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ON THE FREQUENCY OF EUSOCIALITY IN SNAPPING SHRIMPS (DECAPODA: ALPHEIDAE), WITH DESCRIPTION OF A SECOND EUSOCIAL SPECIES

J. Emmett Duffy

ABSTRACT

Recently, the Caribbean snapping shrimp *Synalpheus regalis* was shown to be eusocial by the criteria historically used for honeybees, ants, and termites, i.e., colonies contain a single reproducing female and a large number of non-breeding “workers.” This finding prompted a reexamination of several previously puzzling reports of unusual population structures in other *Synalpheus* species. New collections, and observations made by students of this genus over the last century, suggest that several sponge-dwelling *Synalpheus* species similarly exhibit overlapping generations and monopolization of reproduction by a few individuals, and thus that these species may also be eusocial according to classical entomological criteria. The evidence for this conclusion includes reports of several Caribbean and Indo-Pacific species occurring in large aggregations of “juvenile” shrimp accompanied by few or no mature females. Here I describe one of these species as *Synalpheus chacei*. Like other members of the gambarelloides species group within this genus, *S. chacei* is an obligate inhabitant of living demosponges, and has been collected from at least seven host species in Caribbean Panama, Belize, and the Virgin Islands. Stomach contents comprised primarily detritus and diatoms, suggesting that *S. chacei* feeds on material inhaled in the host sponge’s feeding current. The new species is morphologically similar to *S. bousfieldi*, and is most reliably distinguished from it (and indeed, apparently from all other species of *Synalpheus*) by a unique pair of longitudinal setal combs on the dactyl of the minor first chela. Like *S. regalis*, *S. chacei* lives in colonies of up to several dozen individuals of overlapping generations, in which only a single female breeds, and is thus likely to be eusocial. Interestingly, males of *S. chacei* exhibit an apparent dimorphism in the development of the major chela (fighting claw) which may reflect a concomitant differentiation in behavior among individuals within a colony.

Snapping shrimps in the genus *Synalpheus* are among the dominant motile cryptofauna in coral reef habitats throughout the world, both in terms of abundance (Reed et al., 1982; Snelgrove and Lewis, 1989) and species diversity (Bruce, 1976; Banner and Banner, 1975, 1981, 1983; Chace, 1972, 1989; Dardeau, 1984). In the Caribbean Sea, the majority of *Synalpheus* species belong to Coutière’s (1909) gambarelloides (formerly “laevimanus”) group, characterized by a dense brush of setae on the dactyl of the minor first chela. Nearly all of the gambarelloides species are obligate associates of living sponges. They are generally rather small (most <20 mm total length), spending their entire lives within the internal canals of their hosts, and many species show direct development (Dobkin, 1965, 1969) and gregarious habits (Duffy, 1992). The high diversity of *Synalpheus* (>100 described species, Chace, 1989) has probably resulted both from the highly specific habitat (host) requirements of its species, many of which associate with only a small number of sessile reef invertebrate species in a given area, and from the tendency toward strong spatial differentiation of populations resulting from extremely restricted dispersal (Duffy, 1993, 1996b,c).

Historically, *Synalpheus* has presented many challenges to taxonomists, chief among which is the difficulty of defining and diagnosing species, which are numerous, distinguished by rather subtle morphological distinctions, and which often exhibit substantial morphological variation within putative species. It is now clear that some of this variation is partitioned among previously unrecognized sibling biological species occupying different hosts (Duffy, 1996c), although there can also be substantial variation in body size and morphology among individuals that are certainly conspecific (Dardeau, 1984; Duffy, 1996b,c). Another puzzle presented by these shrimp is the occurrence, noted repeatedly by students of *Synalpheus*, of anomalous population structures, specifically the frequent observation of large groups of apparently juvenile shrimps accompanied by few or no adults. The reports of this situation have stimulated nearly a century of speculation about its potential causes (Coutière, 1907, 1909; Banner and Banner, 1975, 1981, 1983; Dardeau, 1984).

The recent discovery of eusociality in *Synalpheus regalis* (Duffy, 1996a) may offer an explanation for these “juvenile” aggregations. Eusociality (or “true sociality”) is characteristic of the familiar social insects such as ants, termites, and honeybees (Wilson, 1971), as well as the celebrated naked mole-rat (Sherman et al., 1991). Traditionally, eusociality has been recognized by three criteria (Wilson, 1971; but see Sherman et al., 1995; Crespi and Yanega, 1995; Costa and Fitzgerald, 1996 for changing views on the concept of eusociality): (1) cohabitation of different generations, (2) restriction of reproduction to a small number of individuals, and (3) cooperative defense of the “nest”. *S. regalis* meets all of these criteria (Duffy, 1996a). My collections of the new species *Synalpheus chacei* indicate a population structure similar to that of *S. regalis*, as do published collection notes for several other sponge-dwelling *Synalpheus* species, suggesting that eusociality may eventually be confirmed in a number of snapping shrimps from throughout the world’s tropical seas.

METHODS

Live shrimp were obtained from the internal canals of sponges, collected using scuba. Sponges were taken from the vicinity of the Smithsonian Institution’s field station at Carrie Bow Cay, Belize (16°48’N, 88°05’W), and from several reefs near the Smithsonian Tropical Research Institute’s (STRI) field station in the San Blas Islands on the Caribbean coast of Panama (9°34’N, 78°58’W). Colonies of shrimp (i.e., demes inhabiting individual sponges) were removed by dissecting sponges, preserved in ~10% formalin in seawater, and later transferred to 70% ethanol for storage. Carapace length (from base of rostrum to posteromedial margin of carapace) was measured using an ocular reticle. Unless otherwise stated, reported measurements are from the dissected male paratype (USNM 282772). Shrimp were dissected in 70% ethanol, and drawings were made with the aid of a camera lucida.

To gain some insight into the relationship between *S. chacei* and its hosts, I examined stomach contents from ten individuals collected from the sponge *Niphates amorpha* in the San Blas islands, and quantified the contents by pressing the material under a cover slip and identifying the items under 100 haphazardly chosen points in the field of view at a magnification of 250 \times .

SYSTEMATICS

Family Alpheidae Rafinesque, 1815

Genus *Synalpheus* Bate, 1888*Synalpheus chacei* new species

(Figs. 1–5)

Synalpheus bousfieldi (in part: Virgin Gorda specimens) — Chace, 1972.*Synalpheus bousfieldi* — Duffy, 1992.*Synalpheus* near *bousfieldi* — Duffy, 1996a.

Material.—Specimens were taken by divers from the demosponges *Agelas dispar*, *A. clathrodes*, *Hyattella intestinalis*, *Hymeniacion amphilecta*, and *Lissodendoryx* cf. *strongylata* at depths of 2–20 m in the vicinity of Carrie Bow Cay, Belize, and from the demosponges *Niphates amorphia* and *Lissodendoryx colombiensis* growing among mixed coral and sand at depths of 3–10 m in the vicinity of the STRI field station in the San Blas Islands of Panama. The specimens described by Chace (1972) from Virgin Gorda, British Virgin Islands, and tentatively assigned to *S. bousfieldi* (USNM 136109), were also examined.

Types.—Holotype (USNM 282773): adult male, 2.4 mm carapace length; Paratypes (USNM 282772): ovigerous female (figured, in part), 2.9 mm carapace length; adult male (figured), 2.3 mm carapace length; and 61 males and juveniles, comprising the complete colony from a single specimen of the demosponge *Agelas dispar* from 3 m depth, growing under overhanging coral in the spur-and-groove zone of Carrie Bow Cay, Belize, collected 13 December 1990, J. E. Duffy, collector, station 90CBC-36. The type series is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Description.—A small, smooth, compact alpheid, subcylindrical in body form. Rostrum (Fig. 1) bluntly triangular, approximately equal in length to ocular hoods, falling well short of distal margin of first segment of antennular peduncle, ventral surface weakly convex but lacking orbitorostral process. Ocular hoods bluntly triangular, well separated from rostrum.

Pleuron of first abdominal somite of male (Fig. 1) with acute, hooklike tooth at posteroventral corner; second pleuron broadly rounded to slightly concave ventrally, third through fifth pleura with ventral margins produced posteriorly into blunt points; sixth pleuron with blunt point between posteroventral angle and posterolateral angle. Pleura 1–4 of female (Fig. 1) with ventral margins broadly rounded; pleuron 5 produced ventrally into blunt point. Telson (Fig. 1) broadly triangular; anterior width about 3.5 times posterior width; lateral margins nearly straight; dorsal surface bearing two pairs of rather weak spines, one pair situated slightly anterior, and the other posterior, to midlength of segment, both pairs arising from near lateral margins; posterior margin armed with two pairs of spines, the medial pair about twice length of lateral pair; posterior margin between medial spines bearing 2 pairs of dorsally directed simple setae and four posteriorly directed plumose setae.

Stylocerite (Fig. 1) of antennular peduncle convex laterally, with blunt tip, overreaching rostrum but falling somewhat short of midpoint of first segment of antennular peduncle. Segments of antennular peduncle stout, first (visible portion) slightly longer than second and third, the latter two subequal in length.

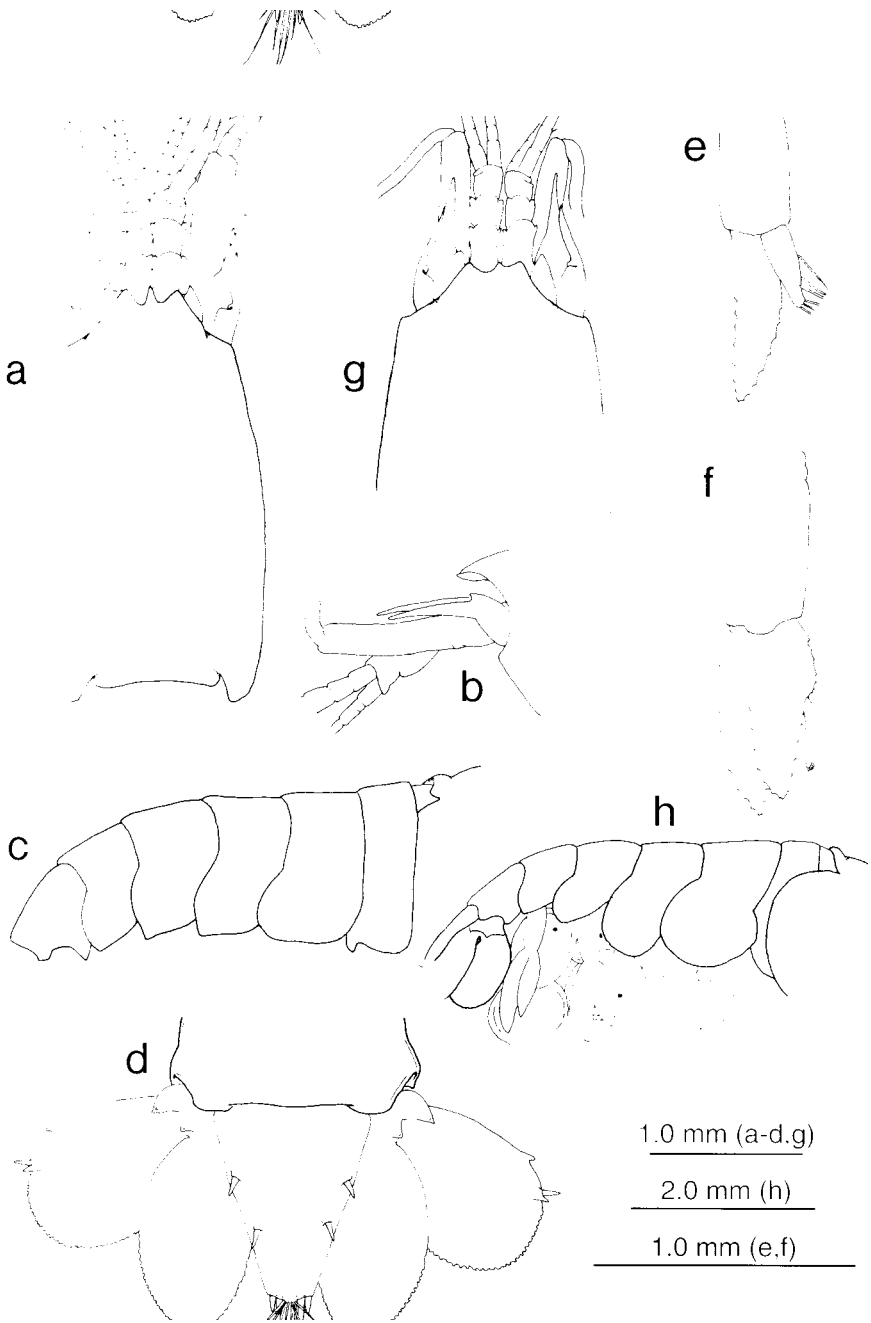


Figure 1. *Synalpheus chacei*, new species. Paratype male (USNM 282772), carapace length 2.4 mm: a, anterior region in dorsal view; b, anterior region in lateral view; c, abdomen in lateral view; d, telson and uropods in dorsal view; e, left first pleopod; f, left second pleopod. Paratype female (USNM 282772), carapace length 2.9 mm: g, anterior region in dorsal view; h, abdomen in lateral view.

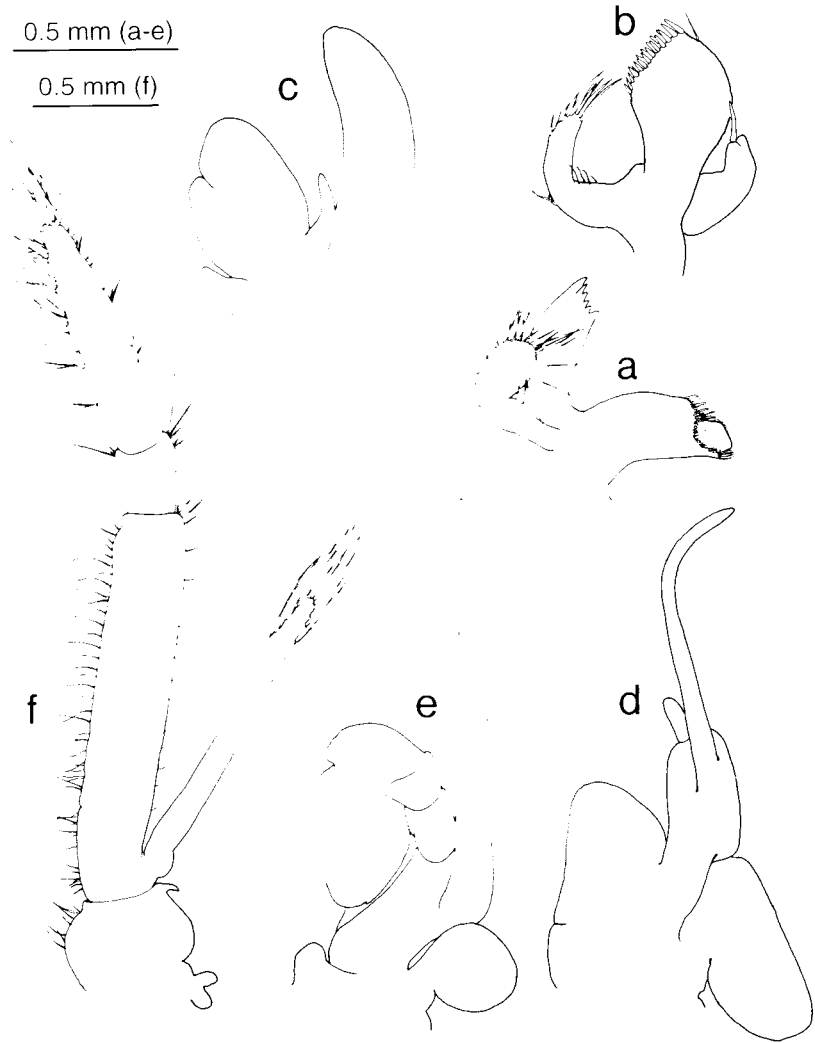


Figure 2. *Synalpheus chacei*, new species, paratype male. a, left mandible; b, left first maxilla; c, left second maxilla; d, left first maxilliped; e, left second maxilliped; f, left third maxilliped.

Antennal scale (scaphocerite, Fig. 1) slender, reaching to between proximal and distal margin of third segment of antennular peduncle, blade completely lacking. Basal antennal segment (basicerite) with dorsal margin unarmed, forming obtuse angle; lateral spine stout, extending approximately to distal margin of second segment of antennular peduncle, two-thirds to three-fourths length of scaphocerite. Distal segment of peduncle (carpocerite) roughly 5 times as long as broad, overreaching antennular peduncle by approximately the length of the latter's third segment.

Mouthparts as figured. Mandible (Fig. 2) with 6 teeth on incisor process, molar process larger than incisor, palp two-segmented. Palp of first maxilliped (Fig. 2) consisting of two

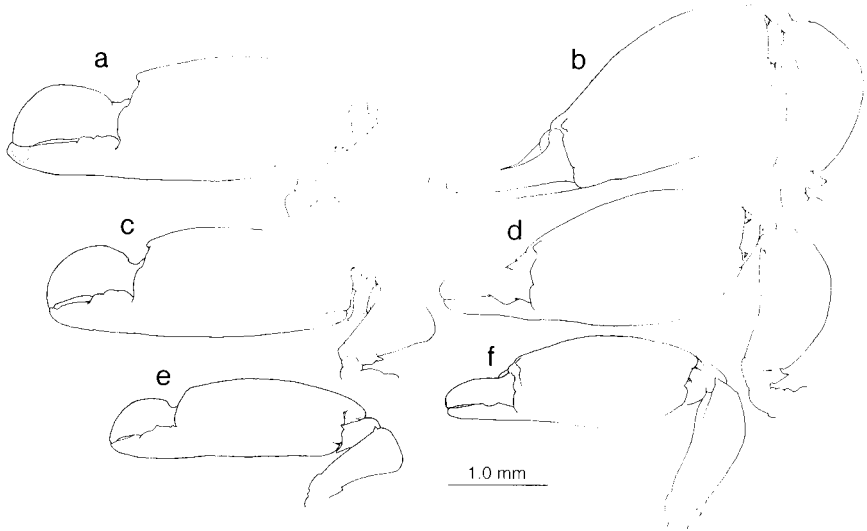


Figure 3. *Synalpheus chacei*, new species. "Falcate" male, carapace length 2.4 mm: a, chela of major first pereiopod in lateral (medial) view; b, same, dorsal (extensor) view. Paratype male: c, chela of major first pereiopod in lateral view; d, same, dorsal view. Paratype female: e, chela of major first pereiopod in lateral view; f, same, dorsal view.

segments. Third maxilliped (Fig. 2) slightly overreaching antennal peduncle, terminating in circlet of 5 spines, exopod nearly reaching distal margin of antepenultimate segment.

Major first pereiopod (Fig. 3) overreaching antennal peduncle by length of chela; chela of males tending toward dimorphism in size and development of fingers: chela of most ("normal") males (e.g., paratype, Fig. 3) subcylindrical, with palm terminating dorsodistally in low, obscure bump, not noticeably curved along axis, approximately 3 times as long as broad, about equal in length to carapace, fingers 0.38 as long as palm, stout and not noticeably compressed laterally; chela of largest ("falcate") males (Fig. 3) curved along axis perpendicular to plane of fingers, 2.9 times as long as broad, 1.08 times carapace length, fingers about 0.44 as long as palm, elongated and laterally compressed, dactyl somewhat sickle-shaped (falcate), with hooklike tip; chela of females (Fig. 3) similar to that of normal males but somewhat smaller, 0.64 of carapace length; carpus of both males and females short and broad; merus more than half as long as palm, extensor margin unarmed distally. Minor first pereiopod (Fig. 4) overreaching antennal peduncle by length of chela; chela about 2.5 times as long as broad, palm slightly inflated, both fingers distinctly bidentate, extensor surface of dactyl (Fig. 4B) bearing two slightly separated, longitudinal rows of curved, dentate setae; carpus about half as long as chela; merus more than three times as long as wide.

Second pereiopod (Fig. 4) overreaching antennal peduncle by length of chela, fingers more than 1.5 times as long as palm, both fingers bearing dense groups of setae. Carpus roughly 1.5 times as long as chela, composed of five articles with relative lengths about 3.5:1:1:1:2, the proximal segment longest. Merus approximately equal in length to carpus and about 1.5 times as long as ischium.

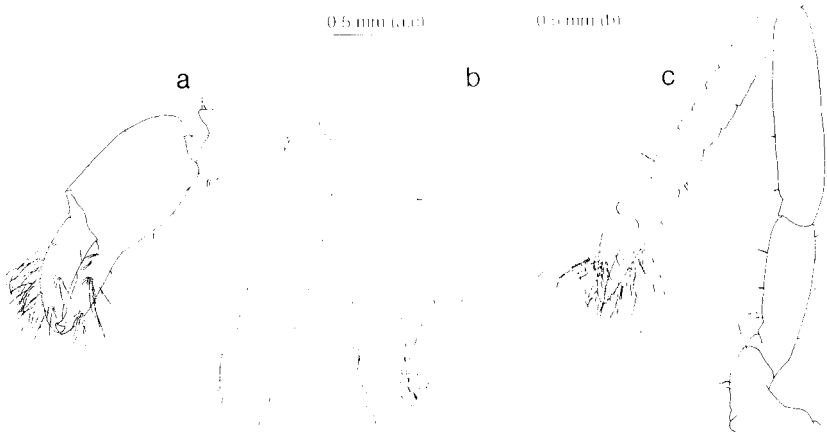


Figure 4. *Synalpheus chacei*, new species, paratype male. a, minor first pereiopod; b, same, detail of dactyl, extensor view; c, left second pereiopod.

Third to fifth pereiopods similar in length and structure, relatively stout, biunguiculate; dactyl with tooth on flexor margin somewhat divergent from curve of segment, subequal in length and basal width to terminal tooth. Third pereiopod (Fig. 5) reaching approximately to distal margin of antennal peduncle; propodus slightly more than four times as long as dactyl, flexor margin armed with 5 movable spines spaced evenly along its length as well as a distal pair of movable spines, both flexor and extensor margins bearing several long setae; carpus about 0.6 as long as propodus, extensor margin bearing well-developed distal lobe, flexor margin with movable spine at distal end; merus unarmed, about 1.5 times as long as propodus; coxa bearing short, stout spine at distal corner of flexor margin. Fourth pereiopod (Fig. 5) similar to third but slightly shorter, extending to around midpoint of carpocerite. Fifth pereiopod (Fig. 5) reaching approximately to anterolateral margin of carapace at antennal sinus; propodus somewhat less than five times as long as wide, flexor margin armed with pair of movable spines at distal margin and six transverse rows of stout serrulate setae in distal half of segment; extensor margin with several long setae; carpus unarmed, about 0.7 as long as propodus; coxa lacking spine on distal part of flexor margin.

Male first pleopod (Fig. 1) with endopod about half of exopod length, bearing three setae distally and two setae on its lateral margin. Male second pleopod (Fig. 1) with endopod subequal in size to exopod; appendix masculina lacking; appendix interna arising at about 0.44 of endopod length, about 0.40 as long as endopod, with about five short curled setae (concinuli).

Uropod lateral branch (Fig. 1) with a single fixed tooth along margin proximal to movable spine, and a single tooth distal to movable spine; lacking transverse articulation. Eggs (Fig. 1) rather large, 0.86–0.91 mm long in clutch from paratype female (mean = 0.88, $n = 10$).

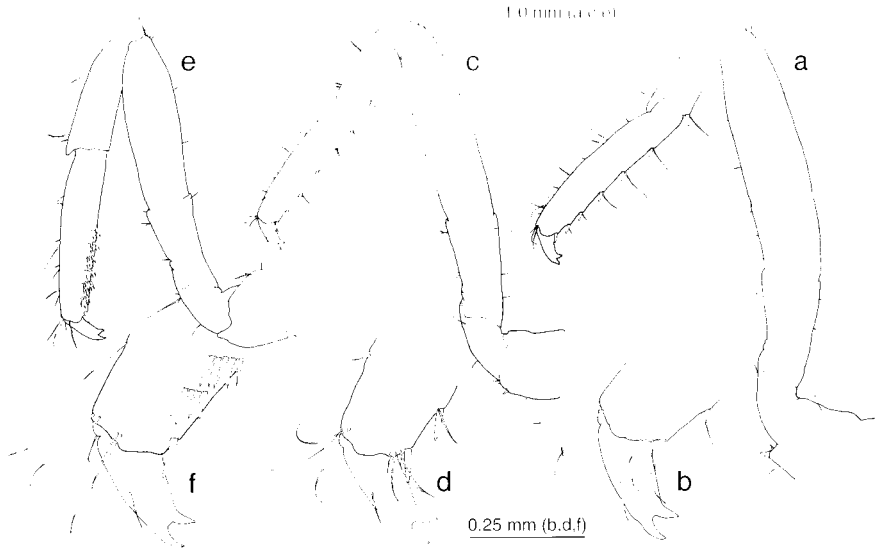


Figure 5. *Synalpheus chacei*, new species, paratype male. a, left third pereiopod; b, same, dactyl; c, left fourth pereiopod; d, same, dactyl; e, left fifth pereiopod; f, same, dactyl.

Variation.—As is typical in this genus, *S. chacei* exhibits sexual dimorphism in the size of the major chela, the female's being proportionally smaller than those of mature males (Fig. 3). More interestingly, there is a suggestion of dimorphism in major chela development among large males as well, with one to several of the larger males within a colony bearing a hypertrophied chela, longer than those of "normal" males in the same colony, and bearing proportionally longer, sickle-shaped fingers (Fig. 3), for which reason I refer to these hypertrophied males as "falcates". It is unclear whether the enlargement of the chela accompanies the molt to maturity, as there are otherwise no external morphological characters that reliably indicate male maturity in *Synalpheus*. In any case, there is no obvious difference between normal and falcate males in carapace length or in the structure of the second pleopod.

S. chacei also exhibits variation among colonies, or among geographically separated populations, in several other characters. One of the more obvious of these is development of the protuberance on the distal margin of the major chela palm, which varies from near absence to a prominent, low bump in different populations.

Color in life.—In life, *S. chacei* is a somewhat nondescript shrimp. The body is generally translucent, sometimes with a faint gold tinge where the cuticle is thickened, and a slightly darker brown tinge to the distal palm and fingers of the major chela. The eggs are a pale grayish-green.

Size (carapace length).—Ovigerous females to 3.0 mm; males and juveniles to 2.4 mm (males and juveniles are not clearly distinguished by any external morphological criteria).

Habitat, Hosts, and Ecology.—Like most other members of the gambarelloides species group (Dardeau, 1984; Duffy, 1992, 1996c), *S. chacei* has been found exclusively in association with living sponges. The type series was collected from within the internal canals of the demosponge *A. dispar*, growing beneath overhanging ledges of the coral *Agaricia tenuifolia* in the spur- and-groove zone of the reef at Carrie Bow Cay, Belize, at a depth of 3 m. Other sponges from which *S. chacei* has been collected in Belize include *A. clathrodes* (Agelasidae), *H. intestinalis* (Spongiidae), *H. amphilecta* (Hymeniacionidae), and *L. cf. strongylata* (Myxillidae). In the San Blas islands of Panama, it has been found in *N. amorphia* (Niphatidae) and *L. colombiensis*. Although these collections indicate a rather wide host range for *S. chacei*, local populations can be quite specialized; in the immediate vicinity of the STRI field station in San Blas, for example, *S. chacei* has been found only in *N. amorphia*, despite the commonness in this area of both of the *Agelas* species used in Belize, and of *L. colombiensis*, which it uses in the Mangles Channel area, some kilometers distant from the STRI station.

The most common item in stomachs of *S. chacei* was amorphous flocculent material, presumably detritus, which was found in all 10 individuals examined and comprised 68.3.7% (mean \pm 1 SE) of stomach contents. The proportion of gut volume occupied by other items appeared to be underestimated by point-counting due to the tendency of the flocculent material to spread out when compressed. The most frequent identifiable item in the guts was centric diatom fragments (14.1 4.0%), also found in all stomachs, followed by mineral grains (1.9 0.4%, 9 of 10 stomachs). All other items occupied <1% of gut volume on average. Commonly found items included crustacean parts (9 stomachs), host sponge spicules (7 stomachs), and eggs of unknown origin (7 stomachs). These data suggest that *S. chacei* is rather omnivorous, feeding primarily on phytoplankton and detritus inhaled by the host sponge's feeding current, but also to some extent on sponge tissue and perhaps on other small animals.

Etymology.—It is a pleasure to name the new species in honor of Dr. Fenner A. Chace, Jr., of the National Museum of Natural History, in recognition of his many contributions to the knowledge of caridean shrimps, the consistently high standards he has set for taxonomic research on this group, and his personal encouragement in this work. Dr. Chace collected the series of specimens from Virgin Gorda and recognized their possible distinction from the morphologically similar *S. bousfieldi* (Chace, 1972) but, lacking adequate comparative material at the time, refrained from describing them as new.

DISCUSSION

S. chacei is a member of Coutière's (1909) gambarelloides (formerly "laevimanus") group, characterized by a brush of setae on the dactyl of the minor first chela, and by the habit in most species of living exclusively within the internal canals of living sponges. The new species appears most closely related to *S. bousfieldi* Chace, 1972 and *S. brooksi* Coutière, 1909 in having a single tooth on the lateral margin of the outer branch of the uropod, bidentate fingers of the minor first chela, scaphocerite lacking a blade, and the dorsal spines of the telson arising from very near its lateral margins. The new species is in fact so similar to *S. bousfieldi* that the specimens collected from Virgin Gorda were discussed by Chace (1972) in his description of *S. bousfieldi* as possibly representing juvenile stages of the adults designated as types. This series of specimens contains a single female (with 14 males and juveniles), and the specimens bear an obscure bump on the

distal margin of the major chela palm and the characteristic pair of longitudinal setal combs on the minor chela dactyl, all as in the type series of *S. chacei*. With the benefit of a much larger series of specimens than those available to Chace, it is now possible to conclude that *S. chacei* and *S. bousfieldi* are different. Probably the most reliable diagnostic character of *S. chacei* is the setation of the dactyl of the minor chela. The characteristic feature of the gambarelloides group, including *S. bousfieldi*, is a thick setal brush on the minor chela dactyl, comprised of numerous tranverse rows of closely spaced, curved setae arising from the dactyl's extensor surface. In contrast, *S. chacei* is unique among the gambarelloides species that I have examined in that this brush is reduced to two longitudinal rows of setae (Fig. 4B). The only other exception to this pattern among Caribbean species occurs in *S. paraneptunus*, which bears a sparse, poorly organized field of setae on the dactyl, and whose placement in the gambarelloides group is doubtful. Other features distinguishing *S. chacei* from *S. bousfieldi* include the palm of the major chela, which terminates in a distinctly produced tooth in the latter species, versus a barely distinguishable bump in *S. chacei*, and the somewhat more produced abdominal pleura in males of *S. chacei*.

The morphological characters distinguishing *S. chacei* from similar species are admittedly quite subtle. Nevertheless, they are consistent both on a microspatial scale and among geographic regions. For example, *S. chacei*, *S. brooksi*, and *S. bousfieldi* can all be found within a few meters of one another, inhabiting different sponge species on the outer reef ridge at Carrie Bow Cay, where they display clear differences in morphology, body size, color, and social organization. Yet samples of *S. chacei* collected from different host species in Panama, Belize, and the Virgin Islands are similar in body size and morphology, and almost invariably contain only a single female per sponge. Thus, while the identification of these shrimp species poses practical problems, there can be little doubt that they are "good", genetically distinct biological species, as has been shown for several cryptic species of the *Synalpheus rathbunae* complex (Duffy, 1996c). The fact that such apparently closely related species may differ substantially in social organization emphasizes the critical need for accurate taxonomy in unraveling their social evolution.

Like the recently described *S. regalis* (Duffy, 1996a,d), *S. chacei* exhibits a population structure that strongly suggests it is eusocial. The classical entomological definition of eusociality is based on three criteria: (1) overlapping generations, (2) reproductive division of labor, and (3) cooperative care of young (Michener, 1958; Wilson, 1971). Like many of its congeners within the gambarelloides group (Dobkin, 1965, 1969), *S. chacei* has direct development, i.e., eggs hatch into benthic, crawling juveniles (J. E. Duffy, pers. observ.). Moreover, the colony of *S. chacei* inhabiting a given sponge frequently shows clearly distinct size classes of juveniles, suggesting that cohorts of newly hatched individuals remain in the sponge where they are born, and that successive generations live together within a sponge. The criterion of "reproductive division of labor" is supported by the finding that, in dissections of over 50 individual sponges from Panama (*S. chacei* was referred to as *S. bousfieldi* in Duffy, 1992) and Belize, the vast majority of *S. chacei* colonies contained a single reproducing female, despite colony sizes sometimes exceeding 80 individuals. Evaluating the third criterion—cooperative brood care—requires behavioral data. Observations of *S. regalis* showed that large non-breeding individuals vigorously attacked intruders, thus defending the colony (including small, relatively inactive juveniles), providing evidence for cooperative brood care in that species (Duffy, 1996a). Preliminary observations of *S. chacei* colonies in the lab similarly show greater aggres-

sive activity in larger individuals than in smaller ones (J. E. Duffy and K. S. Macdonald, unpubl. data). As the colony structures of these two species are similar, it seems likely that larger, non-breeding individuals perform a similar role in colonies of *S. chacei*, and thus that this species can be considered eusocial.

The finding of eusociality in *S. regalis* and *S. chacei* may explain at last the puzzling phenomenon, described repeatedly by students of this genus, of collections comprising large numbers of apparently juvenile shrimps with few or no ovigerous females. This situation has been reported for *S. rathbunae* from "dead sponges" on Puerto Rico (Coutière, 1909), *S. neptunus neptunus* and *S. neptunus germanus* from unidentified sponges from Western Australia (Banner and Banner, 1975), *S. paradoxus*, whose specific name in fact reflects its highly skewed sex ratio, from an unidentified sponge from the Red Sea (Banner and Banner, 1981), *S. crosnieri* from unidentified sponges off Madagascar (Banner and Banner, 1983), and *S. dorae* from a sponge in the genus *Reniera* from northwest Australia (Bruce, 1988). Similarly, while not discussing juvenile characteristics specifically, Chace (1972) reported collections including only one or a few ovigerous females in *S. paranepentus* (from "coral-encrusted rocks"), and *S. rathbunae* ("found by cracking coral"). I have also collected many colonies of the Caribbean species *S. rathbunae* (referred to as *S. "rathbunae B"* in Duffy, 1996c) and *S. filidigitus*. In both of the latter species, as in *S. regalis*, each colony contains only one (in *S. filidigitus*) or a few (in *S. rathbunae*) breeding females (J. E. Duffy, unpub. observ.). Interestingly, most or all of the species discussed above, like *S. regalis*, are rather small shrimps with characteristics reminiscent of the juvenile forms of larger, free-living congeners. For example, with the exception of *S. neptunus* and *S. crosnieri*, all of these species have the carpus of the second cheliped composed of four segments in adults, as it is in young juveniles of many other *Synalpheus* species, most of which have five segments as adults. Similarly, the transverse suture on the lateral branch of the uropod is poorly developed or absent in most of the small, social *Synalpheus* species. In light of these data from the better studied Caribbean species, it seems likely that several previous records of dense juvenile aggregations in *Synalpheus* represent incomplete collections of the colonies of eusocial forms, and thus that eusociality may occur among sponge-dwelling snapping shrimps throughout the world's tropical oceans.

An especially intriguing characteristic of *S. chacei* is the tendency toward dimorphism in the major chela (or fighting claw, Fig. 3), which is used primarily in territorial contests and defense among alpheidids (Hazlett and Winn, 1962; Schein, 1975, 1977; Hughes, 1996; Duffy, 1996a). Examination of several colonies from Caribbean Panama initially suggested that larger males displayed one or the other of two, relatively discrete chela morphs (Fig. 3): "falcates" possess a relatively large, curved chela with long fingers and a sickle-shaped dactyl, whereas non-falcates of the same or similar size possess a smaller, straighter chela with stout fingers (Fig. 3). Such variation in chela development of mature males is not uncommon among crustaceans, occurring in several amphipods (Lowry and Stoddart, 1983; Conlan, 1989, 1990), tanaids (Müller, 1869; Gardiner, 1975), and caridean shrimps (Ra'anan and Sagi, 1985). Male dimorphism is also known in many insects (e.g., Hamilton, 1979). Behavioral studies of several crustacean and insect species have shown that the different male morphs have alternative mating strategies, with the largest or most heavily armed males being "fighters" and the smaller, weaker ones being "sneakers" (Alcock, 1979; Ra'anan and Sagi, 1985; Shuster, 1989).

In social insects, such allometric divergence in morphology generally serves another purpose, resulting in subcastes of workers that are specialized in both structure and behavior for certain tasks (Wilson, 1971; Oster and Wilson, 1978; Itô, 1989; Crespi, 1992). Whether the morphological differentiation of falcates in *S. chacei* represents a behavioral specialization for nest defense, an adaptation for mate competition, or some other, unknown function, will remain a mystery pending further behavioral studies.

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