

LARVAL BIOLOGY OF THAUMATOPSYLLID COPEPODS ENDOPARASITIC IN CARIBBEAN OPHIUROIDS

Gordon Hendler and Il-Hoi Kim

(GH, correspondence, hendler@nhm.org) Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007, U.S.A.;

(IK, ihkim@kangnung.ac.kr) Department of Biology, Kangnung National University, Kangnung 210-702, Republic of Korea

ABSTRACT

The parasitic metanauplius larva of an undescribed species of *Caribeopsyllus*, the second thaumatopsyllid species to be reported from the Caribbean, was discovered in *Ophiothrix angulata* in Belize. In addition, metanauplii of *Caribeopsyllus chawayi*, whose free-living stages were previously known, were found to parasitize *Ophiactis savignyi*. Their ophiuroid hosts usually contained a single larva that caused them no discernable physical damage. *Caribeopsyllus chawayi*, which was initially described from Mexico, is here reported from Belize and is suggested to occur in Brazil. It might occur in the Pacific Ocean, as its host is circumtropical. Larvae of the Belizean thaumatopsyllids are exceptional among copepod nauplii for their large size, four pairs of appendages, true chelate mandibles, elaborate tripartite eyes, accessory photoreceptive structures (Gicklhorn's organ), sexual dimorphism, and endozoic parasitism. *Thaumatopsyllus paradoxus* and *Caribeopsyllus amphiodiae*, the only other thaumatopsyllids with known metanauplii, have the same suite of specializations. However, metanauplii of the latter two species crawl, whereas the Belizean metanauplii swim. Both Belizean species have an antennal arthritis used for feeding and well-developed mandibular setae used for locomotion, which are lacking in *C. amphiodiae*. They leave the host as non-feeding positively phototactic copepodids. Morphological features distinguishing the metanauplii of Belizean species from that of *C. amphiodiae* indicate that the latter should be referred to a new genus if the systematic significance of its unique morphology is corroborated. Similarities between thaumatopsyllids and siphonostomatoids in the ontogenesis of their caudal rami suggest that Thaumatopsyllidae may belong to the Siphonostomatoida, or be closely allied.

KEY WORDS: brittle star, cenogenesis, nauplius, ontogenesis, symbiosis

DOI: 10.1651/09-3187.1

INTRODUCTION

Nearly 100 years ago, Georg Ossian Sars (1913) described the first thaumatopsyllid copepod. He named the species *Thaumatopsyllus paradoxus* Sars, 1913, the "strange miracle flea," alluding to the adult's saltatory swimming movements, its unexpected lack of mouthparts, and its inability to feed. Sars surmised that its larva must feed and might be parasitic, foreshadowing the discovery of *T. paradoxus* larvae in the stomach of ophiuroids (Bresciani and Lützen, 1962). Adults of two new thaumatopsyllid species from the Indo-Pacific subsequently were described (Sewell, 1949; McKinnon, 1994), but the pace of research on the elusive Thaumatopsyllidae and on their larval biology has quickened only recently.

Studies of a thaumatopsyllid associated with burrowing ophiuroids, *Caribeopsyllus amphiodiae* Ho, Dojiri, Hendler, and Deets, 2003, showed that its parasitic larva is unexpectedly long-lived, sexually dimorphic, and has elaborate naupliar eyes (Dojiri et al., 2008; Hendler and Dojiri, 2009). Plankton collections of post-naupliar *Caribeopsyllus chawayi* Suárez-Morales and Castellanos, 1998, revealed seasonal fluctuations in its abundance, although its elusive naupliar stage, presumed to parasitize ophiuroids, remained unknown (Suárez-Morales and Tovar, 2004). An additional discovery, previously overlooked in the carcinological literature but significant in the context of the present study, was of unidentified thaumatopsyllid larvae found in Brazilian ophiuroids (Boffi, 1972; Duarte and Morgado, 1983).

The present investigation was initiated after the first author observed a thaumatopsyllid metanauplius protruding from the damaged body wall of an immature *Ophiothrix angulata* Say, 1825. This association had never before been recorded, and since *O. angulata* is one of the most abundant and frequently observed species of Caribbean ophiuroids (Hendler et al., 1995), the occurrence seemed anomalous. Later in 2006 and in 2008, a systematic search for enterozoic symbionts proved that metanauplii regularly parasitize *O. angulata*, and also revealed that a different species of thaumatopsyllid parasitizes *Ophiothrix savignyi* (Müller and Troschel, 1842). Fortunately, copepodid stages of both Belizean parasites also were obtained. They are described here to establish that *C. chawayi*, originally discovered in Mexico, parasitizes *O. savignyi* in Belize and possibly also in Brazil, and that an unnamed species of *Caribeopsyllus* parasitizes *O. angulata*.

The present contribution documents the morphology of Belizean thaumatopsyllid larvae and elucidates their behavior, habitat preference, and host specificity. Our identification of the parasitic stage of *C. chawayi* sheds light on the species' life cycle and on its exceptional potential for dispersal. We report that unique morphological and life history traits, initially documented in *C. amphiodiae* by Hendler and Dojiri (2009), characterize other (and possibly all) Thaumatopsyllidae, and we elucidate a remarkable diversity of larval behavior and morphology in the family, which clarifies the systematics of these extraordinary copepods.

MATERIALS AND METHODS

Study sites were at Carrie Bow Cay on the Belize Barrier Reef and at various localities in the Belize Shelf Lagoon, which is a vast channel separating the barrier reef and mainland (Rützler and Macintyre, 1982; Macintyre and Rützler, 2000). In February and September, 2006, samples of calcareous algae (*Halimeda* spp.) were collected at Carrie Bow Cay from the shallow back-reef (16°48.13'N, 88°4.69'W) and the spur and groove zone (16°48.2'N, 88°4.60'W) of the inner fore-reef. Samples of benthic substrate from nearby sites in the shelf lagoon included sponges from the Twin Cays island complex (16°49.83'N, 88°5.90'W) and *Halimeda* spp. from a large lagoonal patch reef locally known as a "sand bore" (16°45.535'N, 88°6.759'W), which were collected in February, 2008. During the same month, additional samples were collected at the Pelican Cays island group in the shelf lagoon, including sponges and *Gelidium* sp. algae from Cat Cay (16°39.470'N, 88°10.990'W), sponges and mangrove root biota from Manatee Cay (16°39.961'N, 88°11.575'W), and mangrove root biota and benthic rubble from Lagoon Cay (16°37.818'N, 88°12.500'W).

Most individuals of *Ophiothrix angulata* and *Ophiothrix orstedii* Lütken, 1856 were extracted from *Halimeda* spp. *Ophiothrix angulata* also was found in the fouling community on mangrove roots, on the surface of sponges, and beneath rubble. Most individuals of *O. savignyi* were removed from internal canals of sponges, but some were extracted from *Halimeda*. Ophiuroids were anesthetized in isotonic MgCl₂ solution prior to opening the dorsal wall of the disk and stomach with fine forceps. Measurements of living hosts and parasites were made using a Wild M5 stereomicroscope with an ocular micrometer. Photographs and video recordings were made with a Nikon Coolpix 5400 and eyepiece adapter. Body size of ophiuroids, expressed in terms of disk diameter (dd), was measured at 12× magnification from the base of an arm to the opposite edge of the disk, and anteroposterior body length of the parasites was measured at 50× magnification. Sex (male, female, immature) and presence/absence of gonads were recorded for some samples of ophiuroids. All the specimens of *O. angulata* and *O. orstedii* extracted from a sample were dissected and their parasites were processed. However, collections of *O. savignyi* usually consisted of a few relatively large individuals and a multitude of minute clonal juveniles, and since parasites were not found in tiny juveniles that were assessed, only dissections of large individuals were recorded.

Larvae collected in 2008, on which we based size measurements, morphological descriptions, and line drawings of preserved specimens, comprised 23 metanauplii of *C. chawayi* and one copepodid I stage removed from *O. savignyi*; 10 metanauplii of *Caribeopsyllus* sp. A and one copepodid I stage removed from *O. angulata*, and a copepodid II stage that was presumed to have emerged from *O. angulata*. Specimens preserved in 80% ethanol were cleared in lactic acid for approximately one hour, measured at 100× magnification, and dissected on wooden slides (Humes and Gooding, 1964). They were drawn with the aid of a drawing tube attached to a Nikon Optiphot microscope. Elsewhere in the results, measurements of metanauplii from *O. angulata* were based on the living parasites collected in 2006, in addition to specimens preserved in 2008. Measurements of the dimensions of the metanauplius mouth were based on line drawings in the present report and in Dojiri et al. (2008). Vouchers of developmental stages were deposited in the Crustacea Collection, Natural History Museum of Los Angeles County.

Analyses of the behavior of metanauplii were based on video recordings, made at 16 frames per second of one *Caribeopsyllus* sp. A (0.59 mm long) and one *C. chawayi* (0.73 mm), and two additional *C. amphiodiae* (0.77, 0.64 mm) recorded during a previous study in California, USA (Hendler and Dojiri, 2009). Antennal, mandibular, and maxillular movements were analyzed by comparing successive frames. Estimated rates of motion were very conservative, because the Belizean larvae and their hosts had been anesthetized. Speed of movement (seconds/stroke) was based on the time elapsed during full strokes, i.e., both power and recovery, of individual appendages. The frequency of strokes (full strokes/second) was based on the number of movements of a single appendage recorded during a single one-second interval.

RESULTS

Morphology of Preserved Larval Stages and Living Larvae
Metanauplius Stage of *Caribeopsyllus chawayi*.—Body of largest specimen (Figs. 1E, 2A, 3A, 9C), on which

description is based, measuring 0.98 × 0.82 mm, with truncate anterior end, markedly expanded mid-region, tapered posterior end. Caudal region with 2 groups of caudal setae, each group containing 1 short and 1 longer seta; both setae slender, flexible. Body size-range, 0.19–0.98 mm long and 0.13–0.82 mm wide, based on 23 specimens. Small specimens ovoid, and relatively more slender than large specimens (Fig. 3B).

Antennule (Fig. 3C) unsegmented, strongly tapering, and armed with 21 smooth setae, terminal 2 of which fused at base. Antenna (Figs. 1F, 3D) biramous, proximally bearing prominent extension tipped with acicular arthrite directed toward mouth (Fig. 3E). Exopod consisting of 5 segments; first segment fused with protopod, with inner distal seta; second to fourth segments each with large inner seta; proximal one-third of the latter 3 setae stiff, distal two-thirds flexible and with spinules; fifth segment 55 × 19 μm (2.9 times longer than wide), armed with inner seta and 3 very unequal distal setae. Endopod 1-segmented and armed with 5 elements: 1 small, naked inner seta, 2 small, spiniform inner distal setae, and 1 spine and 1 large seta terminally (this seta more than 2.5 times as long as adjacent spine).

Mouth located between labrum and postoral lip (Fig. 3E), posteromedially to bases of antennae (Figs. 2A, 9C). Labrum with distinct posterior process on both sides with row of minute spinules on ventral surface. Triangular postoral area sclerotized (Fig. 3E). Mandible (Figs. 2A, 3F) biramous, consisting of coxa, basis, exopod, and endopod, and ornamented with numerous spinules on ventral surface. Coxa with massive inner spine. Basis indistinctly demarcated from coxa, with small, transparent seta on inner margin. Exopod 3-segmented; first segment with inner seta; second segment with large inner distal seta; terminal segment as long as wide and with 1 very large and 1 smaller seta distally. Endopod 2-segmented; first segment indistinctly separated from basis and armed with inner hyaline seta and massive inner distal spine; second segment about 3 times longer than wide, with 2 small inner setae, 1 small outer distal seta, and 1 strong terminal claw. Maxillule (Figs. 1F, 3G) bilobate, ornamented with numerous spinules on ventral surface. Neither lobe clearly demarcated from base. Outer lobe extending over inner lobe, with 1 large, 1 medium-sized, and 1 minute seta. Inner lobe with 1 inner seta and 3 terminal, unequal setae.

Beneath exoskeleton of only the 2 largest specimens (0.65 and 0.98 mm long), posterior part of body dorsally showing 3 delicate suture lines (Fig. 3A) and ventrally exhibiting the primordial legs, their setal elements, and caudal setae of copepodid I (Fig. 1E, F).

Copepodid I Stage of *C. chawayi*.—Body measuring 0.94 × 0.35 mm. Major body articulation between fourth and fifth thoracic somites (third and fourth pedigers) (Fig. 4A). Prosome cylindrical, 655 μm long, approximately 1.9 times longer than broad (Fig. 1G). Cephalothorax slightly longer than wide, anteriorly tapered, delimited from first pedigerous somite by incomplete lateral suture lines. Rostrum represented by slightly expanded area without distinct border. Urosome (Fig. 4B) 2-segmented, consisting of

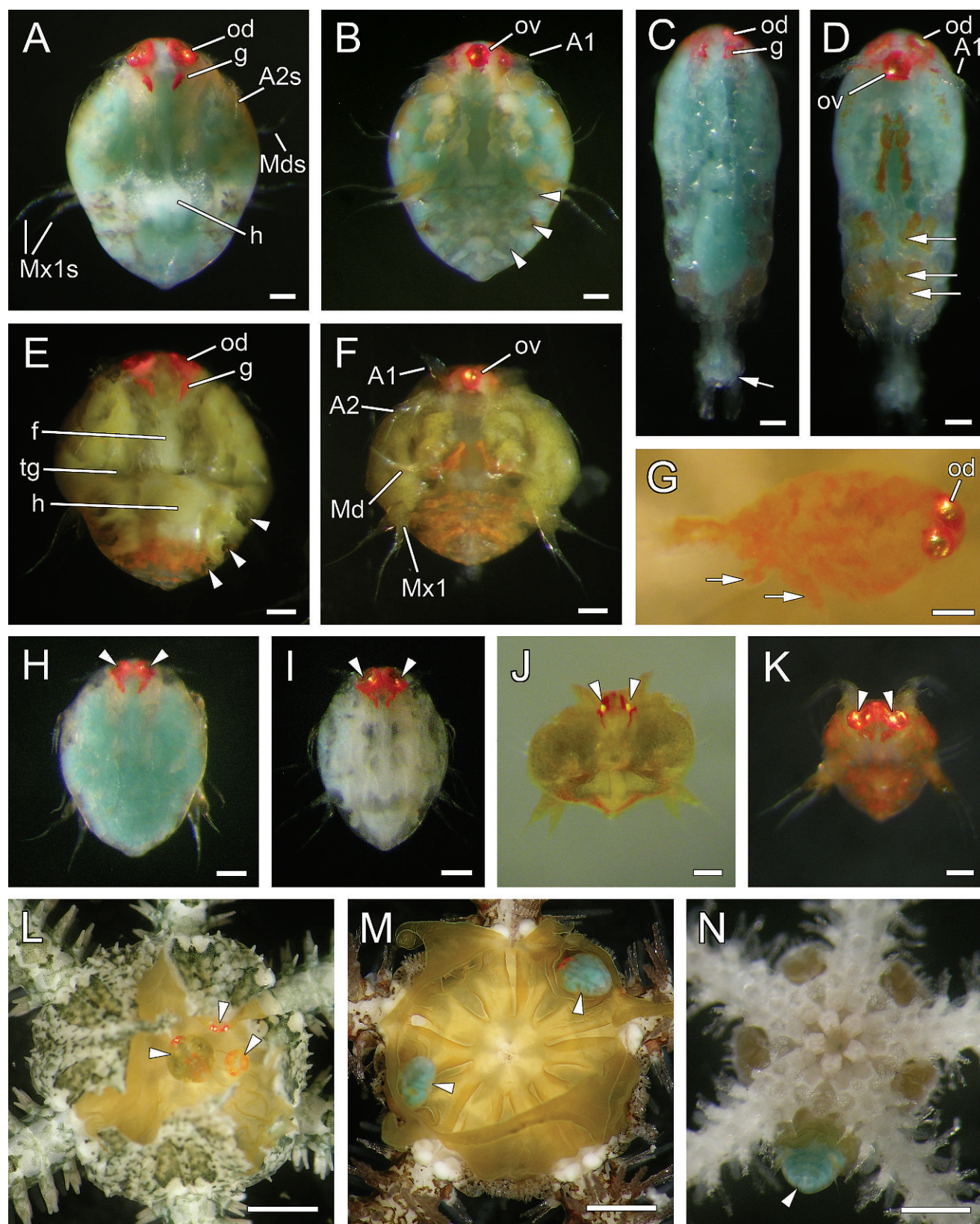


Fig. 1. Living *Caribeopsyllus* sp. A (A-D, H, I, M, N) and *Caribeopsyllus chawayi* (E-G, J, K, L) larvae, showing dorsal and ventral aspects of metanauplius (A, B, E, F) and copepodid (C, D, G) stages, comparing putative male and female metanauplii (H-K), and showing larvae in hosts (L-N). A, *Caribeopsyllus* sp. A metanauplius, 1.02 mm body length, dorsal view, showing dorsally turned setae of antennae (A2s), Gicklhorn's organ (g), posterodorsal hump (h), dorsolateral ocelli (od), and setae of mandibles (Mds) and maxillules (Mx1s); B, *Caribeopsyllus* sp. A metanauplius, ventral view of previous individual, showing antennules (A1), ventral ocellus (ov), and subcuticular primordia of swimming legs (arrowheads); C, *Caribeopsyllus* sp. A

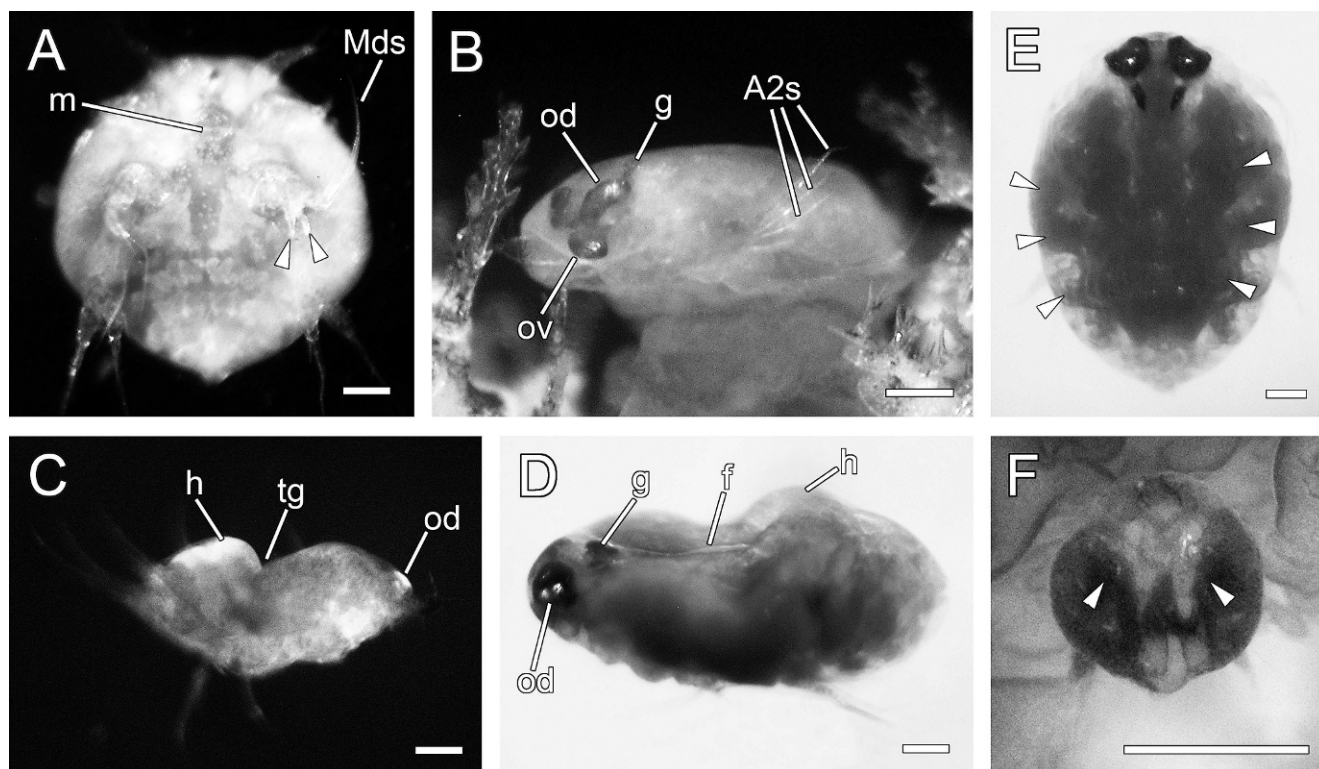


Fig. 2. Living *Caribeopsyllus chawayi* (A, C, F) and *Caribeopsyllus* sp. A (B, D, E), showing appendages (A, B), posterodorsal hump (C, D), and internal organs (E, F) of metanauplii. A, *C. chawayi* metanauplius, 0.79 mm body length, ventral view, showing mouth (m), mandibular setae (Mds), mandibular chela (arrowhead) composed of claw on second endopodal segment opposing spine on first endopodal segment; B, *Caribeopsyllus* sp. A metanauplius, 0.74 mm body length, anterolateral view, clinging to stomach wall of *Ophiothrix angulata* showing fan of antennal setae (A2s), dorsolateral ocelli (od), ventral ocellus (ov), and Gicklhorn's organ (g); C, *C. chawayi* metanauplius, 0.67 mm body length, lateral view, showing posterodorsal hump (h), transverse groove (tg), and convex cap of dorsolateral ocellus (od); D, *Caribeopsyllus* sp. A metanauplius, 1.11 mm body length, lateral view, showing anterior furrow (f) that partially bisects posterodorsal hump (h), dorsolateral ocelli (od), and Gicklhorn's organ (g); E, *Caribeopsyllus* sp. A metanauplius, 0.98 mm body length, dorsal aspect viewed in transmitted light, showing lobate green structures (arrowheads) that may be reproductive or digestive organs; F, *C. chawayi* metanauplius, 0.67 mm body length, dorsal aspect viewed in transmitted light within host's gut, showing lobate green structures (arrowheads) similar to but simpler than those in image E. Scale bars: A-E, 100 μ m; F, 0.5 mm.

fourth pedigerous somite and 1-segmented anterior portion of genito-abdominal trunk (comprising undifferentiated sixth thoracic somite, genital somite, and abdomen). Genito-abdominal trunk $152 \times 123 \mu\text{m}$, with small, conical anterolateral protuberance on both sides and weak lateral constriction near distal third (Fig. 4B). Exoskeleton of genito-abdominal trunk with numerous fine wrinkles. Caudal ramus $87 \times 60 \mu\text{m}$ (1.45 times longer than wide), bearing tuft of several inner distal setules, 5 pinnate setae, and hyaline seta (indicated by a star in Fig. 4B) that is

smooth and flexible, with both the cuticle and interior densely staining in methylene blue. Mouth present as small, simple pore. Esophagus visible but digestive tract not seen. Anal operculum small but recognizable.

Antennule (Fig. 4C) unsegmented, about $185 \mu\text{m}$ long, with 23 setae and tapered distal process; setae consisting of 13 plumose, 1 naked, and 9 small, hyaline, flexible setae. Antenna and oral appendages absent.

Legs 1-3 (Figs. 1G, 4D-F) biramous, with 1-segmented rami. Formulae for leg armature as follows:

copepodid I, 2.13 mm body length, dorsal view, showing Gicklhorn's organ (g), dorsolateral ocelli (od), and globular expansion of abdomen (arrow); D, *Caribeopsyllus* sp. A copepodid I, ventral view of previous individual, showing antennules (A1), dorsolateral ocellus (od), ventral ocellus (ov), and three pairs of swimming legs (arrows); E, *C. chawayi* metanauplius, 0.88 mm body length, dorsal view, showing Gicklhorn's organ (g), dorsolateral ocelli (od), primordia of swimming legs (arrowheads), anterior furrow (f) and posterodorsal hump (h) separated by transverse groove (tg); F, *C. chawayi* metanauplius, 0.73 mm body length, ventral view, showing antennule (A1), antenna (A2), mandibles (Md), maxillules (MX1), and ventral ocellus (ov); G, *C. chawayi* copepodid I, 0.94 mm body length, within host's stomach, showing large dorsolateral ocelli (od) with reflective tapetum, and swimming legs (arrows); H, *Caribeopsyllus* sp. A metanauplius, 0.74 mm body length, dorsal view, putative female showing dense jade-green pigmentation and relatively small, separated dorsolateral ocelli (arrowheads); I, *Caribeopsyllus* sp. A metanauplius, 0.65 mm body length, dorsal view, putative male showing pale pigmentation and relatively large, close-set dorsolateral ocelli (arrowheads); J, *C. chawayi* metanauplius, 0.67 mm body length, oblique dorsal view, putative female showing green pigmentation and relatively small, separated dorsolateral ocelli (arrowheads); K, *C. chawayi* metanauplius, 0.65 mm body length, oblique dorsal view, putative male showing large, close-set dorsolateral ocelli (arrowheads); L, three *Caribeopsyllus chawayi* metanauplii, 0.46-0.98 mm body length (arrowheads), in stomach of *Ophiactis savignyii* (3.0 mm dd); M, two *Caribeopsyllus* sp. A metanauplii (arrowheads), 1.11 and 1.14 mm body length, in stomach of *Ophiothrix angulata* (3.9 mm dd); N, posterior end of a *Caribeopsyllus* sp. A metanauplius (arrowhead), 0.74 mm body length, projecting through body wall of *Ophiothrix angulata* (1.5 mm dd). Scale bars: A-K, 100 μ m; L, M, 1 mm; N, 0.5 mm.

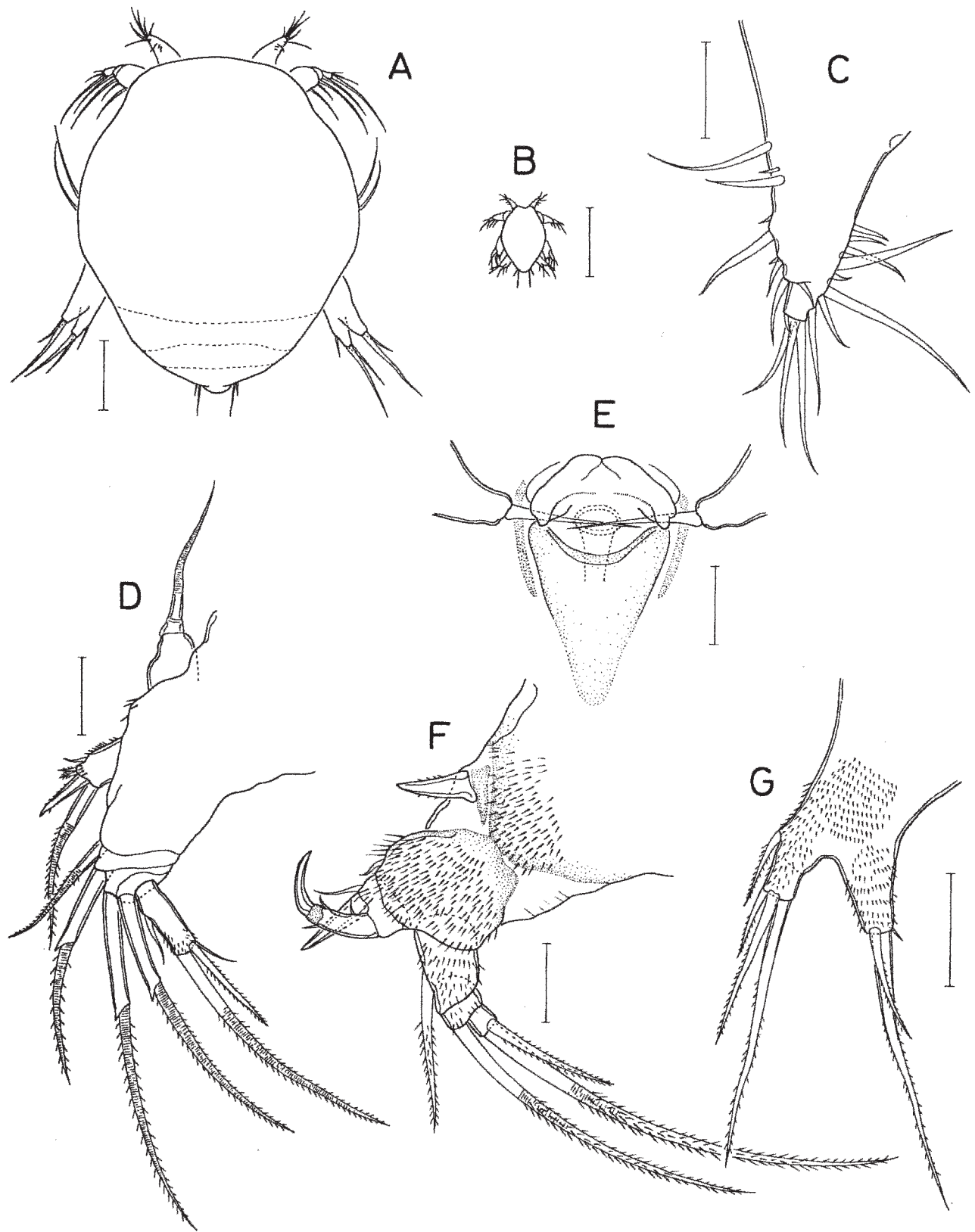


Fig. 3. *Caribeopsyllus chawayi*, metanauplii: A, habitus, dorsal; B, habitus of smallest specimen drawn at same scale as A, dorsal; C, antennule; D, antenna; E, oral area and arthrite of antenna; F, mandible; G, maxillule. Scale bars: A, B, 0.2 mm; C-F, 0.05 mm; G, 0.1 mm.

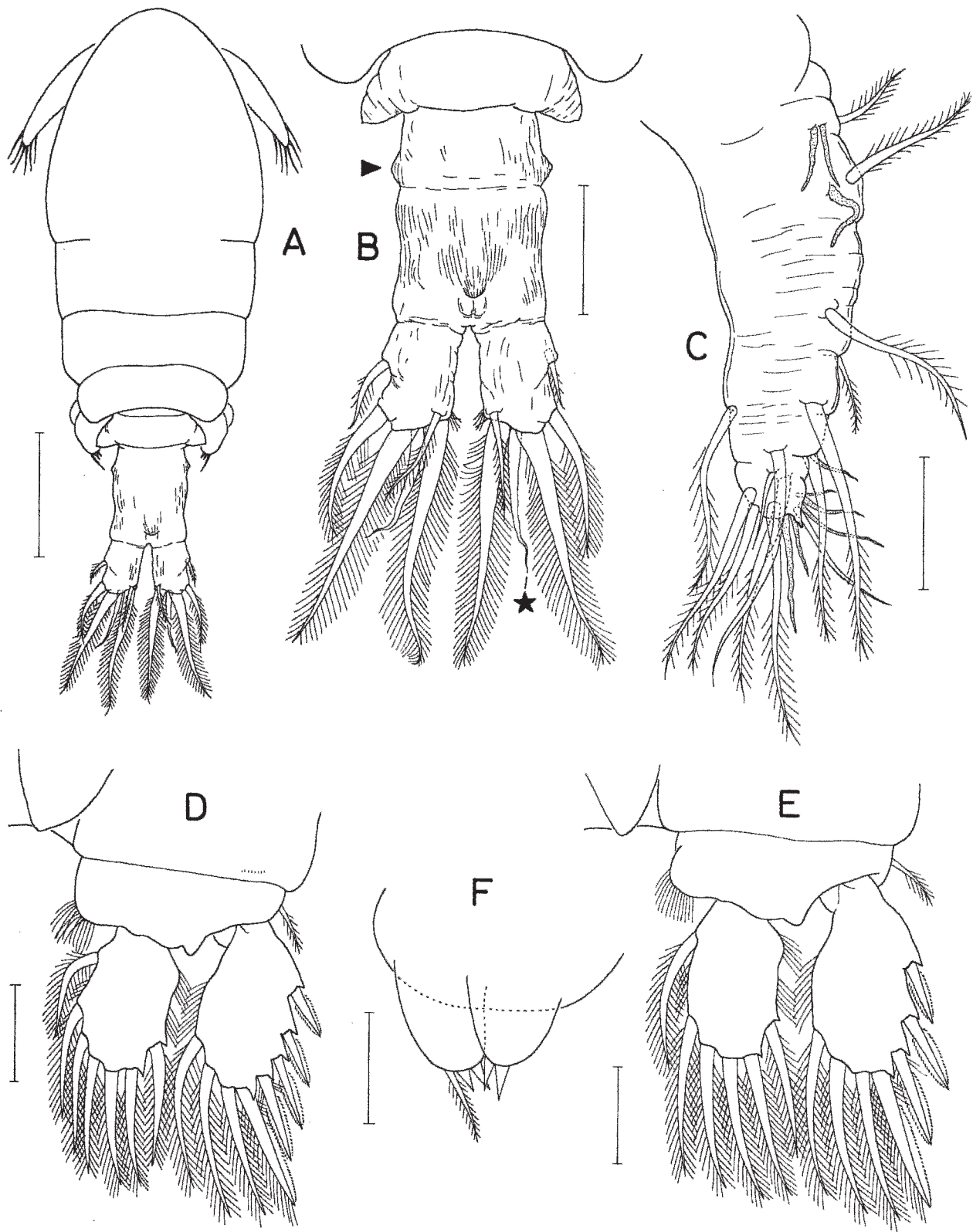


Fig. 4. *Caribeopsyllus chawayi* copepodid I: A, habitus, dorsal; B, urosome, dorsal, showing conical anterolateral protuberances (arrowhead) and hyaline fourth seta (star); C, antennule; D, leg 1; E, leg 2; F, leg 3. Scale bars: A, 0.2 mm; B, 0.1 mm; C-F, 0.05 mm.

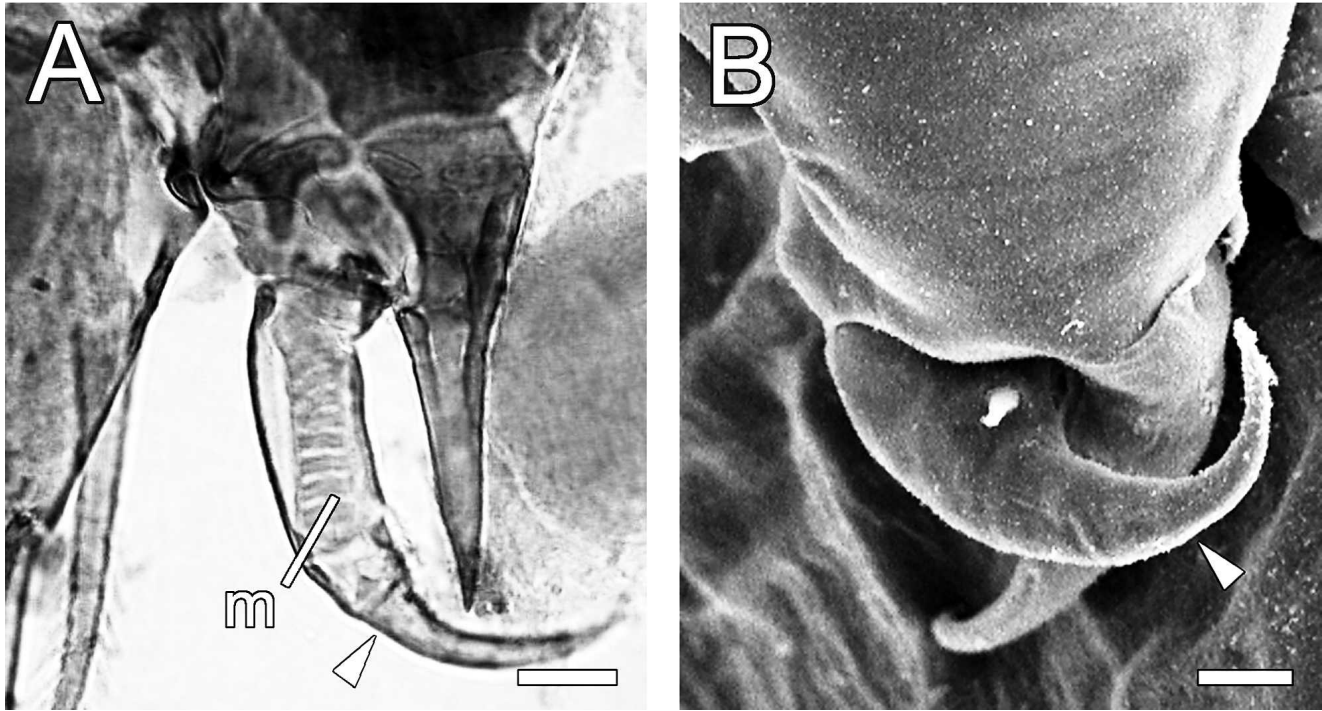


Fig. 5. Morphology of mandibular chela of *Caribeopsyllus metanauplii*. A, *Caribeopsyllus chawayi*, cleared and stained to show striated muscle (m) within second endopodal segment of chela (arrowhead); B, SEM image of *Caribeopsyllus amphiodiae* showing terminal claw of second endopodal segment (arrowhead) retracted against hooked spine on first endopodal segment of mandible. Scale bars: 0.1 mm for both.

Leg 1: coxa 0-0; basis 1-0; exopod IV, I, 3; endopod 1, 6
 Leg 2: coxa 0-0; basis 1-0; exopod III, I, 3; endopod 1, 5
 Leg 3: protopod 0-0; exopod 3; endopod 2.

Medial margin of basis of legs 1 and 2 with setules. Leg 3 with lobiform rami; exopod with pinnate outer seta and 2 small, spiniform setae; endopod with 2 small spiniform setae (Fig. 4F). Leg 4 rudimentary, represented by lobate process with pointed tip, on lateral side of fourth pedigerous somite. Legs 5 and 6 absent.

Appearance of Living Larvae of *C. chawayi*.—The nearly circular body of large metanauplii (> 0.80 mm long) was widened behind the bluntly rounded anterior end, and was broadest at the midpoint (Fig. 1E, F). A transverse groove bisected the midpoint of the body, behind which a posterodorsal hump emerged and tapered towards the constricted posterior end of the larva (Fig. 1E, 2C). A broad dorsal furrow, which narrowed near the eyes, ran antieriad from the groove and between the raised anterolateral edges of the body. The body was opaque yellowish-green variegated with olivaceous regions. There was orange or reddish-orange pigmentation alongside the ventral midline, postero-dorsally on the body, in transverse bands across the caudal region, and at the bases of the appendages (Figs. 1E, F, 2A). Eyes of the larvae were large and brilliant red, consisting of three separate funnel-shaped ocelli, each one with a basal tapetum surrounded by pigmented cells and a transparent convex cap (presence of a refracting lens was not ascertained) (Figs. 1E, F, 2C). In dorsal view, the dorsolateral ocelli obscured the ventral ocellus, and in ventral view, opaque whitish tissue obscured

the dorsolateral ocelli. There were red Gicklhorn's organs distal to the dorsolateral ocelli.

The smallest metanauplii examined, 0.20-0.30 mm long, were translucent and faint yellowish-green with orange and reddish-orange patches in the basal segments of the appendages and toward the sides of the body. Individuals approaching 0.5 mm were opaque yellowish-green with reddish-orange pigmentation alongside the transparent midline. The 0.60-0.70 mm larvae were opaque yellowish-green, with patches of orange, reddish-orange, or red pigment at the bases of appendages, beside the ventral midline of the body, and between the primordial thoracic somites (Fig. 1J, K). The smallest larvae observed (< 0.2 mm long) had a minute naupliar eye with merged ocelli, and individuals 0.30-0.40 mm long had a Y-shaped naupliar eye with three separate ocelli that appeared to be connected by slender red strands. Gicklhorn's organs were present in the smallest larva (0.50 mm) that had recognizable dorsolateral and ventral ocelli. Notably, a 0.65 mm individual had large, closely placed dorsolateral ocelli (Fig. 1K), whereas a 0.67 mm individual had markedly smaller ocelli (Fig. 1J). The latter may be a female, as it also had a dark, olivaceous internal structure, possibly a developing ovary, that was lacking in the previously mentioned individual (Figs. 1J, 2F); however, we did not observe evidence of sexual dimorphism among larger metanauplii. This may be because the large specimens examined were of one sex, and possibly because their reproductive organs were obscured by opaque pigmentation.

The prosome of the actively moving copepodid I contained reddish-orange reticulate masses and whitish

material (Fig. 1G). Basal segments of its swimming appendages were reddish-orange, and the urosome contained paired reddish-orange strands. Large, bright red dorsolateral ocelli were on the lateral midline of the cephalosome, and Gicklhorn's organs lay behind them, on the dorsal surface of the body.

Morphology of the Mandibular Chela of the Metanauplius Larva.—The mandibles of thaumatopsyllid metanauplii bear a pincer-like structure that is used to grip the host. It consists of a terminal claw on the second endopodal segment that opposes a massive, fixed spine on the first endopodal segment (Figs. 2A, 3F, 5, 6E, F). A cleared and stained preparation of the mandible of *C. chawayi* revealed the presence of striated tissue, which is indicative of arthropod voluntary muscle, in the second endopodal segment, and the absence of similar tissue in the spine (Fig. 5A). Separate retractor and protractor muscles were not distinguishable in the endopod, possibly due to the manner in which the specimen was prepared. Although the retracted claw and spine may not meet tip-to-tip, movement of the muscle-operated claw could pinch material against the opposing spine. This is evident from the position of the claw and spine of a specimen of *C. amphiodiae* (Fig. 5B), photographed during a previous study (Dojiri et al., 2008).

Systematic Remarks Regarding *Caribeopsyllus chawayi*.—Suárez-Morales and Tovar (2004) described copepodid stages I-III and V of *C. chawayi*, but their putative copepodid II specimens were actually advanced copepodid I stages (Dojiri et al., 2008). They also revised the description of the adult female (copepodid VI) made by Suárez-Morales and Castellanos (1998), which mistakenly was based on the copepodid V. A single copepodid I specimen was available from among our samples, and we compared it with 6 Mexican copepodid specimens of *C. chawayi* provided by Suárez-Morales.

The Belizean and Mexican copepodid I individuals closely matched one another. Although some characteristic features of the copepodid I were not mentioned by Suárez-Morales and Tovar (2004), all the characteristics of the larvae noted herein are present in specimens from both populations. The most important diagnostic feature of copepodid I of *C. chawayi* is a conical anterolateral protuberance on each side of the genito-abdominal trunk (indicated by an arrowhead in Fig. 4B). The caudal rami of Belizean and Mexican specimens have a similar length:width ratio (1.45 : 1 in the former and 1.49 : 1 in the latter) and a similar tuft of several setules on the inner distal corner. The antennule and legs 1-3 differ only slightly. Although the Belizean specimen was 0.94 mm long, its smaller size than the Mexican specimens is considered to be inconsequential because body lengths of the latter were quite diverse (1.14, 1.18, 1.41, 1.47, and 1.50 mm). Moreover, the Mexican specimens were intermolt individuals that had already developed the cuticle of copepodid II, whereas the newly metamorphosed Belizean copepodid I still had its caudal setae partially imbedded in the caudal rami.

Metanauplius Stage of *Caribeopsyllus* sp. A.—Body (Figs. 1A, B, 2E, 6A, 9D) nearly ovoid, with slightly

convex or slightly truncate anterior margin, expanded mid-region, and tapered posterior end. Body size-range, 0.58-1.14 mm long, based on 9 specimens. Size of dissected specimen 1.03×0.75 mm. Caudal region bearing 2 groups of setae, each group containing 1 short and 1 longer seta; both setae slender, flexible.

Antennule (Fig. 6B) unsegmented, strongly tapering, and armed with 21 setae; 2 of which weakly plumose and the remaining others smooth. Antenna (Figs. 1A, 2B, 6C) biramous, proximally with prominent extension tipped with acicular arthrite directed towards the mouth (Fig. 6D). Exopod consisting of 5 segments; first segment fused with protopod, with small inner distal seta; second to fourth segments each with large inner seta; proximal one-third of the latter 3 setae stiff and distal two-thirds flexible, with spinules; fifth segment $50 \times 21 \mu\text{m}$ (2.38 times longer than wide), armed with inner seta and 3 very unequal distal setae. Endopod 1-segmented and armed with 4 elements: small, naked inner seta; small, spiniform inner distal seta; and terminally 1 spine and 1 seta (this seta at most twice as long as the adjacent spine).

Mouth located between labrum and postoral lip (Fig. 6D), posteromedially to bases of antennae (Fig. 9D). Labrum with rounded posterior process on both sides and row of minute spinules on ventral surface. Postoral area sclerotized (Fig. 6D). Mandible (Fig. 6E) not appreciably different from that of metanauplius of *C. chawayi* and ornamented with numerous spinules on ventral surface (spinules omitted in Fig. 6E). Maxillule (Fig. 6G) also similar to that of *C. chawayi*.

Beneath exoskeleton in 6 specimens (all of them ≥ 0.96 mm long), posterior part of body with 3 delicate dorsal transverse divisions (Fig. 6A) and ventrally exhibiting the primordial legs, their setal elements, and caudal setae of copepodid I (Fig. 1B).

Copepodid I Stage of *Caribeopsyllus* sp. A.—Body (Figs. 1C, D, 7A) 2.13 mm long. Major body articulation between fourth and fifth thoracic somites (third and fourth pedigers). Prosome cylindrical, as wide as dorsoventrally deep. Cephalothorax slightly longer than wide, delimited from first pedigerous somite by incomplete lateral suture lines. Rostrum absent. Urosome unsegmented, but demarcated into 2 parts (consisting of fourth pedigerous somite and undifferentiated genito-abdominal trunk) by abruptly narrowed portion of trunk (Fig. 7B) and ventral sclerotization (Fig. 7C). Genito-abdominal trunk about $315 \mu\text{m}$ long, with narrow anterior part ($154 \mu\text{m}$ wide) and expanded, globular posterior part ($227 \mu\text{m}$ wide and $217 \mu\text{m}$ deep). Exoskeleton of genito-abdominal trunk with numerous fine wrinkles. Caudal rami parallel to each other; each ramus $115 \times 85 \mu\text{m}$ (1.35 times longer than wide), bearing naked, hyaline seta and 5 pinnate setae. Mouth present as small, simple pore. Esophagus visible but digestive tract not seen. Anal area bullate, with distinct anus.

Antennule (Fig. 7D) unsegmented, about $225 \mu\text{m}$ long, with 23 setae and small, pointed distal process; setae consisting of 13 plumose, 2 naked, and 8 small, hyaline, flexible setae. Antenna and oral appendages absent.

Legs 1-3 (Fig. 7E-G) biramous, with 1-segmented rami. Formulae for leg armature as in *C. chawayi*.

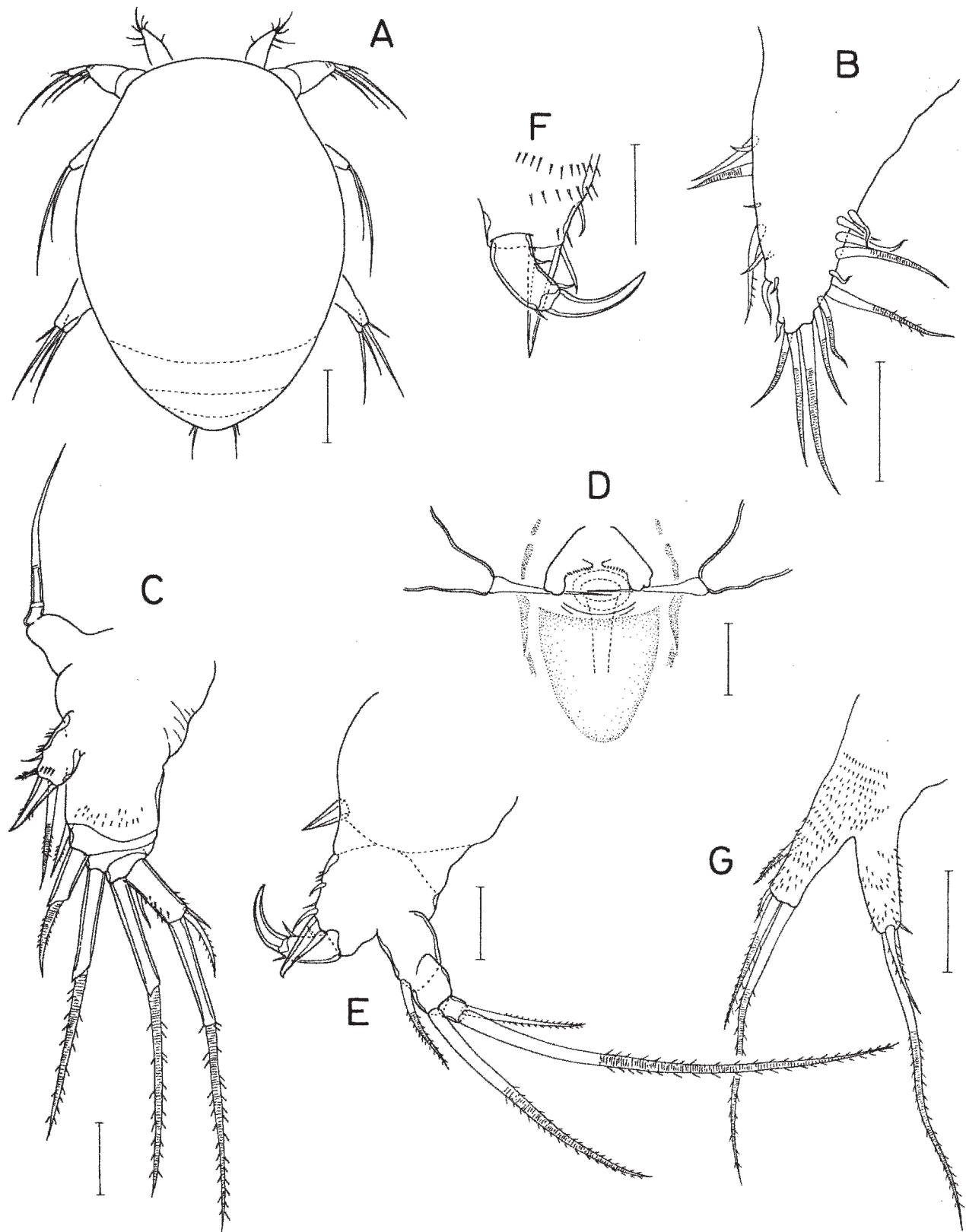


Fig. 6. *Caribeopsyllus* sp. A metanauplius: A, habitus, dorsal; B, antennule; C, antenna; D, oral area and arthrite of antenna; E, mandible; F, endopod of mandible; G, maxillule. Scale bars: A, 0.2 mm; B-E, 0.05 mm; G, 0.1 mm.

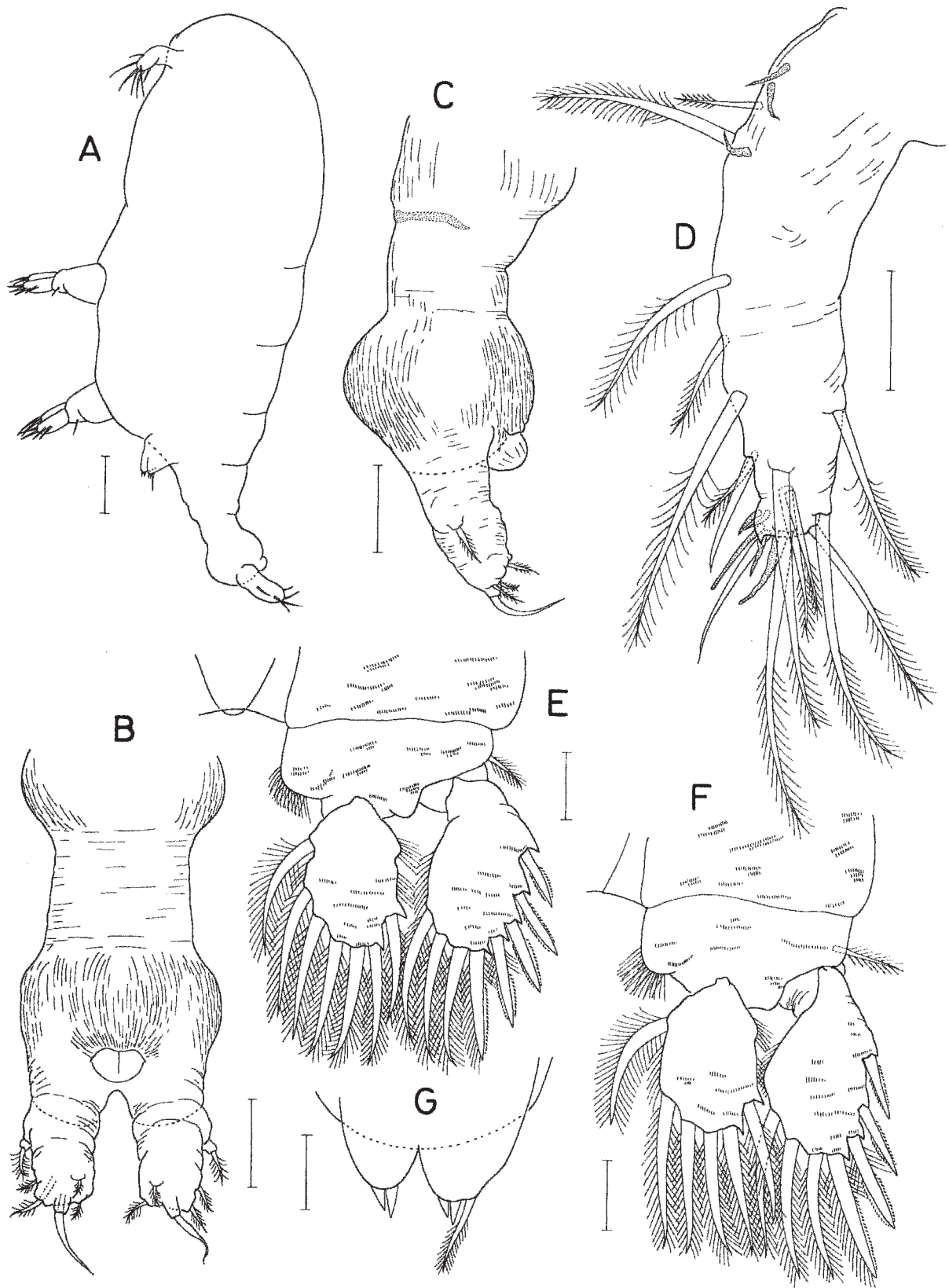


Fig. 7. *Caribeopsyllus* sp. A copepodid I: A, habitus, lateral; B, genito-abdominal trunk, dorsal; C, genito-abdominal trunk, lateral; D, antennule; E, leg 1; F, leg 2; G, leg 3. Scale bars: A, 0.2 mm; B, C, 0.1 mm; D-G, 0.05 mm.

Leg 4 not examined due to destruction of anterior part of fourth pedigerous somite. Legs 5 and 6 absent.

Copepodid II Stage of *Caribeopsyllus* sp. A.—Body (Fig. 8A) 2.03 mm long, slightly smaller than that of copepodid I. Body segmentation as in copepodid I. Urosome (Fig. 8B) indistinctly 2-segmented, consisting of short fourth pedigerous somite and undifferentiated genito-abdominal trunk. Genito-abdominal trunk distinctly narrower than fourth pedigerous somite, $310 \times 188 \mu\text{m}$, bearing leg 5. Caudal rami divergent; each ramus $137 \times 86 \mu\text{m}$ (1.59 times longer than wide), with 6 plumose setae.

Antennule (Fig. 8C) unsegmented, about $252 \mu\text{m}$ long, with 25 setae, anterodistal 4 of which aesthetasc-like. Antenna and oral appendages absent. Mouth present.

Legs 1-3 (Fig. 8D-F) biramous, with 1-segmented rami. Formulae for leg armature as follows:

Leg 1: coxa 0-1; basis 1-0; exopod IV, I, 5; endopod 1, 7

Leg 2: coxa 0-1; basis 1-0; exopod IV, I, 6; endopod 1, 7

Leg 3: coxa 0-1; basis 1-0; exopod IV, I, 6; endopod 1, 7

Rami of legs 1-3 with lateral constriction and incomplete suture at site of impending segmentation in copepodid III stage. Second outer spine on exopod of leg 3 distinctly smaller than adjacent spines.

Leg 4 (Fig. 8G) apparently biramous; sympod with plumose outer seta; exopod with 5 setae; smallest second outer seta naked and other setae plumose; endopod a small lobe with terminal plumose seta. Leg 5 (Fig. 8H) a lobe with long plumose seta and small naked seta. Leg 6 represented by 2 very small processes posterior to leg 5 (Fig. 8H).

Appearance of Living Larvae of *Caribeopsyllus* sp. A.—The subovoidal body of large metanauplii (≥ 0.80 mm long) was widened behind the truncate anterior end, and was broadest anterior to the midpoint (Figs. 1A, B, 2E). A posterodorsal hump emerged just past the midpoint and tapered towards the bluntly pointed posterior end of the body (Figs. 1A, 2D). A wide furrow ran anteriorly from the hump, along the dorsal midline and between the raised anterolateral edges of the body. The body was opaque jade green and olivaceous, with transverse bands across the caudal region. There was brownish-yellow pigmentation in the appendages, and there were brownish-yellow patches beside the ventral midline that were more conspicuous on the ventral surface than on the dorsal surface of the body. The ocelli and Gicklhorn's organs of the larva resembled those of *C. chawayi* (Figs. 1A, B, 2B, D, E).

The smallest metanauplii examined, 0.10-0.20 mm long, were whitish and translucent. The appendages were amber-colored in larvae 0.40 mm and larger. The body was whitish and opaque in 0.50 mm animals, pale green in 0.60 mm animals, and jade green with brownish-yellow markings in 0.70 mm animals. The smallest larva had a Y-shaped naupliar eye composed of three minute ocelli that appeared to be connected by slender red strands. Gicklhorn's organs were associated with the dorsolateral ocelli of individuals as small as 0.60 mm. A whitish 0.65 mm long individual had large, close-set dorsolateral ocelli (Fig. 1I), whereas a greenish 0.74 mm individual had

relatively small, well separated ocelli (Fig. 1H). The individual with large eyes may have been a male, as appeared to be the case in *C. chawayi*. However, males and females were not distinguished among the large metanauplii. Most of them had eyes of similar size and a multi-lobed green organ (Fig. 2E). A histological study will be required to determine which large metanauplii of *Caribeopsyllus* sp. A are female and whether the green organ is an ovary.

The prosome of copepodid stages I and II was jade green, variegated with bluish-green pigmentation and with scattered flecks of brown pigment (Fig. 1C, D). There were patches of intense green, brownish-yellow, and brown pigmentation beside the ventral midline. The antennules contained red strands. A strand of whitish material extended through the urosome into the white anal somite. The bases of the swimming appendages were yellowish-brown and reddish-brown. The ocelli and Gicklhorn's organs resembled those of the copepodid of *C. chawayi*.

Systematic Remarks Regarding *Caribeopsyllus* sp. A.—We refer the species parasitizing *O. angulata* to *Caribeopsyllus* based on the close resemblance of its metanauplius and copepodid stages to those of the type species of the genus, *C. chawayi*. There are no appreciable differences in the armature of antennules and legs between the two species. However, the antennal endopod bears 5 elements in *C. chawayi* metanauplii, but 4 (lacking a small spiniform seta) in *Caribeopsyllus* sp. A (Figs. 3D, 6C). In addition, the terminal seta on the endopod is distinctly larger in *C. chawayi* than in *Caribeopsyllus* sp. A. It is about 3 times longer than the adjacent spine in *C. chawayi*, but only about twice the length of the adjacent spine in *Caribeopsyllus* sp. A (Figs. 3D, 6C). Although the posteriorly humped body-shape of their metanauplii is similar, body proportions and coloration of the two species are different. Furthermore, the copepodid I stage of *Caribeopsyllus* sp. A is considerably larger (2.13 mm) than that of *C. chawayi* (0.94 mm), and the posterior part of its genito-abdominal trunk is markedly expanded and globular.

Larval Behavior

Metanauplii of both Belizean species used mandibular chelae to grasp the host's stomach wall (Fig. 1L, M, 2A, B). Individuals that were not anesthetized swam within the host's stomach, as well as after they had been removed from the host, by rapidly flexing the paired setose appendages. Resting individuals held the long, flexible antennal setae against the dorsal surface of their body (Fig. 1A, 2B), but the long setae of their mandibles and maxillules projected sideways from the body (Fig. 1A, B, F).

The swimming Belizean metanauplii moved their contralateral appendages in unison, but *C. amphiodiae* crawls by moving contralateral appendages alternately, and not in a consistent sequence. Maximum frequency of appendage movement was 4/sec ($\bar{x} = 3.00 \pm 0.26$ SE, $n = 10$) in *Caribeopsyllus* sp. A, and 6/sec ($\bar{x} = 2.50 \pm 0.50$ SE, $n = 2$) in *C. chawayi*. Speed of appendage movement was greater in metanauplii of swimming *Caribeopsyllus* sp. A ($\bar{x} = 0.15 \pm 0.01$ SE sec/stroke, $n = 15$) and *C. chawayi* ($\bar{x} =$

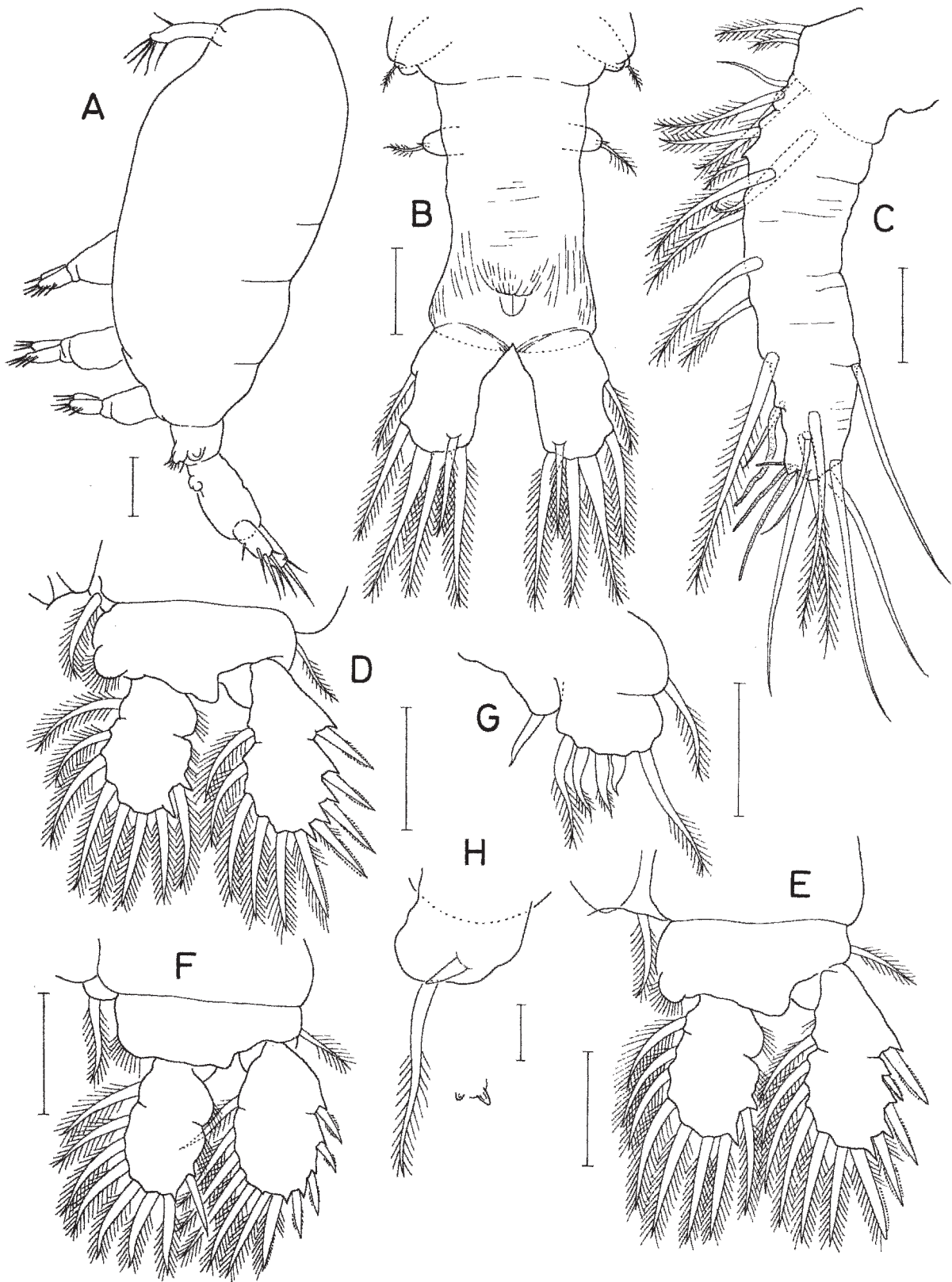


Fig. 8. *Caribeopsyllus* sp. A copepodid II: A, habitus, lateral; B, urosome, dorsal; C, antennule; D, leg 1; E, leg 2; F, leg 3; G, leg 4; H, legs 5 and 6. Scale bars: A, 0.2 mm; B, D-F, 0.1 mm; C, G, 0.05 mm; H, 0.02 mm.

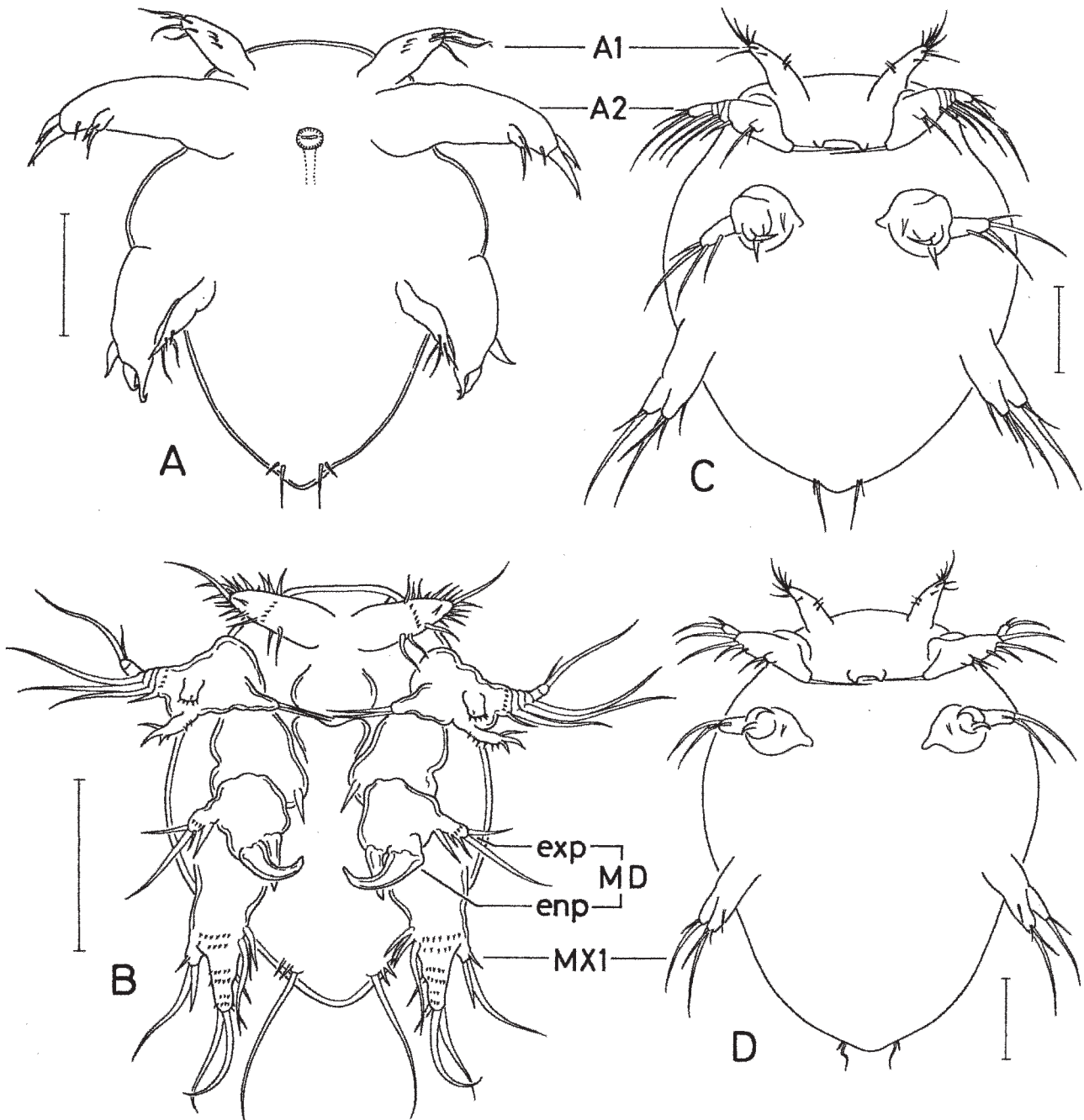


Fig. 9. Ventral views of four thaumatopsyllid metanauplii. A, *Caribeopsyllus amphiodiae* (redrawn from Dojiri et al., 2008); B, *Thaumatoopsyllus paradoxus* (redrawn from Bresciani and Lützen, 1962); C, *Caribeopsyllus chawayi*; D, *Caribeopsyllus* sp. A. Scale bars: 0.2 mm for all.

0.27 ± 0.04 SE sec/stroke, $n = 7$), than in the crawling metanauplii of *C. amphiodiae* ($\bar{x} = 1.05 \pm 0.06$ SE sec/stroke, $n = 32$). Despite the anesthetized condition of the Belizean metanauplii, the frequency of their appendage movements was comparable to those of free-swimming calanoid nauplii studied by Paffenhöfer and Lewis (1989).

Emergence of thaumatopsyllids from the host has not been directly observed, but Hendler and Dojiri (2009) provided evidence that the emergent stage of *C. amphiodiae* could be an advanced metanauplius or a copepodid

stage. The presence of actively moving stage I copepodids of the Belizean species in their host's stomach suggests that a copepodid (not a metanauplius) is the emergent stage in *Caribeopsyllus* sp. A and *C. chawayi*. A copepodid II stage of *Caribeopsyllus* sp. A was found in seawater in which several species of ophiuroids had been held for several hours. In that brief period, it likely emerged from an individual of *O. angulata* in the container (possibly as a copepodid I). It repeatedly and rapidly swam upward in a Petri dish of seawater, and then sank for an instant,

sometimes pausing momentarily at the bottom of the dish before swimming upward again. The copepodid moved toward the lighted edge of the dish, and when the light beam from a fiber optic microscope lamp was shifted along the perimeter of the dish it followed the light.

Characteristics of Hosts and Size of Parasites

The larvae of *C. chawayi* were found only in *O. savignyi* (Fig. 1L), and the larvae of *Caribeopsyllus* sp. A were found only in *O. angulata* (Fig. 1M). The red eyes and green bodies of *Caribeopsyllus* sp. A could sometimes be discerned through the host's distended body wall. In samples of *Halimeda* spp. collected at Carrie Bow Cay in October, 2006, 3 of the 11 *O. angulata* (27%) that were examined were parasitized, but none of the other ophiuroids was parasitized, including 22 juvenile *Ophiocoma pumila* Lütken, 1859, 8 *Ophiocomella ophiactoides* (H. L. Clark, 1901), and 90 *Ophiothrix orstedii*. In samples of *Halimeda* spp. collected from Carrie Bow Cay in February and March 2008, 10 of 55 *O. angulata* (18%) were parasitized, but 55 *O. orstedii* were not parasitized.

Metanauplii of *C. chawayi* were generally of smaller size ($\bar{x} = 0.58 \pm 0.04$ SE mm, range 0.19-0.98, $n = 23$), than those of *Caribeopsyllus* sp. A ($\bar{x} = 0.69 \pm 0.06$ SE mm, range 0.16-1.14, $n = 20$). Most of the parasites were small compared to their hosts. The ratio between the length of the largest metanauplius and the dd of the host approached 0.5 for *C. chawayi* ($\bar{x} = 0.23 \pm 0.02$ SE, range 0.09-0.47, $n = 17$) and also for *Caribeopsyllus* sp. A ($\bar{x} = 0.34 \pm 0.03$ SE, range 0.18-0.49, $n = 12$). Thus, even the largest larva could not occlude its host's gut, although the cumulative impact of several parasites on a host might be somewhat greater (Fig. 1L, M). Only one infected *O. angulata* was physically damaged, a 1.50 mm dd individual containing a 0.74 mm long *Caribeopsyllus* sp. A that had stretched and ruptured the body wall from within (Fig. 1N). The injury, however, may have been caused accidentally during the sampling procedure.

The larvae of *C. chawayi* were found in two individuals of *O. savignyi* with regenerating arms (dd = 2.53, 3.22 mm), which had relatively recently undergone fission (= asexual reproduction) that had split apart the host's disk. They also occurred in large hosts with 6 arms of approximately equal size. The 17 *O. savignyi* parasitized by *C. chawayi* lacked gonads. Most hosts, in fact, were smaller than relatively rare sexually mature individuals. The *O. savignyi* that we examined ranged from 1.38 to 5.75 mm dd ($\bar{x} = 3.17 \pm 0.08$ SE mm, $n = 117$). Those with gonads were of 4.06 to 5.75 mm dd ($\bar{x} = 4.83 \pm 0.20$ SE mm, $n = 11$), whereas infected individuals were of only 1.69 to 4.14 mm dd ($\bar{x} = 3.09 \pm 0.16$ SE mm, $n = 17$). The possibility that small, sexually inactive ophiuroids were preferentially parasitized was only weakly supported by the available data, which pertain solely to relatively large, sponge-dwelling ophiuroids, very few of which (17 of 117 individuals dissected) had gonads.

Infected *O. angulata* tended to be small and comprised sexually mature and immature ophiuroids. Individuals of *O. angulata* that were examined ranged from 1.00 to 8.66 mm dd ($\bar{x} = 4.09 \pm 0.13$ SE, $n = 149$), but those parasitized by *Caribeopsyllus* sp. A were of only 1.38-3.91 mm dd ($\bar{x} =$

2.53 ± 0.25 SE mm, $n = 9$). Although we did not record the presence or absence of gonads for 8 infected individuals, we observed that 5 other infected *O. angulata* lacked gonads. Moreover, of the 149 individuals that were sexed, those that contained gonads ranged from 2.38 to 8.66 mm dd ($\bar{x} = 4.60 \pm 0.13$ SE, $n = 114$), but 4 of the 13 hosts were smaller than any of the sexually mature individuals.

Distribution and Incidence of Parasites

All the *O. angulata* parasitized by *Caribeopsyllus* sp. A were collected from the back reef and the spur and groove zones on the barrier reef near Carrie Bow Cay, Belize. Most of the infected ophiuroids lived in *Halimeda opuntia* (Linnaeus) Lamouroux, 1816, and some occurred in mixed samples of *H. opuntia* and *Halimeda goreau* Taylor, 1962. Parasites were not detected in 159 *O. angulata* collected from various substrates in shelf lagoon localities including Cat, Manatee, Lagoon, and Twin cays, and an unnamed sand bore. On the other hand, *C. chawayi* was found in *O. savignyi* collected from *Halimeda* spp. on a submerged sand bore in the shelf lagoon. It parasitized *O. savignyi* in an *Amorphinopsis* sp. sponge at Twin Cays, but not those found in *Lissodendoryx isodictyalis* (Carter, 1882). It also parasitized *O. savignyi* in a *Hyrtios* sp. sponge at Cat Cay, but did not occur in individuals removed from *Haliclona* cf. *vermeuleni* De Weerd, 2000, and *Mycale laevis* (Carter, 1882) at Manatee Cay.

At Carrie Bow Cay, the only locale where *Caribeopsyllus* sp. A occurred, 11 of 66 (16.7%) of the *O. angulata* that were sampled were parasitized. The incidence of parasitism appeared to vary temporally, as 2 of 11 ophiuroids (27.3%) collected in September, 2006, and 8 of 55 (14.5%) collected in February, 2008, were parasitized. Although 14.5% (17 of 117) of all the *O. savignyi* examined were parasitized, the actual prevalence of parasitism was considerably lower since very small individuals, which were not parasitized but that dominated the population of *O. savignyi*, were not dissected in proportion to their occurrence.

Approximately 77% of the infected *O. savignyi* and *O. angulata* were parasitized by only 1 metanauplius. A single copepodid I of *C. chawayi* was found in one *O. savignyi*, and a copepodid I of *Caribeopsyllus* sp. A was found in one *O. angulata*, but the remainder of the parasites were metanauplii. Ten of 13 infected *O. angulata* contained 1 parasite, 1 had 2, 1 had 3, and 1 had 6 parasites. Thirteen of 17 infected *O. savignyi* contained 1 parasite, 2 had 2, 1 had 3, and 1 had 4 parasites.

DISCUSSION

Apomorphic and Cenogenetic Larval Features

Naupliar stages of four thaumatopsyllid species have been identified, including *T. paradoxus*, *C. amphiodiae*, *C. chawayi*, and *Caribeopsyllus* sp. A. All four species have larvae that are endoparasites of ophiuroids, and free-living adults that lack mouthparts and the ability to feed (Bresciani and Lützen, 1962; Dojiri et al., 2008; Hendler

and Dojiri, 2009; present study). They share a suite of remarkable synapomorphic features, which appear early during ontogenesis (Dojiri et al., 2008; Hendler and Dojiri, 2009; present study). The parasitic larvae are metanauplii by definition, as they bear four pairs of appendages. They grow to approximately 1 mm in length, which is exceptionally large relative to most copepod nauplii (Longhurst, 1986). The presence of four pairs of appendages in the free-swimming nauplius I stage of *C. amphiodiae* (see Dojiri et al., 2008; Hendler and Dojiri, 2009), and in the smallest metanauplii of *Caribeopsyllus* sp. A and *C. chawayi*, suggests that all Thaumatopsyllidae may have a paedomorphic life cycle, lacking an initial orthonauplius stage with only three pairs of appendages.

Although they dwell in the dark, the metanauplii of three species have elaborate naupliar eyes and conspicuous Gicklhorn's organs. We presume that contradictory observations regarding eyes of the larvae of *T. paradoxus* (Bresciani and Lützen, 1962; Fosshagen, 1970; Suárez-Morales and Tovar, 2004) may be based on incomplete descriptions. As is noted by Hendler and Dojiri (2009) the nauplius I of *C. amphiodiae* is negatively phototactic and likely gravitates toward the host's benthic habitat, whereas adults of *T. paradoxus* are attracted to lighted traps (Hovda and Fosshagen, 2003). Adult *T. paradoxus* and the positively phototactic copepodid II of *Caribeopsyllus* sp. A presumably swim toward the illuminated water column.

Although sexually dimorphic nauplii are virtually unknown among other copepods, with the exception of two species that were characterized as having "progenetic metanauplii" (Huys, 2001; Huys et al., 2006), evidence from the four thaumatopsyllid species studied suggests that their metanauplii may generally be dimorphic. In addition, the large, advanced metanauplii of the three species of *Caribeopsyllus* have elaborate naupliar eyes and precociously developing subcuticular copepodid structures, including the third and fourth pedigerous somites that arise internal to the naupliar exoskeleton; furthermore, they give rise to non-feeding adults. Thus, they have larval characteristics that were hypothesized by Hendler and Dojiri (2009) to have permitted the evolution of non-feeding adults in phylogenetically disparate groups of animals: large size, ontogenetically advanced morphological structures, and a capacity to store the nutrient reserves used for reproduction.

Thaumatopsyllid metanauplii have striking specializations for locomotion and feeding, which may be ontogenetically transitory (cenogenetic) larval adaptations for their unusual parasitic life style. Their mandible, used to grip the host, bears a chela which is clearly a cenogenetic structure that is present only in the naupliar stage. It consists of a terminal claw on the second endopodal segment, which contains striated muscle, and which opposes a massive, fixed spine on the first endopodal segment (Figs. 2A, 5, 6F). To our knowledge chelate mandibles have not been found to occur in the nauplii of other copepods, although some monstrillid and harpacticoid nauplii have hooked claws (Dahms, 1991; Ogawa et al., 1997; Grygier and Ohtsuka, 2008).

Metanauplii of *C. chawayi* and *Caribeopsyllus* sp. A have relatively slender appendages with well developed setae (Figs. 3A, 6A, 9C, D), and they swim by moving paired, contralateral appendages in a coordinated manner, similarly to free-swimming, planktotrophic copepod nauplii. On the other hand, the non-swimming metanauplius of *C. amphiodiae* (Fig. 9A) crawls by flexing its appendages in an irregular sequence. Its appendages bear fewer and relatively, shorter setae and spines than those of *Caribeopsyllus* sp. A, *C. chawayi*, and *T. paradoxus* (Fig. 9B). The mandibular exopod is a large, smooth spine in *C. amphiodiae* (Fig. 9A), whereas in *C. chawayi*, *Caribeopsyllus* sp. A., and *T. paradoxus* it is 3-4 segmented, covered with numerous setal elements, and bears long, well-developed setae (Figs 3F, 6E, 9B-D). In addition, the maxillule of *C. amphiodiae* is relatively smaller than that of the species with swimming metanauplii. The naupliar appendages of *T. paradoxus* are more robust than those of the swimming species, and although it crawls, its maxillules are relatively larger and have better developed setation than those of *C. amphiodiae* (Fig. 9A, B). Thus, the morphology of their naupliar appendages is similar for *Caribeopsyllus* sp. A. and *C. chawayi*, which have swimming metanauplii, and differs from that of *C. amphiodiae* and *T. paradoxus*. The crawling metanauplii of the latter two species, however, have dissimilar appendages.

The metanaupliar antenna of *Caribeopsyllus* sp. A, *C. chawayi*, and *T. paradoxus* has an arthrite that can be drawn across the mouth. However, there is one arthrite in the Belizean *Caribeopsyllus* spp., and an arthrite with an associated seta that may be a second arthrite, in *T. paradoxus*. The metanauplius of *T. paradoxus* also has a well developed labrum compared to the *Caribeopsyllus* species (Bresciani and Lützen, 1962: Fig. 5). The "naupliar arthrite," according to Ferrari and Dahms (2007), is a muscularly-controlled, articulating structure, which is generally (but not exclusively) found in copepod nauplii that feed. It is thought to transport food to the mouth (Izawa, 1987; Ferrari and Dahms, 2007), although the action of the arthrite has not been directly observed. Metanauplii of *C. amphiodiae*, which lack an antennal arthrite, probably ingest extremely fine particles and fluid using capillary action (Hendler and Dojiri, 2009); and an individual 0.49 mm in length had a mouth 0.03 mm in width. Metanauplii of *Caribeopsyllus* sp. A and *C. chawayi* (1.04 and 0.97 mm in length, respectively) both had mouths approximately 0.02 mm wide. Thus, *T. paradoxus* and the Belizean species may use the naupliar arthrite to gather particles of food; nevertheless the Belizean species and *C. amphiodiae* (which lacks an arthrite) must ingest microscopic particles of similarly small size.

Larval Features and Phylogenetic Relationships

Species of copepods are typically distinguished based on differences in shape and armature of the adult's feeding and swimming appendages. Among Thaumatopsyllidae the number of taxonomically useful characters is quite limited as the adults lack feeding appendages and have swimming appendages that are alike. Thus, naupliar characters

potentially could be of immense taxonomic value for thaumatopsyllid systematics due to the homogeneous morphology of the adults.

When *C. amphiodiae* was first described, its adults were differentiated from those of *C. chawayi* by the presence of 1 spine and 6 setae (formula I, 6) on the third exopodal segment of leg 1, and the lack of an outer seta on the protopod and a 2-segmented exopod on leg 4 (Ho et al., 2003). Subsequently, Suárez-Morales and Tovar (2004) proved that the holotype of *C. chawayi* was a copepodid V. The authentic adult female they described had the same appendage formula that Ho et al. (2003) proposed to distinguish *C. amphiodiae*. Nevertheless, *C. chawayi* is characterized by a pair of lateral processes at the junction between the cephalosome and first pedigerous somite, the length of the abdomen, shape of the cephalothorax, and the processes on the outer margin of the exopod of leg 1. Other thaumatopsyllid species have been diagnosed mainly based on the morphology of legs 4 and 5, since legs 1-3 are so similar among them.

Although their adults are rather similar, striking differences between the metanauplii of *C. amphiodiae*, on the one hand, and those of *C. chawayi* and *Caribeopsyllus* sp. A on the other, suggest that the first species is not congeneric with the latter two. However, it is noteworthy that conspicuous interspecific differences that we have found among thaumatopsyllid larvae may represent cenogenetic characters, i.e., transitory features that develop early in ontogenesis, or may accurately reflect phylogenetic affinities among the species. The two possibilities are not mutually exclusive. The appendage structures of the metanauplius of *C. amphiodiae*, which differ markedly from those of *C. chawayi*, *Caribeopsyllus* sp. A., and *T. paradoxus*, may represent cenogenetic adaptations of the larva to its infaunal, deposit-feeding host, which is morphologically and ecologically quite unlike the epifaunal ophiuroids parasitized by the other three species. The apical segment on the antennal exopod of the 3 *Caribeopsyllus* species bears 4 setae, but the apical segment bears only 2 setae in *T. paradoxus*. Only the latter species has an antennal arthrite and seta (or possibly 2 arthrites); *C. amphiodiae* lacks an arthrite and has fewer exopodal segments than the other species. The sorts of disparities among *Thaumatopsyllus* and *Caribeopsyllus* metanauplii are surprising among confamilial copepods.

Naupliar characters generally have been neglected in systematic studies of copepods (Dahms, 2004), and disparities between phylogenetic analyses based on larval and adult features of congeneric copepods have been attributed to the use of cenogenetic features as characters (Lopez, 1980; Björnberg, 1986; Dahms et al., 1991; Dahms, 2000; Goetze, 2003). However, corresponding naupliar body structures of putatively congeneric copepods may be quite similar (or dissimilar), and can be useful for characterizing genera (Koga, 1970; Dahms, 1990; Dahms et al., 2005, 2007; Chullasorn et al., 2009). Fortunately, concordance could be assessed between a phylogeny of thaumatopsyllids based on genome sequence data, and one inferred from the morphological characters of larvae (compare Björnberg, 1986 versus Goetze, 2003). Therefore,

we suggest that a molecular systematic analysis of *Caribeopsyllus* species could be used to gauge the systematic significance of their larval morphology. If molecular evidence corroborates the systematic affinities suggested by naupliar and adult morphology, proposal of a new genus for *C. amphiodiae* would be warranted.

The ordinal classification of Thaumatopsyllidae has been problematic since the family's debut in the scientific literature. Thaumatopsyllids have been regarded as Monstrilloidea (Sars, 1913), Cyclopoida (Bresciani and Lützen, 1962; Huys and Boxshall, 1991; McKinnon, 1994; Boxshall and Halsey, 2004), Thaumatopsylloidea (Ho et al., 2003; Ferrari and Dahms, 2007), and Siphonostomatoida (Sewell, 1949; Fosshagen, 1970), depending on the characters considered by different authors. Although resolution of this problem will require a consideration of both molecular and morphological data, we can suggest two ontogenetic character transformations that may help clarify the placement of the family. According to Huys et al. (2007), the transient modification of seta IV (indicated by a star in our Fig. 4B) on the caudal rami of copepodid I into a flattened hyaline element is an autapomorphy for the Siphonostomatoida. In addition, the authors point out a characteristic reduction from 7 to 6 setae on the adult caudal ramus in the siphonostome Caligidae and Monstrillidae. We note that both traits are expressed by thaumatopsyllid species with described copepodid I stages, namely *C. chawayi* and *C. amphiodiae*. In our newly molted specimen of *Caribeopsyllus* sp. A the corresponding structure was incompletely developed (still embedded in the caudal ramus) and lacked the same flexibility and affinity for methylene blue found in the copepodid I of *C. chawayi*. Assuming the thaumatopsyllid characters are not homoplasies, this suggests the possibility that the Thaumatopsyllidae may indeed be Siphonostomatoida, or closely allied.

Distribution and Dispersal of Species of *Caribeopsyllus*

Previously, the geographic ranges of thaumatopsyllid species appeared not to overlap (Suárez-Morales and Castellanos, 1998), although information on their distribution was almost entirely limited to the species' type localities. *Thaumatopsyllus paradoxus* was reported in Scandinavia (Bresciani and Lützen, 1962; Fosshagen, 1970), *Orientopsyllus investigatoris* Sewell, 1949, off the Nicobar Islands, *Australopsyllus fallax* McKinnon, 1994, from Australia, *C. amphiodiae* off California (Ho et al., 2003), and *C. chawayi* from southeastern Mexico (Suárez-Morales and Castellanos, 1998). However, our discovery of *Caribeopsyllus* sp. A doubles the number of thaumatopsyllid species known from the Caribbean, establishes that two thaumatopsyllid species have overlapping ranges, and extends the known range of *C. chawayi* for at least 216 km along the Mesoamerican Barrier Reef System from the Yucatan Peninsula to Belize. The copepodids and adult stages of *Caribeopsyllus* sp. A, which likely occur in the same region, have not been reported. In the future, they could be sought in nearshore plankton and recognized by comparison with the copepodids described herein, or could

be obtained from metanauplii that are reared using the methodology of Dojiri et al. (2008).

Parasitism of *Caribeopsyllus* sp. A on *Ophiothrix angulata*, and its absence from *Ophiothrix orstedii* and several other co-occurring species of ophiuroids, suggests that it is host-specific. Although *O. angulata* occurs from Bermuda to Uruguay, the presence of *Caribeopsyllus* sp. A on the Belize Barrier Reef, and its seeming absence from the shelf lagoon, suggests that ecological factors may constrain its range. Although *O. angulata* occurred abundantly and was well sampled at the lagoonal cays, individuals from the lagoon were not found in *Halimeda* spp., as they were on the barrier reef. Thus, a survey of *O. angulata*, specifically of individuals living in algae, is required to evaluate the occurrence of *Caribeopsyllus* sp. A in the lagoon.

It appears that *Caribeopsyllus* sp. A does not castrate its host, since some infected ophiuroids were sexually mature. The possibility that it inhibits the growth or gonad development of *O. angulata* could be tested experimentally, or evaluated indirectly by obtaining more data on the reproductive condition of hosts. It also remains to be determined whether the prevalence of *Caribeopsyllus* sp. A in small ophiuroids is influenced by host size, by characteristics of the algal microhabitat of *O. angulata* (described by Hendler and Littman, 1986), or by the genotype of the ophiuroids. With regard to this last possibility, it is notable that certain individuals of *O. angulata* characterized by their coloration, small size, abundance in coralline algae, and reproductive periodicity, were described as a “variety” (var. *poecila*), which “clearly intergrades” with other nominal varieties of *O. angulata*, by H. L. Clark (1918: 319). The specificity of *Caribeopsyllus* sp. A for *O. angulata* individuals resembling “var. *poecila*” suggests that the putative variety may be a distinct but cryptic species that the parasite prefers.

Caribeopsyllus chawayi was found at cays in the Belize Shelf Lagoon, and evidently parasitizes *O. savignyi* at various stages of asexual reproduction and living in a variety of substrates. Although its metanauplii were only found in sexually inactive hosts, additional data on their occurrence in *O. savignyi* are required to determine whether the larvae cannot (or do not) infect large, sexually ripe ophiuroids, and whether they cause parasitic castration in small ophiuroids.

Caribeopsyllus chawayi was not collected on the Belizean forereef, but it likely occurs there since it was discovered on the forereef of Mahahual, Quintana Roo, Mexico (Suárez-Morales and Tovar, 2004), where its host *O. savignyi* has been found nearby (see Laguarda-Figueras et al., 2004). Potentially, *C. chawayi* could be spread widely throughout the geographic range of *O. savignyi*, which is circumtropical (Hendler et al., 1995). However, *O. savignyi* (sensu lato) reportedly comprises multiple lineages and possibly more than one species (Roy and Sponer, 2001, 2002). A molecular systematic study (Roy and Sponer, 2002) documented two clades of *O. savignyi* that appeared, based on relative branch lengths, to have diverged before the advent of long-distance shipping could have contributed to their dispersal. One clade is restricted to the Atlantic, but

a history of genetic exchange between Atlantic and Pacific populations of the second clade is indicated by the occurrence of one haplotype in both oceans. To test the possibility that *C. chawayi* has dispersed between oceans, an extensive survey of Pacific populations of *O. savignyi* for the presence of thaumatosyllid parasites will be necessary.

Although the brief life-span of non-feeding adult thaumatosyllids limits their capacity to disperse (Hendler and Dojiri, 2009), the potential for dispersal by *C. chawayi* larvae may be enormous compared with other thaumatosyllids because peripatetic *O. savignyi* can raft for great distances on floating objects (De Felice, 1999; Paulay et al., 2002). The possibility that *C. chawayi* parasitizes more than one species (which would also enhance its potential for dispersal) is bolstered by the discovery of “thespesiosyllid” (= thaumatosyllid) metanauplii in *O. savignyi* and in *Ophiactis lymani* Ljungman, 1871, in Brazil (Boffi, 1972; Duarte and Morgado, 1983). It remains to be seen whether the infected Brazilian ophiuroids are parasitized by *C. chawayi*, or perhaps by two different and possibly undescribed thaumatosyllid(s), because the specific identity of the Brazilian parasites cannot be inferred from published descriptions.

ACKNOWLEDGEMENTS

The success of this study is attributable in large part to Klaus Rützler, David Pawson, and the Smithsonian CCRE program staff and scientists, who for many years have encouraged and supported research on the biology of Caribbean ophiuroids. We are indebted to Eduardo Suárez-Morales for providing specimens of *Caribeopsyllus chawayi*, to Klaus Rützler who identified the sponges we sampled, to Haris Lessios who guided our interpretation of the phylogeography of *Ophiactis*, and to Geoff Boxshall, Mark Grygier, Hans-Uwe Dahms, and Jan Pechenik for their helpful comments on drafts of the manuscript. We are also obliged to the late Karen Friedmann for funds used in this project, and grateful to colleagues who facilitated the field work including Mike Carpenter, Claudette DeCourley, Harald Gruber, Brian Helmuth, Ed James, Dustin Kemp, Sara Lewis, Dan Miller, Ton Okkerse, Joerg Ott, Laurie Penland, Randi Rotjan, Karin Schagen, Francis Torres, Eva Toth, and Hendrik Wuyts. Brian Koehler prepared the photographic figures. This is CCRE contribution 866.

REFERENCES

- Björnberg, T. K. S. 1986. The rejected nauplius: A commentary. *Syllogeus* 58: 232-236.
- Boffi, E. 1972. Ecological aspects of ophiuroids from the phytal of S.W. Atlantic Ocean warm waters. *Marine Biology* 15: 316-328.
- Boxshall, G. A., and S.H. Halsey. 2004. An Introduction to Copepod Diversity, Part II. The Ray Society, London. pp. 422-966.
- Bresciani, J., and J. Lützen. 1962. Parasitic copepods from the west coast of Sweden including some new or little known species. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn* 124: 367-408.
- Carter, H. J. 1882. Some sponges from the West Indies and Acapulco in the Liverpool Free Museum described, with general and classificatory remarks. *Annals and Magazine of Natural History* (5) 9(52): 266-301, 346-368, pls.11-12.
- Chullasorn, S., W.-X. Yang, H.-U. Dahms, P. Kangtia, M. Holynska, W. Anansatiporn, L. O. Sanoamuang, and J. S. Hwang 2009. Naupliar development of *Eucyclops* cf. *serrulatus tropicalis*, *Euc.* cf. *spatulatus*, and *Ectocyclops medius* Kiefer, 1930 (Copepoda: Cyclopidae). *Zoological Studies* 48: 12-32.
- Clark, H. L. 1901. The echinoderms of Porto Rico. *Bulletin of the United States Fish Commission* 20 (Part 2): 231-263, pls. 14-17.

- . 1918. Brittle-stars, new and old. *Bulletin of the Museum of Comparative Zoology* 62: 265-338, 8 pls.
- Dahms, H.-U. 1990. The first nauplius and the copepodite stages of *Thalestris longimana* Claus, 1863 (Copepoda, Harpacticoida, Thalestridae) and their bearing on the reconstruction of phylogenetic relationships. *Hydrobiologia* 202: 33-60.
- . 1991. Usefulness of postembryonic characters for phylogenetic reconstruction in Harpacticoida (Crustacea, Copepoda). *Bulletin of the Plankton Society of Japan, Spec. Vol.*: 87-104.
- . 2000. Phylogenetic implications of the crustacean nauplius. *Hydrobiologia* 417: 91-99.
- . 2004. Postembryonic apomorphies proving the monophyletic status of the Copepoda. *Zoological Studies* 43: 446-453.
- , S. Lorenzen, and H. K. Schminke. 1991. Phylogenetic relationships within the taxon *Tisbe* (Copepoda, Harpacticoida) as evidenced by naupliar characters. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 29: 450-465.
- , N. V. Schizas, and T. C. Shirley. 2005. Naupliar evolutionary novelties of *Stenhelia peniculata* (Copepoda, Harpacticoida) from Alaska affirming taxa belonging to different categorical rank. *Invertebrate Zoology* 2: 1-14.
- , S. Chullasorn, P. Kangtia, F. D. Ferrari, and J. S. Hwang. 2007. Naupliar development of *Tigriopus japonicus* Mori, 1932 (Copepoda: Harpacticidae). *Zoological Studies* 46: 746-759.
- De Felice, R. C. 1999. Fouling marine invertebrates on the hull of the *USS Machinist* in Pearl Harbor prior to its move to Apra Harbor, Guam. Final report submitted to U.S. Fish and Wildlife Service, Pacific Islands Ecoregion, Honolulu, Hawai'i. Hawai'i Biological Survey contribution 1999-013. 16 pp.
- De Weerdt, W. H. 2000. A monograph of the shallow-water Chalinidae (Porifera, Haplosclerida) of the Caribbean. *Beaufortia* 50(1): 1-67.
- Dojiri, M., G. Hendler, and I.-H. Kim. 2008. Larval development of *Caribeopsyllus amphiodiae* (Thaumatopsyllidae: Copepoda), an enterozoic parasite of the brittle star *Amphiodia urtica*. *Journal of Crustacean Biology* 28: 281-305.
- Duarte, L. F. L., and E. H. Morgado. 1983. Crustaceos parasitos de invertebrados associados á esponja *Zygomycale parishii* (Bowerbank) e ao briozoário *Schizoporella unicornis* (Johnston, 1847). *Iheringia, Série Zoologia* 62: 3-11.
- Ferrari, F. D., and H.-U. Dahms. 2007. Post-embryonic Development of the Copepoda. *Crustaceana Monographs* 8. Brill, Leiden; Boston. vi, 229 pp.
- Fosshagen, A. 1970. *Thespesiopsyllus paradoxus* (Sars) (Copepoda, Cyclopoida) from western Norway. *Sarsia* 42: 33-40.
- Goetze, E. 2003. Cryptic speciation on the high seas: global phylogenetics of the copepod family Eucalanidae. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 270: 2321-2331.
- Grygier, M.J., and S. Ohtsuka. 2008. A new genus of monstrilloid copepods (Crustacea) with anteriorly pointing ovigerous spines and related adaptations for subthoracic brooding. *Zoological Journal of the Linnean Society* 152: 459-506.
- Hendler, G., and M. Dojiri. 2009. The contrariwise life of a parasitic, paedomorphic copepod with a non-feeding adult: ontogenesis, ecology, and evolution. *Invertebrate Biology* 128: 65-82.
- , and B. S. Littman. 1986. The ploys of sex: relationships among the mode of reproduction, body size and habitats of coral-reef brittlestars. *Coral Reefs* 5: 31-42.
- , J. E. Miller, D. L. Pawson, and P. M. Kier. 1995. *Sea Stars, Sea Urchins, and Allies: Echinoderms of Florida and the Caribbean*. Smithsonian Institution Press, Washington and London. xi, 390 pp.
- Ho, J.-S., M. Dojiri, G. Hendler, and G. B. Deets. 2003. A new species of Copepoda (Thaumatopsyllidae) symbiotic with a brittle star from California, U.S.A., and designation of a new order Thaumatopsyllida. *Journal of Crustacean Biology* 23: 582-594.
- Hovda, J. I., and A. Fosshagen. 2003. Hyperbenthic calanoids and *Thespesiopsyllus paradoxus* (Sars) collected with a light trap in western Norway. *Sarsia* 88: 89-94.
- Humes, A. G., and R. U. Gooding. 1964. A method for studying the external anatomy of copepods. *Crustaceana* 6: 238-240.
- Huys, R. 2001. Splanchnotrophid systematics: a case of polyphyly and taxonomic myopia. *Journal of Crustacean Biology* 21: 106-156.
- , and G. A. Boxshall. 1991. *Copepod Evolution*. The Ray Society, London. 468 pp.
- , J. Llewellyn-Hughes, P. D. Olson, and K. Nagasawa. 2006. Small subunit rDNA and Bayesian inference reveal *Pectenophilus ornatus* (Copepoda *incertae sedis*) as highly transformed Mytilicolidae, and support assignment of Chondracanthidae and Xarifiidae to Lichomolgoida (Cyclopoida). *Biological Journal of the Linnean Society* 87: 403-425.
- , S. Conroy-Dalton, P. D. Olson, J. N. Spinks, and D. A. Johnston. 2007. Extraordinary host switching in siphonostomatoid copepods and the demise of the Monstrilloida: Integrating molecular data, ontogeny and antennular morphology. *Molecular Phylogenetics and Evolution* 43: 368-378.
- Izawa, K. 1987. Studies on the phylogenetic implications of ontogenetic features in the poecilostome nauplii (Copepoda: Cyclopoida). *Publications of the Seto Marine Biological Laboratory* 32: 151-217.
- Koga, F. 1970. On the nauplius of *Centropages yamadai* Mori, Copepoda. *Journal of the Oceanographical Society of Japan* 126: 95-102.
- Laguarda-Figueras, A., M. Abreu Perez, J. Torres Vega, F. A. Solis-Marin, and A. De La Luz Duran Gonzalez. 2004. Ophiuroids (Echinodermata: Ophiuroidea) from the Mexican Caribbean: Puerto Morelos, Quintana Roo, Mexico. *Avicennia* 17: 13-34.
- Lamouroux, J. V. F. 1816. *Histoire des polypiers, coralligènes flexibles, vulgairement nommés zoophytes*. Caen, France, De l'imprimerie de F. Poisson. lxxxiv, 560 pp., pls. 1-19, 1 chart.
- Ljungman, A. 1871. Förteckning öfver uti Vestindien af Dr. A. Göes samt under korvetten Josefinas expedition i Atlantiska Oceanen samlade Ophiurider. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 1871: 615-658.
- Longhurst, A. R. 1986. Instar increments in copepod growth. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1671-1674.
- Lopez, G. W. 1980. Description of the larval stages of *Tisbe cucumariae* (Copepoda: Harpacticoida) and comparative development within the genus *Tisbe*. *Marine Biology* 57: 61-71.
- Lütken, C. F. 1856. Bidrag til Kundskab om Slangestjernerne. II. Oversigt over de vestindiske Ophiurer. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjöbenhavn* 1856: 1-19.
- . 1859. Additamenta ad historiam Ophiuridarum. Beskrivelser af nye eller hidtil kun ufuldstændigt kjendte Arter af Slangestjerner. Anden Afdeling. *Det Kongelige Danske Videnskabelige Selskabs Skrifter. Naturvidenskabelig og Mathematisk Afdeling*. (5) 5 (1861): 177-271, 5 pls.
- Macintyre, I. G., and K. Rützler (eds.), 2000. *Natural History of the Pelican Cays, Belize*. Atoll Research Bulletin 466-480, viii, 333 pp.
- McKinnon, A. D. 1994. *Australopsyllus fallax* gen. et sp. nov., the third known species of the family Thaumatopsyllidae (Copepoda: Cyclopoida). *Sarsia* 79: 27-32.
- Müller, J., and F. H. Troschel. 1842. *System der Asteriden*. Friedrich Vieweg und Sohn, Braunschweig, Germany. xx, 134 pp., 12 pls.
- Ogawa, W., K. Matsuzaki, and H. Misaki. 1997. A new species of *Balaenophilus* (Copepoda: Harpacticoida), an ectoparasite of a sea turtle in Japan. *Zoological Science* 14: 691-700.
- Rützler, K., and I. Macintyre (eds.), 1982. *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize*. Smithsonian Contributions to the Marine Sciences 12, xiv, 539 pp.
- Paffenhöfer, G. A., and K. D. Lewis. 1989. Feeding behavior of nauplii of the genus *Eucalanus* (Copepoda, Calanoida). *Marine Ecology Progress Series* 57: 129-136.
- Paulay, G., L. Kirkendale, G. Lambert, and C. Meyer. 2002. Anthropogenic biotic interchange in a coral reef ecosystem: a case study from Guam. *Pacific Science* 56: 403-422.
- Roy, M. S., and R. Sporer. 2001. The recent evolutionary history of *Ophiactis savignyi* (Echinodermata: Ophiuroidea), pp. 307-311. In, M. Barker (ed.), *Echinoderms 2000*. Balkema, Rotterdam.
- , and ———. 2002. Evidence of a human-mediated invasion of the tropical western Atlantic by the 'world's most common brittlestar.' *Proceedings of the Royal Society of London, Series B, Biological Sciences* 269: 1017-1023.
- Sars, G. O. 1913. *Thaumatopsyllus paradoxus* G.O. Sars, a remarkable copepod from the Norwegian coast apparently referable to the monstrilloid group. *Archiv for Mathematik og Naturvidenskab* 33: 3-11, 1 pl.
- Say, T. 1825. On the species of the Linnean genus *Asterias*, inhabiting the coast of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 5: 141-154.
- Sewell, R. B. S. 1949. The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida. *John Murray Expedition 1933-34, Scientific Report* 9: 17-199.

Suárez-Morales, E., and I. A. Castellanos. 1998. *Caribeopsyllus chawayi*, new genus, new species (Copepoda: Cyclopoida: Thaumatopsyllidae), from a Mexican reef area. *Journal of Crustacean Biology* 18: 199-204.

———, and E. Tovar. 2004. Postnaupliar stages of a thaumatopsyllid copepod from a reef area of the western Caribbean Sea. *Sarsia* 89: 223-244.

Taylor, W. R. 1962. Two undescribed species of *Halimeda*. *Bulletin of the Torrey Botanical Club* 89: 172-177.

RECEIVED: 11 June 2009.

ACCEPTED: 26 September 2009.