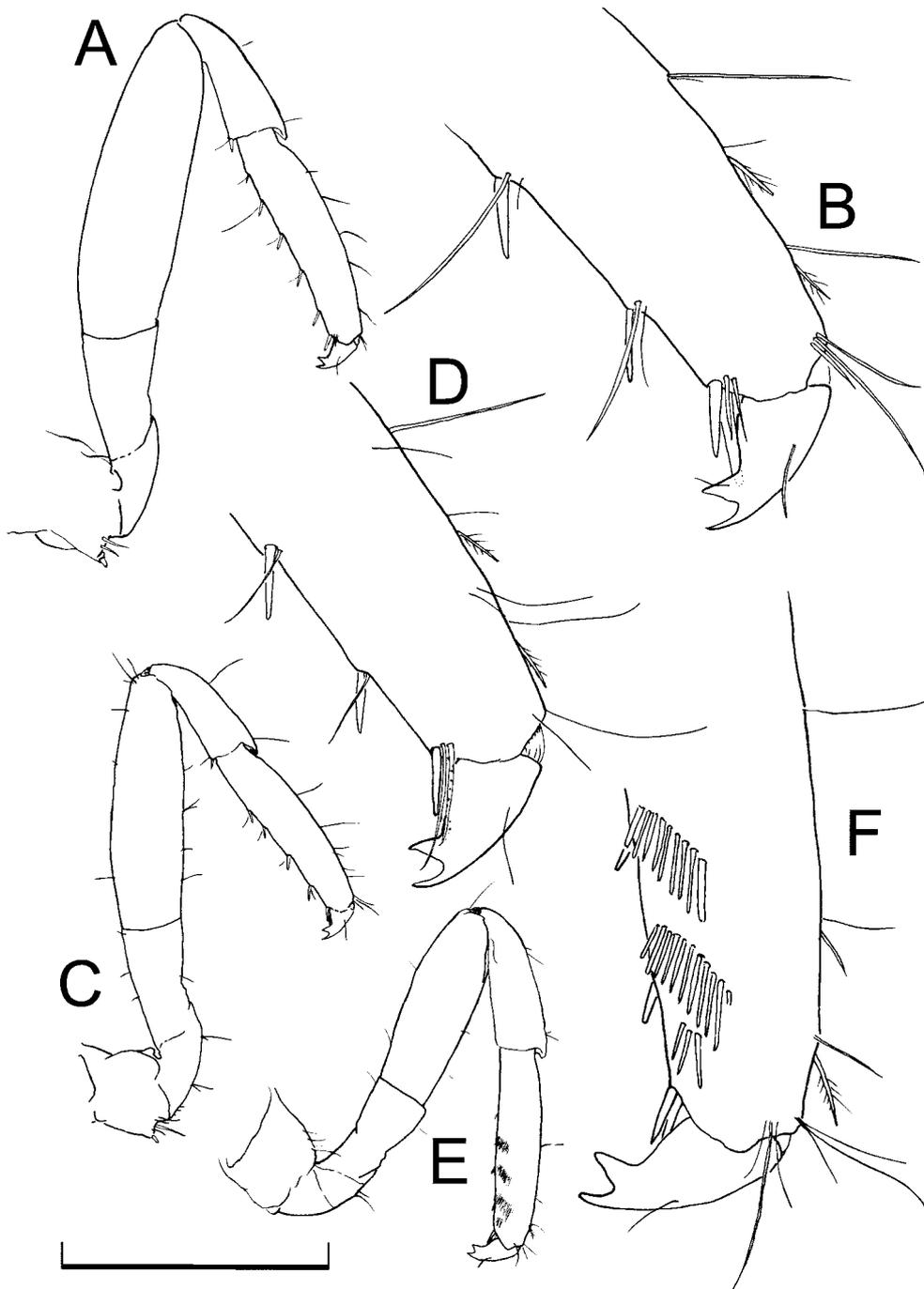


FIGURE 9. *Zuzalpheus elizabethae*, n. sp. Paratype male 2.7 mm (USNM 1019044): a, right third pereopod; b, same, detail of distal portion; c, right fourth pereopod; d, same, detail of distal portion; e, right fifth pereopod; f, same, detail of distal portion. Scale bar = 1 mm for a, c, e; and 0.24 mm for b, d, f.

Etymology. We name this species after Dr. Elizabeth Canuel, Virginia Institute of Marine Science, in appreciation of her assistance with our early field research on *Zuzalpheus* and continuous support while studying these shrimps.

Variations. The number of fixed teeth on the exterior margin of the uropodal exopod is most frequently 2, occasionally 1 or 3, with rare records of 4 and 5 only in one of the uropods. In a few specimens one or both of the second to fourth pleura have 2 points instead of the normal 1, in almost every one of these instances, again

it only happens on just one of the two sides of the abdominal segment. The holotype has a supernumerary pleopodal ramus emerging anteriorly to the first right pleopod, a peculiar abnormality that has not been recorded previously.

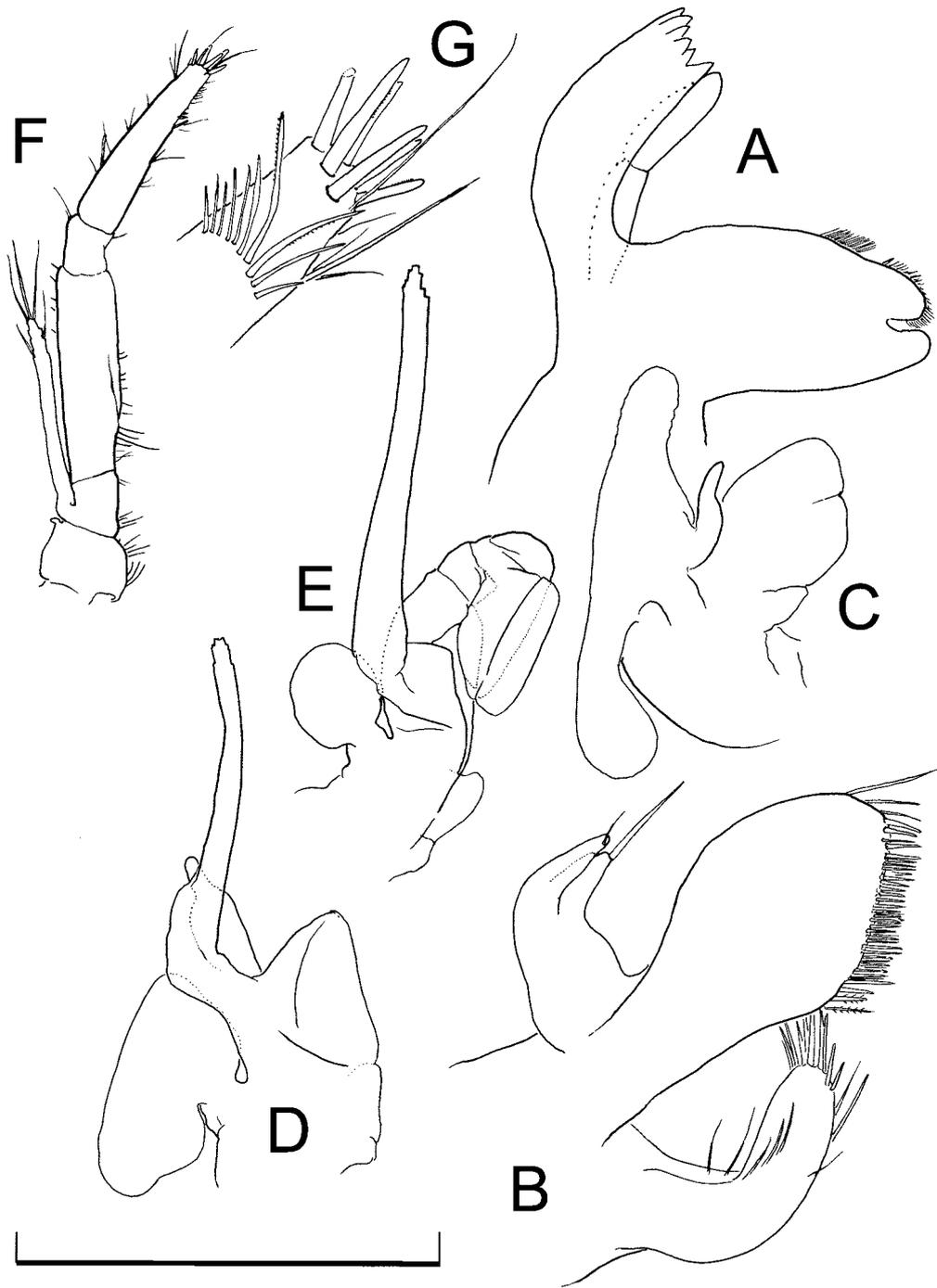


FIGURE 10. *Zuzalpheus elizabethae*, n. sp. Mouthparts. Paratype male 2.7 mm (USNM 1019044): a, right mandible; b, right first maxilla; c, right second maxilla; d, right first maxilliped; e, right second maxilliped; f, right third maxilliped; g, same, detail of tip. Scale bar = 1 mm for a, b, g; 2 mm for c, d, e; and 4 mm for f.

Hosts and ecology. In Belize, we have collected *Zuzalpheus elizabethae*, n. sp. most frequently from species of *Lissodendoryx*, including *L. cf. strongylata* and *L. sp.* on the outer reef ridge, and from *L. colombiensis* in shallow water, as well as from *Hymeniacidon caerulea*. There are also occasional records from other

sponges. This species lives in eusocial colonies, consisting of tens to hundreds of individuals with only one or two breeding females. Whereas all other eusocial *Zuzalpheus* species in our area are reliably found in all or most specimens of at least one host species (Duffy *et al.* 2000, Macdonald *et al.* 2006), *Z. elizabethae* exhibits a more “fugitive” distribution, being found in only occasional specimens of the several hosts from which it has been recorded.

Distribution. Florida Keys, USA (J.E. Duffy unpublished); Lee Stocking Island, Bahamas (K.S. Macdonald, pers. comm.); San Blas Islands, Panama (as *S. “rathbunae A”*, Duffy 1996c); Belize Barrier Reef (this study).

Remarks. *Z. elizabethae* n. sp. is one of a complex of morphologically similar species related to *Z. rathbunae*. Aside from the genetic differences already documented (Duffy 1996c), the following morphological characters appear consistent in separating them (Table 2). The anterior corner of the first pleura in males of both *Z. elizabethae*, n. sp., and *Z. regalis* is clearly produced into an acute angle, whereas it is broadly rounded in *Z. rathbunae*. Also, the tubercle dorsally overhanging the base of the dactyl on the major first chela lacks the accessory spinule and is distinctly acute and upwardly oriented in *Z. rathbunae*, but it is blunter and has a small spine in the two other species. Additionally, *Z. regalis* differs from *Z. elizabethae*, n. sp., by having the abdominal pleura less pointed, a conspicuous fringe of long setae on the lower margin of the first abdominal pleura, and more slender fingers on the second chelae. Samples of *Z. elizabethae*, n. sp., collected from *Lissodendoryx colombiensis* in Panama have a remarkably high incidence of an abdominal parasitic isopod; every specimen appeared to be a partially feminized male, with the abdominal pleura broadly rounded, and an occasional hint of the anterior angle on the first one. The major chela in the Panamanian specimens is indistinguishable from that of *Z. elizabethae*, n. sp., but the final identity of these samples remains to be established.

TABLE 2. Morphological characters useful in distinguishing four species related to *Zuzalpheus rathbunae* Coutière.

	<i>Z. elizabethae</i>	<i>Z. filidigitus</i>	<i>Z. rathbunae</i>	<i>Z. regalis</i>
Major Pereopod 1 chela, anterodorsal palmar margin	inflated + spine	inflated + spine	flared, no spine	inflated + spine
Minor Pereopod 1 chela, dactyl	simple	accessory spine	simple	simple
Male 1 st pleura, posterior corner	long, hooked	short, hooked	long, acute	long, hooked
Male 2nd pleura	acute point	widely obtuse	acute point	thick point

***Zuzalpheus filidigitus* (Armstrong, 1949) n. comb.**

(Figs. 11–12, Plate 3)

Synalpheus filidigitus Armstrong 1949: 15, fig. 5; Duffy 1996c; Duffy and Macdonald 1999: 284; Ríos 2003: 79, figures 2–10 and 2–11, plate II.

Material examined. (1) **Holotype** ♂ (AMNH 9572), 2.4 mm, Barahona Harbor, Dominican Republic, 1932–1933. **Paratypes:** hundreds of specimens (AMNH 9573), same data as holotype.

(2) 5 ♂ (USNM 1019061, VIMS 01CBC0502), 2.3–2.4 mm, Curlew Ridge, Belize, 27 Apr 2001, from a colony of 88 ♂ and a single ovigerous ♀ (2.9 mm), in demosponge *Xestospongia* sp. growing among dead *Madracis* sp., 15 m.

(3) 1 ovigerous ♀ (VIMS 93CBC0302), 2.2 mm, 18 ♂ (VIMS 93CBC0303–93CBC0320), 1.4–2.4 mm, outer ridge at Carrie Bow Cay, Belize, 18 March 1993, in *Oceanapia* sp., 15 m.

(4) 1 ovigerous ♀ (VIMS 93CBC0702), 1.8 mm, 6 ♂ (VIMS 93CBC0703–93CBC0708), 1.4–1.6 mm, from a colony of 7 individuals, outer ridge at Carrie Bow Cay, Belize, 18 March 1993, in *Xestospongia* cf. *proxima*, 15 m.

(5) 11 ♂ (VIMS 94CBC2602–94CBC2612), 1.5–2.2 mm, from a colony of 13 individuals, outer ridge at Carrie Bow Cay, Belize, 23 August 1994, in *Xestospongia* cf. *subtriangularis*, 17 m.

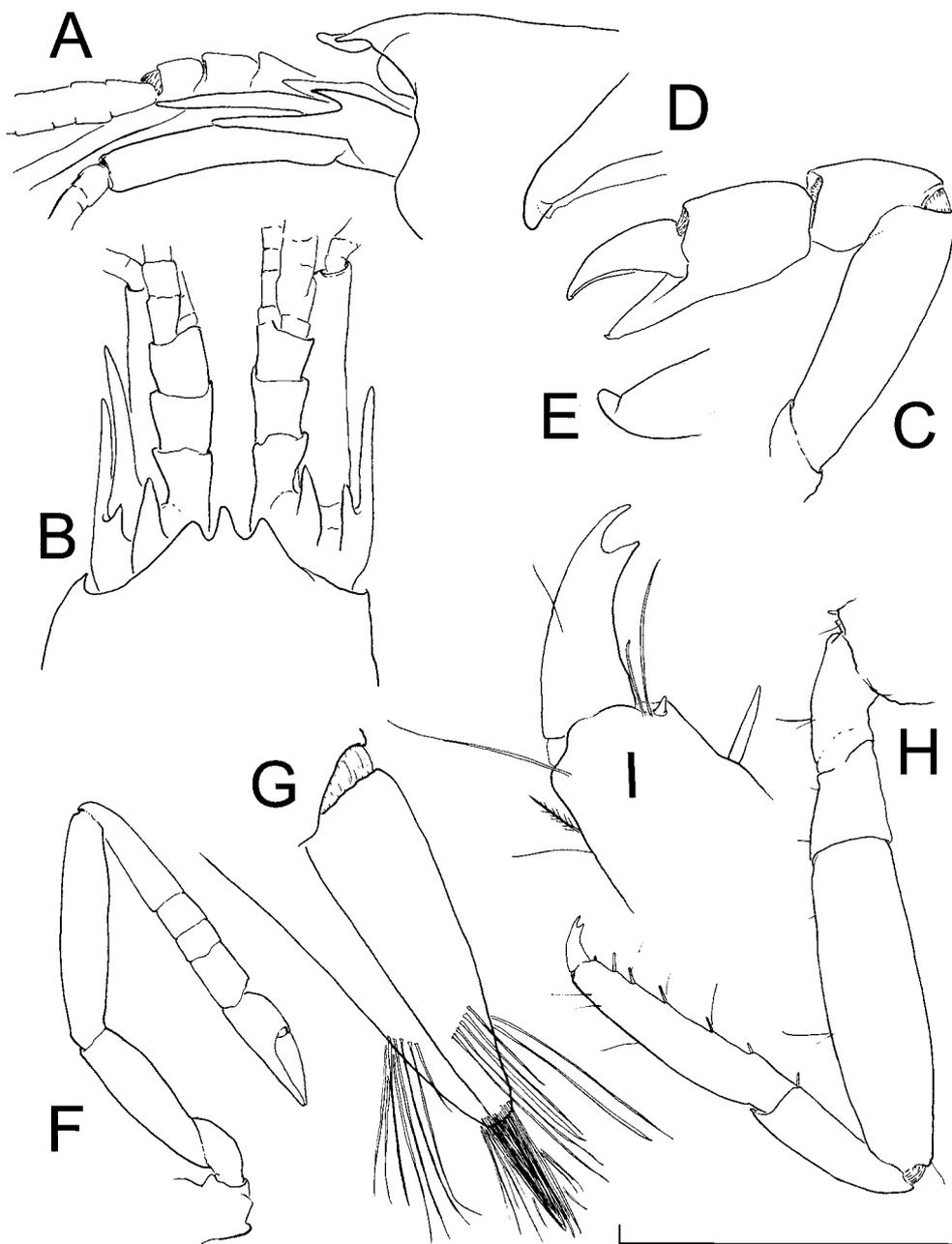


FIGURE 11. *Zuzalpheus filidigitus* (Armstrong 1949). Male holotype 2.4 mm (AMNH 9572): a, anterior region of carapace and cephalic appendages, lateral view (right scaphocerite missing); b, same, dorsal view. Male 2.3 mm (USNM 1019061): c, left minor first pereopod (setal combs on dactyl omitted), lateral view; d, same, tip of dactyl, ventrolateral view; e, same, tip of fixed finger, lateral view; f, left second pereopod, lateral view; g, same, tip of chela with some setae removed, lateral view; h, left third pereopod, lateral view; i, same, detail of distal portion, lateral view. Scale bar = 1.3 mm for a, b, c, f; 1.0 mm for h; and 0.25 mm for d, e, i, g.

Diagnosis. Body subcylindrical; carapace smooth, with pterygostomial corner obtusely angular, and posterior margin with cardiac notch distinct. Rostrum triangular, clearly narrower than and slightly surpassing

ocular hoods, distally upturned and with ventral margin convex. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, broadly triangular, separated from rostrum by deep adrostral sinus. Ocular processes absent. Ocellary beak in lateral view rod-like. Stylocerite slender; tip acute; reaching about as far as distal margin of 1st segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 very small basal ventral processes. *Basicerite* with sharp spine on dorsal margin not surpassing stylocerite, longer lateral spine reaching distal half of second segment of antennular peduncle. *Scaphocerite* blade absent, lateral spine robust, clearly overreaching antennular peduncle; mesial corner at base of scaphocerite obtuse. Carpocerite slightly surpassing scaphocerite. *Maxilliped 3* with distal cirlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment.

Major pereopod 1 massive, fingers clearly not longer than half length of palm; fixed finger reduced, slightly shorter than dactyl; in ventral view, outer face of fixed finger without distinct protuberance. Palm of chela with distal superior margin produced into prominent blunt tubercle, latter with short secondary spine on ventral surface. Merus with extensor margin strongly convex, ending in obtuse angle, sometimes with a hint of shallow angular projection.

Minor pereopod 1 with palm clearly less than 2 times longer than high; fingers about as long as palm; dactyl with flexor surface excavate, with subdistal bump and tooth near apex; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor surface obliquely concave, and no hint of subdistal tooth. Extensor margin of merus convex, ending in obtuse angle.

Pereopod 2 chela distally tapering, dactyl and fixed finger terminating in sets of anteriorly directed stiff simple setae, giving fingers a produced or filiform appearance; carpus 4-segmented, about as long as merus. *Pereopod 3* slender; dactyl biunguiculate, with proximal tooth thicker than distal one; merus without movable spines on flexor margin; mesial lamella on coxa present. *Pereopods 4 and 5* normal.

Pleura 1 of male with posteroventral corner produced into short broadly acute hook; posteroventral corner of male *pleura 2* produced into obtuse angle. *Pleopod 1* of male with 3 terminal setae on endopod; *pleopod 2* of male with marginal setae on exopod originating near midpoint; appendix interna on male *pleopods 2–5* present. *Telson* with space between posterior marginal spines about one-third width of posterior margin; marginal convex lobe absent; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush all absent. *Uropods* with 1–2 (occasionally 3) fixed teeth on outer margin of exopod anterior to movable spine.

Color (Plate 3). Translucent with pale to bright yellow ovaries and developing embryos; the digestive gland is a yellowish-salmon color.

Variations. The number of fixed teeth on the lateral margin of the uropodal exopod is almost always 2, with few smaller specimens having only one. Four specimens in the colony examined lack a rostrum, while the queen has an asymmetrical frontal border due to a broadened adrostral sinus on the right side. Two of the specimens (USNM 1019061) lack the protuberance overhanging the base of the dactyl on the major chela, just as Armstrong (1949) recorded in a few of his specimens. Among the hundreds of paratypes (AMNH 957), Armstrong (1949) separated 14 specimens and labeled them as “variations”; in this vial there is a detached small cheliped with a trifid dactyl, otherwise these shrimps seem to belong in *Z. filidigitus*. The female in the examined colony is a “large queen” (Duffy and Macdonald 1999), well differentiated from the rest of the members by having a larger body size, broad abdominal pleura, and two minor chelipeds on the first pereopods.

Ecology. At Carrie Bow Cay *Z. filidigitus* seems to be restricted to the sponges *Xestospongia* spp. and *Oceanapia* sp., with incidental records from *Hyattella intestinalis*, all growing among branches of coral, usually *Madracis mirabilis*. Like *Z. regalis* and *Z. chacei*, *Z. filidigitus* is a eusocial species forming colonies with one or rarely a few reproductive females and tens of males and juveniles (Duffy and Macdonald 1999).

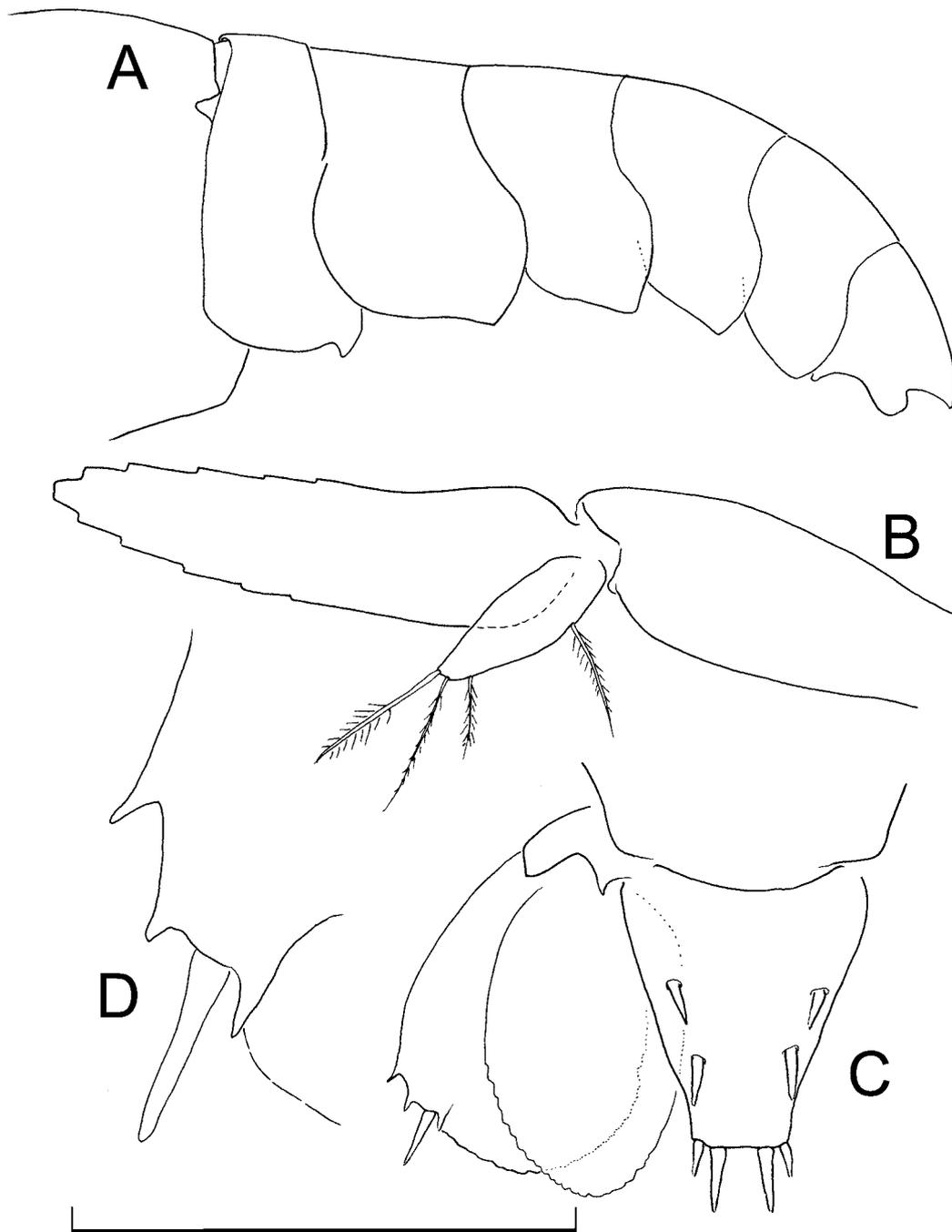


FIGURE 12. *Zuzalpheus filidigitus* (Armstrong 1949). Male 2.4 mm (USNM 1019061): a, abdomen, lateral view. Incomplete moult (VIMS 01CBC0502): b, first pleopod; c, telson and left uropod, dorsal view; d, distolateral corner of left uropod, dorsal view. Scale bar = 1.6 mm for a; 0.41 mm for b; 1.0 mm for c; and 0.31 mm for d.

Distribution. Western Atlantic: Dominican Republic (Armstrong 1949), Belize Barrier Reef (this study).

Remarks. *Zuzalpheus filidigitus* is one of a complex of four closely related species (Duffy 1996c) that bear a sharp spine on the dorsal margin of the basicerite, lack any trace of a blade on the scaphocerite, and have only four segments in the carpus of the second chelae. The four species in the “*Zuzalpheus rathbunae* complex” can be separated by a combination of consistent morphological characters (Table 2). When Armstrong (1949) erected *S. filidigitus*, he noted the similarity of this species to *Z. rathbunae* and listed five characters to distinguish them: length of spine on dorsal margin of basicerite, tubercle overhanging base of major chela dactyl, merus of minor chela, fingers of second chelae, and merus of third pereopod. The name that

Armstrong (1949) gave to the species comes from what he called "threadlike" fingers on the chela of the second pair of pereopods; as shown in his figure 5c. Dardeau (1984) concurred with Armstrong and described the fingers as filiform, without any further comments. Examination of several specimens from Belize under high magnification suggests that the threadlike appearance of the fingers is actually due to the presence of distal and subdistal brushes of stiff simple setae on both the dactyl and the fixed finger, which obscure the tips of the fingers and give them a filiform appearance. Additional observations are necessary to verify that those specimens without the filiform tips have not just lost them due to trauma.

***Zuzalpheus goodei* (Coutière, 1909) n. comb.**

(Plate 3)

Synalpheus goodei Coutière, 1909: 58–61, fig. 33; Dardeau 1984: 40–47, *pro pars*, fig. 18–21, *nec S. osburni* Schmitt 1933; Ríos 2003: 87–90, plate IV.

? *Synalpheus goodei*: Verrill, 1922: 116, Plates 37–40.

Material examined. (1) 2 ♂ (USNM 1019062, VIMS 95CBC2605), 4.5 and 5.8 mm, Twin Cays, Belize, 26 June 1995, in *Xestospongia wiedenmayeri* van Soest 1980, among mangrove roots, 1.5 m.

(2) 1 ovigerous ♀ (VIMS 01CBC3502), 4.7 mm, 1 ♂ (VIMS 01CBC3503), 4.1 mm, The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize, 30 April 2001, in *Pachypellina podatypa*, 2 m.

(3) 1 ovigerous ♀ (VIMS 93CBC1702), 4.6 mm, 1 ♂ (VIMS 93CBC1703), 5.1 mm, The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize, 19 March 1993, in *Pachypellina podatypa*, 2 m.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. Rostrum lanceolate, narrower and longer than ocular hoods, with convex inferior margin prolonged posteriorly beyond anteriormost edge of carapace, and distally upturned. Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process broad. Ocellary beak in lateral view, thick. Stylocerite stout; mesial margin slightly concave; tip acute; reaching distal fifth of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with acute dorsal margin, and with longer ventrolateral spine reaching distal margin of second segment of antennular peduncle. Scaphocerite blade reduced, robust sharp lateral spine with lateral margin slightly concave, clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present. Carpocerite overreaching scaphocerite. Third maxilliped with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment.

Major pereopod 1 massive, fingers slightly longer than half length of palm; fixed finger slightly shorter than dactyl; in ventral view, outer face of fixed finger without any protuberance. Palm of chela with distal superior margin produced into prominent tubercle and distal acute spine. Merus, extensor margin strongly convex, with distal flat angular projection.

Minor pereopod 1 with palm less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor surface distally excavate, terminating in two strong distal teeth, subequal in length, and an accessory protuberance, all situated perpendicularly to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor surface obliquely concave, and two subdistal accessory protuberances. Extensor margin of merus distally convex, ending in obtuse angle.

Pereopod 2 with carpus 5-segmented, about as long as merus.

Pereopod 3 stout; dactyl biunguiculate, with flexor tooth thicker than extensor; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pleura 1 of male with posterior corner produced ventrally into shallow triangular hook; second pleura of male with posterior corner obtusely prolonged. *Pleopod 1* of male, with about 8 terminal setae on endopod;

second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines about one-third of distal margin; marginal convex lobe inconspicuous; posterior corners adjacent to spines rectangular. Anal flaps, perianal setae, and postanal setal brush present. *Uropods* with 5 to 12, usually 7 or 8, fixed teeth on outer margin of exopod.

Color (Plate 3). Translucent milky white with sparse pink chromatophores; distal portions of chelae with marginal highlights of greenish gold; tip of major chela, orange to brown; ripe ovaries, light gray to brown; digestive gland, olive green. This account does not match what Verrill (1922) recorded in great detail studying specimens from Bermuda. Because the identity of the material from Belize is supported by the examination of the syntypes (also from Bermuda), the specimens analyzed by Verrill may belong in a different species.

Variations. The dorsolateral corner on the basicerite ends usually in a sharp acute angle, but occasionally it is reduced to a right angle. The blade of the scaphocerite is always narrow and shorter than the adjacent spine, but it can reach the distal margin of any one of the three segments of the antennular peduncle or just half the length of the stylocerite. In some specimens the blade is reduced to a convex emargination, but even in such cases the presence of marginal setae remains constant. There seems to be a growth-related pattern to the degree of the development of the hook on the posterior corner on the first abdominal pleura; in some smaller males there is only a triangular ventrally directed flap. Also, the number of fixed teeth on the lateral margin of uropodal exopods is reduced in smaller specimens.

Hosts and ecology. We have found *Z. goodei* in *Xestospongia wiedenmayeri* growing on mangrove roots, and in *Pachypellina podatypa* (de Laubenfels 1934) in shallow reef environments. It forms heterosexual pairs or groups of several individuals with roughly equal sex ratios.

Distribution. Western Atlantic: Bermudas, Tampa Bay, Florida, USA (Coutière 1909); Gulf of Mexico (Coutière 1909; Dardeau 1984); Cuba (Martínez Iglesias and García Raso 1999); Dominica, Tobago (Chace 1972); Belize Barrier Reef (this study).

Remarks. *Zuzalpheus goodei* is superficially similar to *Z. williamsi*, but they can be easily separated by the differences mentioned under the account for *Z. williamsi*. Dardeau (1984) synonymized *Synalpheus osburni* Schmitt, 1933 with this species. However, examination of the holotype (AMNH 3599) from Puerto Rico suggests that it should be considered a valid species within *Zuzalpheus*. Still the only known specimen, the holotype of *Z. osburni* (Schmitt, 1933) has a remarkable feature, *i.e.*, a spine on the distal border of the palm of the minor chela. Other differences with *Z. goodei* include the strikingly elongated rostrum, the total absence of a blade on the scaphocerite or any traces of setae on the mesial margin of the lateral spine, the protuberance overhanging the spine on the distal margin of the palm of the major chela, and the shape of the dactyl of the smaller chela. Discovery of additional specimens of *Z. osburni*, including males, will likely provide more characters to distinguish these two species.

***Zuzalpheus herricki* (Coutière, 1909) n. comb.**

(Plate 3)

Synalpheus herricki Coutière, 1909: 74–78, fig. 44; Dardeau 1984: 55–64, figs. 27–30 (and synonymy, maybe excluding *Synalpheus tanneri* Coutière, 1909).

Material examined. (1) 2 ovigerous ♀ (VIMS 05CBC3704) 4.0–5.7 mm, outer ridge of Curlew Reef, Belize (16°44'54.1"N, 88°04'21.7"W), 15 July 2005, in *Hymeniacidon amphilecta*, 15 m.

(2) 1 ovigerous ♀ (VIMS 93CBC3801), 4.1 mm, 2 ♂ (VIMS 93CBC3803, 93CBC3804), 3.4 and 4.1 mm, fore-reef at Carrie Bow Cay, Belize, 23 March 1993, in *Hymeniacidon amphilecta*, 5–7 m.

(3) 1 ovigerous ♀ (VIMS 93CBC5820), 4.3 mm, 1 ♂ (VIMS 93CBC5803), 5.3 mm, outer ridge at Carrie Bow Cay, Belize, 27 March 1993, in *Hymeniacidon amphilecta*, 13 m.

(4) 1 ovigerous ♀ (VIMS 99CBC3307), 1 ♂ (VIMS 99CBC3308), outer ridge of Carrie Bow Cay, Belize,

6 December 1999, in *Hyattella intestinalis*, 17 m.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomial corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. *Rostrum* wider than ocular hoods, about as long as ocular hoods, and distally upturned; margins in dorsal view, convex. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly triangular, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes produced into a fingerlike structure. Ocellary beak in lateral view not rodlike. Stylocerite slender; mesial margin convex; tip acute; distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without mesio-ventral tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorso-lateral corner, and with longer ventrolateral spine clearly overreaching tip of stylocerite. *Scaphocerite* with blade absent, and with robust, acute lateral spine with lateral margin slightly concave, not overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal cirlet of spines on distal segment, and without ventro-distal spine on antepenultimate segment

Major pereopod 1 massive, fingers clearly less than half length of palm; fixed finger about as long as dactyl; in ventral view, outer face of fixed finger without lateral protuberance. Palm of chela with distal superior margin produced into tapering acute spine. Merus, extensor margin strongly convex, with distal angular projection.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with two distinct distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, and 2 distinct teeth subequal in length. Extensor margin of merus convex, ending in obtuse angle.

Pereopod 2 carpus with five segments; and distinctly longer than merus.

Pereopod 3 slender; dactyl biunguiculate, with subequal teeth; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pleura 1 of male with posterior corner acutely produced ventrally; second pleura of male rounded to obtuse. *Pleopod 1* of male, with many terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. Telson, space between distal spines equal or less than one third of distal margin; marginal convex lobe present; posterior corners adjacent to spines rectangular. Anal flaps, perianal setae, and postanal setal brush all absent. *Uropods* with a single fixed tooth on outer margin of exopod.

Color (Plate 3). Body translucent whitish with brown-tinged distal palm and fingers of major chela. Ovaries and eggs pale green to drab olive.

Hosts and ecology. In Belize we have collected only a few specimens of *Zuzalpheus herricki*, which came from the sponges *Hymeniacidon amphilecta* and *Hyattella intestinalis*, on the outer reef ridge at Carrie Bow Cay from depths of 15–20 m.

Distribution. Western Atlantic: Anclote, Florida, USA (Coutière 1909); possibly from Eleuthera, Bahamas (Chace 1972); Gulf of Mexico (Coutière 1909; Dardeau 1984); Belize Barrier Reef (this study).

Remarks. *Zuzalpheus herricki* can be distinguished from all other West Atlantic *Zuzalpheus* by the unique concavities along the ventral margins of male abdominal pleura 3 and 4, giving the ventral margins of these pleura a W-shaped appearance. Another character useful in diagnosing *Z. herricki* is the dactyl of the major chela, which in Belizean specimens terminates in a distinct, ventrally directed tooth, separated from the rest of the dactyl by a constriction or indentation on the flexor margin of the dactyl. This feature is also visible in Dardeau's (1984) figures 27 and 28 of the lectotype from Anclote, Florida. Dardeau (1984) redescribed this species, designating a lectotype, and summarized its long and confused taxonomic history. As he noted, the lateral branch of the uropod in *Z. herricki* typically has a single fixed tooth lateral to the movable spine, although multiple teeth occur in some specimens. In our key to *Zuzalpheus*, we have thus followed Dardeau

(1984) in including this species in the group characterized by a single fixed tooth lateral to the movable spine.

***Zuzalpheus idios*, n. sp.**

(Figs. 13–17, Plate 3)

Synalpheus sp.3, new species Ríos 2003:91, figures 2–12 through 2–16, plate II.

Synalpheus “brooksi D”: Morrison *et al.* 2004; Macdonald *et al.* 2006

Material examined. (1) **Holotype** ♂ (USNM 1019047, VIMS 01CBC8007), 5.0 mm, **allotype** ovigerous ♀ (USNM 1019048, VIMS 01CBC8006), 5.1 mm; **paratypes**: 2 ♂ (USNM 1019049, VIMS 01CBC8007), 4.3 and 4.7 mm, Carrie Bow Cay, Belize, 4 May 2001, in demosponge *Hymeniacidon amphilecta*, 6m.

(2) 3 ovigerous ♀ (VIMS 90CBC0205, 90CBC0208, 90CBC0213) 3.3–4.4 mm, 6 ♂ (VIMS 90CBC0209–90CBC0215), 3.4–4.3 mm, outer ridge at Carrie Bow Cay, Belize, 6 December 1990, in *Hymeniacidon amphilecta*, 17 m.

(3) 1 ovigerous ♀ (VIMS 93CBC7601), 4.7 mm, 2 ♂ (VIMS 93CBC7603, 93CBC7604), 4.4 and 3.2 mm, spur and groove reef at Carrie Bow Cay, Belize, 5 April 1993, in *Hymeniacidon amphilecta*, 9 m.

(4) 1 ovigerous ♀ (VIMS 93P5011), 4.4 mm, 3 ♂ (VIMS 93P5012–93P5014), 4.0–4.6 mm, from a larger colony, Cayos Limones, San Blas Islands, Panama, 4 October 1993, in *Lissodendoryx colombiensis*, 12 m.

Description of holotype. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomial corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. *Rostrum* about as long as ocular hoods, but distinctly narrower, distally upturned; margins in dorsal view straight. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process triangular, flanged posteriorly onto lower side of eye. Ocellary beak in lateral view not rod-like, broader at base. *Stylocerite* acute, but tip blunt; mesial margin slightly concave; surpassing midpoint of first segment; latter without ventromesial tooth, and with two basal ventral processes. *Basicerite* without spine on dorsolateral corner, and with longer ventrolateral spine reaching distal half of second segment of antennular peduncle. *Scaphocerite* blade absent, acute lateral spine robust, with lateral margin slightly concave, slightly surpassing basicerite spine, not overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circlet of spines on distal segment and without ventrodorsal spine on antepenultimate segment. Remaining mouthparts as figured.

Major pereopod 1 massive, fingers clearly shorter than half length of palm; fixed finger slightly shorter than dactyl; in ventral view, outer face of fixed finger without any marked lateral protuberance. Palm of chela with distal superior margin produced into tapering conical blunt tubercle not conspicuously directed upward; in frontal view, tubercle does not show ventral surface and does not rise above palmar profile. Merus, extensor margin strongly convex, ending in obtuse angle.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with 2 distinct distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, and 2 distinct teeth subequal in length. Extensor margin of merus convex, ending in right angle.

Pereopod 2 with carpus 5-segmented, subequal to merus.

Pereopod 3 slender; dactyl biunguiculate, with flexor tooth clearly thicker than extensor; propodus with row of 7 mobile spines on flexor margin and one pair of distal mobile spines flanking base of dactylus; carpus with distal mobile spine on flexor margin; merus almost 4 times longer than wide, without movable spines on flexor margin; mesial lamella on coxa present. *Pereopod 4* similar to third, slightly weaker. *Pereopod 5* weaker than fourth; propodus with only 2 spines on flexor margin, and 5 transverse combs of stout setae on ventral face; carpus without distal spine.

Pleura 1 of male with posterior corner distinctly produced ventrally and anteriorly into small hook; sec-

ond pleura of male broadly rounded; third to fifth pleura of male progressively acute, but not pointed. *Pleopod 1* of male, with 6 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. *Telson* with central space between distal spines about one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with a single fixed tooth on outer margin of exopod distinctly removed from the mobile one, this latter slightly longer and more slender than adjacent inner fixed tooth.

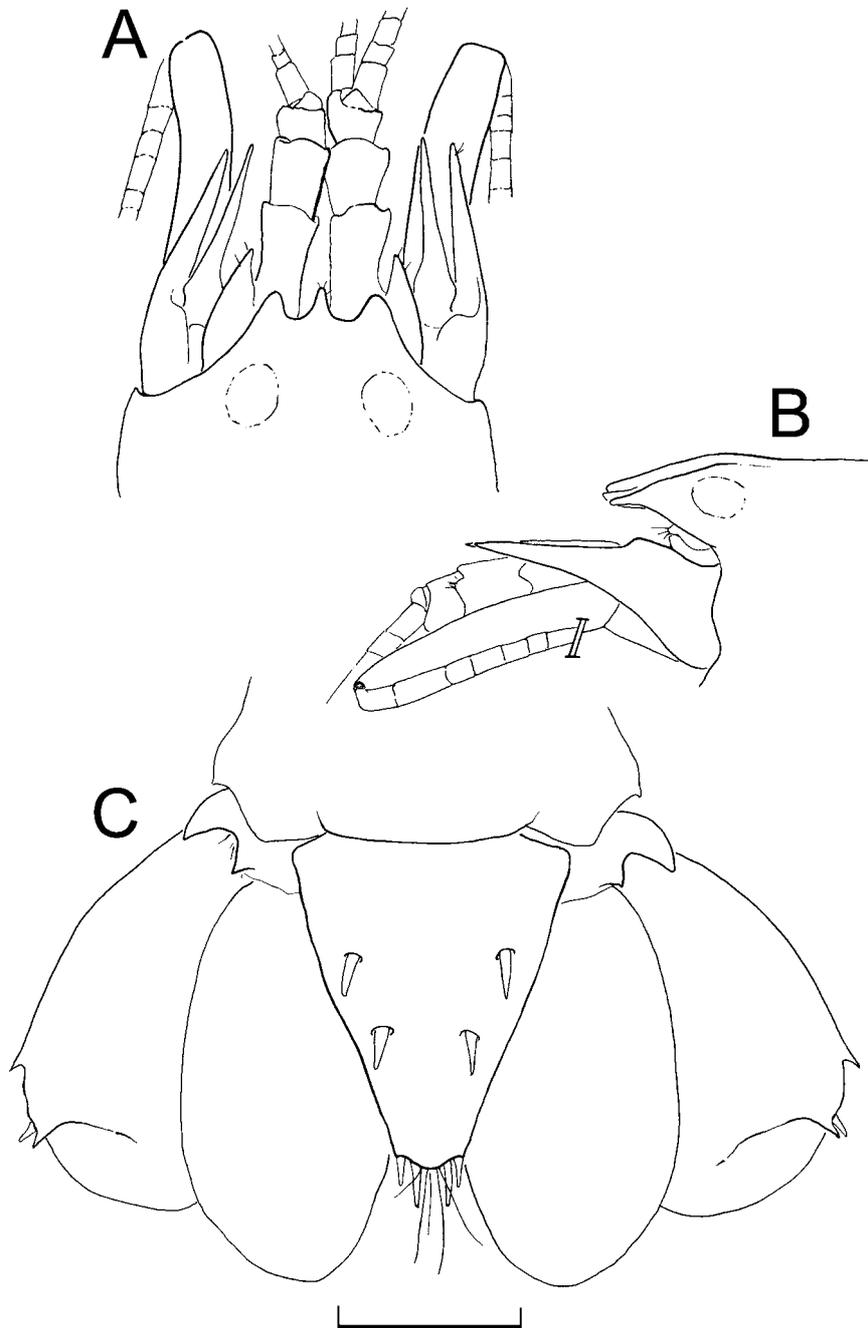


FIGURE 13. *Zuzalpheus idios*, n. sp. Allotype ovigerous female 5.1 mm (USNM 1019048): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, telson and uropods, dorsal view. Scale bar = 1 mm for a, b; and 0.76 mm for c.

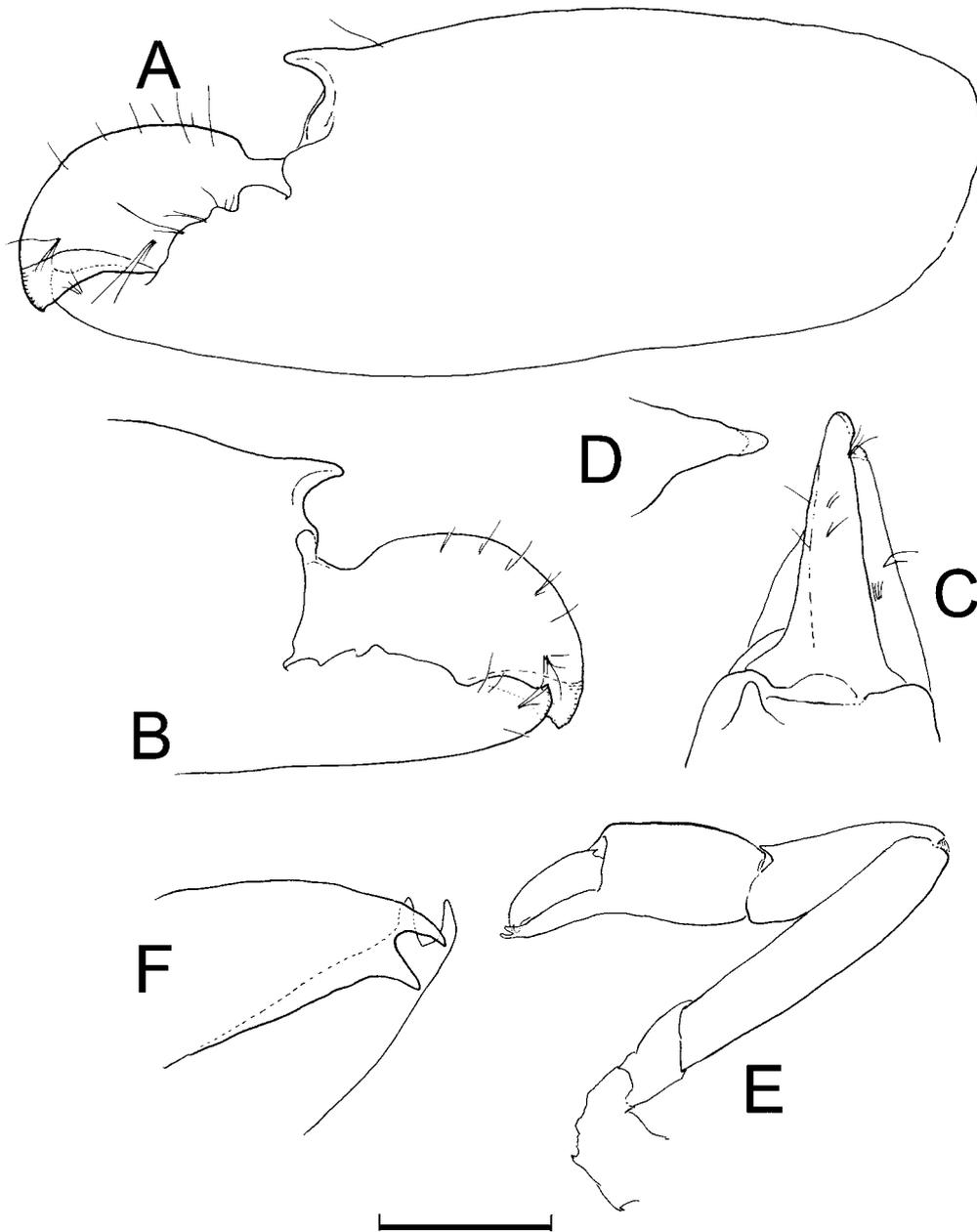


FIGURE 14. *Zuzalpheus idios*, n. sp. Allotype ovigerous female 5.1 mm (USNM 1019048): a, chela of major first pereopod in lateral view; b, same, anterior region alternate lateral view; c, same, dorsal view; d, same, tip of fixed finger, ventral view. Paratype male 4.7 mm (USNM 1019049): e, minor first pereopod, lateral view; f, distal portion of same, alternate lateral view. Scale bar = 1 mm for a, b, c, d; 1.2 mm for e; and , 0.24 mm for f.

Color (Plate 3). Specimens from *Hymeniacidon amphilecta* have a milky translucent appearance with regularly scattered red chromatophores on the carapace and major chela; cutting edges on fingers of major chela amber, distal palm and fingers of major chela orange. Developing eggs and ovaries deep scarlet to brick-red to brownish-orange. Specimens from *Lissodendoryx colombiensis* in Panama were mostly transparent with scattered contracted chromatophores, and had a light purple hue most apparent in smaller specimens, also with dark red ovaries and eggs.

Etymology. From the Greek, meaning “one’s own” or “pertaining to oneself”. The name signifies the distinctiveness of this species despite its strong resemblance to *Z. brooksi*.

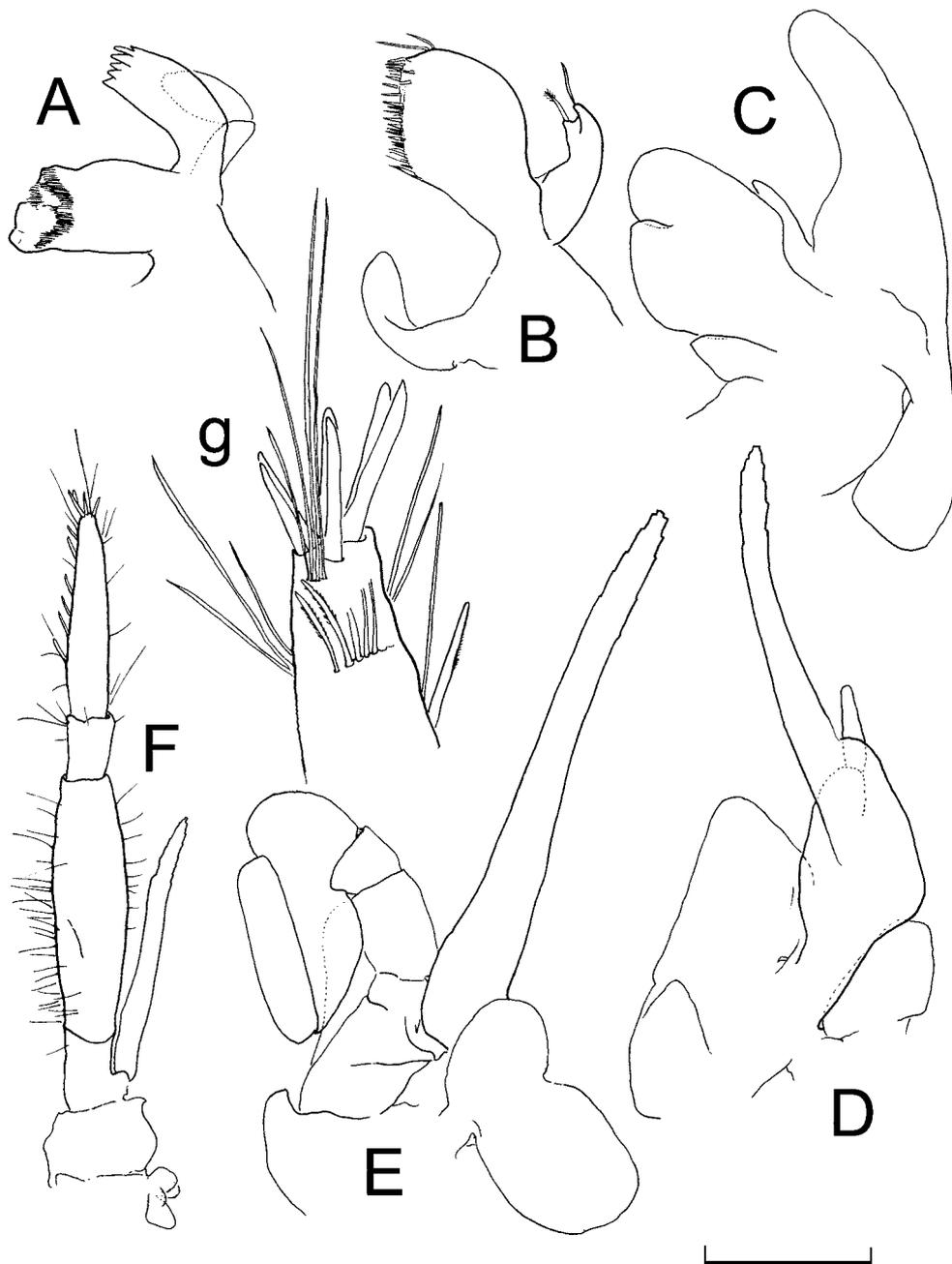


FIGURE 15. *Zuzalpheus idios*, n. sp. Mouthparts. Paratype male 4.7 mm (USNM 1019049): a, mandible; b, first maxilla; c, second maxilla; d, first maxilliped; e, second maxilliped; f, third maxilliped; g, same, detail of tip. Scale bar = 0.5 mm for a, b, c, d, e; 1 mm for f; and 0.2 mm for g.

Variation. In some males, the abdominal pleura posterior to the second one form an acute angle ventrally, without prolonging into an acuminate projection. Some juveniles have 4 segments in the carpus of the second pereopod, while occasional larger specimens have six. Arrangement of teeth on the uropodal exopod is constant, except in small juveniles where the external tooth has the appearance of being not fully developed.

Hosts and ecology. *Zuzalpheus idios*, n. sp., lives in groups of up to several tens of specimens with numerous ovigerous females and juveniles present. It inhabits canals of the demosponges *Hymeniacidon amphilecta* in Belize and *Lissodendoryx colombiensis* in Panama.

Distribution. Belize Barrier Reef (this study), San Blas Islands, Panama (J.E. Duffy unpublished), possibly Florida Keys, USA (J.E. Duffy unpublished).

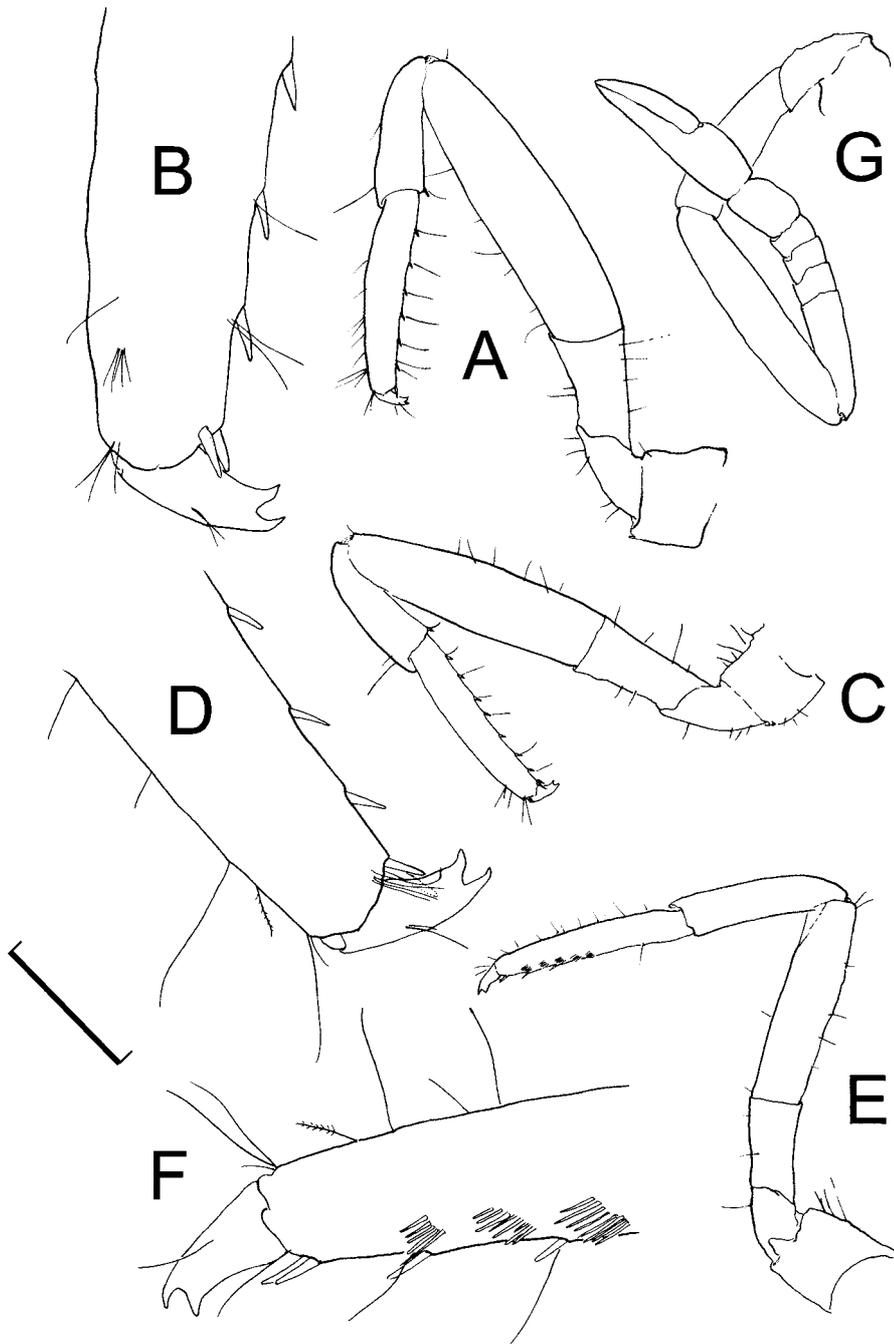


FIGURE 16. *Zuzalpheus idios*, n. sp. Paratype male 4.7 mm (USNM 1019049): a, third pereopod; b, same, detail of distal portion; c, fourth pereopod; d, same, detail of distal portion; e, fifth pereopod; f, detail of distal portion; g, second pereopod. Scale bar = 1 mm for a, c, e, g; and 0.2 mm for b, d, f.

Remarks. The differences in host association between this species and *Z. brooksi* (Coutière) are supported by a subtle suite of morphological characters. In *Z. idios*, the conical projection overhanging the base of the dactyl in the major chela is slightly blunter and oriented more directly anteriorly, as opposed to upwardly in *Z. brooksi*. Also, *Zuzalpheus idios*, n. sp., grows to slightly larger sizes than *Z. brooksi*. Its color in life is quite distinct from that of *Z. brooksi*.

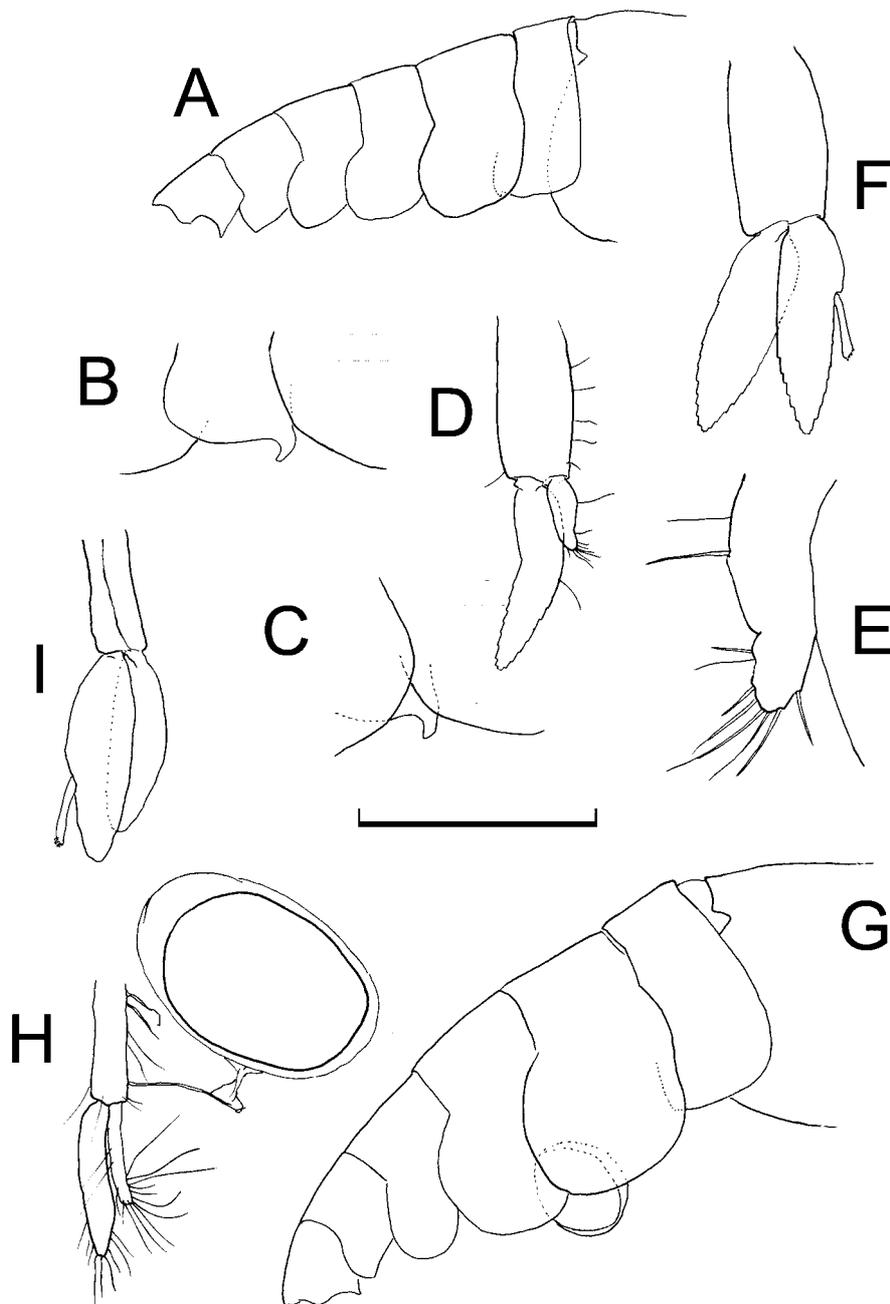


FIGURE 17. *Zuzalpheus idios*, n. sp. Holotype male 5.0 mm (USNM 1019047): a, abdomen, lateral view. Paratype male 4.3 mm (USNM 1019049): b, detail of first abdominal pleura, lateral view. Paratype male 4.7 mm (VIMS 01CBC8007): c, detail of first abdominal pleura, lateral view; d, first pleopod, lateral view; e, same, detail of Appendix interna; f, second pleopod, lateral view. Allotype ovigerous female 5.1 mm (USNM 1019048): g, abdomen, lateral view; h, first pleopod, lateral view; i, second pleopod, lateral view. Scale bar = 1 mm for d, f; 1.3 mm for b, c; 1.5 mm for h, i; 3 mm for a, g; and 0.3 mm for e.

***Zuzalpheus kensleyi*, n. sp.**

(Figs. 18–22, Plate 3)

Synalpheus sp. 4, new species Ríos 2003:104, figures 2–17 through 2–21, plate III.

Synalpheus “intermediate”: Morrison *et al.* 2004. Macdonald *et al.* 2006

Material examined. (1) **Holotype** ♂ (USNM 1019050, VIMS 93CBC1503), 6.0 mm, **allotype** ovigerous ♀ (USNM 1019051, VIMS 93CBC1502), 6.1 mm, The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize, 19 March 1993, in cryptic yellow tube sponge growing among dead coral rubble, 2 m.

(2) **Paratype** ovigerous ♀ (USNM 1019052, VIMS 93CBC6303), 5.0 mm, The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize 31 March 1993, in cryptic yellow tube sponge growing among dead coral rubble, 2 m.

(3) 1 ovigerous ♀ (VIMS 01CBC3802), 4.1 mm, 1 ♂ (VIMS 01CBC3803), 4.0 mm, The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize, 30 April 2001, in cryptic yellow tube sponge growing among dead coral rubble, 2 m.

(4) 1 ♂ (VIMS 02CBC0201), 3.2 mm, The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize 20 June 2002, no host found, 2 m.

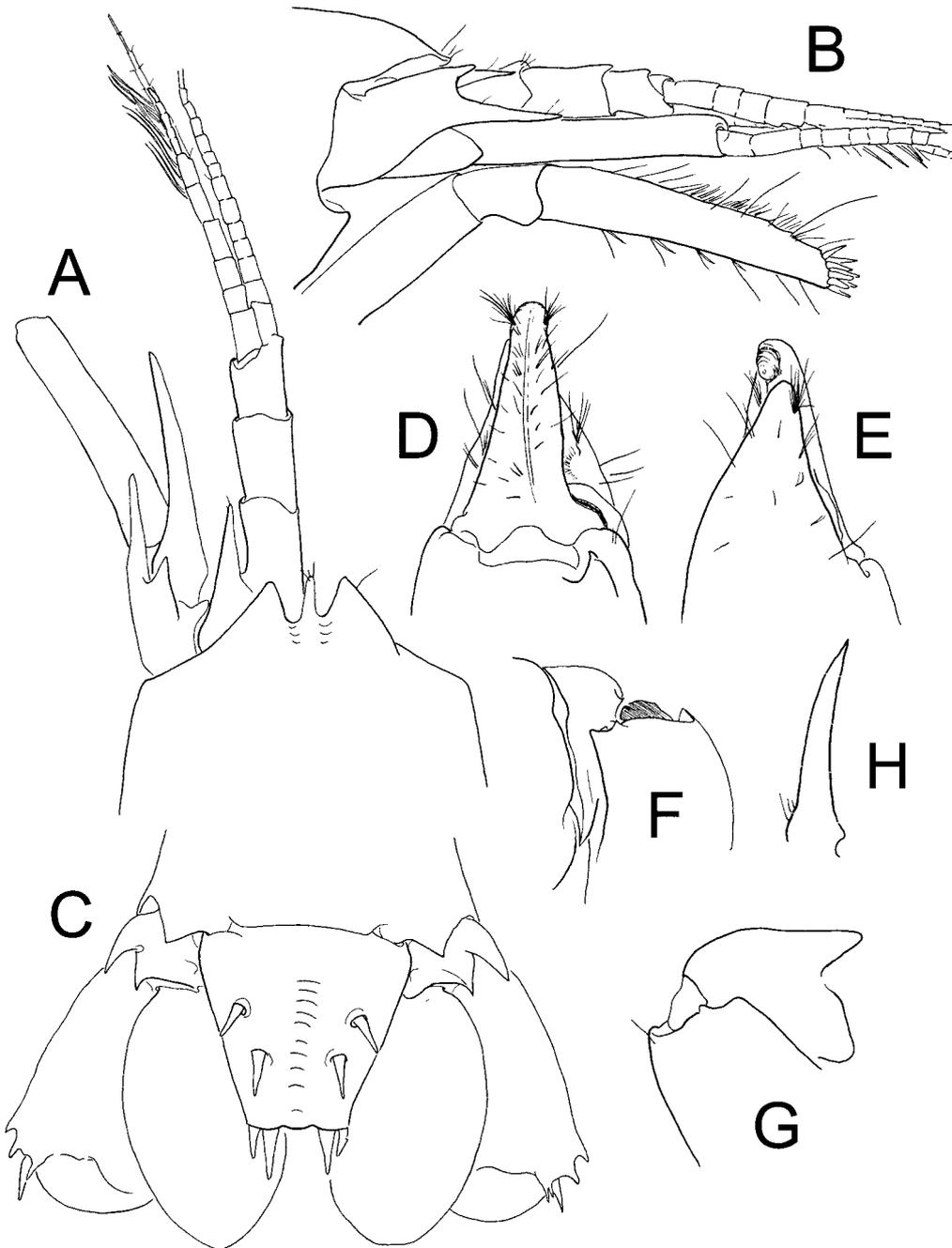


FIGURE 18. *Zuzalpheus kensleyi*, n. sp. Holotype male 6.0 mm (USNM 1019050): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, telson and uropods, dorsal view; d, dactyl of major first pereopod, dorsal view; e, fixed finger of major first pereopod, ventral view; f, distal part of merus of major first pereopod, lateral view; g, distal part of merus of minor first pereopod, lateral view. Allotype ovigerous female 6.1 mm (USNM 1019051): h, right scaphocerite, dorsal view. Scale bar = 1.5 mm for a, b, c, g, h; and 2 mm for d, e, f.

(5) 1 ♂ (VIMS 04CBC3201), The Pinnacles (Sand Bores), SW of Carrie Bow Cay, Belize 14 March 2004, in *Hyattella intestinalis*, 2 m.

(6) 1 ovigerous ♀ (VIMS 03P2001), 1 ♂ (VIMS 03P2002), Isla San Cristobal, Bocas del Toro region, Panama 5 August 2003, in *Hymeniacion caerulea*, 1 m.

Description of holotype. Body subcylindrical. Carapace smooth, with sparse short simple setae. *Rostrum* distinctly narrower and slightly longer than ocular hoods; without reaching distal margin of first segment of antennular peduncle; distally upturned; orbitorostral process absent. Pterygostomian corner produced into bluntly acute angle. Posterior margin with distinct cardiac notch. First segment of antennular peduncle without ventromesial tooth. Antenna with 2 basal ventral processes. *Basicerite* dorsal margin with acute spine, lateral spine barely reaching middle of scaphocerite; latter not reaching distal margin of carapocerite, without blade, with mesial projection at base. *Maxilliped 3* without ventrodistal spine on antepenultimate segment; remaining mouthparts as figured.

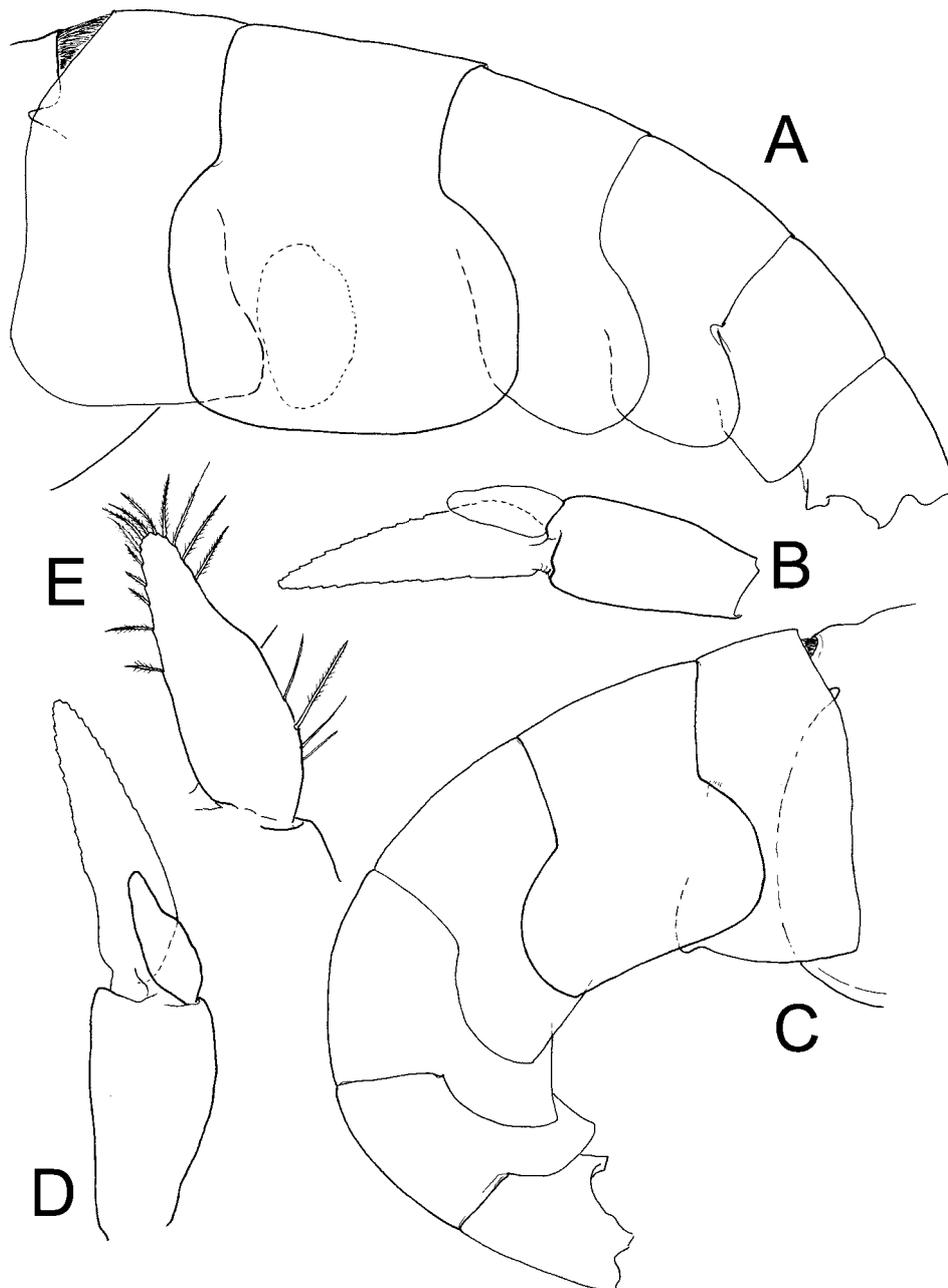


FIGURE 19. *Zuzalpheus kensleyi*, n. sp. Allotype ovigerous female 6.1 mm (USNM 1019051): a, abdomen with one egg, lateral view. Paratype female 5.0 mm (USNM 1019052): b, right first pleopod. Holotype male 6.0 mm (USNM 1019050): c, abdomen, lateral view; d, right first pleopod; e, same, detail of endopod. Scale bar = 2 mm for a, c; 1 mm for b, d; and 0.44 mm for e.

Major pereopod 1 massive, dactyl slightly overreaching fixed finger; distal superior margin of palm produced into prominent tubercle with descending spine on tip; extensor margin of merus with flat angular projection.

Minor pereopod 1 palm longer than fingers; dactyl with flexor surface excavate, with three teeth, subequal in length, perpendicular to dactyl axis; 12 transverse setal combs on extensor surface; fixed finger with flexor surface obliquely concave, distal tooth and subdistal accessory bump; extensor margin of merus with angular projection.

Pereopod 2 more slender than the others, with carpus 5-segmented, longer than merus.

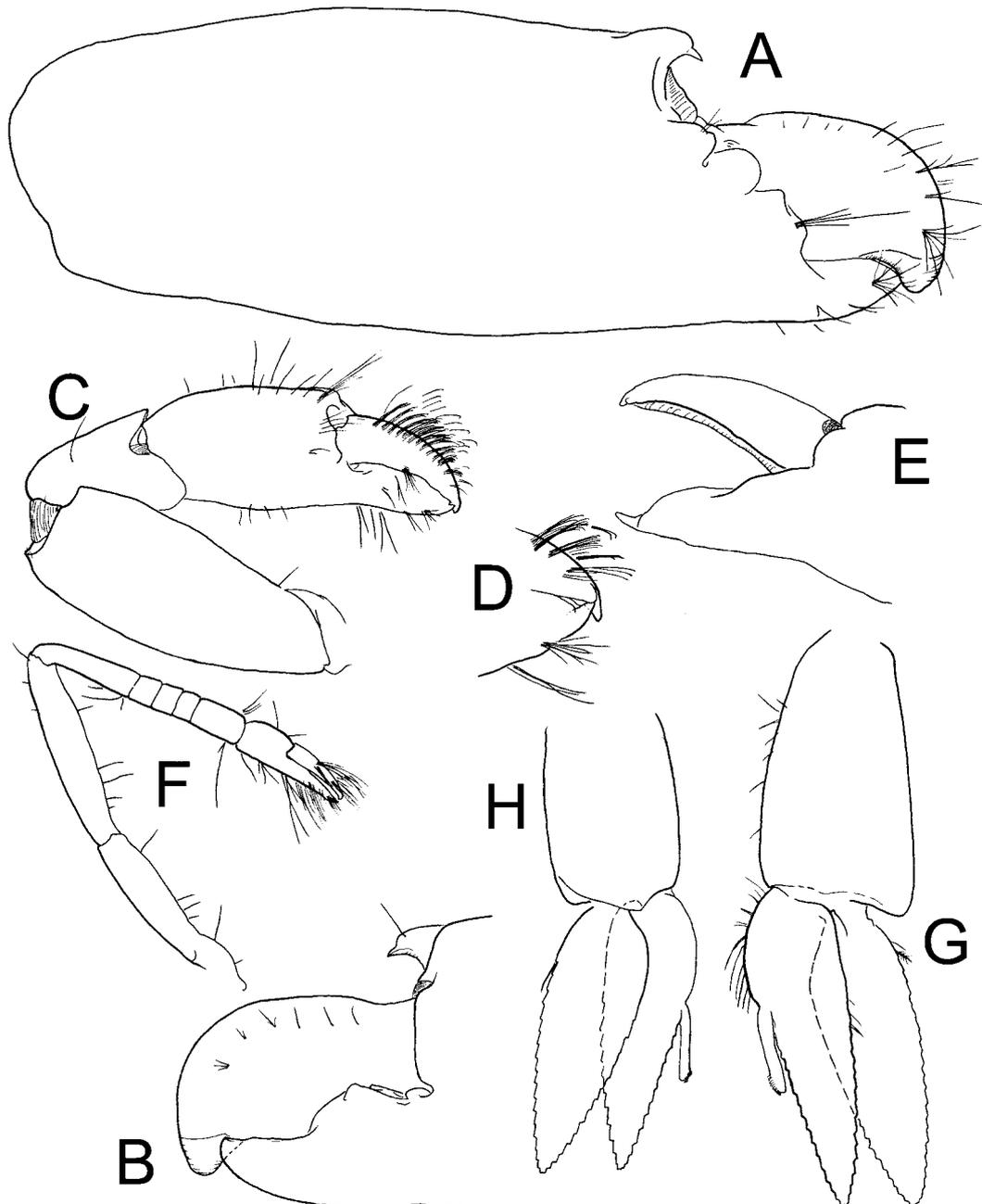


FIGURE 20. *Zuzalpheus kensleyi*, n. sp. Holotype male 6.0 mm (USNM 1019050): a, major first pereopod in lateral view; b, same, anterior portion of external face, lateral view; c, minor first pereopod lateral view; d, same, tip of fingers, lateral view; g, right second pleopod. Paratype female 5.0 mm (USNM 1019052): e, distal portion of minor first pereopod, lateroventral view; f, second pereopod, lateral view; h, right second pleopod. Scale bar = 2 mm for a, b, c, f; and 1 mm for d, e, g, h.

Pereopod 3 dactyl biunguiculate, with proximal tooth clearly stouter than distal one; propodus with 8 mobile marginal spines evenly distributed and paired mobile spines flanking base of dactyl; carpus with single distoventral mobile spine; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pereopod 4 very similar to 3rd, but slightly weaker. *Pereopod 5* weaker than 4th, propodus with marginal spines irregularly arranged, and with 6 combs of setae transversely arranged on distal half.

Pleura 1 of male weakly produced on posterior corner; pleura 2–5 of male obtuse; first pleopod endopod with many terminal setae; origin of marginal setae on pleopod 2 exopod close to base. All pleura of female broadly rounded; appendix interna present on endopod of second to fifth pleopods in both sexes. *Telson* stout, subtrapezoidal, middle space between posterior marginal spines greater than one-third width of posterior margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. *Uropods* with 2 fixed teeth on outer margin of exopod anterior to mobile spine, latter clearly longer than adjacent mesial fixed tooth.

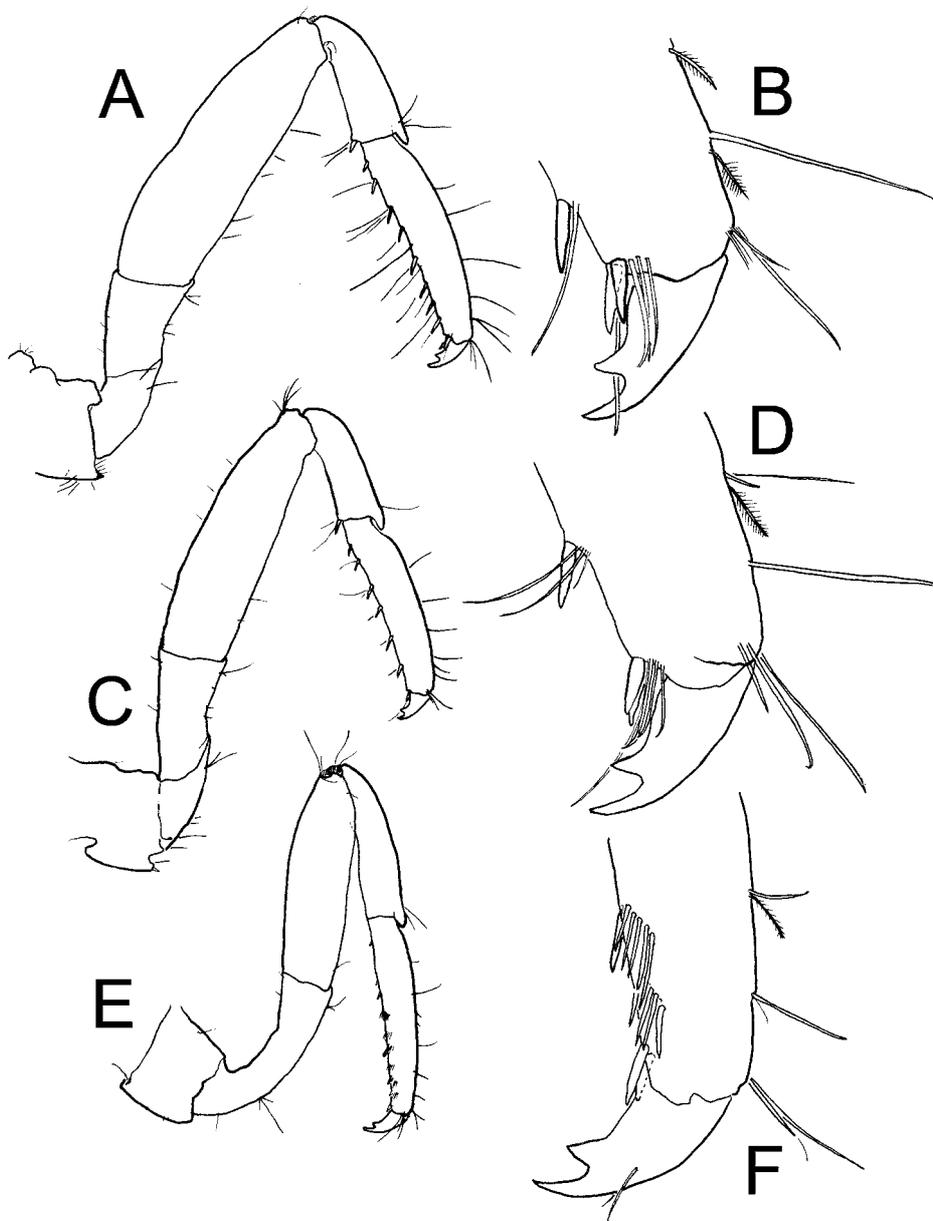


FIGURE 21. *Zuzalpheus kensleyi*, n. sp. Paratype female 5.0 mm (USNM 1019052): a, third pereopod, lateral view; b, same, detail of distal portion; c, fourth pereopod, lateral view; d, same, detail of distal portion; e, fifth pereopod, lateral view; f, same, detail of distal portion. Scale bar = 2 mm for a, c, e, and 0.39 mm for b, d, f.

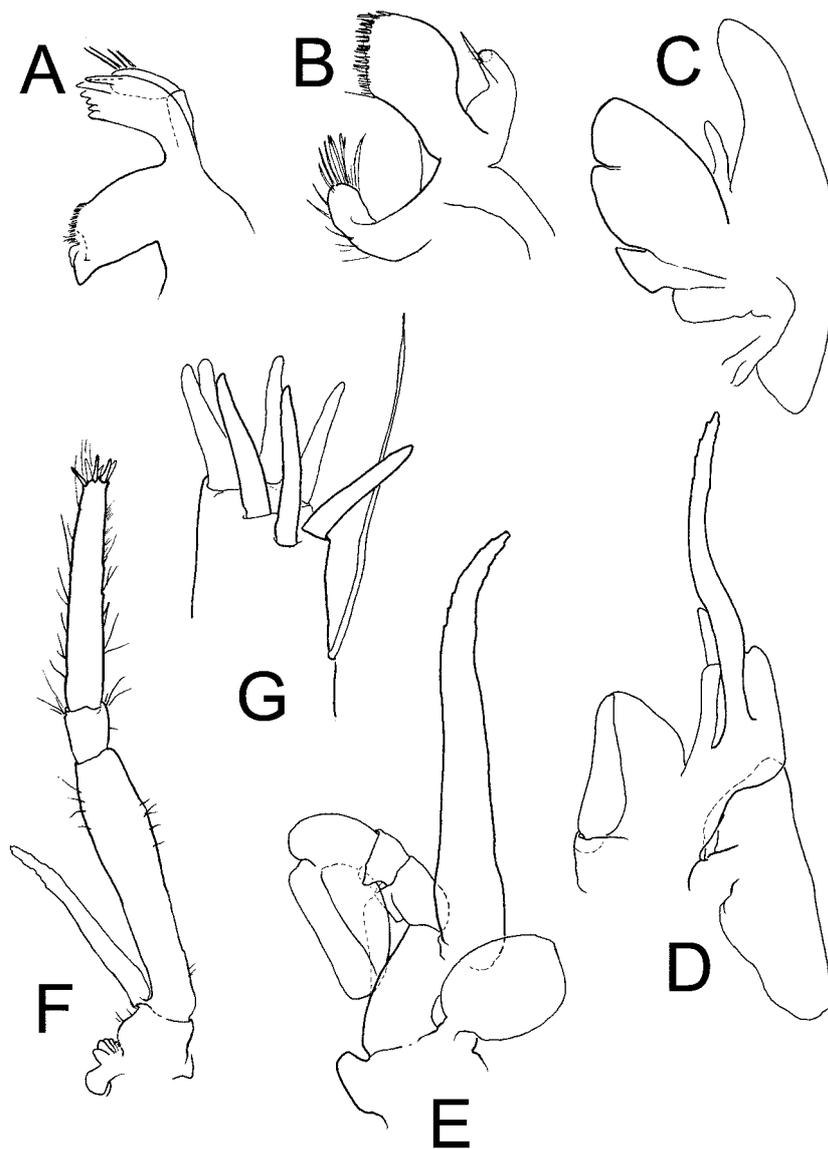


FIGURE 22. *Zuzalpheus kensleyi*, n. sp. Mouthparts. Paratype female 5.0 mm (USNM 1019052): a, left mandible; b, left first maxilla; c, left second maxilla; d, left first maxilliped; e, left second maxilliped; f, right third maxilliped; g, same, detail of tip. Scale bar = 1 mm for a, b, c, d, e, 2 mm for f, and 0.4 mm for g.

Color (Plate 3). Translucent to dull gold with few sparse chromatophores, distal portion of major chela brown. Ovaries and developing embryos pale green.

Etymology. We are honored to name this species after the late Dr. Brian Kensley, National Museum of Natural History, Smithsonian Institution, in appreciation of his many contributions to crustacean taxonomy and his support for our research at Carrie Bow Cay.

Variations. A single slight variation, unrelated to sex or size, was recorded from the scaphocerite. Among the six specimens available (3.2–6.1 mm), three have a slight basal emargination, but only two have setae on that emargination, the remaining three show no traces of a blade or emargination. The supernumerary tooth adjacent to the mobile spine on the right uropodal exopod of the holotype is probably a minor abnormality, as none of the remaining specimens possess this character.

Hosts and ecology. In Belize all but one of our specimens were found in an unidentified yellow tube sponge growing anastomosed among coral rubble on shallow patch reefs. A single specimen was found in *Hyattella intestinalis* in the same habitat. In cursory collections from the Bocas del Toro region of Caribbean Panama, we found a few specimens in *Hymeniacion caerulea* growing among shallow coral rubble.

Distribution. Belize Barrier Reef (this study); Bocas del Toro region, Panama (J.E. Duffy, unpublished)

Remarks. Dissection of an embryo from the allotype suggests that the first stage is a megalopa, due to the presence of fully developed biramous pleopods and rudimentary first and second pereopods with recognizable chelae. *Zuzalpheus kensleyi*, n. sp., resembles *Z. goodei*, *Z. williamsi* and *Z. paraneptunus*, but they can be easily separated by several characters. In contrast to *Z. kensleyi*, n. sp., *Z. paraneptunus* has a very reduced array of setal combs on the extensor surface of the dactyl of the minor first chela, stronger apical teeth and excavate fingers on that chela, and lacks the acute spine on the dorsal margin of the basicerite. Both *Z. goodei* and *Z. williamsi* have more teeth on the outer margin of the uropodal exopod, and the first pleura of the males is strongly produced into an acute hook-like projection.

***Zuzalpheus longicarpus* (Herrick, 1891) n. comb.**

(Fig. 23)

Alpheus saulcyi variety *longicarpus* (Herrick, 1891) in part; Coutière 1897b:369.

Synalpheus laevimanus variety *longicarpus*: Coutière 1898a:189, 1898b:221; 1899; 1900:357.

Synalpheus longicarpus: Coutière, 1907:610, 1909: 53, fig. 31; Christoffersen 1979:344 in part; Williams 1984:104 in part; Dardeau 1984:64 in part; Ríos 2003:117, figures 2–22.

Material examined. (1) 1 ♂, 5.9 mm (VIMS 93CBC5506), 1 ♀, 5.1 mm (VIMS 93CBC5515), South Water Cay, Belize, 28 March 1993, in *Sphaciospongia vesparium*, 1.5 m.

(2) 5 ♂, 5.5, 6.7, 7.5, 7.5, 7.5 mm, 2 ♀, 7.9 and 8.1 mm, 2 ovigerous ♀, 6.7 and 7.5 mm (VIMS 91NC0101), off Morehead City, North Carolina, 3 July 1991, in yellow sponge otherwise resembling *Sphaciospongia vesparium*.

(3) 5 ♂, 5.1, 7.0, 7.3, 7.5, 7.6 mm, 1 ♀, 8.4 mm (USNM 1019063, VIMS 93P3001), Guigalatupo reef, San Blas Islands, Panama, 28 September 1993, in *Sphaciospongia vesparium*, 1 m.

Diagnosis. Body subcylindrical; carapace smooth, glabrous, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch diminished. *Rostrum* lanceolate, distally upturned, clearly narrower and slightly longer than ocular hoods. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, acute, margins straight, separated from rostrum by deep adrostral sinus. Ocular processes present, but not elongated. Ocellary beak in lateral view rod-like. *Stylocerite* slender; mesial margin straight, or convex; tip acute; reaching about as far as distal margin of first antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorsolateral corner, and with longer ventrolateral spine overreaching tip of stylocerite. *Scaphocerite* blade reduced, acute lateral spine robust, with lateral margin straight, reaching about as far as antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal cirlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment

Major pereopod 1 massive, fingers shorter than half length of palm; fixed finger reduced, considerably shorter than dactyl; in ventral view, outer face of fixed finger without any protuberance. Palm of chela somewhat inflated proximally, with distal superior margin produced into prominent tubercle with acute spine directed forward. Merus, extensor margin straight or slightly convex, with distal angular projection.

Minor pereopod 1 with palm more than twice as long as high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with 2 strong distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, with 2 strong teeth, subdistal one slightly smaller than distal one. Extensor margin of merus convex, ending in acute angle.

Pereopod 2 with carpus 5-segmented, not longer than merus.

Pereopod 3 slender; dactyl biunguiculate, with extensor tooth clearly thicker at base than flexor; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pleura 1 of male with posterior corner hook-like, acutely produced ventrally and anteriorly; second through fifth pleurae of male strongly acuminate. *Pleopod 1* of male, with about six terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines equal or less than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines rectangular. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with 3 to 6 fixed teeth on outer margin of exopod, slightly apart from the longer mobile spine adjacent the internal fixed tooth.

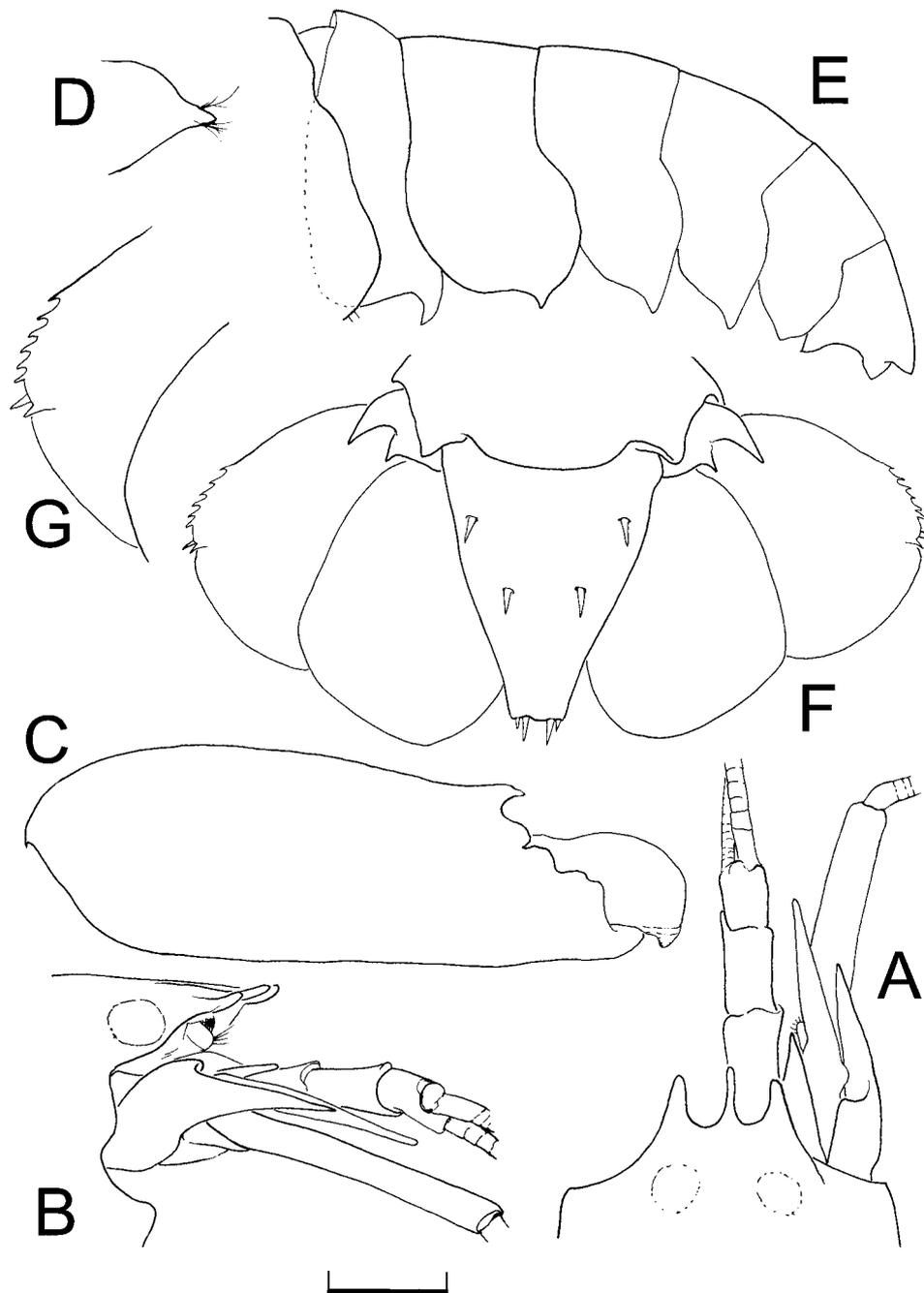


FIGURE 23. *Zuzalpheus longicarpus* (Herrick 1891). Male 7.6 mm (USNM 1019063): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, tilted lateral view; e, abdomen, lateral view; f, telson and uropods, dorsal view; g, detail of left uropod, dorsal view. Ovigerous female 7.3 mm (USNM 1019063): c, chela of major first pereopod, lateral view; d, same, tip of fixed finger, ventral view. Scale bar = 1 mm for a, b, f, 1.4 mm for c, d, e, and 0.74 mm for g.

Color. Translucent straw color with scattered chromatophores; distal portions of chelae purple to black; ovaries dull yellow, embryos dull brick-orange.

Variations. One of the most frequent variations is the widening of the orbital hoods (in dorsal view), which may be associated with the larger specimens. In those instances they resemble the hoof-shaped hoods in *Zuzalpheus dardeau*, n. sp. The blade on the scaphocerite is usually reduced to less than half the length of the adjacent lateral spine, but occasionally exceeds this length. The spine overhanging the dactylar articulation on the major cheliped usually emerges at the most distal point of the protuberance, but occasionally arises from its ventral slope, as occurs in several other species. The number of fixed teeth on the outer corner of the uropodal exopod is most frequently from 4 to 6, but it can be anywhere from 3 up to 8. In a single specimen there was a postanal brush of stiff setae like the one in *Zuzalpheus dardeau*, n. sp., but less dense.

Hosts and ecology. We have found *Zuzalpheus longicarpus* living only inside the canals of the loggerhead sponge *Sphaciospongia vesparium*, as mentioned by several authors (e. g. Pearse 1950; Chace 1972; Dardeau 1984; Erdman and Blake 1987; Duffy 1992). Herrick (1891) reported that his type specimens came from *Hircinia arcuta*, currently known as *Ircinia strobilina* (Lamarck 1816), a large dark sponge superficially similar in appearance to *Z. vesparium*.

Distribution. Western Atlantic: North Carolina (Coutère 1909; J.E. Duffy unpublished); Cuba (Martínez Iglesias and García Raso 1999); Jamaica (Coutère 1909); Virgin Islands (Chace 1972); Gulf of Mexico (Coutère 1909; Dardeau 1984); Yucatan peninsula (Coutère 1909; Chace 1972); Belize Barrier Reef (this study); Windward Islands (Chace 1972); Tobago (Chace 1972); Curacao (Coutère 1909); Brazil (Christoffersen 1979). With the discovery of several new species closely related to *Z. longicarpus* (Table 1), the geographical boundaries of previous records under this name should be treated with caution.

Remarks. We have found only a very few specimens of this species in Belize. In Belizean specimens of *Sphaciospongia vesparium*, for example, *Z. dardeau* n. sp. is the more common large species of the genus and appears to “take the place” of *Z. longicarpus*, cohabiting in that sponge with *Z. brooksi* and *Z. pectiniger*, as *Z. longicarpus* does elsewhere. *Z. longicarpus* may be distinguished from the several other, morphologically similar species by the slender orbital hoods, reduced cardiac notch, relatively small spines on the dorsal surface of the telson, and apical insertion of the spine overhanging the dactylar articulation on the major cheliped (Table 1).

Z. longicarpus and related species are among the largest and most common species of *Zuzalpheus* in shallow waters of the western Atlantic, so it is not surprising that the name has been widely used in the literature. Yet, because the holotype designation is problematic, the history of the name is truly a quagmire. Herrick (1891:385) described the larvae of several species of Alpheidae, recognizing at least two varieties in what he called *Alpheus saulcyi* Guérin, but he refers to types only in his table 1, wherein he registers his specimen number 13 as the type of his variety *longicarpus*, but does not mention its inclusion in any Museum collection. Coutière (1898a) had access to abundant material of this species, including two typical specimens sent by Herrick. In that brief contribution, Coutière (1898a) published the first inclusion of the species in the genus *Synalpheus*, and also provided dorsal views of the anterior regions of four shrimp, two of which (his Figs. 2” and 2”) represent the first known illustrations of *S. longicarpus*. Coutière additionally established the identity of this taxon in his magnum opus (1899), which includes an illustration of a mandible from a type (his Fig. 153), an antennule and the minor first chela of a cotype (his Figs. 116, 123, and 241), and the tip of the telson from another specimen (his Fig. 394).

Although Coutière (1907) first published the binomen *Synalpheus longicarpus*, the species was defined later in his monograph of the American species belonging in that genus (Coutière 1909), wherein a useful diagnosis is included along with figures that have been repeatedly reproduced (Hay and Shore 1918; Verrill 1922; Williams 1965 and 1984).

Probably overwhelmed by the striking and apparently continuous intraspecific variation in the abundant material that he examined, Christoffersen (1979) decided to include *S. pandionis* (Coutière) as a junior syn-

onym of *S. longicarpus*. *S. pandionis* was then resurrected by Dardeau (1984), and Christoffersen (1998) later accepted Dardeau's conclusions. Interestingly, in the figures provided both by Christoffersen (1979) and Dardeau (1984), it is possible to recognize some of their specimens as a different species (see remarks under *Zuzalpheus dardeau*, n. sp.), as is also the case of the SEM photographs of Ray (1974). The "*Synalpheus longicarpus*" depicted in plate 65 from Boone (1930) is clearly a misidentification since that specimen is lacking the comb of setae on the extensor surface of the dactyl of the smaller chela, and the uropodal exopods are barren of teeth.

Additional details on the taxonomic history of this species can be found in the general introduction of Coutière's (1909) revision of *Synalpheus*, and in Verrill (1922). Dardeau (1984:73) could not locate the holotype, and the cotypes mentioned by Coutière (1899) are the only type material that might still be extant. Designation of a neotype is beyond the scope of the present contribution, mainly because of the difficulty of proving the nonexistence of the holotype or trying to find the cotypes.

***Zuzalpheus mcclendoni* (Coutière, 1910) n. comb.**

Synalpheus mcclendoni Coutière, 1910:487, fig. 3; Chace 1972:95, figs. 33, 34; Ray 1974:148, fig. 133–135; Ríos 2003:124–128.

Synalpheus macclendoni Dardeau 1984: 74, fig. 37–39.

Material examined. (1) 1 ♂, 3.2 mm (USNM 1019064, VIMS 93CBC7701), Carrie Bow Cay, Belize, 5 April 1993, in unidentified yellow boring sponge, 2.5 m.

(2) 1 ♂ (VIMS 94CBC3402), 2.5 mm, outer ridge at Carrie Bow Cay, Belize, 23 August 1994, no host found, 17 m.

(3) 1 ♂ (VIMS 93CBC3205), 2.5 mm, fore-reef slope, Carrie Bow Cay, Belize, 22 March 1993, in *Agelas clathrodes*, 22 m.

(4) 1 ♂ (VIMS 93CBC6103), outer ridge at Carrie Bow Cay, Belize, 29 March 1993, in unidentified columnar mustard-colored sponge, 14 m.

(5) 2 ♂ (VIMS 93CBC7402), fore-reef slope, Carrie Bow Cay, Belize, 31 March 1993, in *Agelas clathrodes*, 22 m.

Diagnosis. Body subcylindrical; carapace smooth, glabrous, with pterygostomian corner forming obtuse angle, and posterior margin with cardiac notch distinct. *Rostrum* triangular, somewhat narrower and slightly longer than ocular hoods, not conspicuously upturned, and sometimes with a shallow ventral convex keel behind the base. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, acute, separated from rostrum by deep adrostral sinus. Ocular process small, but prolonged backwards into distinct keel on mesioventral edge of eye. Ocellary beak in lateral view rectangular. *Stylocerite* strong; mesial margin slightly concave; tip blunt; slightly overreaching distal margin of first segment of antennular peduncle; this latter segment with ventromesial tooth, and with two basal ventral processes. *Basicerite* with superior corner not prolonged and with long ventrolateral spine slightly overreaching tip of stylocerite. *Scaphocerite* blade present, longer acute lateral spine robust, clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circling of spines on distal segment and without ventrodorsal spine on antepenultimate segment

Major pereopod 1 massive, chela elongated, fingers about half length of palm, flattened, curved inwards, and tips crossing; in ventral view, outer face of fixed finger without any protuberance. Palm of chela with distal superior margin typically tapering into strong acute spine. Merus, extensor margin strongly convex, with distal flat angular projection.

Minor pereopod 1 with palm about twice as long as high; fingers shorter than palm; dactyl with flexor margin blade-like, subdistal accessory tooth, and two bumps, in addition to distal tip; transverse dorsal setal

combs on extensor surface of dactyl very conspicuous; fixed finger with flexor surface blade-like, and subdistal bump in addition to distal tip. Extensor margin of merus slightly convex, ending in right angle.

Pereopod 2 with carpus 5-segmented, about as long as merus.

Pereopod 3 slender; dactyl biunguiculate, with flexor tooth thicker than extensor; merus without spines; mesial lamella on coxa present. *Pereopods 4 and 5* normal.

Pleura 1 of male with posterior corner obscurely produced ventrally and anteriorly into small hook-like tooth; second pleura of male broadly rounded. *Pleopod 1* of male, with about four terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines greater than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush all absent. *Uropods* with a single fixed tooth on outer margin of exopod, about as strong as fixed inner tooth, but shorter than slender mobile spine.

Color. In Belizean specimens from *Agelas clathroides*, the body was generally transparent; major chela bears a striking pattern of prominent red chromatophores on disto-dorsal surface of palm and flexor margins of fingers, and double transverse bands of dark blue pigment immediately proximal to the red area. We have also observed this distinctive color pattern in specimens from the same host in the San Blas islands of Panama and in the Florida Keys; they are presumably conspecific. In contrast, a single specimen from Panamá differed strikingly from these others in having an overall creamy uniform yellow to white background color with some yellowish wash on distal portions of the major chela; this presumably represents an undescribed species.

Variations. The ocular hoods are usually straight, but occasionally in some specimens they look as Ray (1974) remarked: "they show a slight inward curving with their inner surfaces slightly sloping mesoventrally". The stylocerite usually reaches the midpoint of the second segment of the antennular peduncle, but sometimes it barely overreaches the first segment, as in Figure 3n of Coutière (1910) and Figure 33b of Chace (1972). The superior border of the palm of the major chela typically tapers into a streamlined point, but in a couple of individuals there was a basal constriction on the distal spine.

One male from Panama had two major chelae on the first pair of pereopods. To our knowledge this is the only record of this kind of abnormal symmetry in any species of *Zuzalpheus*. Females with two minor chelae are typical in some of the eusocial species, such as *Z. filidigitus* (Duffy 1998; Duffy and Macdonald 1999).

Hosts and ecology. *Z. mcclendoni* is uncommon in our collections from Belize. We have found several single specimens in *Agelas clathroides*, one specimen in an unidentified yellowish boring sponge lining smooth cylindrical canals in coral rock, and a few specimens unassociated with hosts, presumably dislodged from them during rubble collection.

Distribution. Western Atlantic: Dry Tortugas, Florida, USA (Coutière 1910), Florida Keys, USA (J.E. Duffy unpublished); Bahamas (Dardeau 1984); Cuba (Martínez Iglesias and García Raso 1999); St. Lucia, Tobago Cays, and Yucatan peninsula of Mexico (Chace 1972); San Blas Islands, Panamá (Duffy 1992), Belize Barrier Reef (this study).

Remarks. Recognizing its similarity to *Z. sanctithomae*, Coutière (1910) erected *Synalpheus mcclendoni* succinctly, restricting his description to a few characters that would distinguish the two species, and including only five illustrations. Chace (1972) further complemented the knowledge of this species with a full set of drawings, but, in what appears to be a mere typographical error, his key to the species introduced an unfortunate misunderstanding. In couplet 9 of his key to *Synalpheus*, Chace (1972) separated *S. mcclendoni* from *S. sanctithomae*, among other characters, on the basis of the shape of the major chela, which he stated is "not noticeably twisted" in *S. mcclendoni* and "twisted" in *S. sanctithomae*. In fact, the opposite is true. Coutière (1910) explicitly mentioned that the fingers of the major chela are curved inwards in *S. mcclendoni*, and this is what gives the chela the twisted appearance noted by Chace (1972). Ray (1974) gave an extended diagnosis of *S. mcclendoni*, mentioning the inward curvature of the fingers of the major chela, and provided SEM images illustrating it. Dardeau (1984) perpetuated the confusion by misspelling the specific name as "*mac-*

clendoni", and including Chace's mistaken couplet in his key. Ironically, the specimens Dardeau (1984) designated with the incorrect spelling may belong to an undescribed species: he mentioned that the material he examined, syntypes included, differ from the specimens studied by Chace (1972) in the form of the palmar spine on the major chela and the first pleura of males. Both of these characters are variable in *Z. mcclendoni*, but other details, such as color and host preferences, suggest that there is indeed a second species. The question of which of the species should retain the name *mcclendoni* awaits a closer examination of the type material deposited in the USNM. Notably, figure 3n in Coutière (1910) depicts a scaphocerite shorter than the ones we observed, which were more similar to figure 33b in Chace (1972).

At Carrie Bow Cay we have collected an undescribed species morphologically very similar to *Z. mcclendoni*, but with a strikingly different color pattern (blue, white and red) on the major chela. Coinciding with most of the specimens examined by Dardeau (1984), these shrimp were living inside a sponge in the genus *Agelas*.

***Zuzalpheus pandionis* (Coutière, 1909) n. comb.**

(Figs. 24–25, Plate 4)

Synalpheus pandionis Coutière, 1909:67, fig. 39; Ríos 2003:128, figures 2–23 and 2–24, plate IV.

Synalpheus pandionis extentus Coutière, 1909:69, fig. 40.

Material examined. (1) 5 syntypes (USNM 38400), 3 ♀ and 2 males, from off Saint Thomas, 6 February 1899, 20–23 fms.

(2) 1 ♂, 5.9 mm (USNM 1019065, VIMS 94CBC3302), 1 ovigerous ♀, 6.8 mm (USNM 1019066, VIMS 94CBC33-01), outer ridge of Carrie Bow Cay, Belize 23 August 1994, in *Lissodendoryx* cf. *strongylata*, 14 m.

(3) 1 ♂, 6.6 mm (VIMS 95CBC0502), 1 ♀, 6.0 mm (VIMS 95CBC0502), outer ridge of Carrie Bow Cay, Belize, 21 June 1995, in *Lissodendoryx* cf. *strongylata*, 14 m.

(4) 1 ♂, 5.4 mm (VIMS 95CBC2002), 1 ovigerous ♀, 6.2 mm (VIMS 95CBC2001), outer ridge of Carrie Bow Cay, Belize, 23 June 1995, in *Lissodendoryx* cf. *strongylata*, 14 m.

(5) 1 ♂, 4.3 mm (VIMS 98CBC0101), fore-reef at South Water Caye, Belize, 3 December 1998, in *Hymeniacidon amphilecta*, 12 m.

Diagnosis. Body subcylindrical; carapace smooth, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. *Rostrum* in dorsal view lanceolate, about as long as ocular hoods, but clearly narrower; in lateral view, distally upturned, with a ventrally convex longitudinal septum behind the base. Latter not reaching beyond half the height of the eye. Inferior edge of ocular hoods converging to about half the height of each side of septum. Ocular hoods dorsally convex; in dorsal view, squarely rounded anteriorly, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes produced into a broad structure on the lower half of eye. Ocellary beak in lateral view, truncate. *Stylocerite* slender; mesial margin slightly concave; tip acute; distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorsolateral corner, and with longer ventrolateral spine not reaching distal half of third segment of antennular peduncle. *Scaphocerite* blade elongated, acute lateral spine robust, with lateral margin slightly concave, reaching about as far as lateral spine of basicerite; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal cirlet of spines on distal segment and without ventrodistal spine on antepenultimate segment.

Major pereopod 1 massive, fingers clearly shorter than half length of palm; fixed finger reduced, noticeably shorter than dactyl; in ventral view, outer face of fixed finger with an obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute downwardly directed spine on its ventral face. Merus, extensor margin strongly convex, with distal angular projection.

Minor pereopod 1 with palm more than twice as long as high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with terminal tooth flanked by smaller subdistal tooth; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, and subdistal accessory bump. Extensor margin of merus convex.

Pereopod 2 with carpus 5-segmented, about as long as merus.

Pereopod 3 stout; dactyl biunguiculate, with extensor tooth clearly more slender than flexor; merus without movable spines on flexor margin; mesial lamella on coxa present.

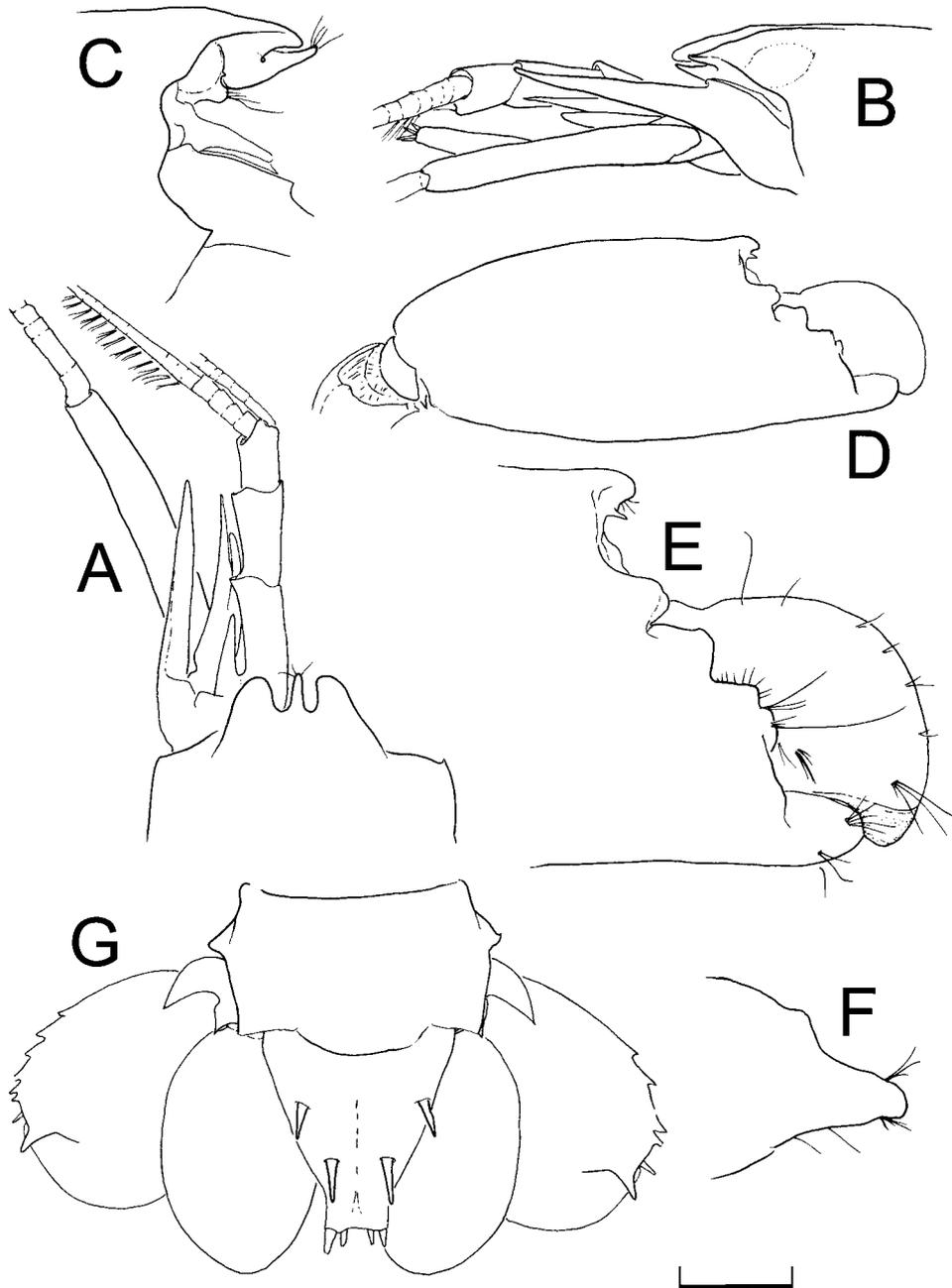


FIGURE 24. *Zuzalpheus pandionis* (Coutière 1909). Male 6.6 mm (VIMS 95CBC0502): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, same, alternate lateral view with cephalic appendages pushed down; d, chela of major first pereopod, lateral view; e, same, detail of distal portion, lateral view; f, same, tip of fixed finger, ventral view; g, telson and uropods, dorsal view. Scale bar = 1 mm for a, b, e, f, g, 0.7 mm for c, and 2 mm for d.

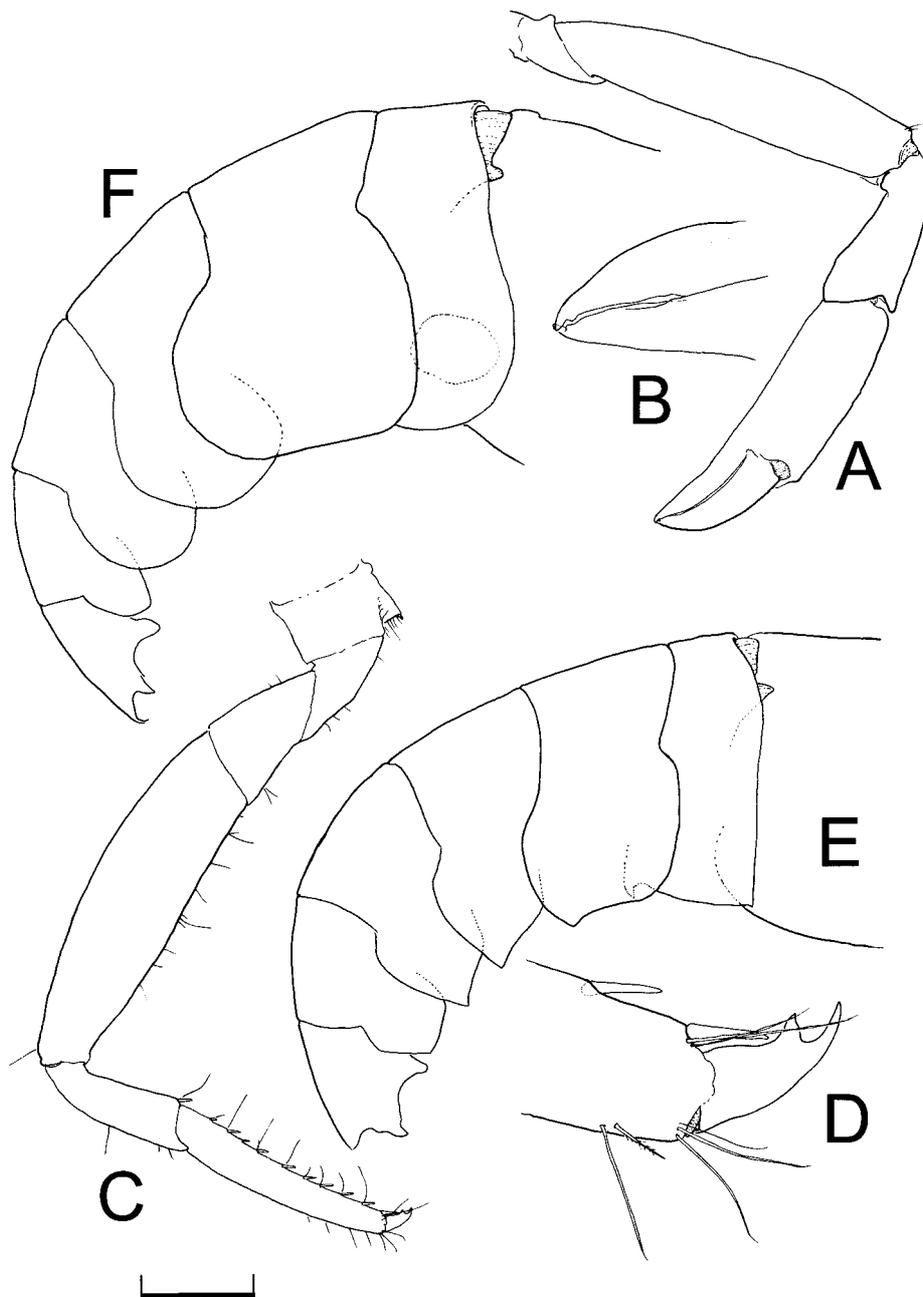


FIGURE 25. *Zuzalpheus pandionis* (Coutière 1909). Male 6.6 mm (VIMS 95CBC0502): a, minor first pereopod, lateral view; b, same, detail of distal portion (setal combs on dactyl omitted), alternate lateral view; c, right third pereopod; d, same, detail of distal portion; e, abdomen, lateral view. Ovigerous female 6.8 mm (USNM 1019066): f, abdomen showing one egg, lateral view. Scale bar = 1 mm for a, c, 1.3 mm for e, f, 0.5 mm for b, and 0.2 mm for d.

Pleura 1 of male with posterior corner acutely produced ventrally; second pleura of male produced into acute angle. Appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines about one-third of distal margin, frequently without conspicuous convex lobe. Ventral face of telson without anal flaps nor perianal setae, but with postanal setal brush. *Uropods* with 3–6 teeth on outer margin of exopod; mobile spine distinctly removed from wide fixed tooth.

Color (Plate 4). Specimens from *Lissodendoryx* sp. were solid uniform bright orange-red, the color of mature papaya fruit, with fingers and distal palm of major chela more intense red-orange, and orange-red ovaries and embryos.

Variations. On rare occasions, the distal margin of both the ocular hoods and the ocellary beak are not completely straight but slightly concave. The most frequent number of fixed teeth on the uropod is 4, whereas 3 is very rare, and 5 or 6 are more common.

Hosts and ecology. *Zuzalpheus pandionis* was found living in heterosexual pairs, most frequently inside a bright orange-red sponge identified as *Lissodendoryx* cf. *strongylata* on the outer reef ridge. Other hosts include *Agelas clathrodes*, *Hyattella intestinalis* and *Hymeniacidon amphilecta*. Most of the samples came from 10–15 m deep.

Distribution. Western Atlantic: Bahamas (Lemaitre 1984); Cuba (Martínez Iglesias and García Raso 1999); Virgin Islands (Coutère 1909; Chace 1972); Gulf of Mexico (Dardeau 1984); Belize Barrier Reef (this study); San Blas Islands, Panama (J.E. Duffy unpublished). With the discovery of several new species closely related to *Z. pandionis* (Table 1), the geographical boundaries of previous records under this name should be treated with caution.

Remarks. The original type series of *Z. pandionis* includes five specimens, all fragmented. Nevertheless, it was possible to confirm both their conspecificity and the series of characters that allow the distinction of this species (Table 1). The most useful of these characters include: broad ocular hoods, ventral surface of rostrum with longitudinal posterior septum, fixed finger of major first chela with obtuse ventrolateral protuberance, and the shape of the uropodal exopod. Chace (1972) made *Synalpheus grampusi* a synonym of *Z. pandionis*; he chose this name despite the page location of each name in the publication by Coutière (1909). That turned out to be an accurate decision, because (as Chace had remarked) the three specimens in the type series of *S. grampusi* seem to belong in two species: the two larger males, but not the smaller female, have a blade on the scaphocerite. Coutière (1909) distinguished *S. pandionis* from *S. grampusi* based largely on the presence of that blade. Considering that both the description and the illustration of *S. grampusi* lack the blade, it is most appropriate to maintain the name *Z. pandionis* for the species bearing a blade on the scaphocerite. The female in the type series of *S. grampusi* is further considered under the remarks for *Zuzalpheus yano*, n. sp.

Christoffersen's (1979) synonymization of *S. pandionis* and *S. longicarpus* (Herrick) was discussed above under remarks for *Z. longicarpus*. These two species can be separated by several characters in *Z. longicarpus* (Table 1), including the elongated ocular hoods, the reduced cardiac notch, the lack of basal protuberance on the fixed finger of the major chela, the stronger distal teeth on the dactyl of the smaller chela, and the much reduced spines on the dorsal surface of the telson.

The holotype of *Synalpheus pandionis extentus* Coutière (1909) does not look much different than some of the specimens from Belize and Panama, and for this reason the subspecies is considered here as a synonym of *Z. pandionis*. Furthermore, this female was apparently collected together with the type series of *Z. pandionis*.

***Zuzalpheus paraneptunus* (Coutière, 1909) n. comb.**
(Plate 4)

Synalpheus paraneptunus, Coutière 1909:86–89, Fig. 52; Dardeau 1984:92–98, Figs. 47–50 (and synonymy).

Material examined. (1) 1 ovigerous ♀ (VIMS 01CBC5504), 3.1 mm, 1 ♂ (VIMS 01CBC5505), 2.9 mm, The Pinnacles (Sand Bores) SW of Carrie Bow Cay, Belize, 2 May 2001, in *Xestospongia proxima*, 2 m.

(2) 1 ovigerous ♀ (VIMS 01CBC0504), 4.6 mm, 1 ♂ (VIMS 01CBC0503), 4.5 mm, outer ridge at Curlew Cay, 27 April 2001, in *Xestospongia proxima*, 15–18 m.

(3) 1 ovigerous ♀ (VIMS 03CBC5801), 3.4 mm, 1 ♂ (VIMS 03CBC5802), 2.8 mm, The Pinnacles (Sand Bores) SW of Carrie Bow Cay, Belize, 28 April 2003, in *Pachypellina podatypa*, 2 m.

(4) 1 ♀ (VIMS 94CBC9201), 2.4 mm, 1 ♂ (VIMS 94CBC9203), 2.4 mm, fore-reef slope at Carrie Bow Cay, Belize, 30 August 1994, in *Oceanapia* sp., 18 m.

(5) 1 ♀ (VIMS 96CBC2001), 3.3 mm, 1 ♂ (VIMS 96CBC2002), 3.2 mm, outer ridge at Carrie Bow Cay, Belize, 13 June 1996, in *Oceanapia* sp., 17 m.

(6) 1 ovigerous ♀ (98CBC5003), 3.3 mm, 1 ♂ (VIMS 98CBC5004), 2.7 mm, outer ridge at Carrie Bow Cay, Belize, 8 December 1998, in *Xestospongia* cf. *subtriangularis*, 17 m.

(7) 1 ovigerous ♀ (VIMS 99CBC5302), 3.8 mm, 1 ♂ (VIMS 99CBC5304), 3.2 mm, outer ridge at Carrie Bow Cay, Belize, 9 December 1999, in unidentified soft white sponge, 17 m.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner very obtusely angular, and posterior margin with cardiac notch distinct. *Rostrum* clearly narrower than ocular hoods, about as long as ocular hoods, and distally upturned; margins in dorsal view, concave or convex. Orbitostral process absent. Ocular hoods dorsally convex; in dorsal view, acute, margins concave or convex, separated from rostrum by deep adrostral sinus. Ocular processes present, but not elongated. Ocellary beak in lateral view rodlike. *Stylocerite* slender; mesial margin slightly concave; tip acute; clearly exceeding distal margin of first segment of antennular peduncle; this latter segment without mesio-ventral tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorso-lateral corner, and with longer ventrolateral spine clearly overreaching tip of stylocerite. Scaphocerite with blade reduced, and with robust, acute lateral spine with lateral margin slightly concave, clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circlet of spines on distal segment, and without ventro-distal spine on antepenultimate segment

Major pereopod 1 massive, fingers clearly less than half length of palm; fixed finger reduced, much shorter than dactyl; in ventral view, outer face of fixed finger with an obtuse basal protuberance. Palm of chela with distal superior margin produced into tapering acute spine. Merus, extensor margin strongly convex, with distal angular projection.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor surface excavate, with two distal teeth, subequal in length and oriented perpendicular to long axis of dactyl; transverse dorsal setal combs on extensor surface of dactyl present but reduced to irregular field rather than thick brush; fixed finger with flexor surface excavate, and 2 distinct teeth subequal in length. Extensor margin of merus convex, with distal angular projection.

Pereopod 2 carpus with five segments (rarely four); and equal or shorter than merus.

Pereopod 3 stout; dactyl biunguiculate, with clearly unequal teeth; and extensor tooth wider at base than flexor; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pleura 1 of male with posterior corner weakly produced, or rounded; second pleura of male rounded to obtuse. *Pleopod 1* of male with few terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines more than one third of distal margin; marginal convex lobe present; posterior corners adjacent to spines acute; projections not longer than wide. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with usually two or more fixed teeth on outer margin of exopod.

Color (Plate 4). Transparent, distal palm and fingers of major chela usually tinged dark brown, varying from dull orange to blue-black; ovaries and eggs bright grass green to bright yellow.

Hosts and ecology. In Belize this species is not very common, but we have collected it from a variety of hosts including *Hyattella intestinalis*, *Oceanapia* sp., *Pachypellina podatypa*, *Xestospongia* cf. *proxima*, at depths ranging from 1–20 m. Usually, one or a few heterosexual pairs are found in an individual sponge, sometimes with a few juveniles also present. According to Coutière (1909, p. 87), “the eggs give rise to zoëae”.

Distribution. Western Atlantic: Florida Keys, USA (J.E. Duffy, unpublished); Bahamas (Lemaitre 1984); Cuba (Martínez Iglesias and García Raso 1999); Jamaica (Coutière, 1909); Puerto Rico (Schmitt 1935); Gulf

of Mexico (Dardeau 1984); Yucatan peninsula, Leeward Islands, Windward Islands (Chace 1972); Belize Barrier Reef (this study); Bonaire (Schmitt 1936); San Blas Islands, Panama (Duffy 1992); Colombia (Coutière, 1909).

Remarks. *Zuzalpheus paraneptunus* is a morphologically distinctive species that is difficult to confuse with any other West Atlantic species. The excavate, spoon-shaped fingers of the minor first chela, together with the sparse field of setae on the dactyl thereof, are unique in this region. Indeed, the reduction of the setal brush on the minor chela dactyl, which is diagnostic for *Zuzalpheus*, has suggested to several authors that the “gambarelloides group” (herein elevated to genus level as *Zuzalpheus*) may not be homogeneous (Coutière, 1909, Dardeau 1984). Morrison *et al.* (2004) found strong support for a sister-taxon relationship between *Z. paraneptunus* and the new species *Z. kensleyi* (called *S.* “intermediate” in that publication), described herein, suggesting that *Z. paraneptunus* is indeed closely related to the other species of *Zuzalpheus*. Nonetheless, as suggested by Dardeau (1984), the membership and geographic distribution of the new genus will remain somewhat uncertain until a careful phylogenetic comparison can be made with some of the Indo-Pacific species in the Coutièrei (previously *Biunguiculatus*) group, which share some morphological characteristics with *Z. paraneptunus* (Banner and Banner 1975).

***Zuzalpheus pectiniger* (Coutière, 1907) n. comb.**

(Plate 4)

Synalpheus pectiniger Coutière, 1907:611; Coutière, 1909:78–82, fig. 48; Dardeau:98–102, figs. 51–53 (and synonymy).

Material examined. (1) 14 ♂, 4.3–4.4 mm, 6 ovigerous ♀, 3.9–5.3 mm (VIMS 93CBC2902), Twin Cays, Belize, 22 March 1993, in *Sphaciospongia vesparium*, 1.5 m.

(2) 1 ovigerous ♀ (VIMS 93CBC2012), 4.0 mm, 1 ♂ (VIMS 93CBC2013), 4.2 mm, Blue Ground Range, W of Carrie Bow Cay, Belize, 19 March 1993, in *Sphaciospongia vesparium*, 1.5 m.

(3) 3 ♂ (VIMS93CBC2102, 93CBC2113, 93CBC2114), 2.9 mm, 4.0 mm, 4.1 mm, Blue Ground Range, Belize, 19 March 1993, in *Sphaciospongia vesparium*, 1.5 m.

(4) 4 ovigerous ♀ (VIMS 93CBC2605, 93CBC2609, 93CBC2610, 93CBC2611), 4.6 mm, 4.6 mm, 4.8 mm, 4.6 mm, 4 ♂ (VIMS 93CBC2603, 93CBC2606, 93CBC2607, 93CBC2608), 4.2 mm, 5.0 mm, 3.7 mm, 4.1 mm, Twin Cays, Belize, 21 March 1993, in *Sphaciospongia vesparium*, 1.5 m.

(5) 1 ♂ (VIMS 95F4107), 4.3 mm, Three Sisters Reef, Florida Keys, USA, 19 May 1995, in *Sphaciospongia vesparium*, 4.2 m.

Diagnosis. Body subcylindrical; carapace smooth, glabrous, with pterygostomian corner broadly obtuse, and posterior margin with cardiac notch diminished. *Rostrum* carinate, about as long as, but slightly narrower than, orbital hoods, distally upturned; margins in dorsal view convex. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view acute, separated from rostrum by deep circular adrostral sinus. Ocular process broad. Ocellary beak in lateral view broad at base, not rod-like. *Stylocerite* slender, tip acute, reaching about as far as distal margin of first antennular peduncle; this latter segment without mesio-ventral tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorso-lateral corner, and with ventrolateral spine reaching distal half of second segment of antennular peduncle. *Scaphocerite* without blade; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal cirlet of spines on distal segment, and without ventro-distal spine on antepenultimate segment.

Major pereopod 1 massive, fingers shorter than half length of palm; fixed finger reduced to less than half length of dactyl; in ventral view, fixed finger widely triangular, almost rounded distally and without any obvious protuberance on outer face. Palm of chela with distal superior margin produced into acute conical projection, somewhat flattened dorsoventrally, overhanging base of dactyl. Merus extensor margin slightly convex

with flat distal angular projection.

Minor pereopod 1 with palm less than twice as long as high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with 3 strong distal teeth, equal in length, and parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, with 2 strong teeth subequal in length, and adjacent bump; merus with extensor margin slightly convex with flat distal angular projection.

Pereopod 2 with carpus 5-segmented, slightly longer than merus.

Pereopod 3 slender; dactyl biunguiculate, with flexor tooth slightly thicker than terminal tooth; merus without movable spines on flexor margin; mesial lamella on coxa present. Pereopods 4 and 5 normal.

Pleura 1 with dorsal anterior margin produced into distinct convex lobe; pleura of male usually strongly acuminate, sixth with 2 distinct spines; ovigerous females with pleura broadly rounded. *Pleopod 1* of male, endopod with six terminal setae and four near base; pleopod 2 of male with marginal setae on exopod originating at base; appendix interna on second to fifth pleopods, present. *Telson* with space between posterior marginal spines less than one third width of posterior margin; marginal convex lobe absent. Anal flaps, perianal setae, and postanal setal brush all absent. *Uropods* with outer margin of exopod having 1–3 fixed teeth distinctly removed from mobile spine, and usually without adjacent inner fixed tooth.

Color (Plate 4). Transparent with a distinctly pink facial region, due to expanded chromatophores, juxtaposed with the black stomach. Distal palm and fingers of major chela with brownish to blue-black tinge. Digestive gland dark olive, ovaries and embryos pale golden yellow.

Variations. Putative males (*i. e.*, non ovigerous specimens) show abdominal pleurae with various degrees of elongation, in the extreme case resembling needle-like projections, in other cases with the tip strongly hooked anteriorly. Interestingly, the first pleura, which is typically considered the diagnostic secondary sexual character in most species of *Synalpheus*, frequently remains broadly rounded in putative male *Z. pectiniger* even when the posterior ones are acutely pointed. In most specimens both pairs of spines on the dorsal surface of the telson are located on the anterior half, but specimens with the posterior pair implanted slightly beyond the midlength of telson are not rare.

Hosts and ecology. *Zuzalpheus pectiniger* is evidently a strict host specialist in the loggerhead sponge *Sphaciospongia vesparium*, in which it is a characteristic inhabitant throughout its geographic range. We know of no reliable records from any other host or habitat. It can be found in groups of up to a few hundred individuals, generally with approximately equal sex ratio in the larger size classes.

Distribution. Western Atlantic: Florida Keys, USA (Coutière 1909; Duffy 1993); Bahamas (Coutière 1909; Lemaitre 1984); Cuba (Martínez Iglesias and García Raso 1999); Virgin Islands (Coutière 1909; Chace 1972); Gulf of Mexico (Coutière 1909; Wass 1955; Tabb and Manning 1961; Rouse 1970; Lyons et al. 1971; Menzel 1971; Dardeau 1984; Erdmann and Blake 1987); Yucatan peninsula, Mexico (Chace 1972); Belize Barrier Reef (this study); San Blas Islands, Panama (Duffy 1992); Windward Islands (Chace 1972); Netherlands Antilles (Coutière 1907, 1909; Westinga and Hoetjes 1981).

Remarks. Identification of *Z. pectiniger* is relatively straightforward when specimens in good condition are available, as the tridentate dactyl of the minor chela is unique among West Atlantic *Zuzalpheus*. The large chela is also a reliable taxonomic character because of both the short fixed finger and the slanted conical projection overhanging the base of the dactyl.

***Zuzalpheus regalis* (Duffy, 1996) n. comb.**

(Fig. 26, Plate 4)

Synalpheus regalis Duffy 1996b: 564, fig. 1–5; Ríos 2003:136, figure 2–25, plate IV.

Material examined. (1) **Holotype** ♂ (USNM 280092), 2.4 mm (rostrum excluded), from a colony of 89 ♂

(USNM 280093, 280095) and a single ovigerous ♀ (USNM 280094), Carrie Bow Cay, Belize, 28 March 1993, in *Xestospongia* cf. *subtriangularis* (Duchassaing 1850), 15 m.

(2) 13 individuals, 2.6–3.3 mm (VIMS 01CBC4803), and a single ovigerous ♀ (VIMS 01CBC4806) from a colony of 258, outer ridge at Curlew reef, Belize, 1 May 2001, inside sponge *Xestospongia* cf. *subtriangularis*, 15 m.

(3) 1 ovigerous ♀ (VIMS 96CBC3401), 2.7 mm, 60 ♂ (VIMS 96CBC3402), 1.3–2.9 mm, outer ridge at Carrie Bow Cay, Belize, 17 June 1996, in *Xestospongia* cf. *subtriangularis*, 15 m.

(4) 1 ovigerous ♀ (VIMS 01CBC4303), 3.9 mm, from a colony of 1 ovigerous ♀ and 204 others, outer ridge at Curlew reef, Belize, 1 May 2001, in *Hyattella intestinalis*, 15–20 m.

(5) 6 individuals, 2.4–2.7 mm (VIMS 04CBC0904), and a single ovigerous ♀ (VIMS 04CBC0905), 3.2 mm, from a colony of 1 ovigerous ♀ and 71 others, outer ridge at Curlew reef, Belize, 12 March 2004, in *Hyattella intestinalis*, 15–20 m.

(6) 10 individuals, 2.6–3.0 mm (VIMS 05CBC0902, 05CBC0903), and a single ovigerous ♀ (VIMS 04CBC0905), 3.9 mm, from a colony of 1 ovigerous ♀ and 101 others, outer ridge at Long reef, Belize, 10 July 2005, in *Hyattella intestinalis*, 20–25 m.

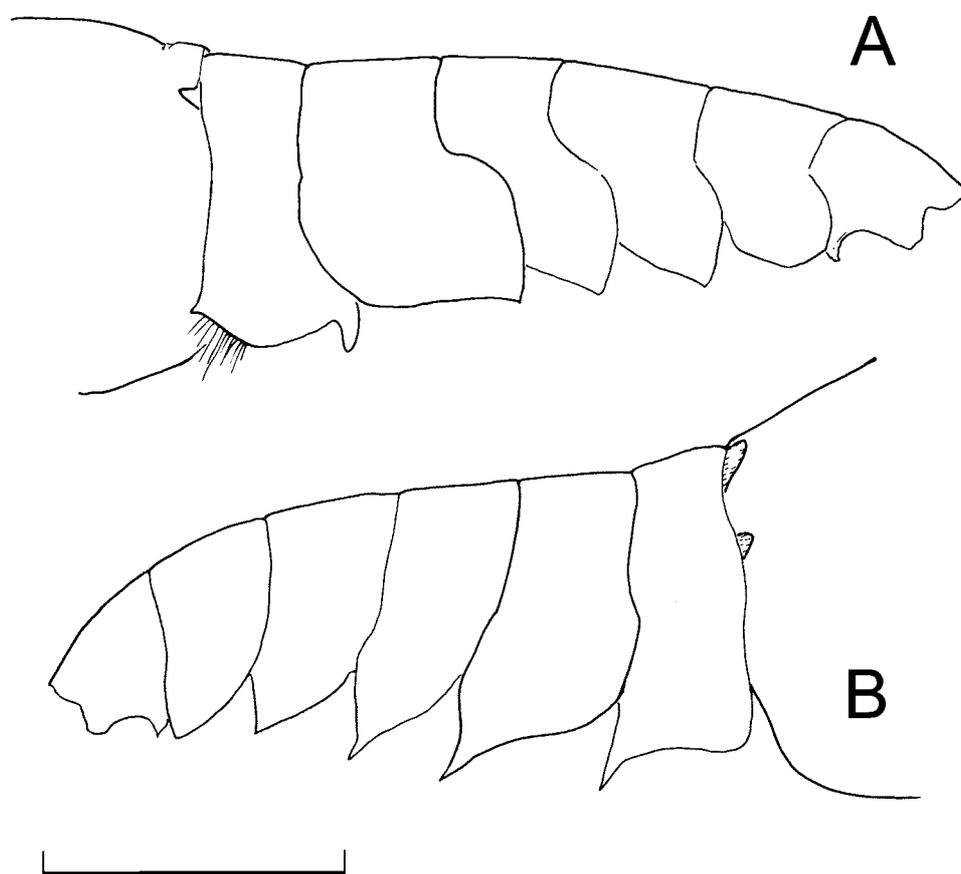


FIGURE 26. *Zuzalpheus regalis* (Duffy 1996). Male 2.5 mm (VIMS 93CBC4802): a, abdomen, lateral view. *Zuzalpheus rathbunae* (Coutière 1909). Male 2.4 mm (VIMS 88SB12503): b, abdomen, lateral view. Scale bar = 1 mm.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner very obtusely angular, and posterior margin with cardiac notch distinct. *Rostrum* lanceolate, about as long as, but much narrower than, ocular hoods, and distally upturned. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly rounded, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes virtually absent, just a slightly swollen obtuse protuberance. Ocellary beak in lateral view

not rod-like. Stylocerite thick, mesial margin slightly concave, tip acute, distinctly shorter than distal margin of first segment of antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. Basicerite with strong sharp spine on dorsal margin, and with longer ventrolateral spine reaching about half length of second segment of antennular peduncle. Scaphocerite blade absent, acute lateral spine robust, with lateral margin slightly concave, normally not reaching distal margin of antennular peduncle; mesial corner at base of scaphocerite, obtuse. *Maxilliped 3* with distal circlet of spines on distal segment, and without ventrodiscal spine on antepenultimate segment

Major pereopod 1 massive, fingers shorter than half length of palm; fixed finger slightly shorter than dactyl; in ventral view, outer face of fixed finger with subtly obtuse protuberance. Palm of chela with distal superior margin produced into prominent rounded tubercle, occasionally with accessory acute spine on distoventral face. Merus, extensor margin strongly convex, ending in obtuse angle.

Minor pereopod 1 with palm less than 2 times longer than high; fingers clearly shorter than palm; dactyl simple, with flexor surface obliquely concave; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor surface obliquely concave, and no hint of second tooth. Extensor margin of merus convex, ending in obtuse angle.

Pereopod 2 with carpus 4-segmented, about as long as merus.

Pereopod 3 dactyl, biunguiculate, flexor tooth thicker than extensor tooth; merus without movable spines on flexor margin; mesial lamella on coxa present. *Pereopods 4 and 5* normal.

Pleura 1 of male with anterior corner prolonged into acute angle, and posterior corner acutely produced ventrally; pleura 2–5 of male produced into acute angle. *Pleopod 1* of male, with 3 or 4 setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines about one-third of distal margin; marginal convex lobe, absent; posterior corners adjacent to spines, obtuse. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with 2 to 4 fixed teeth on outer margin of exopod, usually removed from longer mobile spine.

Color (Plate 4). Translucent orange with sparse red chromatophores in anteriodorsal part of carapace; distal palm and fingers of major chela bright orange to brown orange; ovaries and developing embryos pale green (Duffy 1996c).

First larva. In the laboratory, three larvae were obtained from a wild-caught ovigerous female. The larvae were crawling megalopae very similar to those of *Z. elizabethae*, n. sp., but at an earlier stage. The pleopods are biramous, but unlike the ones in *S. elizabethae*, n. sp., they do not have any setae. Also, the telson is less rectangular and has only the two pairs of setae on the distal margin, without any spines.

Variations. The anterior corner of the male first pleura normally has a ventrally oriented acute angle; relatively few of the specimens examined here had a broadly rounded corner as the one illustrated from the holotype (Duffy 1996b), and this condition usually is associated with probable feminization due to abdominal parasitic isopods. The lateral spine of the scaphocerite seems to grow allometrically, it usually does not reach the distal edge of the antennular peduncle, but in the larger specimens it does reach that edge and occasionally it surpasses it slightly. The number of fixed teeth on the lateral edge of the uropodal exopod varies from 1 in the smallest specimens up to 4 or 5 in the rare largest ones, but the most frequent numbers are 3, 2, and 4. Some of the intraspecific variability seems to be associated with particular colonies (Duffy 1996c).

Hosts and ecology. We have found *Zuzalpheus regalis* almost exclusively within *Xestospongia* cf. *subtriangularis* and *Hyattella intestinalis*. On a few occasions we have collected this shrimp from *Lissodendoryx* cf. *strongylata* and *Hymeniacion caerulea*. Eusocial colonies in a marine animal were first described in *Z. regalis*: dense populations (up to 300 individuals) of this species have a single reproductive female, distinct cohorts from a single colony are genetically related, and a certain degree of labor division has been described (Duffy 1996a; Duffy *et al.* 2002).

Distribution. Western Atlantic: known only from the vicinity of the type locality at Carrie Bow, Belize.

Remarks. There are three additional species in the western Atlantic that are similar to *Z. regalis*. These are *Zuzalpheus elizabethae*, n. sp., *Z. rathbunae*, and *Z. filidigitus*. These small shrimp are genetically distinct (Duffy 1996c) and can be separated by several morphological characters (Table 2). The ventral projections on the abdominal pleura in *Z. regalis* are more rounded than those of *Z. rathbunae* and *Z. elizabethae*, n. sp. The second chela has thicker fingers in *Z. elizabethae*, n. sp. and lastly, *Z. rathbunae* has an acute projection over the base of the dactyl of the major chela, instead of the more rounded protuberance of the other two species.

***Zuzalpheus ruetzleri* (Macdonald and Duffy 2006) n. comb.**
(Plate 4)

Synalpheus “*bousfieldi* blade”, in Morrison *et al.*, 2004, and in Macdonald *et al.*, 2005.

Material examined. (1) **Holotype:** ♂, (USNM 1092312, VIMS 01CBC4502), 3.6 mm, Sand Bores, Belize, 30 April 2001, in *Hymeniacidon* cf. *caerulea*, 1–2 m.

(2) **Allotype:** ♀, (USNM 1092313, VIMS 01CBC4501), 4.1 mm, Sand Bores, Belize, 30 April 2001, in same individual *H. cf. caerulea* as holotype.

(3) **Paratypes.** 1 ♂ (USNM 1092314, original VIMS 01CBC6101), 3.1 mm, Sand Bores, Belize, 2 May 2001, in *H. cf. caerulea*, 1–2 m. 2 ♀ (USNM 1092315, VIMS 01CBC5601, 01CBC5602), 3.5 mm, 3.2 mm, Sand Bores, Belize, 2 May 2001, in *H. cf. caerulea*, 1–2 m. 1 ♀ (AMNH 18494, VIMS 01CBC6301), 4.4 mm, Sand Bores, Belize, 2 May 2001, in *H. cf. caerulea*, 1–2 m. 1 ♂ (USNM 1092316, VIMS 01CBC6302), 4.0 mm, Sand Bores, Belize, in same *H. cf. caerulea* as VIMS 01CBC6301.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. *Rostrum* longer than orbital teeth, and slightly narrower, distally upturned; margins in dorsal view straight. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly acute, separated from rostrum by deep adrostral sinus. Ocular process triangular, flanged posteriorly onto lower side of eye. *Stylocerite* acute, with blunt tip; mesial margin concave; surpassing midpoint of first segment of antennular peduncle; latter without ventromesial tooth, with two basal ventral processes. *Basicerite* with dorsomesial corner rounded, lateral spine reaching distal half of third segment of antennular peduncle. *Scaphocerite* with well-developed blade, reaching to almost half length of lateral spine; acute lateral spine robust, slightly surpassing basicerite spine, slightly overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal cirlet of spines on distal segment, without ventrodiscal spine on antepenultimate segment.

Major pereopod 1 massive, fingers clearly less than half length of palm; fixed finger slightly shorter than dactyl. Palm of chela with distal superior margin forming a protuberance, which is secondarily produced distally, slightly curved downward, toward dactyl.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with 2 distinct distal teeth, subequal in length, and parallel to dactyl axis; transverse dorsal setal combs on dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, and 2 distinct distal teeth subequal in length.

Pereopod 2 with carpus 5-segmented, subequal to merus. Both fingers terminating in narrow, curved tooth.

Pereopod 3 slender; dactyl biunguiculate, with flexor tooth clearly thicker than extensor tooth; mesial lamella on coxa present. Pereopods 4 and 5 normal.

Pleura 1 of male with posterior corner distinctly produced ventrally into small, anteriorly directed hook; second pleura of male broadly rounded; third to fifth pleura of male progressively acute, but not pointed. *Pleopod 1* of male, with 2 terminal setae on endopod; second pleopod of male with marginal setae on exopod

originating in distal 1/2; appendix interna present on second to fifth male pleopods. *Telson* with marginal convex lobe; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with a single fixed tooth on outer margin of exopod distinctly removed from the mobile one, which is longer and more slender than adjacent inner fixed tooth.

Color (Plate 4). Non-descript, translucent with dull gold tinge to thickened parts of cuticle; distal palm and fingers of major chela brownish; ovaries and eggs pale pink to olive green to chestnut brown.

Variation. The length of the scaphocerite blade ranges from 1/3 to 2/3 length of lateral spine of scaphocerite. The relative length of the distal teeth on the fingers of the minor first pereopod also vary, with the distal tooth larger than the proximal tooth in some specimens, while in others the teeth are subequal.

Hosts and ecology. In Belize, *Zuzalpheus ruetzleri* appears to be a specialist on the cryptic midnight-blue sponge *Hymeniacion cf. caerulea*. It is almost invariably found as a single heterosexual pair within a sponge.

Distribution. San Blas Islands, Panama (Macdonald and Duffy 2006), Belize Barrier Reef (Macdonald and Duffy 2006; this study).

Remarks. *Zuzalpheus ruetzleri* belongs to the complex of morphologically similar species that includes *Z. brooksi*, *Z. bousfieldi* and *Z. chacei*. *Z. ruetzleri* is similar in color pattern to *Z. bousfieldi*, which also can inhabit *H. cf. caerulea*, making identification practical only with a microscope. However, the presence of a blade on the scaphocerite is a remarkably consistent character differentiating these two species, and the two morphological types (bladed and unbladed) appear to mate assortatively.

***Zuzalpheus sanctithomae* (Coutière, 1909) n. comb.**

(Plate 5)

Synalpheus sanctithomae, Coutière 1909:61–62, Fig. 35; Christoffersen 1979:352, Figs. 29, 30; Dardeau 1984:104 (and synonymy)

Material examined. (1) Syntype ♂ and ♀ (USNM 24782), 3.2 and 3.3 mm (rostrum excluded), respectively, off St. Thomas, Virgin Islands.

(2) 1 ovigerous ♀ (VIMS 03CBC1810), 3.2 mm, 1 ♂ (VIMS 03CBC1816), 2.7 mm, outer ridge at Carrie Bow Cay, Belize, 19 April 2003, in *Hyattella intestinalis*, 15–20 m.

(3) 2 ovigerous ♀ (VIMS 04CBC3901, 04CBC3902), 2.7 and 2.9 mm, 3 ♂ (VIMS 04CBC3904, 04CBC3905, 04CBC3906), 2.6, 2.9, 2.9 mm, outer ridge at Curlew Reef, Belize, 15 March 2004, in *Hymeniacion caerulea*, 20 m.

(4) 1 ovigerous ♀ (VIMS 03CBC6301), 3.5 mm, 1 ♂ (VIMS 03CBC6302), 3.1 mm, fore-reef slope, N end of Gladden Reef, Belize, 28 April 2003, in *Hymeniacion caerulea*, 8–11 m.

(5) 1 ovigerous ♀ (VIMS 95CBC4401), 2.9 mm, outer ridge at Carrie Bow Cay, Belize, 1 July 1995, in *Lissodendoryx* sp., 15–20 m.

Diagnosis. Body subcylindrical; carapace smooth, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. *Rostrum* clearly narrower than ocular hoods, about as long as ocular hoods, and distally upturned; margins in dorsal view, concave. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, bluntly triangular, margins concave or convex, separated from rostrum by deep adrostral sinus. Ocular processes present, but not elongated. Ocellary beak in lateral view rodlike. *Stylocerite* slender; mesial margin straight; tip blunt; reaching about as far as distal margin of first antennular peduncle; this latter segment with mesio-ventral tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorso-lateral corner, and with longer ventrolateral spine clearly overreaching tip of stylocerite. *Scaphocerite* with blade present, and with robust, acute lateral spine with lateral margin slightly concave, not overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped*

3 with distal circlet of spines on distal segment, and without ventro-distal spine on antepenultimate segment

Major pereopod 1 massive, fingers clearly not longer than half length of palm; fixed finger reduced, much shorter than dactyl; in ventral view, outer face of fixed finger with an obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute spine. Merus, extensor margin strongly convex. With distal angular projection.

Minor pereopod 1 with palm clearly less than two times longer than high; fingers clearly shorter than palm; dactyl with flexor surface obliquely concave, distal tip with subdistal accessory bump; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor margin straight, blade-like, and subdistal accessory bump. Extensor margin of merus convex, ending in right angle.

Pereopod 2 carpus with five segments; and equal or shorter than merus.

Pereopod 3 slender; dactyl biunguiculate, with extensor tooth wider at base than flexor tooth; merus without movable spines on flexor margin; mesial lamella on coxa present.

Pleura 1 of male with posterior corner distinctly produced ventrally and anteriorly, hook-like; second pleura of male rounded to obtuse. *Pleopod 1* of male with few terminal setae on endopod; second pleopod of male with marginal setae on exopod originating near midpoint; appendix interna on male pleopods 2–5 present. *Telson*, space between distal spines greater than one third of distal margin; marginal convex lobe present; posterior corners adjacent to spines acute. Projections not longer than wide. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with a single fixed tooth on outer margin of exopod.

Color (Plate 5). Live specimens are faint to bright orange in overall appearance, with distal palm and fingers of major chela more intensely orange. The ovaries and embryos are bright to olive green.

Hosts and ecology. In Belize we have collected *Zuzalpheus sanctithomae* most commonly from *Hymeniacidon caerulea*, but also from *Agelas clathrodes*, *Hyattella intestinalis*, and *Lissodendoryx* sp., at depths ranging from 1–20 m. It occurs usually as a single heterosexual pair in an individual sponge.

Distribution. Western Atlantic: Florida Keys (Gore 1981); Virgin Islands (Coutière, 1909); Belize (this study); Panama (J.E. Duffy, unpublished); Brazil (Christoffersen 1979).

Remarks. Identification of *Zuzalpheus sanctithomae* has been somewhat confused in the past due to a typographical error in Chace's (1972) key to the Western Atlantic *Synalpheus*, as described under our remarks on *Z. mcclendoni*.

***Zuzalpheus ul*, n. sp.**

(Figs. 27–30, Plate 5)

Synalpheus sp. 5, new species Ríos 2003:140, figures 2–26 through 2–29, plate I.

Material examined. (1) **Holotype** ♂, 3.5 mm (USNM 1019053, VIMS 01CBC4605), **allotype** ovigerous ♀, 3.9 mm (USNM 1019054, VIMS 01CBC4604), Sand Bores, Belize, 30 April 2001, in *Hymeniacidon caerulea*, 2 m.

(2) Ovigerous ♀, 4.0 mm, 2 ♂, 3.0, 3.8 mm (VIMS 90SB1008), San Blas Islands, Panama, 13 April 1990, no host recorded, 1 m; ♂, 5.1 mm, ovigerous ♀, 3.4 mm (VIMS 90SB0702), Porvenir and Aguadargana Islands, Panama, 12 April 1990, no host recorded.

Description of holotype. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomian corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. *Rostrum* clearly narrower than ocular hoods, slightly longer than ocular hoods, and distally upturned; margins in dorsal view, straight. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, squared off and blunt anteriorly, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes present, but not elongated. Ocellary beak in lateral view not rod-like. *Stylocerite* slender; mesial margin slightly concave; tip

acute; distinctly shorter than distal margin of first segment of antennular peduncle; latter without ventromesial tooth, and with 2 basal ventral processes. *Basicerite* without spine on dorsolateral corner, and with longer ventrolateral spine clearly overreaching tip of stylocerite. *Scaphocerite* blade reduced, acute lateral spine robust, with lateral margin slightly concave, not overreaching antennular peduncle, slightly shorter than basicerite lateral spine; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment; other mouthparts as figured.

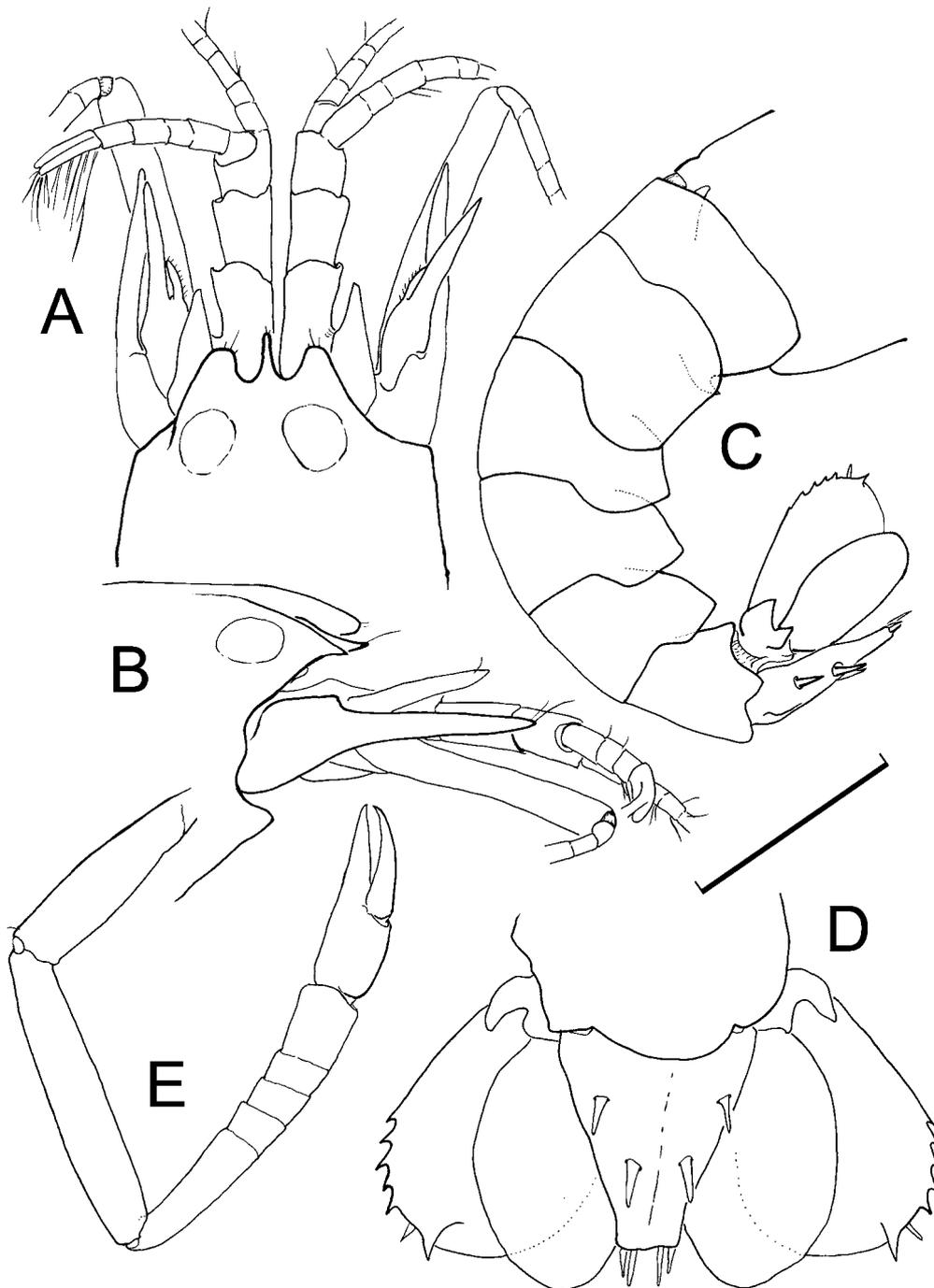


FIGURE 27. *Zuzalpheus ul*, n. sp. Holotype male 3.5 mm (USNM 1019053): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, abdomen, lateral view; d, telson and uropods, dorsal view; e, left second pereopod. Scale bar = 1.0 mm for a, b, d, 1.5 for c, and 0.9 mm for e.

Major pereopod 1 massive, fingers shorter than half length of palm; fixed finger reduced, noticeably shorter than dactyl; in ventral view, outer face of fixed finger without pronounced protuberance. Palm of chela with distal superior margin produced into prominent tubercle with acute downwardly directed spine on its ventral face. Merus, extensor margin convex, with distal angular projection.

Minor pereopod 1 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 very conspicuous; fixed finger with flexor margin straight, blade-like, and subdistal accessory bump. Extensor margin of merus convex, ending in obtuse angle.

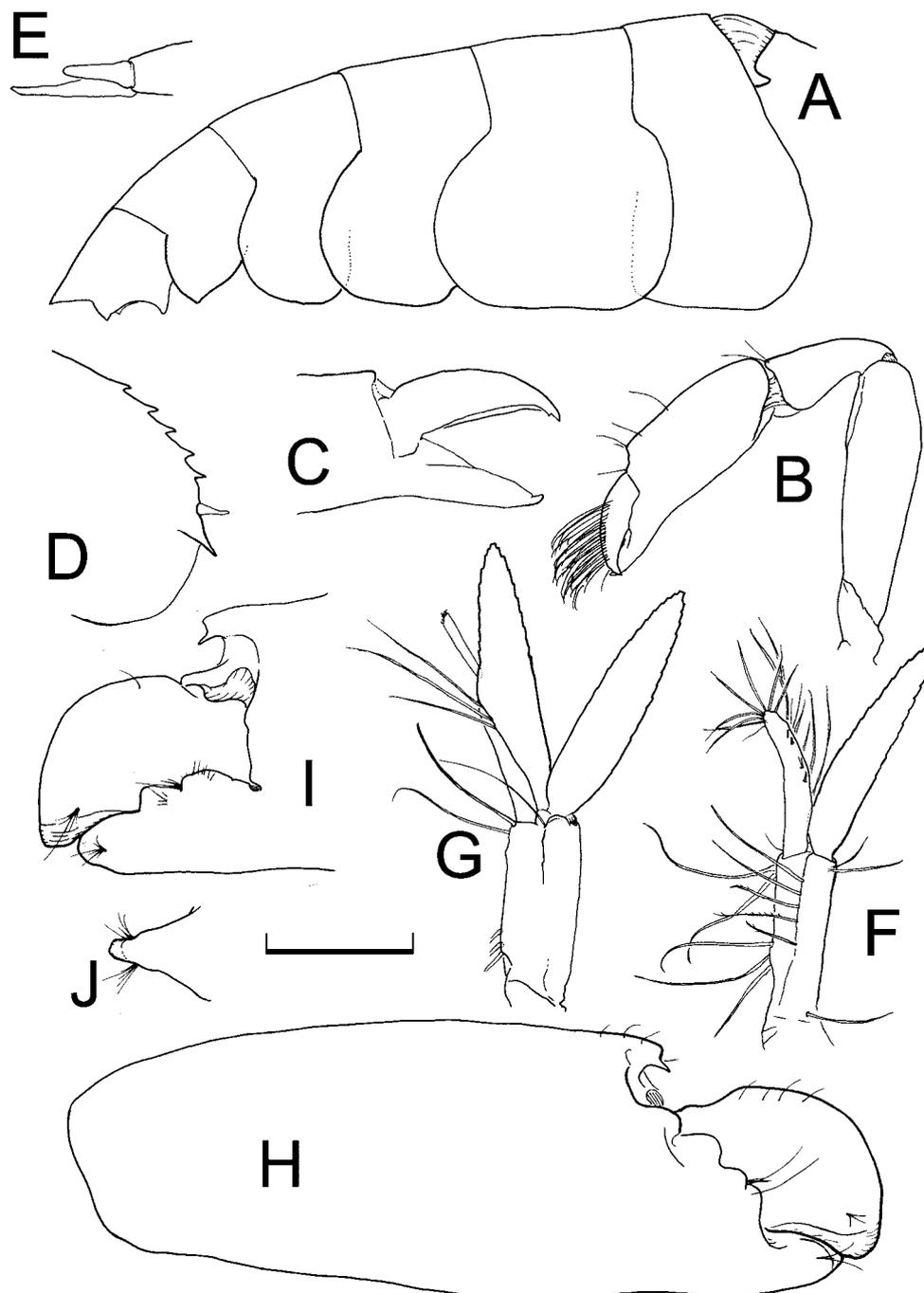


FIGURE 28. *Zuzalpheus ul.*, n. sp. Allotype female 3.9 mm (USNM 1019054): a, abdomen, lateral view; b, minor first pereopod, lateral view; c, same, detail of distal portion (setal combs omitted), alternate lateral view; d, outer margin of exopod of right uropod; e, right corner of telson, lateral view; f, left first pleopod; g, left second pleopod. Holotype male 3.5 mm (USNM 1019053): h, chela of major first pereopod, lateral view; i, same, detail of distal portion, alternate lateral view; j, same, tip of fixed finger, ventral view. Scale bar = 1 mm for a, b, 0.6 mm for c, f, g, 0.5 for d, e, and 0.9 for h, i, j.

Pereopod 2 with carpus 5-segmented, slightly longer than merus.

Pereopod 3 stout; dactyl biunguiculate, with clearly unequal teeth; and flexor tooth wider at base than extensor tooth; propodus with nine mobile spines on flexor margin and one pair on distal end; carpus with 1 mobile distal spine; merus without any spine on flexor margin; mesial lamella on coxa present. *Pereopod 4* similar to third, but weaker. *Pereopod 5* similar to fourth, but slender, without distal spine on carpus, and with 7 rows of setal combs on ventral face of propodus.

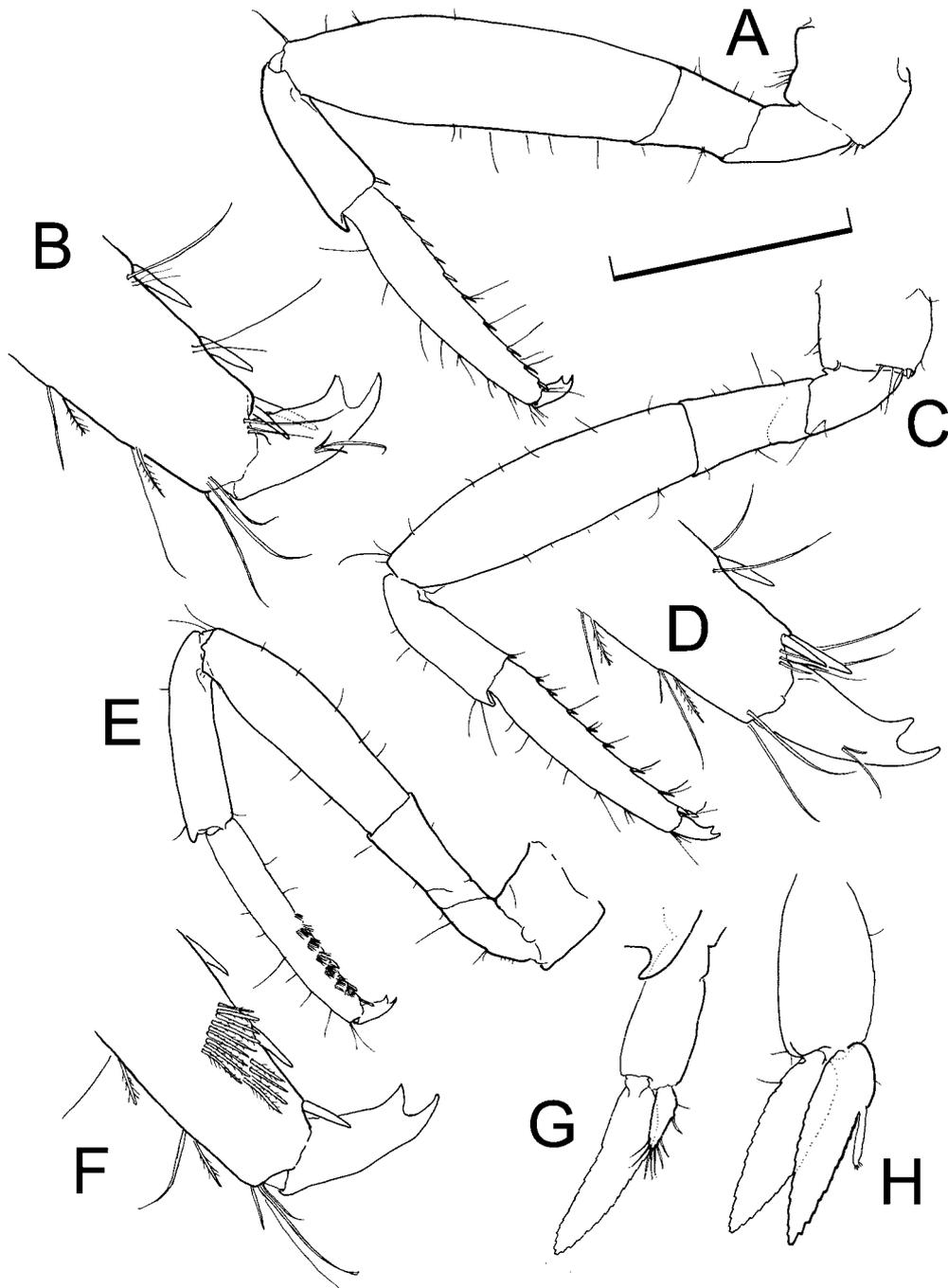


FIGURE 29. *Zuzalpheus ul*, n. sp. Holotype male 3.5 mm (USNM 1019053): a, left third pereopod; b, same, detail of distal portion; c, left fourth pereopod; d, same, detail of distal portion; e, left fifth pereopod; f, same, detail of distal portion; g, left first pleopod; h, left second pleopod. Scale bar = 1 mm for a, c, e, g, h, and 0.28 mm for b, d, f.

Pleura 1 of male with posterior corner distinctly produced ventrally and anteriorly, hook-like; second pleura of male with lower margin slightly concave, posterior corner broadly rounded; third to fifth pleura with posterior margin forming acute angle, not sharp. *Pleopod 1* of male with seven terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines about one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines obtuse. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with 5 fixed teeth on outer margin of exopod.

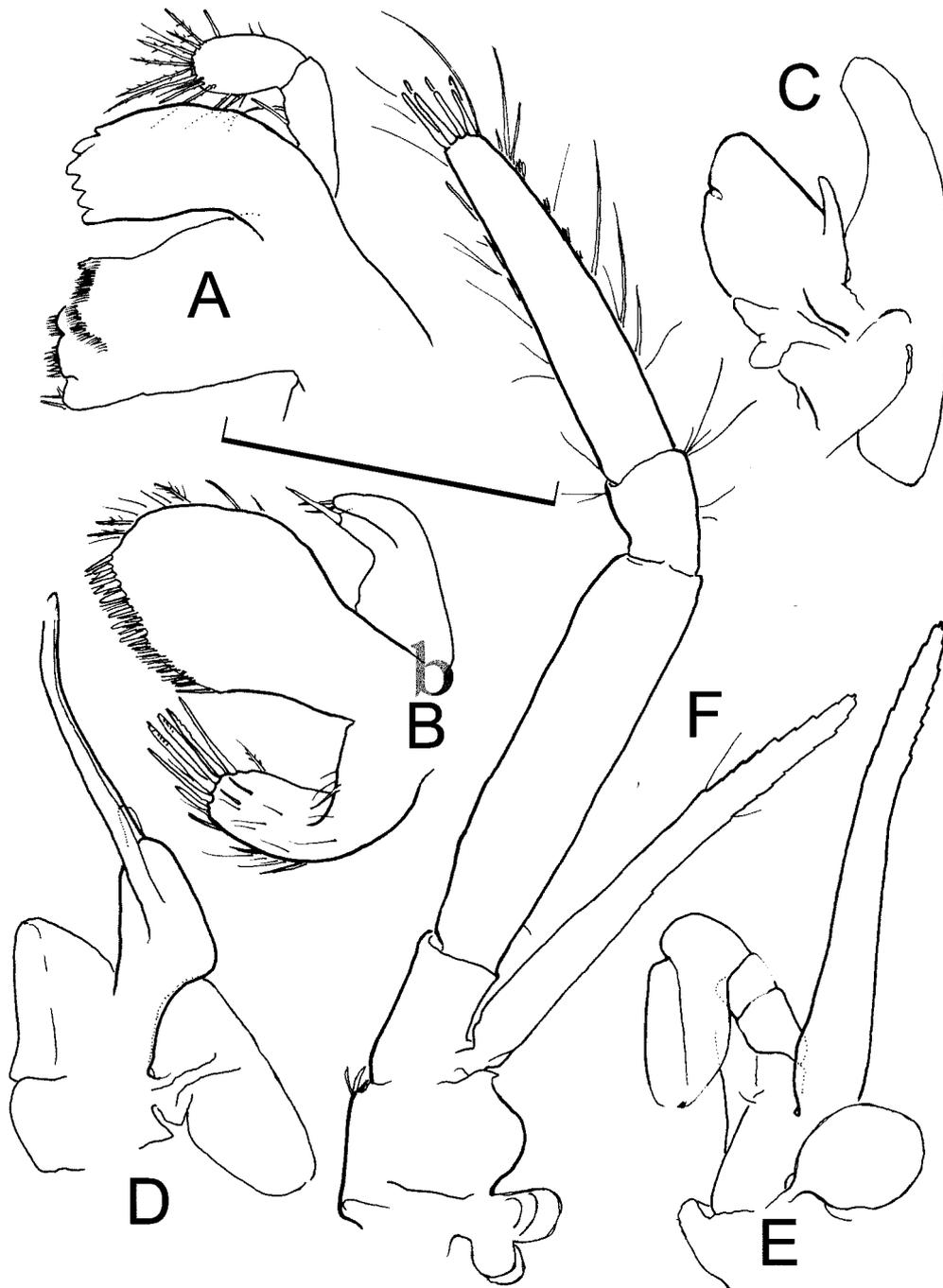


FIGURE 30. *Zuzalpheus ul*, n. sp. Mouthparts. Holotype male 3.5 mm (USNM 1019053): a, left mandible; b, left first maxilla; c, left second maxilla; d, left first maxilliped; e, left second maxilliped; f, left third maxilliped. Scale bar = 1 mm for a, b, and 1.8 mm for c, d, e, f.

Color (Plate 5). Live specimens are translucent with scattered reddish chromatophores regularly distributed. The distal edges of the major chela have a dull to bright orange tone. The digestive gland is maroon-green and the eyes are white. An ovigerous female had a faint hue of white along the lateral margins of the body and bright orange ovaries.

Etymology. The specific name is a Mayan word that describes a location in a space; it could be translated as “inside” or “within, with a sense of under”. It alludes to the sponge-dwelling habits of this and many other species of *Zuzalpheus*.

Variations. Several of the specimens have an abnormally reduced rostrum not reaching beyond half the length of the ocular hoods; one ovigerous female is lacking the rostrum altogether. The blade on the scaphocerite is conspicuously reduced, but always present, at least on one side, and it normally has short marginal setae throughout. In one female paratype, the spine overhanging the base of the dactyl on the major chela is slightly twisted inward. The number of fixed teeth on the outer margin of the uropodal exopod varies from 4 to 6, rarely 7, with 5 teeth most frequent.

Ecology. *Zuzalpheus ul*, n. sp., is one of several species found in canals of the midnight blue sponge *Hymeniacidon caerulea*. It has also been found inside a white unidentified soft sponge.

Distribution. San Blas Islands, Panama; Belize Barrier Reef (this study).

Remarks. This species is closely related to *Zuzalpheus pandionis*, *Z. dardeau*, n. sp., and *Z. yano*, n. sp., but can be distinguished from them by the presence of a minute blade on the scaphocerite, a rounded posterior corner on the second male pleura, and clearly unequal spines on the posterior margin of the telson (Table 1). Also, full grown individuals of *Z. ul*, n. sp., are never as large as those of the other species. Some of the specimens identified as *Synalpheus grampusi* by Coutière (1909) resemble *Z. ul*, n. sp., but the predicament of trying to retain that old name would prompt more instability in the taxonomy of the genus. See additional remarks under both *Z. pandionis* and *Z. yano*, n. sp.

***Zuzalpheus williamsi* (Ríos and Duffy, 1999) n. comb.**

(Plate 5)

Synalpheus williamsi Ríos and Duffy 1999: 541, fig. 1–6; Ríos 2003:152, figures.

Material examined. (1) **Holotype** ♂ (USNM 276158), 3.6 mm, **allotype** ovigerous ♀, 4.5 mm (USNM-276159), Carrie Bow Cay, Belize, 13 June 1996, in *Hymeniacidon caerulea*, 18 m.

(2) **Paratypes:** ♂, 4.4 mm, 2 ovigerous ♀, 4.3, 4.8 mm (USNM 276160), Carrie Bow Cay, Belize, 4 April 1993, in *H. caerulea*, 13 m;

(3) **Paratype** ♂, 2.3 mm (CNCR 17987) Carrie Bow Cay, Belize, 12 June 1996, in *H. caerulea*, 18 m.

(4) **Paratype** ♂, 3.7 mm (MNHN Na 13561) Ulagsukun Reef, Panamá, 17 January 1991, in *H. caerulea*, 1–2 m.

(5) 1 ♂ (VIMS 91P6301), 4.1 mm, Mamitupo Reef, San Blas Islands, Panama, 19 Jan 1991, in orange tubular sponge, 1–2 m.

Diagnosis. Body subcylindrical; carapace smooth, sparsely setose, with pterygostomial corner produced into bluntly acute angle, and posterior margin with cardiac notch distinct. *Rostrum* about as long as, but clearly narrower than, ocular hoods, and distally upturned; margins in dorsal view, straight; ventral margin convex. Orbitorostral process absent. Ocular hoods dorsally convex; in dorsal view, acute, separated from rostrum by deep adrostral sinus. Ocular processes broad. Ocellary beak in lateral view, with inner margin concave and exterior convex. *Stylocerite* slender; mesial margin slightly concave; tip acute; reaching about as far as distal margin of first antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. *Basicerite* with broad spine on dorsal margin, and with longer ventrolateral spine

reaching distal half of second segment of antennular peduncle. *Scaphocerite* blade broad, slightly reduced, acute lateral spine robust, with lateral margin slightly concave, clearly overreaching antennular peduncle; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circlet of spines on distal segment and without ventrodiscal spine on antepenultimate segment

Major pereopod 1 massive, fingers clearly not longer than half length of palm; fixed finger reduced, much shorter than dactyl; in ventral view, outer face of fixed finger with a strong obtuse basal protuberance. Palm of chela with distal superior margin produced into prominent tubercle with secondary acute spine on ventral surface. Merus, extensor margin strongly convex, with distal flat angular projection.

Minor pereopod 1 with palm clearly less than 2 times longer than high; fingers clearly shorter than palm; dactyl with flexor surface excavate, with subdistal accessory bump oriented perpendicular to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor surface obliquely concave, and subdistal accessory bump. Extensor margin of merus convex, with flat distal angular projection.

Pereopod 2 with carpus 5-segmented, slightly longer than merus.

Pereopod 3 slender; dactyl biunguiculate, with flexor tooth slightly thicker than extensor tooth; merus without movable spines on flexor margin; mesial lamella on coxa present. Pereopods 4 and 5 normal.

Pleura 1 of male with posterior corner distinctly produced ventrally into anteriorly directed hook; second pleura of male broadly rounded. *Pleopod 1* of male, with 4 or 5 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base; appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines greater than one-third of distal margin; marginal convex lobe present; posterior corners adjacent to spines rectangular. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with 3 to 6 fixed teeth on outer margin of exopod.

Color (Plate 5). Translucent faint gold to golden brown, with tips of chelae (fingers and distal part of palm included) of first pereopods bright orange to red; second legs golden; third to fifth, transparent; and traces of blue in the gut and in the branchiae. These traces were the same dark blue as the host sponge, *Hymeniacidon caerulea*, and they still can be seen in some of the preserved specimens (Ríos and Duffy 1999).

Variations. The number of immovable teeth on the lateral margin of the uropodal exopod varies from three to six, with a mode of four; this variation may relate to size and perhaps sex, considering that the smaller specimens have fewer teeth, and that the only 2 specimens with 6 teeth were males (Ríos and Duffy 1999).

Hosts and ecology. *Zuzalpheus williamsi* is most often found within the midnight-blue sponge *Hymeniacidon caerulea*. We have recorded occasional specimens in an unidentified orange tubular sponge growing among coral rubble (Ríos and Duffy 1999), and in another unidentified yellow sponge.

Distribution. Western Atlantic: San Blas islands, Panama; Belize Barrier Reef (this study).

Remarks. *Z. williamsi* can be unequivocally distinguished from the morphologically similar *Z. goodei* by several features of the latter, which include lack of ventrolateral protuberance on the fixed finger of the major chela; a wider submesial fixed tooth, a shorter mobile spine, and more fixed teeth on the outer margin on the uropodal exopod; the presence of a tuft of setae behind the anal opening; and the absence of marginal setae around the anal opening.

***Zuzalpheus yano*, n. sp.**

(Figures 31–34, Plate 5)

Synalpheus sp. 6, new species Ríos 2003:155, figures 2–30 through 2–33.

Synalpheus “*pandionis* small” Morrison *et al.* 2004.

Material examined. (1) **Holotype** ♂, 6.0 mm (USNM 1019055, VIMS 01CBC7402), **allotype** ovigerous ♀, 7.2 mm (USNM 1019056, VIMS 01CBC7401), Twin Cays, Belize, 26 April 2001 in *Lissodendoryx colombiensis*, 1–2 m.

(2) **Paratypes:** 1 ♂ (USNM 1019057, VIMS 94CBC14-14), 5.3 mm, Twin Cays, Belize, 20 August 1994, in *Lissodendoryx colombiensis*, 1–2 m. 1 ovigerous ♀ (USNM 1019058, VIMS 94CBC24-07), 5.5 mm, Twin Cays, Belize, 22 August 1994, in *Lissodendoryx colombiensis*, 1–2 m.

(3) 1 ovigerous ♀ (VIMS 94CBC1407), 6.4 mm, Twin Cays, Belize, 20 August 1994, in *Lissodendoryx colombiensis*, 1–2 m.

(4) 1 ♂ (VIMS 98CBC0902), 5.0 mm, 1 ovigerous ♀ (VIMS 98CBC0901), 5.4 mm, Sand Bores, Belize, 3 December 1998, in *Lissodendoryx* cf. *strongylata*, 1.5 m deep.

(5) 1 ovigerous ♀ (VIMS 93CBC6302), 5.3 mm, 1 ♂ (VIMS 93CBC6305), 4.6 mm, Sand Bores, Belize, 31 March 1993, in unidentified yellow tube sponge, 2 m.

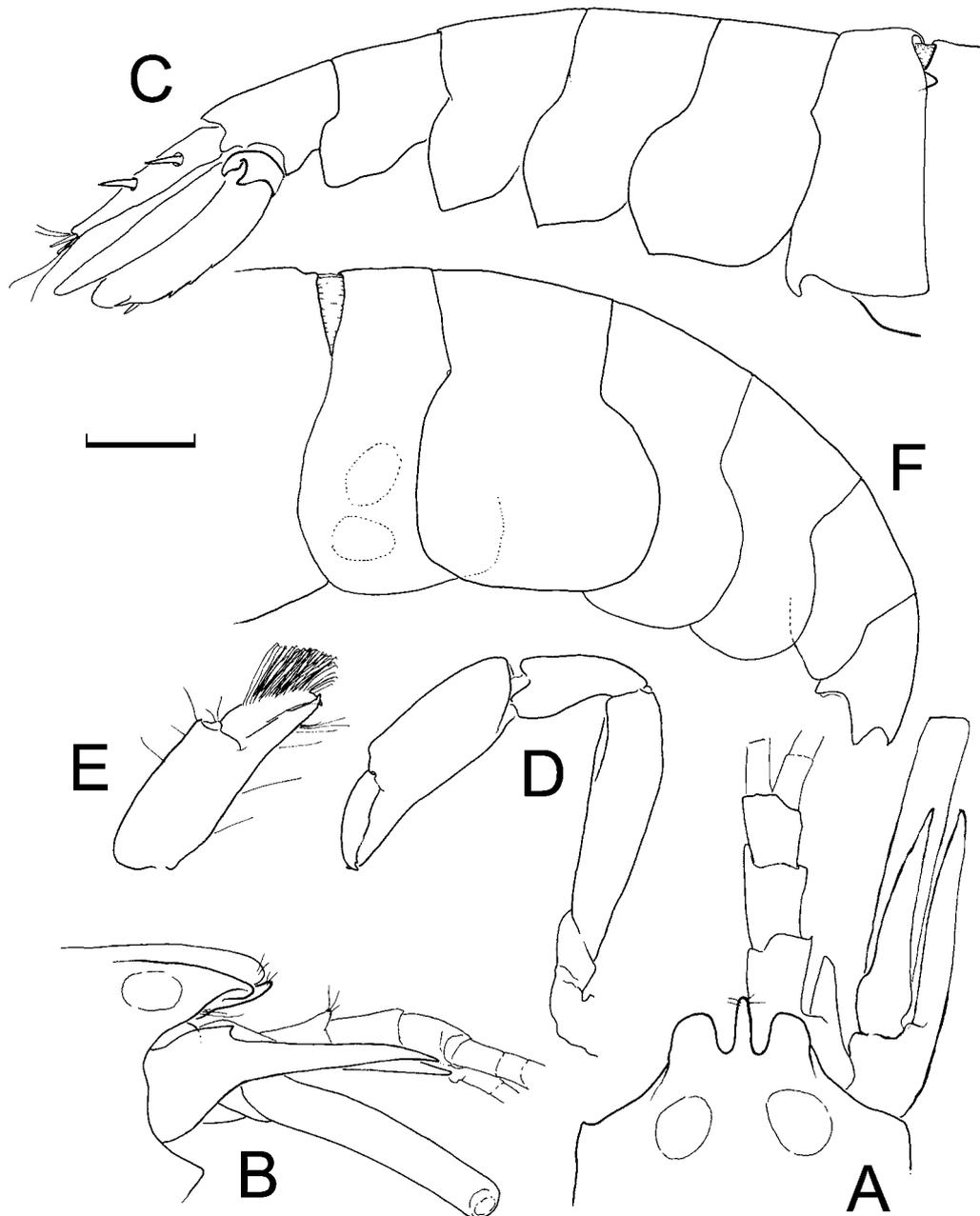


FIGURE 31. *Zuzalpheus yano*, n. sp. Paratype male 5.3 mm (USNM 1019057): a, anterior region of carapace and cephalic appendages, dorsal view; b, same, lateral view; c, abdomen, lateral view; d, minor first pereopod, lateral view; e, chela of same, alternate lateral view. Paratype ovigerous female 5.5 mm (USNM 1019058): f, abdomen showing two eggs, lateral view. Scale bar = 1.4 mm for a, b, and 1 mm for c, d, e, f.

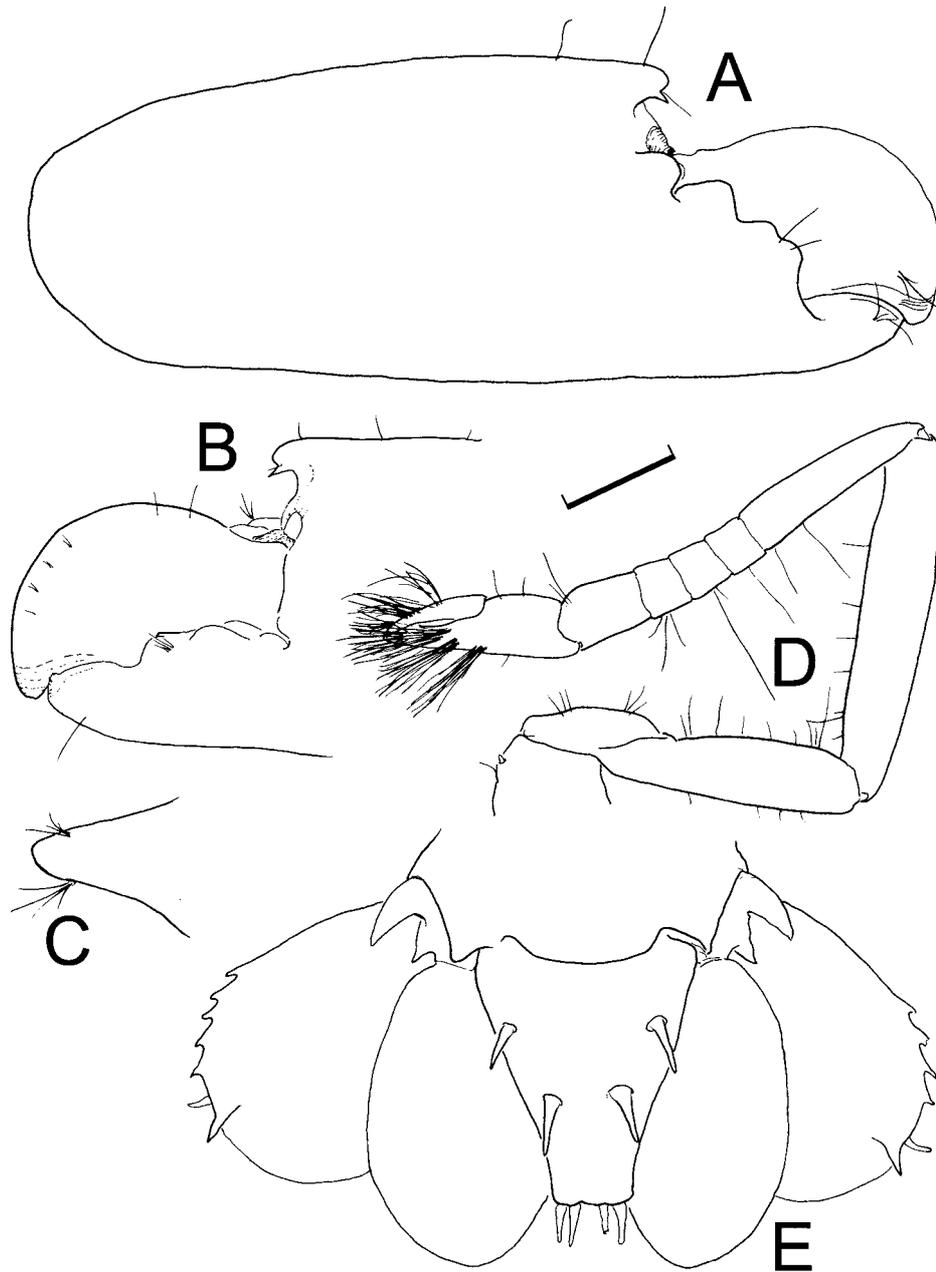


FIGURE 32. *Zuzalpheus yano*, n. sp. Paratype male 5.3 mm (USNM 1019057): a, chela of major first pereopod, lateral view; b, same, detail of distal portion, alternate lateral view; c, same, tip of fixed finger, ventral view; d, left second pereopod, lateral view; e, telson and uropods, dorsal view. Scale bar = 1 mm for a, b, 0.7 mm for c, e, and 0.6 for d.

Description of holotype. Body subcylindrical; carapace smooth, with scattered short setae; pterygostomian corner produced into blunt acute angle, and posterior margin with cardiac notch distinct. *Rostrum* lanceolate, slightly upturned and laterally compressed; narrower, but about as long as orbital hoods; these latter dorsally convex with flattened mesial slope wider than lateral edge, and converging under base of rostrum; in dorsal view, ocular hoods squared off and blunt anteriorly, margins convex, separated from rostrum by deep adrostral sinus. Ocular processes conspicuously broad. Ocellary beak in lateral view, broad. *Stylocerite* slender; mesial margin slightly concave; tip acute; reaching nearly as far as distal margin of first antennular peduncle; this latter segment without ventromesial tooth, and with 2 basal ventral processes. *Basicerite* with dorsolateral corner slightly produced into blunt acute angle; longer ventrolateral spine clearly overreaching tip of stylocerite. *Scaphocerite* blade totally absent, acute lateral spine robust, with lateral margin slightly con-

cave, barely overreaching antennular peduncle, and reaching slightly shorter than basicerite lateral spine; mesial projection at base of scaphocerite present. *Maxilliped 3* with distal circlet of spines on distal segment, and without ventrodistal spine on antepenultimate segment; remaining mouthparts as figured.

Major pereopod 1 massive, fingers shorter than half length of palm; fixed finger somewhat shorter than dactyl; in ventral view, outer face of fixed finger without any pronounced protuberance. Palm of chela with distal superior margin produced into prominent tubercle with downwardly directed acute spine on its ventral surface. Merus, extensor margin strongly convex, with distal angular projection.

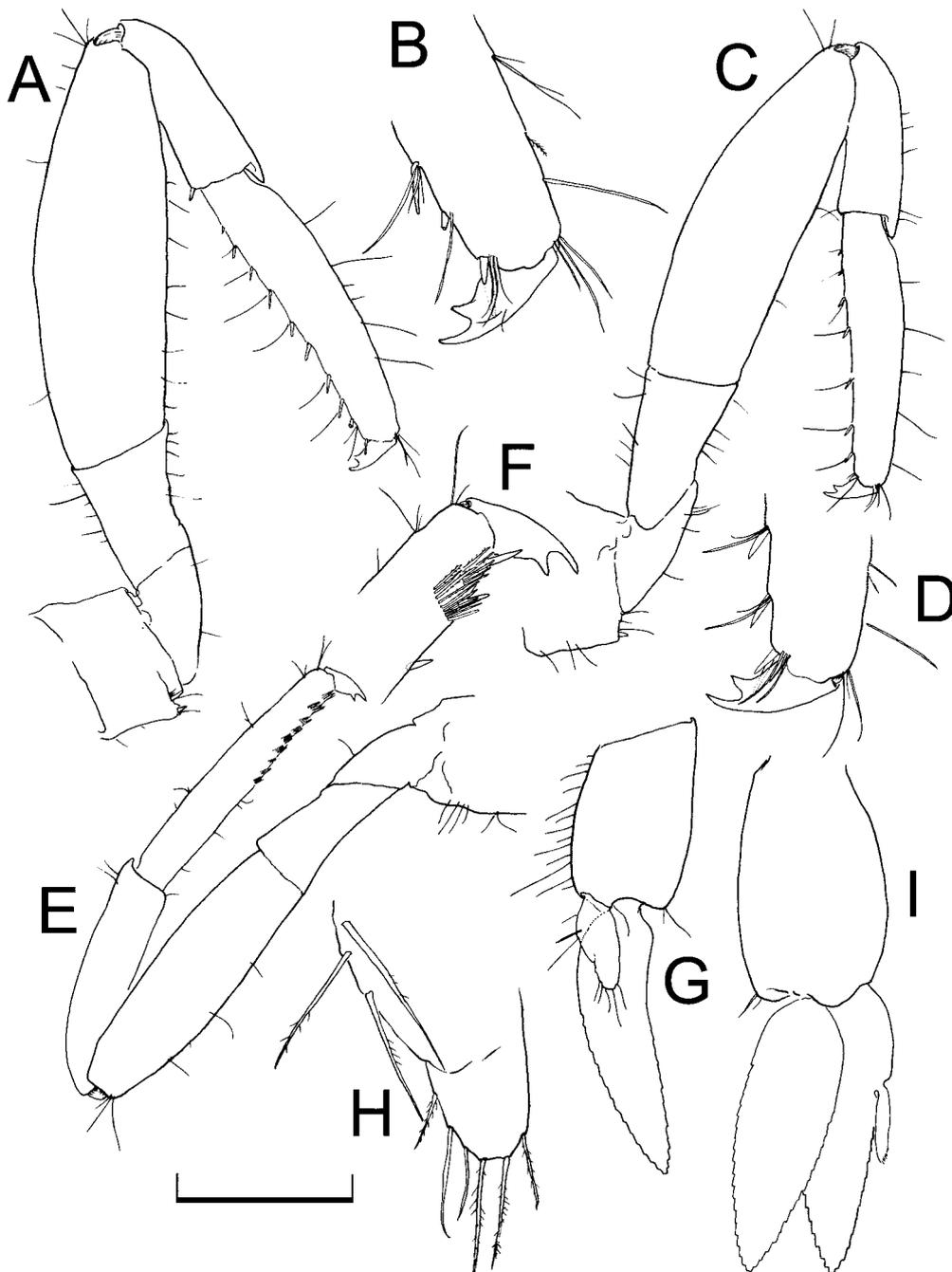


FIGURE 33. *Zuzalpheus yano*, n. sp. Paratype male 5.3 mm (USNM 1019057): a, right third pereopod; b, same, detail of distal portion; c, right fourth pereopod; d, same, detail of distal portion; e, right fifth pereopod; f, same, detail of distal portion; g, right first pleopod; h, same, detail of distal portion of endopod; i, right second pleopod. Scale bar = 1 mm for a, c, e, 0.4 mm for b, d, f, 0.8 for g, i, and 2 mm for h.

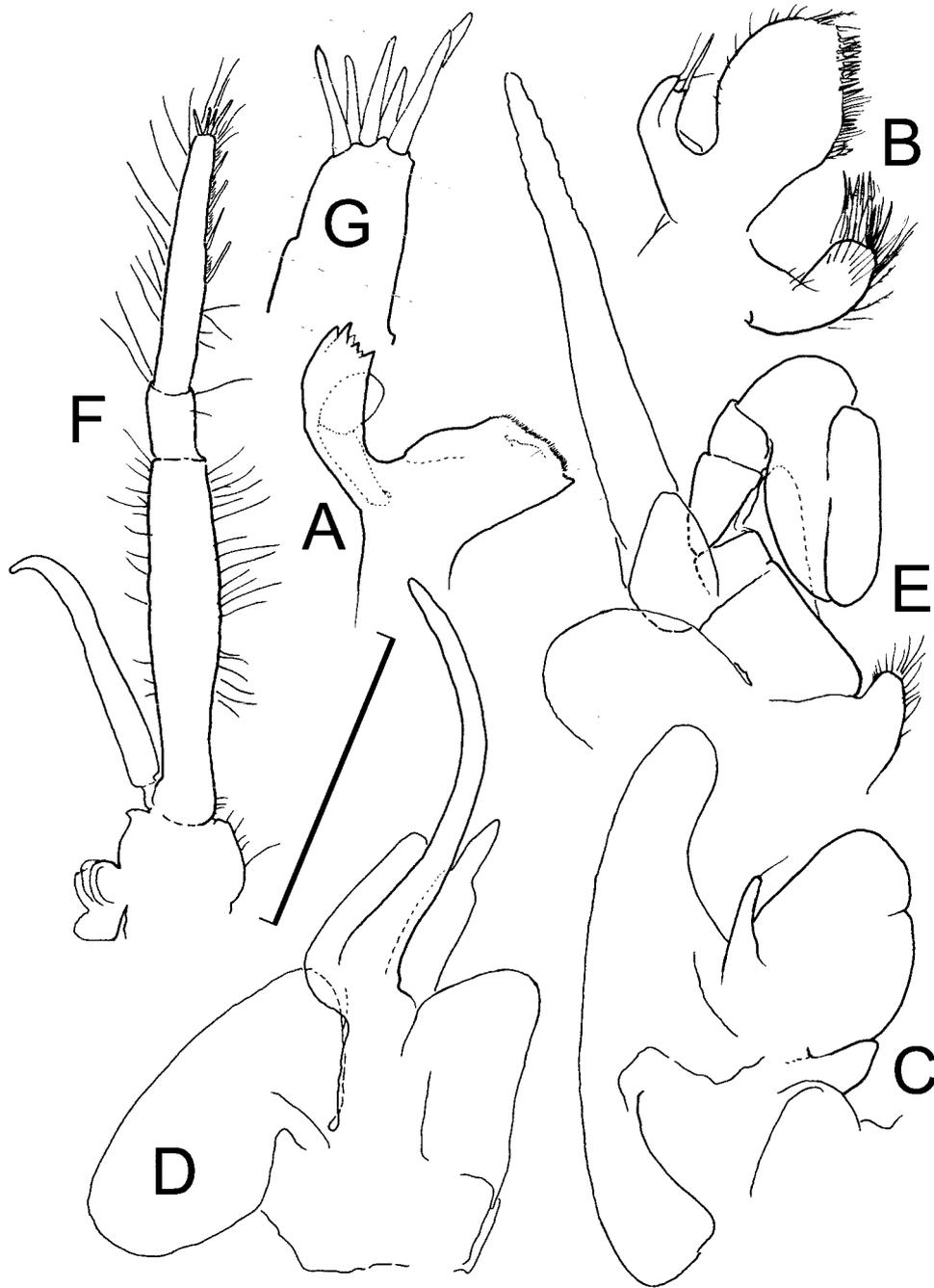


FIGURE 34. *Zuzalpheus yano*, n. sp. Mouthparts. Paratype male 5.3 mm (USNM 1019057): a, right mandible; b, right first maxilla; c, right second maxilla; d, right first maxilliped; e, right second maxilliped; f, right third maxilliped; g, same, detail of distal portion, alternate lateral view. Scale bar = 1 mm for a, b, c, d, e, 2 mm for f, and 0.5 mm for g.

Minor pereopod 1 with palm about 2 times longer than high; fingers clearly shorter than palm; dactyl with flexor margin straight, blade-like, with 2 distinct but unequal terminal teeth oriented parallel to dactyl axis; transverse dorsal setal combs on extensor surface of dactyl very conspicuous; fixed finger with flexor surface obliquely concave, and subdistal accessory bump. Extensor margin of merus convex, ending in right angle.

Pereopod 2 with carpus 5-segmented, distinctly longer than merus.

Pereopod 3 stout; dactyl biunguiculate, with flexor tooth thicker than extensor tooth; propodus of right leg with row of 8 (left leg with 9) mobile spines on lower margin and one pair on distal end; carpus with one mobile distal spine on flexor margin; merus without spines on flexor margin; mesial lamella on coxa present.

Pereopod 4 similar to third, but weaker. Pereopod 5 similar to fourth but slender, with 12 parallel rows of transverse setal combs, 3 mobile spines, and 1 distal pair of mobile spines on ventral face of propodus; carpus without distal spine.

Pleura 1 of male with posterior corner distinctly produced ventrally into anteriorly directed hook; second to fourth pleura of male with lower margin produced into acute angle; fifth pleura similar but more blunt. *Pleopod 1* of male, with 8 terminal setae on endopod; second pleopod of male with marginal setae on exopod originating close to base on external margin; appendix interna on second to fifth male pleopods, present. *Telson*, space between distal spines about one-third of distal margin; marginal convex lobe absent; posterior corners adjacent to spines not produced. Anal flaps, perianal setae, and postanal setal brush absent. *Uropods* with 5 fixed teeth on outer margin of exopod.

Color (Plate 5). Dull orange-brown to reddish in overall appearance, with brown tips of the major first chela. This latter feature was still evident in some preserved specimens as a translucent fringe. Ovaries and embryos are brick-red.

Etymology. The specific name is a Mayan word for "another" or "different" and was chosen to underscore the fact that this is yet another new species of *Zuzalpheus* in the complex related to *Z. pandionis*.

Variations. The number of fixed teeth on the outer margin of the uropodal exopod varies from 4 to 6, rarely 3 or 7, but the most frequent number is 5.

Hosts and ecology. We have found this species most frequently within the sponge *Lissodendoryx colombiensis*. Other occasional hosts include the sponges *Hymeniacidon caerulea*, *Pachypellina podatypa*, and an unidentified yellow sponge.

Distribution. Western Atlantic: Belize (this study), Bocas del Toro region, Panama (JED, pers. obs.).

Remarks. There is considerable morphological similarity between *Z. yano*, n. sp., and a group of species that includes *Z. longicarpus* and *Z. pandionis* (Table 1). *Z. yano* most closely resembles *Z. ul*, n. sp., which preferentially inhabits *Hymeniacidon caerulea*. However, *Z. yano*, n. sp., attains larger sizes, never has any trace of a blade on the scaphocerite, and has the second to fourth male pleurae more pointed.

Coutière (1909) erected *Synalpheus grampusi* for a group of specimens that resemble *Z. yano*, n. sp., but after examining the type series we are confident in erecting a new species. In the description of *S. grampusi*, Coutière (1909) recognized several diagnostic characters also present in *Z. yano*, n. sp., most notably the rounded ocular hoods, the shape of the chelae, the fixed teeth on the uropod, and the absence of a blade on the scaphocerite. However, the two largest syntypes (USNM 38399) of *S. grampusi* have a blade on the scaphocerite, which is why Chace (1972) decided to synonymize it with *S. pandionis* (see remarks under this species). Coutière (1909) called "anomalous" the specimen depicted in his figure 36a, and it is this illustration that most strongly resembles both his description of *S. grampusi* and *Z. yano*, n. sp., Chace (1972) suspected that the type series of *S. grampusi* includes a mixture of taxa, and suggested that "a new name might have to be assigned" for *S. grampusi* if proven valid. Furthermore, according to Article 72.4.1 of the International Code of Zoological Nomenclature (ICZN 1999), since Coutière (1909) referred to the specimens without blade as "anomalous", they should not be considered as syntypes. Consequently the only appropriate name-bearing specimens are those with a blade, *i. e.* the pair of largest specimens in lot USNM 38399, but the third specimen in the lot (a smaller ovigerous female without blade) is not a real syntype. We conclude that trying to conserve the name "*Synalpheus grampusi*" would only further confuse the taxonomy of the group.

Key to the species of *Zuzalpheus* and *Synalpheus* of the West Atlantic

Previous authors have emphasized the difficulty of constructing a reliable key to *Synalpheus* (Chace 1972; Dardeau 1984), particularly for juveniles and single specimens, and we concur. We have relied heavily on the keys of Chace and Dardeau, but have also made numerous changes. We have attempted to list the clearest

diagnostic characters first in each couplet. Where these are characters of chelae or other appendages frequently missing from specimens, we have tried to include other, sometimes less clearly diagnostic, characters of the carapace and abdomen that are usually present in even damaged specimens. Characters in parentheses are present in the designated taxon but cannot be used to exclude other species. Data on host associations and color in life are not included in the following key (see the species accounts) but are often very useful complements to morphological characters in identifying live specimens.

1. Dactyl of minor first chela with brush of long, distally curved setae on extensor surface (reduced to sparse group in *S. paranephtunus*); stylocerite no longer than first segment of antennular peduncle (*Zuzalpheus*) 2
- Dactyl of minor chela with scattered tufts of straight setae, but without thick brush on extensor surface; stylocerite distinctly longer than first segment of antennular peduncle. (Scaphocerite with well-developed blade, in most species wider than lateral spine, lateral spine distinctly longer than that of basicerite) (*Synalpheus*) 31
- 2(1). Both pairs of dorsal spines of telson arising in posterior half of telson. (Ocular hoods and rostrum blunt, broader than long) *Z. heardi*
- Anterior pair of dorsal spines of telson arising in anterior half of telson.....3
- 3(2). Both pairs of dorsal spines of telson arising in anterior half of telson.....4
- Posterior pair of dorsal spines of telson arising in posterior half of telson.....5
- 4(3). Carapace carinate (i.e., with longitudinal ridge) in anterior dorsal midline; ocular hoods distinctly broader than rostrum at base; scaphocerite with small blade; dactyl of minor chela bidentate distally; fixed finger of major chela subequal in length to dactyl *Z. anasimus*
- Carapace not carinate in anterior dorsal midline; ocular hoods similarly broad as rostrum at base; scaphocerite without blade; dactyl of minor chela strongly tridentate distally; fixed finger of major chela distinctly shorter than dactyl..... *Z. pectiniger*
- 5(3). Carpus of second pereopod composed of four segments 6
- Carpus of second pereopod composed of five segments..... 11
- 6(5). Basicerite (i.e., basal segment of antennal peduncle) with strong dorsal spine7
- Basicerite (i.e., basal segment of antennal peduncle) lacking dorsal spine10
- 7(6). Second through fifth pleura of male each tapering to acute tip ventrally 8
- Second through fifth pleura of male obtuse, each terminating in blunt, rounded angle ventrally9
- 8(7). First pleura of male with anteroventral corner produced into acute point; palm of major first chela with distal tubercle armed with small spine *Z. elizabethae*
- First pleura of male with anteroventral corner rounded, broadly obtuse; palm of major first chela with distal tubercle lacking spine *Z. rathbunae*
- 9(7). First pleura of male with anteroventral corner produced into acute point; fingers of second pereopods lacking terminal tufts of long setae *Z. regalis*
- First pleura of male with anteroventral corner rounded, broadly obtuse; fingers of second pereopods bearing terminal tufts of long setae, giving fingers a narrow, tapering appearance..... *Z. filidigitus*
- 10(6). Third maxilliped terminating in cluster of setae (uniquely among species of *Zuzalpheus*); second through fifth pleura of male each tapering to acute tip ventrally; lateral spine of basicerite nearly equal in length to that of scaphocerite *Z. barahonensis*
- Third maxilliped terminating in cirlet of 8–10 stout spines (as in most species of *Zuzalpheus*); second through fifth pleura of male obtuse, each terminating in blunt, rounded angle ventrally; lateral spine of basicerite distinctly shorter than that of scaphocerite *Z. agelas*
- 11(5). Dorsal margin of basicerite with distinct spine directed anterodorsally *Z. kensleyi*
- Dorsal margin of basicerite rounded, rectangular, or with short point.....12

- 12(11). Both fixed finger and dactyl of minor first pereopod with excavate inner (flexor) surfaces, dactyl with setae on extensor surface sparse, not clearly organized into rows *Z. paraneptunus*
 Fixed finger of minor first pereopod blade-like, without excavate inner surface, dactyl with thick brush of setae on extensor surface.....13
- 13(12). Lateral branch of uropod with single fixed tooth on lateral margin anterior to movable spine.....14
 Lateral branch of uropod with two or more fixed teeth on lateral margin anterior to movable spine 24
- 14(13). Scaphocerite with blade15
 Scaphocerite without blade17
- 15(14). Scaphocerite blade extending less than $\frac{1}{2}$ length of lateral spine; fingers of minor first chela distally bidentate*Z. ruetzleri*
 Scaphocerite blade extending $\frac{3}{4}$ or more the length of lateral spine; fingers of minor first chela not distally bidentate16
- 16(15). Major first chela with fingers curved laterally; distal margin of telson broad, with fan of plumose setae*Z. mcclendoni*
 Major first chela with fingers not curved laterally, approximately straight; distal margin of telson narrow, with fewer than six plumose setae..... *Z. sanctithomae*
- 17(14). Third pereopod with thin lateral flanges on flexor margins of merus and carpus, forming concavity on ventral (flexor) surfaces of both segments *Z. androsi*
 Third pereopod without lateral flanges, merus and carpus smooth and ovoid in cross-section.....18
- 18(17). Dactyl of minor first pereopod with two parallel longitudinal rows of long setae on extensor surface .
*Z. chacei*
 Dactyl of minor first pereopod with brush of long setae, sometimes consisting of many short transverse rows, on extensor surface19
- 19(18). Ocular hoods extremely short and broad, much broader than long; telson with both pairs of “dorsal” spines arising directly from lateral margins *Z. brevifrons*
 Ocular hoods at least as long as broad; telson with anterior pair or both pairs of dorsal spines arising from dorsal surface20
- 20(19). Third and fourth pleura of male with concavity on ventral edge, producing a W-shaped margin; dactyl of major first pereopod with distinct subterminal constriction on flexor margin, forming ventrally directed tooth at distal end of dactyl*Z. herricki*
 Third and fourth pleura of male with ventral margins broadly rounded; dactyl of major first pereopod with smoothly curving flexor margin, lacking distinct constriction or distinct terminal tooth.....21
- 21(20). Palm of major first chela terminating in slightly curved spine directed downward, toward dactyl (anterior pair of dorsal spines on telson arising from very near lateral margin)22
 Palm of major first chela terminating in acute tubercle directed forward or slightly upward; anterior pair of dorsal spines on telson distinctly removed from lateral margin23
- 22(21) Lateral spines of basicerite and scaphocerite short, not reaching beyond distal margin of second segment of antennular peduncle; telson squat, length rarely greater than $\frac{3}{4}$ width*Z. carpenteri*
 Lateral spines of basicerite and scaphocerite long, reaching beyond midpoint of third segment of antennular peduncle; telson not squat, length subequal to or greater than width.....*Z. bousfieldi*
- 23(21). Palm of major first chela terminating in conical tubercle directed upward.....*Z. brooksi*
 Palm of major first chela terminating in tubercle directed forward.....*Z. idios*
- 24(13). Lateral spine of basicerite less than $\frac{3}{4}$ length of lateral spine of scaphocerite25
 Lateral spine of basicerite more than $\frac{3}{4}$ length of lateral spine of scaphocerite28
- 25(24). Basicerite with dorsal margin rounded or forming an obtuse angle26
 Basicerite with dorsal margin forming acute point27
- 26(25). Chela of major first pereopod with fixed finger less than half length of dactyl; cardiac notch distinct .

.....	<i>Z. disparodigitus</i>	
Chela of major first pereopod with fixed finger more than half length of dactyl; cardiac notch indistinct, shallow, with strongly obtuse superior angle	<i>Z. longicarpus</i>	
27(25). Fixed finger of major first chela with distinct lateral protuberance at base; lateral branch of uropod with 3–6 fixed teeth	<i>Z. williamsi</i>	
Fixed finger of major first chela without distinct lateral protuberance at base, lateral margin appearing straight or gently rounded in ventral view; lateral branch of uropod with 6–10 fixed teeth ...	<i>Z. goodei</i>	
28(24). Ocular hoods slender, approximately triangular, tapering to blunt distal points; fingers of minor first chela distinctly bidentate, with two rod-shaped distal teeth each	<i>Z. dardeaui</i>	
Ocular hoods squared to broadly rounded; fingers of minor first chela with teeth obscure, reduced to shallow bumps		29
29(28). Scaphocerite without blade	<i>Z. yano</i>	
Scaphocerite with blade		30
30(29). Telson with lateral and mesial pairs of spines on posterior margin approximately equal in length; lateral branch of uropod with small lobe visible between posteriormost fixed tooth and movable spine; fixed finger of major first chela with distinct lateral protuberance at base	<i>Z. pandionis</i>	
Telson with lateral pair of spines on posterior margin distinctly shorter than mesial pair; lateral branch of uropod with posteriormost fixed tooth closely adjacent to movable spine, and no lobe visible; fixed finger of major first chela without distinct lateral protuberance at base	<i>Z. ul</i>	
31(1). Ocular hoods triangular, not much broader than rostrum		32
Ocular hoods elongate, much broader than rostrum		35
32(31). Rostrum with distinct ventral process separating eyes; palm of major first chela lacking distal tooth or spine; merus of pereopod 3 short and broad, less than 2.5 times as long as broad	<i>S. curacaoensis</i>	
Rostrum with ventral process lacking or vestigial, not preventing contact between the eyes; palm of major first chela with distal tooth or spine; merus of pereopod 3 about 4 times as long as broad		33
33(32). Ocular hoods and rostrum obtuse, reduced to shallow bumps; stylocerite rounded distally; basicerite rounded dorsally	<i>S. obtusifrons</i>	
Ocular hoods and rostrum acute; stylocerite tapering to slender tip; basicerite acute dorsally		34
34(33). Palm of major chela with distinct spine and a single blunt tubercle on distal margin; dactyl of major first chela squared off, with anterior margin nearly flat and perpendicular to long axis of chela	<i>S. minus</i>	
Palm of major chela with spine and two blunt tubercles on distal margin; dactyl of major first chela smoothly curved	<i>S. brevicarpus</i>	
35(31). Dactyls of three posterior pairs of pereopods with triangular projection on flexor margin, distal tooth approximately perpendicular to axis of dactyl and distinctly broader than proximal tooth		36
Dactyls of three posterior pairs of pereopods lacking triangular projection on flexor margin, distal and proximal teeth subparallel to axis of dactyl and similar in breadth		37
36(35). Triangular projection on flexor margin of dactyls of three posterior pairs of pereopods low and obtuse	<i>S. fritzmuelleri</i>	
Triangular projection on flexor margin of dactyls of three posterior pairs of pereopods large and acute	<i>S. hemphilli</i>	
37(35). Basicerite unarmed dorsally		38
Basicerite armed dorsally with strong spine		39
38(37). Palm of major first chela lacking distal spine; rostrum bearing strongly produced ventral process with cavity on posteroventral surface	<i>S. scaphoceris</i>	
Palm of major first chela with strong distal spine; rostrum with ventral process not strongly produced, posteroventral surface evenly convex	<i>S. townsendi</i>	

39(37). Palm of major first chela lacking distal spine	<i>S. tenuispina</i>
Palm of major first chela armed distally with curved spine.....	40
40(39). Merus of pereopod 3 unarmed; dactyls of three posterior pairs of pereopods with distal tooth on flexor margin narrower than proximal tooth.....	<i>S. apioceros</i>
Merus of pereopod 3 armed on distal half of flexor margin with series of movable spines; dactyls of three posterior pairs of pereopods with distal tooth on flexor margin broader than proximal tooth.....
.....	<i>S. dominicensis</i>

Discussion

Based on our review of the external morphology of shrimp in the genus *Synalpheus* Bate, 1888, mainly from the western Atlantic, and on associated molecular data (Morrison *et al.* 2004), we have concluded that the species historically included in the informal Gambarelloides group (Coutière 1908, 1909) are sufficiently distinct to represent a new genus. Consequently we have erected *Zuzalpheus*, n. gen., for 34 species, including six new to science (Table 3). The most reliable diagnostic characters that separate *Zuzalpheus* from *Synalpheus* are the brush of setae on the dactyl of the minor first cheliped, recognized by Coutiere (1909) in his establishment of the laevimanus (subsequently gamarelloides) group of species, and the mesial lamella on the coxae of the third leg, which we have not found in any of the species of *Synalpheus* we have examined from outside the new genus *Zuzalpheus*.

Synalpheus has been a source of vexation to taxonomists for over a century. The genus is second only to *Alpheus* in number of species within the species-rich family Alpheidae. Unlike *Alpheus*, however, the species of *Synalpheus* and *Zuzalpheus* have a relatively uniform general morphology with only slight, often subtle variations. Species of both the latter genera are generally small, with cryptic habits, and display apparently high intraspecific morphological variability and frequent morphological aberrations. Interestingly, such variations sometimes show high frequencies among the genetically related individuals within a given sponge, suggesting a hereditary basis (Duffy 1996a, 1996c). Dardeau (1984) also noted the commonness of intraspecific variability and aberrations in *Synalpheus*, and speculated on the possible causes, alluding to the lack of knowledge on the biology of *Synalpheus*. A better understanding of morphological variation in alpheids requires both a rigorous distinction among cryptic species, as we have tried to do in this contribution, and appreciation of what might be called normal variation. For example, sexual dimorphism is incompletely understood due to the likelihood of environmentally influenced sex determination, as has been documented in the alpheid genus *Athanas* (Suzuki 1970; Gherardi and Calloni 1993) and evidently in some species of *Zuzalpheus* (E. Tóth and R.T. Bauer, *pers. comm.*). Second, some characters appear to be related to size, and presumably age. Finally, in highly social species, distinctive morphological modifications of the queens are probably also influenced by social circumstances, as in *Z. filidigitus*, in which the queen's major chela is transformed into a second symmetrical minor chela (Duffy and Macdonald 1999). Lastly, caution has to be exercised also with parasitized specimens or those undergoing regeneration of appendages due to traumatic alterations.

Keeping such "normal" variation in mind, our collections of live animals have allowed us to exploit the sponge-dwelling habit of *Zuzalpheus*, and the pair-forming habit of many species, to assist in separating morphologically cryptic species. Separation of putatively conspecific collections by host of origin has allowed us to see that morphological variation, though subtle, is often discontinuous, and thus provides diagnostic character combinations. Consequently, given the generally strong host specificity (Macdonald *et al.* 2006), a positive identification of the host sponge usually hints at the identity of the shrimp (Duffy 1996c). In other cases, however, closely related species can occupy the same host (*e. g.*, *Z. brooksi* and *Z. idios*; *Z. dardeau* and *Z. yano*). These cases, which probably reflect secondary contact after allopatric speciation, are more difficult taxonomically, but can be resolved through careful examination of multiple specimens in conjunction with

color in life. Indeed, color patterns of live shrimp often differ distinctively between morphologically similar species (see color plates), and, along with host association, often provide the first clues to identity in the field. Finally, the occurrence of heterosexual pairs in many (non-eusocial) *Zuzalpheus* species allows an assessment of whether shrimp mate assortatively according to color and morphological traits; this pairing has been especially helpful in deciding whether putative taxa occupying the same host species are conspecific or not (Knowlton and Mills 1992; Knowlton et al. 1993).

TABLE 3. Left: List of species included in *Zuzalpheus*. Right: Species from outside the western Atlantic that may belong in the genus based on literature descriptions of morphology. † not recorded from Belize; * not recorded from the western Atlantic.

<i>Zuzalpheus</i>	
<i>Z. agelas</i> (Pequegnat & Heard, 1979)	* <i>Z. (?) crosnieri</i> Banner & Banner, 1983
† <i>Z. anasimus</i> (Chace, 1972)	* <i>Z. (?) parfaiti</i> Coutière, 1898
<i>Z. androsi</i> (Coutière, 1909)	* <i>Z. (?) sladeni</i> Coutière, 1908
† <i>Z. barahonensis</i> (Armstrong, 1949)	* <i>Z. (?) spongicola</i> Banner & Banner, 1981
<i>Z. bousfieldi</i> (Chace, 1972)	
<i>Z. brevifrons</i> (Chace, 1972)	
<i>Z. brooksi</i> (Coutière, 1909)	
<i>Z. carpenteri</i> (Macdonald and Duffy 2006)	
<i>Z. chacei</i> (Duffy, 1998)	
<i>Z. dardeaui</i> , n. sp.	
† <i>Z. disparodigitus</i> (Armstrong, 1949)	
<i>Z. elizabethae</i> , n. sp.	
<i>Z. filidigitus</i> (Armstrong, 1949)	
* <i>Z. gambarelloides</i> (Nardo, 1847)	
<i>Z. goodei</i> (Coutière, 1909)	
† <i>Z. heardi</i> (Dardeau, 1984)	
<i>Z. herricki</i> (Coutière, 1909)	
<i>Z. idios</i> , n. sp.	
<i>Z. kensleyi</i> , n. sp.	
<i>Z. longicarpus</i> (Herrick, 1891)	
<i>Z. mcclendoni</i> (Coutière, 1910)	
* <i>Z. mulegensis</i> (Ríos, 1992)	
* <i>Z. occidentalis</i> (Coutière, 1909)	
† <i>Z. osburni</i> (Schmitt, 1933)	
<i>Z. pandionis</i> (Coutière, 1909)	
<i>Z. paranepentus</i> (Coutière, 1909)	
<i>Z. pectiniger</i> (Coutière, 1907)	
† <i>Z. rathbunae</i> (Coutière, 1909)	
<i>Z. regalis</i> (Duffy, 1996)	
<i>Z. ruetzleri</i> (Macdonald and Duffy, 2006)	
<i>Z. sanctithomae</i> (Coutière, 1909)	
<i>Z. ul</i> , n. sp.	
<i>Z. williamsi</i> (Ríos and Duffy, 1999)	
<i>Z. yano</i> , n. sp.	

It has been 20 years since Dardeau (1984) made the last major contribution to the knowledge of the Gambarelloides group, but the taxonomy of *Synalpheus* and *Zuzalpheus* is still far from settled. For example, we believe we have substantially clarified the taxonomy of this genus from Belize. Yet, after 15 years of collecting, putative new species and problematic specimens occasionally turn up on nearly every field expedition. Moreover, our collections suggest that *Synalpheus* shrimp outside the genus *Zuzalpheus*, which we do not consider here, are equally rich in undescribed cryptic species, as also found in *Alpheus* (Knowlton and Keller 1983, 1985; Knowlton 1986; Knowlton and Mills 1992; Knowlton *et al.* 1993, Anker 2001). As specifically suggested both by Banner and Banner (1975) and by Dardeau (1984), detailed information on microhabitat gained through careful fine-scale sampling has greatly helped in separating species. This revised taxonomy should aid further studies on the ecology, evolution, and behavior (Duffy 2007) of this fascinating group of animals.

Shrimp in the genus *Zuzalpheus* are all, as far as is known, obligate inhabitants of living sponges, and most are relatively specialized in that they use only a small subset of the sponge species in their environment. Indeed, a careful analysis of the Belizean species concluded that over half the species are local specialists on a single sponge species (Macdonald *et al.* 2006). A few of these, such as *Z. pectiniger*, are known from only a single host species throughout their entire range, despite having been collected many times over the last century or more. At the other extreme are species such as *Z. chacei* that use several hosts in a given locality, and yet other hosts in different regions. The sponges that support the largest number of host-specialist species include *Agelas* spp. and *Sphaciospongia vesparium*, both of which commonly reach large size, are long-lived, and geographically widespread. The massive dimensions and diversity of internal space sizes (Duffy 1992) in sponges such as *Sphaciospongia vesparium* probably also help to explain why several species of *Zuzalpheus* frequently can be found inhabiting a single sponge. Sponges of this species, for example, may simultaneously house *Z. brooksi*, *Z. pectiniger*, *Z. longicarpus*, and occasionally *Z. mcclendoni* and *Z. dardeau*, n. sp.

Life in sponges has presumably influenced evolution and speciation in *Zuzalpheus* by subdividing shrimp populations into patchy, sedentary demes with restricted gene flow among them (Duffy 1993). Because sponges differ greatly in size, architecture, abundance, and chemistry, early studies on the evolutionary ecology of *Zuzalpheus* (Duffy 1996b,c) focused on the hypothesis that divergence among conspecific races of shrimp using different host species might provide a general mechanism for speciation in these animals, resulting in the modern diversity of *Zuzalpheus*. This hypothesis is consistent with the finding that *Z. brooksi* populations collected from *Sphaciospongia vesparium* are less dense, larger-bodied, and differ in parasite prevalence compared with conspecifics in the co-occurring sponge *Agelas clathrodes* (Duffy 1996b). It also appears consistent with the different host associations of some closely related species (Duffy 1996c). With the benefit of the larger picture provided by our revised taxonomy (this study) and analysis of host use patterns (Macdonald *et al.* 2006), we can reevaluate the generality of this hypothesis more rigorously.

Contrary to the original hypothesis of host-mediated divergence, it now appears that closely related species commonly share host species, and sometimes even individual hosts. Examples include the co-occurrence in *Sphaciospongia vesparium* of *Z. longicarpus* and *Z. dardeau*; co-occurrence in *Xestospongia* spp. of *Z. rathbunae*, *Z. regalis*, and *Z. filidigitus*; and co-occurrence in *Agelas* spp. of *Z. brooksi*, *Z. carpenteri*, and *Z. chacei*. On a practical level, this pattern of host use renders identification very challenging, as closely related and morphologically similar species often can be found using a given host species in the same region, sometimes in the same individual host. This surely explains a significant part of the historical difficulty of identifying and diagnosing *Synalpheus* species. From an evolutionary perspective, this sharing of host species among sister species of shrimp suggests that speciation in these shrimp probably proceeds initially via allopatric divergence of populations, perhaps on small geographic scales due to their restricted dispersal, followed by secondary contact under changing conditions. Perhaps the high host specificity of sponge-dwelling *Zuzalpheus* (Macdonald *et al.* 2006) results from subsequent ecological character displacement, i.e., divergence in host use driven by competition among the closely related sister taxa. This process has been invoked to explain

many cases of divergent resource use among sister taxa (Schluter 2000). While our taxonomic revision sets the stage for addressing these questions, detailed sampling and study across a wide geographic range will be necessary to answer them with confidence.

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Z. agelas male



Z. androsi female



Z. bousfieldi female



Z. bousfieldi male



Z. brevifrons female



Z. brooksi female

PLATE 1. *Zuzalpheus agelas*, male. (VIMS 04CBC4301) from *Agelas clathrodes*, Long Reef, Belize. *Zuzalpheus androsi*, female (VIMS 03CBC0901) from *Hyattella intestinalis*, Carrie Bow Cay, Belize. *Zuzalpheus bousfieldi*, female (VIMS 03CBC1201) from *Hyattella intestinalis*, Carrie Bow Cay, Belize. *Zuzalpheus bousfieldi*, male (VIMS 03CBC1202) from *Hyattella intestinalis*, Carrie Bow Cay, Belize. *Zuzalpheus brevifrons*, female (VIMS 03CBC3601) from unidentified sponge, Sand Bores, Belize. *Zuzalpheus brooksi*, female (VIMS 05FK14) from *Spheciospongia vesparium*, Key Largo, Florida, USA.



Z. carpenteri female



Z. carpenteri male



Z. chacei female



Z. dardeauui female



Z. dardeauui male



Z. elizabethae female

PLATE 2. *Zuzalpheus carpenteri*, female (VIMS 04CBC4202) from *Agelas clathrodes*, Long Reef, Belize. *Zuzalpheus carpenteri*, male (VIMS 04CBC4201) from *Agelas clathrodes*, Long Reef, Belize. *Zuzalpheus chacei*, female (VIMS 01CBC1101) from *Lissodendoryx* cf. *strongylata*, Curlew Reef, Belize. *Zuzalpheus dardeauui*, female (VIMS 01CBC7407) from *Lissodendoryx colombiensis*, Twin Cays, Belize. *Zuzalpheus dardeauui*, male (VIMS 01CBC706) from *Lissodendoryx colombiensis*, Twin Cays, Belize. *Zuzalpheus elizabethae*, female (VIMS 03CBC0801) from *Lissodendoryx* sp., Carrie Bow Cay, Belize.



Z. filidigitus female



Z. herricki female



Z. goodei female



Z. goodei male



Z. idios female



Z. kensleyi female

PLATE 3. *Zuzalpheus filidigitus*, female (VIMS 01CBC0901) from *Xestospongia* cf. *proxima*, Curlew Reef, Belize. *Zuzalpheus herricki*, female (VIMS 05FK0602) from *Hippospongia* sp., Tavernier Key, Florida, USA. *Zuzalpheus goodei*, female (VIMS 03CBC3701) from *Pachypellina podatypa*, Sand Bores, Belize. *Zuzalpheus goodei*, male (VIMS 03CBC3702) from *Pachypellina podatypa*, Sand Bores, Belize. *Zuzalpheus idios*, female (VIMS 01CBC8001) from *Hymeniacidon amphilecta*, Carrie Bow Cay, Belize. *Zuzalpheus kensleyi*, female (VIMS 01CBC3802) from unidentified yellow sponge, Sand Bores, Belize.



Z. pandionis female



Z. paraneptunus female



Z. pectiniger female



Z. pectiniger male



Z. regalis female



Z. ruetzleri female

PLATE 4. *Zuzalpheus pandionis*, female (VIMS 03CBC1701) from *Lissodendoryx* sp., Carrie Bow Cay, Belize. *Zuzalpheus paraneptunus*, female (VIMS 01CBC0704) from *Oceanapia* sp., Curlew Reef, Belize. *Zuzalpheus pectiniger*, female (VIMS 05FK1501) from *Sphaciospongia vesparium*, Key Largo, Florida, USA. *Zuzalpheus pectiniger*, male (VIMS 05FK1502) from *Sphaciospongia vesparium*, Key Largo, Florida, USA. *Zuzalpheus regalis*, female (VIMS 01CBC02) from *Xestospongia* cf. *subtriangularis*, Curlew Reef, Belize. *Zuzalpheus ruetzleri*, female (VIMS 01CBC6301) from *Hymeniacidon caerulea*, Sand Bores, Belize.



Z. sanctithomae female



Z. williamsi female



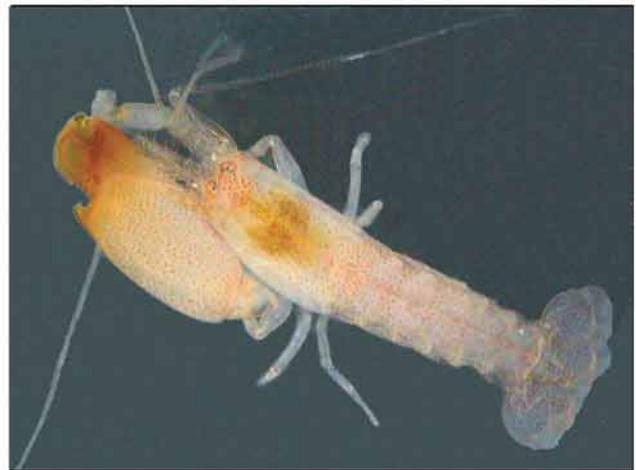
Z. ul female



Z. ul male



Z. yano female



Z. yano male

PLATE 5. *Zuzalpheus sanctithomae*, female (VIMS 01CBC6001) from *Hymeniacidon caerulea*, Sand Bores, Belize. *Zuzalpheus williamsi*, female from *Hymeniacidon caerulea*. *Zuzalpheus ul*, female (VIMS 01CBC4002) from *Hymeniacidon caerulea*, Sand Bores, Belize. *Zuzalpheus ul*, male (VIMS 01CBC4001) from *Hymeniacidon caerulea*, Sand Bores, Belize. *Zuzalpheus yano*, female (VIMS 03P2401) from *Lissodendoryx colombiensis*, Isla Pastores, Bocas del Toro region, Panama. *Zuzalpheus yano*, female (VIMS 03P2401) from *Lissodendoryx colombiensis*, Isla Pastores, Bocas del Toro region, Panama. *Zuzalpheus yano*, male (VIMS 03P2403) from *Lissodendoryx colombiensis*, Isla Pastores, Bocas del Toro region, Panama.