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Ecology and Behavior of Maxillipius Commensalis, a Gorgonophile Amphipod from Madang, Papua New Guinea (Crustacea: Amphipoda: Maxillipiidae)

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ECOLOGY AND BEHAVIOR OF *MAXILLIPIUS COMMENSALIS*, A GORGONOPHILE AMPHIPOD FROM MADANG, PAPUA NEW GUINEA (CRUSTACEA: AMPHIPODA: MAXILLIPIIDAE)

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ABSTRACT

Maxillipius commensalis Lowry, is reported as an ectocommensal on arborescent gorgonaceans from coral reefs at Madang, Papua New Guinea. The family is reviewed and the male of this species is described. In-situ behavior studies show the amphipods to crowd close together in large numbers on one side of a gorgonian stalk. The terminal articles of the sixth pereopods are greatly elongated and whip-like and are waved at the sides in a circular motion, possibly facilitating spacing or feeding. When disturbed, the amphipods react en masse as a coherent group rather than as individuals.

The strange gorgonophile amphipod, *Maxillipius commensalis* Lowry, is reported from octocorals in the Madang Lagoon, Papua New Guinea. First described from southern New Guinea by Lowry (1984), the author now adds descriptions of the male, and notes on sexual dimorphism. A review of the family and genera is also provided. While this information is available elsewhere (Barnard and Karaman, 1991), it may not be readily accessible to many workers in the tropics and thus is included here. Lowry (1984) reported the color of *M. commensalis* from Port Moresby as red, while specimens from the Madang Lagoon are creamy white. Aside from this difference, there appears to be no significant morphological difference in males or females from both areas. Notes on in-situ behavior on reefs at Madang and laboratory observations are also presented.

Maxillipiidae Ledoyer, 1973

Diagnosis.—Body depressed; head weakly depressed, eyes weakly bulging. Antenna 2 longer than 1, articles 1–3 of antenna 1 short, becoming progressively shorter; accessory flagellum absent. Mandibular incisor present, molar large, weakly triturative, rakers present, palp vestigial or absent. Inner lobes of lower lip present. Maxillae ordinary, except inner plate of maxilla 1 vestigial and palp of maxilla 1 uniarticulate. Inner plates of maxillipeds very small or slender, poorly armed, outer plates very large, palp huge. Coxa 1 vestigial, hidden by coxa 2, other coxae very short, overlapping. Gnathopods feeble, poorly setose, scarcely subchelate, but gnathopod 1 broader and shorter than 2. Article 2 of pereopod 5 unexpanded or weakly lobate, of pereopods 6–7 expanded and lobate; pereopod 6, article 6 greatly elongate and whip-like, dactyl minute. Peduncle of uropod 3 elongate, rami longer than peduncle. Telson short, apparently not fleshy, much broader than long, uncleft.

Description.—Body weakly carinate on pleon. Head with medium rostrum, eyes bulging, medium to large. Article 1 of antenna 1 short. Incisors extended, toothed, laciniae mobiles present, 2–3 rakers present; molar large, maul-shaped, weakly triturative, palp absent or represented by hump and seta. Outer lobes of lower lip appressed, inner lobes small and adhering to outer lobes, or large and fleshy, mandibular lobes sharp and broad. Inner plate of maxilla 1 small, naked, outer plate with 8–10 spines, palp long and 1-articulate. Plates of maxilla 2 slender, apically setose, inner plate occasionally with 1–2 medial setae. Inner plates of maxillipeds narrow, small, with 2–3 apical setae each, outer plates with oblique apicomedial margin bearing slender, single and paired setae, palp article 2 flabellate, sparsely setose-spinose medially, article 3 curved, dactyl unguiform.

Article 2 of gnathopods 1–2 slender, article 3 short; article 4 of gnathopod 1 weakly lobate, article 5 longest and broadest, lobate or not, propodus short, broadly ovate, mittenform, palm oblique or vestigial, setose, dactyl large to small, simple; gnathopod 2, article 4 short, carpus elongate, unlobed, propodus elongate, rectangular, slightly shorter and much narrower than carpus, palm minute or absent, transverse, posterior margin of propodus poorly armed, straight, dactyl stout, curved, sharp.

Pereopods 3–4 slender, article 4 very short, article 2 of pereopod 5 unexpanded, of pereopods 6-7 moderately expanded, with sharp posteroventral lobe. Oostegites huge, present on coxae 2-4.

Epimeron 2 larger than 3. Urosomites separate, 1 largest. Rami of uropods 1–3 lanceolate, outer rami of uropods 1–2 shorter than inner. Peduncle of uropod 3 elongate, rami (almost) as long as peduncle or longer, simple. Telson very short, broad, entire, with 2 apical setule notches.

Sexual Dimorphism.—(New information, based on *M. commensalis.*) Male antenna 1 with weak callynophore bearing few aesthetascs, remainder of flagellum without aesthetascs. Female without callynophore, usually with aesthetascs on articles beyond article 1. Some aberrant females with weakly developed callynophore. Otherwise, very similar to males.

Relationship.—Similar to Melphidippidae but coxa 1 vestigial, telson much broader than long, mandibular palp absent and palp of maxilliped very broadened. Like Colomastigidae but urosomites separate, gnathopod 1 dominant, antennal flagella well developed, palp of maxilliped expanded (versus outer plate and its article expanded in Colomastigidae).

Differing from Dexaminidae in the separate urosomites, vestigial coxa 1, and short, uncleft telson. From Pardaliscidae in the large molar. From Stilipedidae (=Astyridae) in the large molar, lack of mandibular palp, and severe reduction of coxae. From Amphilochidae in the severe reduction of coxae and short telson. From Podoceridae in the short peduncle of antenna 1, weak, simple gnathopod 2 and large uropod 3. From Iciliidae in the elongate peduncle of uropod 3 with equal rami, reduced coxa 1 covered by coxa 2, short peduncle of antenna 1, lack of mandibular palp, uniarticulate palp of maxilla 1, and feeble plates of the maxillipeds.

KEY TO THE GENERA OF MAXILLIPIIDAE

Gnathopod 1 carpochelate; article 1 of maxilliped palp larger than article 2 . . . . *Maxillipides*

Gnathopod 1 not carpochelate; article 1 of maxilliped palp much smaller than article 2 . . . . *Maxillipius*

Maxillipides Ledoyer

Maxillipides Ledoyer, 1984:86 (*Maxillipides laticarpus* Ledoyer, 1984, original designation).

Species.—*M. laticarpus* Ledoyer, 1984.

Distribution.—Marine, New Caledonia, shallow water, seagrass, 1 species.

Maxillipius Ledoyer

Maxillipius Ledoyer, 1973:32 (*Maxillipius rectitelson* Ledoyer, 1973, original designation).

Species.—*Maxillipius commensalis* Lowry, 1984:196; *M. rectitelson* Ledoyer, 1973, 1986.

Distribution.—Marine, Madagascar, seagrass bed (*Enhalus acoroides*), shallow water, to New Guinea, on gorgonian, *Melithaea, Echinogorgia, Villogorgia, Verrucella.*

Key to the Species of *Maxillipius*

Coxa 2, anterior margin acuminate, articles 5–6 of gnathopod 1 narrow and elongate .... *Maxillipius commensalis*

Coxa 2 with blunt anterior margin, articles 5–6 of gnathopod 1 broad and short ....*M. rectitelson*

Maxillipius commensalis Lowry
Figures 1–5

Maxillipius commensalis Lowry, 1984: 196.

Material.—USNM 239489 (voucher), six specimens: male "t" 1.20 mm (side view illustration), female "u" 1.75 mm, female "v" 1.83 mm (dorsal illustration), female "w" 2.00 mm, female "x" 1.33 mm, male "y" (not measured); USNM 239490 (voucher), 87+ specimens; Papua New Guinea, Madang, Tab Anchorage, near Wangat Island, 1 March 1990, 25 m, on gorgonians *Echinogorgia* sp. 1, J. D. Thomas, collector, Station JDT\PNG 70.

Diagnosis.—Coxa 2 acuminate; articles 5–6 of gnathopod 1 narrow and elongate.

Description.—Male "t." Callynophore composed of slightly elongate first flagellar article with several internal structures; bearing 2 rows of 3 and 4 aesthetascs.

Anteroventral corners of pereonites 2–4 overlapping next segment forward (unusual in Gammaridea), posteroventral corners of pereonites 4–6 overlapping next segment backward (normal).

Gills present on coxae 2–7, 2–5 of similar length, 6 smaller, 7 much smaller and comma-shaped. Pleopods with elongate peduncles, rami slightly shorter, subequal, each with 7 articles.

Peduncle of uropod 1 with 2 dorsolateral spines, apical wire-like seta, apicomedial corner with one spine, medial margin with one spine, outer ramus with one weak subapical spine; peduncle of uropod 2 with weak apicolateral seta-spine, inner ramus with one marginal spine; uropod 3 without spines, peduncle elongate.

Female.—Oostegites on coxae 2–5, huge on coxae 2–4, small on coxa 5.

Illustrations.—Dorsal drawing of female "v" not flattened, thus pleon foreshortened, conspicuous internal muscular bundles drawn in dotted lines, left pereopod 6 shown twice, in forward and rearward positions, oval of arrows showing rotational direction and limits. While most thoracic legs are shown thrust beneath the body in this specimen, in life they are normally splayed to the side (note aberrant left antenna with weakly developed callynophore, right antenna 1 of normal female morphology). Parts not illustrated: Pereopod 4 like pereopod 3 but article 5 with 1 (versus 2) setae.

Distribution.—Madang Lagoon region, Papua New Guinea, on five species of gorgonians, (Paramuriceidae: *Echinogorgia* sp. 1, 2, 3; Villogorgia sp. 1; Ellisellidae: *Verrucella* sp. 1) to 28 m.

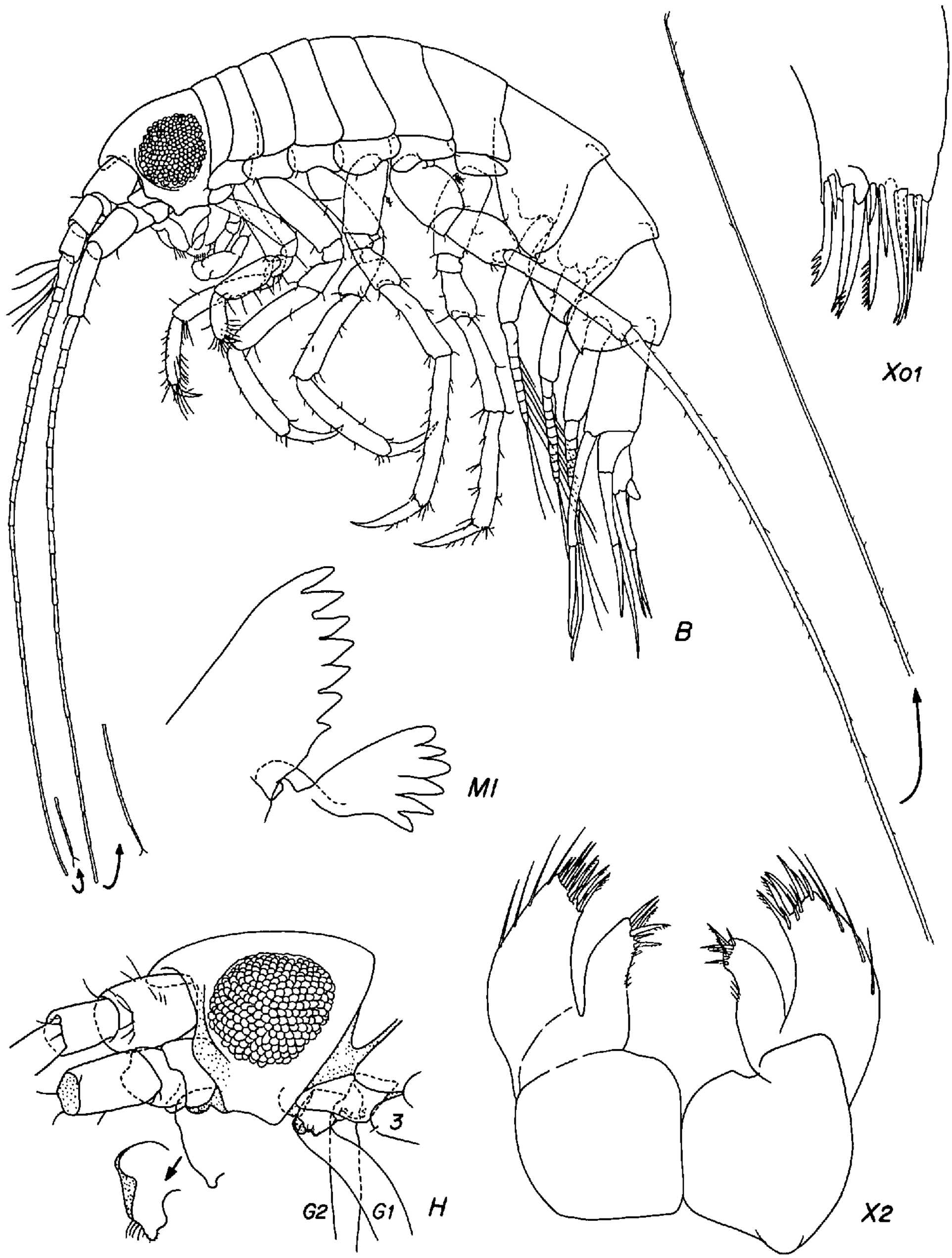

Figure 1. *Maxillipius commensalis,* unattributed figures are all male "t," 1.20 mm. Capital letters in figures refer to body parts; lower case letters to the left of capital letters refer to specimens, letters and numbers to the right of capital letters refer to modifiers as listed below: A, antenna; B, body; C, coxa; G, gnathopod; H, head; K, pleopod; M, mandible; P, pereopod; R, uropod; U, upper lip; W, urosome; X, maxilliped; Y, oostegite; Z, gill; i, inner plate or ramus; l, left; m, medial, o, outer plate or ramus; r, right; s, setae removed. Arrows in the figures indicate rotational movement, or continuation of appendages too long for convenient placement in the figures.

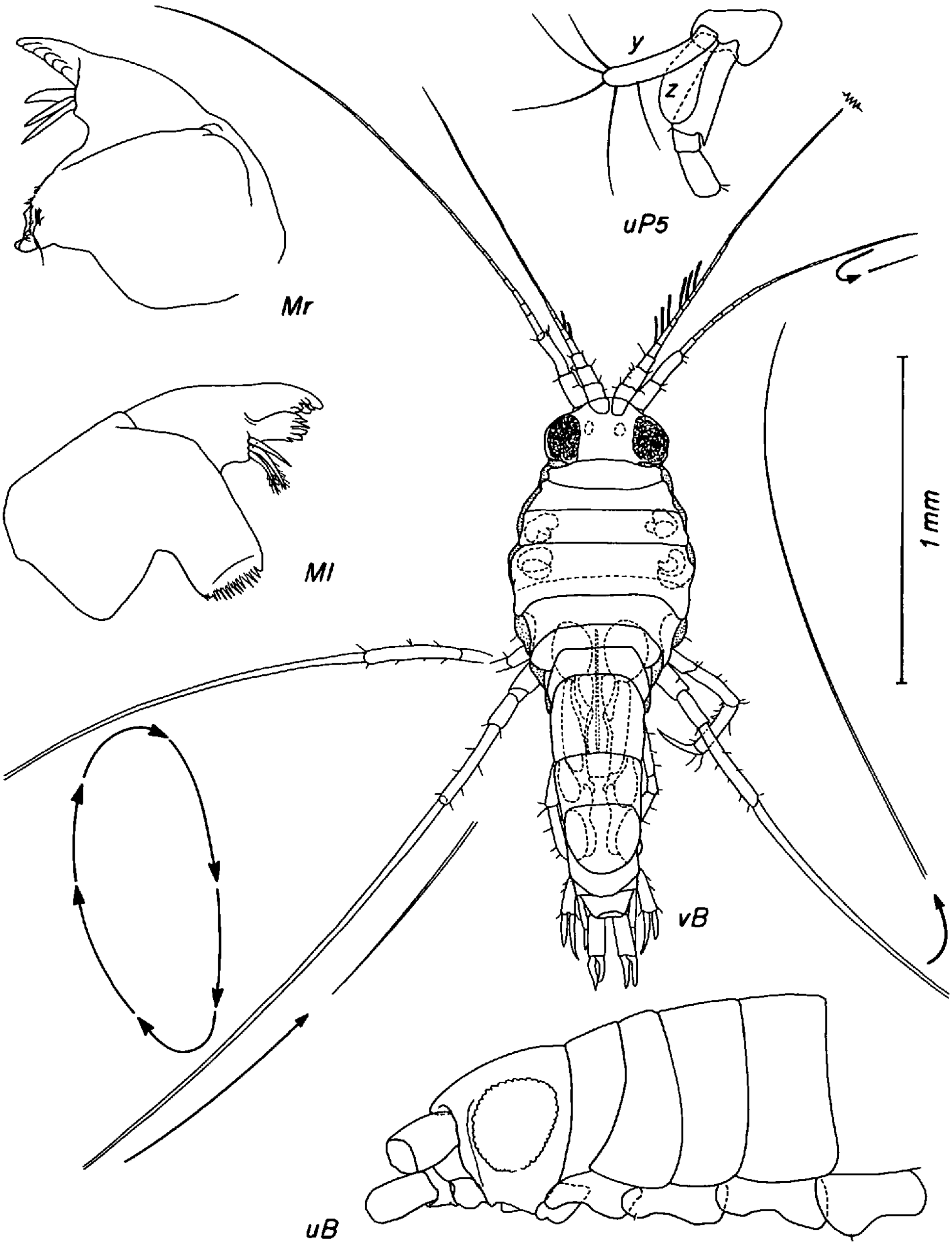

Figure 2. *Maxillipius commensalis*, male "t" 1.20 mm; female "u" 1.75 mm; female "w" 2.00 mm.

Methods

On the reefs of Madang, specimens of *M. commensalis* were collected from gorgonians by placing large zip-lock bags over the branches of the gorgonians and quickly "milking" the stem by hand from base to tip to dislodge the amphipods into plastic bags, which were then sealed underwater. Specimens were returned to the laboratory and placed in petri dishes with sea water and provided with small stalks of host gorgonians. The amphipods usually survived up to three days in the lab following this

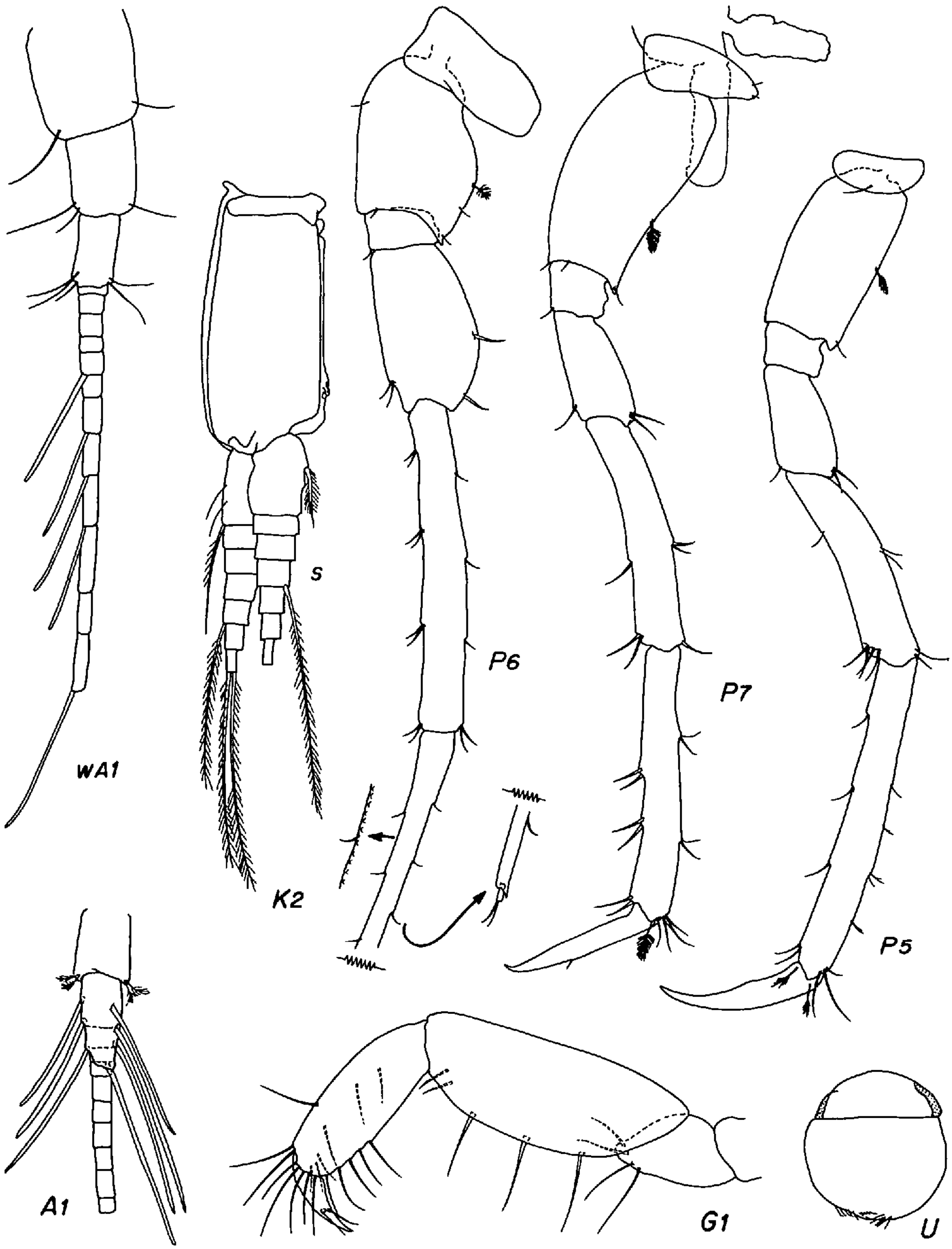

Figure 3. *Maxillipius commensalis*, male "t" 1.20 mm; female "w" 2.00 mm.

procedure. *M. commensalis* is very fragile and extreme care must be taken when handling both live and preserved material to avoid breaking the long, whip-like articles of pereopod 6 and antennae. Transfer of both live and preserved amphipods to petri dishes or vials should be done liquid to liquid by pipette or dropper. Transference across surface tension films readily fragments the filaments of pleopod 6 and antennae.

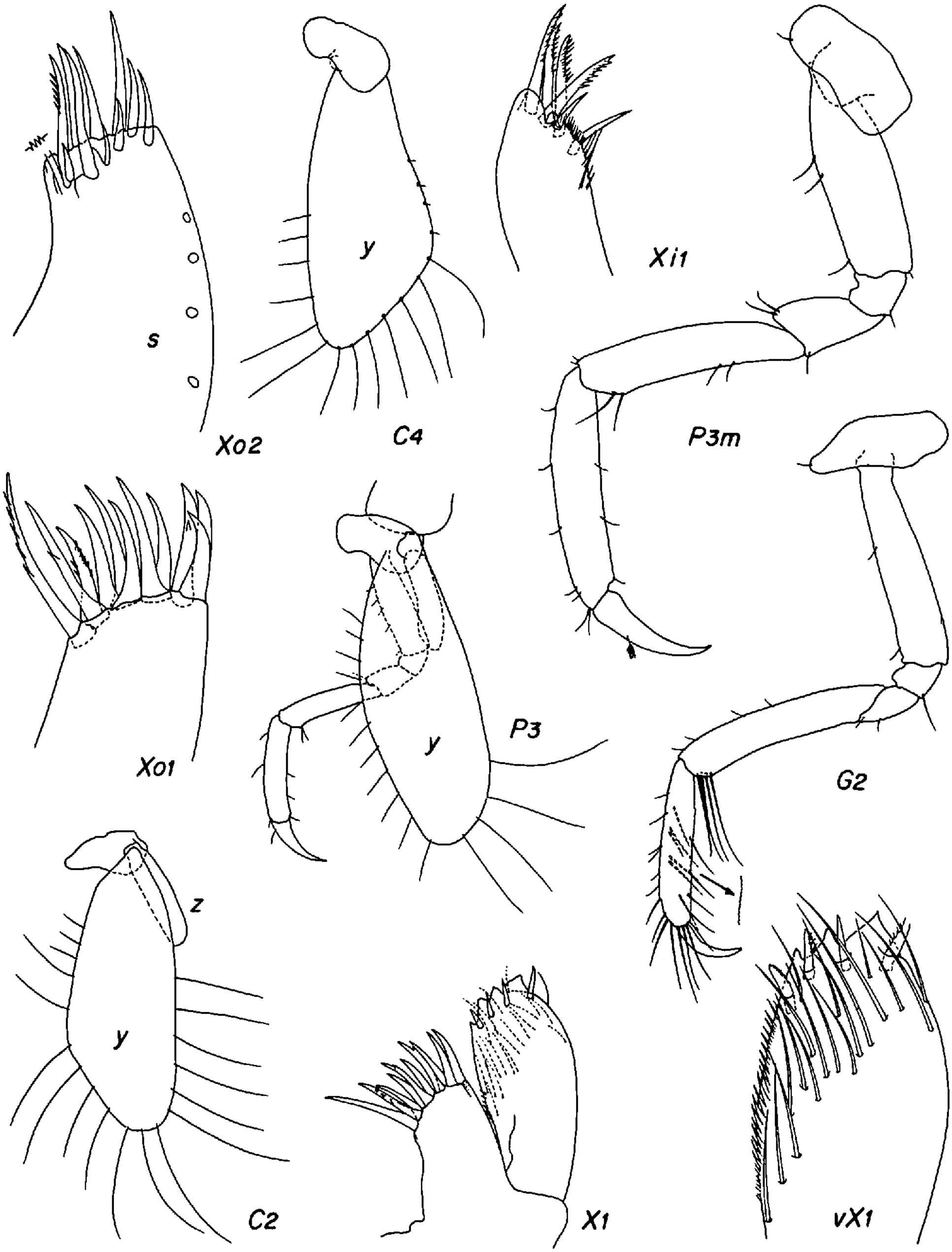

Figure 4. *Maxillipius commensalis*, male "t" 1.20 mm; female "v" 1.83 mm.

BEHAVIOR

Aggregation on gorgonians appears capricious, but when *Maxillipius* is present, a gorgonian stalk and all of its branches are fully covered with amphipods. This "blanket" of individuals covering the gorgonian is generally on the side of stalks and branches facing current flow. By placing a small probe next to a terminal

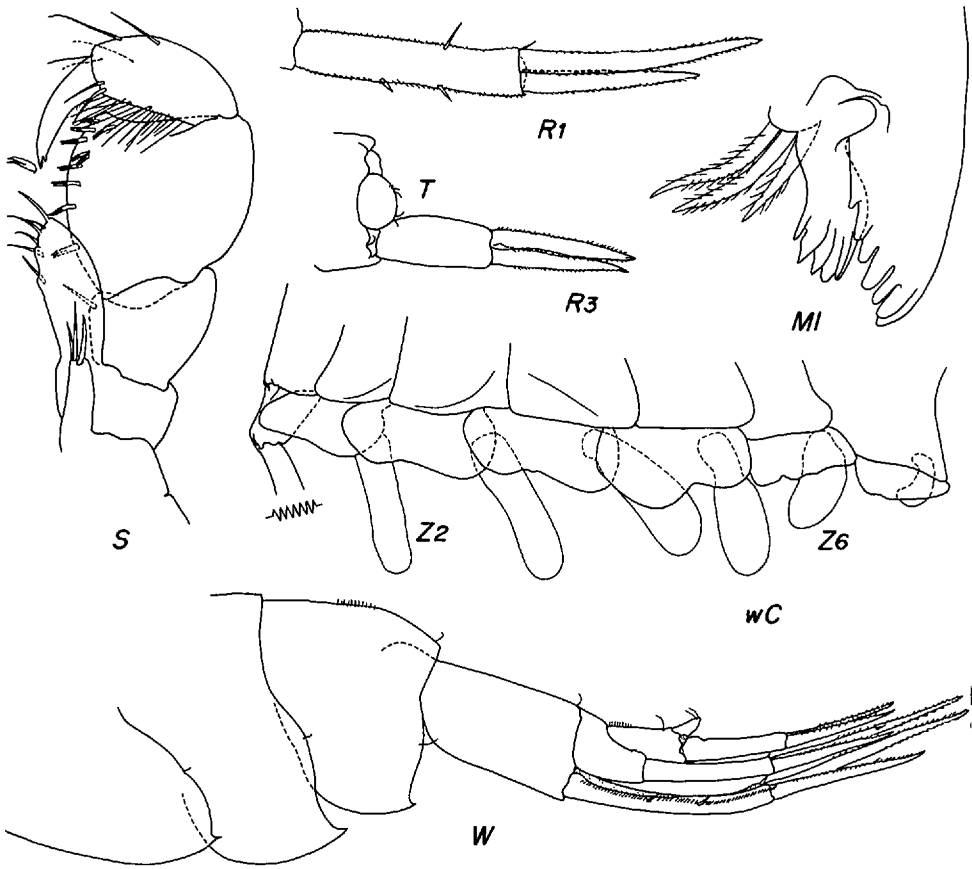

Figure 5. *Maxillipius commensalis,* male "t" 1.20 mm; female "w" 2.00 mm.

individual on a stem one can essentially "herd" a localized group of amphipods to the opposite side of the stalks and branches. Quick movements in the water near the colony results in an instantaneous migration of the entire colony of amphipods to the far side of the gorgonian surface. Disturbing the amphipods sufficiently to cause them to swim away from the host is virtually impossible. Experiments placing *Maxillipius* in the water column showed them to be extremely sluggish swimmers due to the increased hydraulic drag from the long terminal articles of the antennae and pereopod 6. On the host, the amphipods are crowded together as close as allowed by the laterally extended pereopod 6, which appears similar to a tactile antenna. These articles are fully extended on each side of the amphipod, and are slowly to rapidly rotated, or swept, in an elliptical fashion, clockwise on the left side, counterclockwise on the right. The legs are rotated alternately or in tandem. One assumes a tactile response occurs when the leg touches the leg of another individual so that a proper spacing occurs between individuals. The distance between individuals is a fraction of a millimeter. The spider-like appearance and the creamy color of the amphipod gives the appearance of polyps covering the gorgonian stalks.

In laboratory experiments, each sweep or rotation of pereopod 6 was termed a "beat." I counted a maximum average of approximately 100 beats per minute.

Antenna 2 also was rotated at a rate of about 75 beats per minute, gnathopod 2 at about 150 beats per minute and the maxillipeds appeared to "shiver" 2 or 3 times faster than gnathopod 2. Sometimes leg 6 is extended rearward and waved in sagittal and antisagittal beats. Occasionally the whip-like ends of pereopod 6 are brought forward to the mouthpart field and held by the gnathopods while they are drawn through and cleaned of attached material. They are also brought forward in this fashion when they are apparently free of attached material. It is unknown whether the attached matter on the pereopods has been swept or filtered from the water column, or consists of mucous and other material gathered from the surface of the host gorgonian.

The sweeping, or "beat" rate increases rapidly when the animal is touched or disturbed with a fine probe. The rate quickly diminishes to pre-disturbance rates if the amphipod is left alone, or, upon movement away from disturbance.

Individuals frequently stand on pereopods 3 and 5, rear upwards at a 10° angle above horizontal plane of the gorgonian stem and shake the urosome. Sometimes the standing mode is accomplished with, for example, only right pereopod 3 and left pereopod 7; or other combinations may occur. Pleopods generally beat only intermittently. The side view of the body as illustrated is unnatural. The urosome is strongly flexed beneath the rear part of the body so that the apex of uropod 3 reaches forward to the level of pereonite 3. Pereopod 3 is held laterally to the gnathopods, and pereopod 4 laterally to pereopod 3; gnathopod 1 is held outside of gnathopod 2 (drawing reflects this position). There was no discernible difference in behavior placement between males and females. Ovigerous females usually carried 2-4 large yellow eggs in the greatly enlarged marsupium.

Discussion

The preference of *M. commensalis* for certain species of gorgonians is subject to speculation (e.g., *Echinogorgia, Villogorgia,* and *Verrucella* sp.). Physical morphology does not seem to play a part in selection as there appears to be a multitude of gorgonians of similar size and shape. Two factors that bear consideration are: 1. predation of amphipods by fish; and 2. chemical defense of the gorgonians by biologically active compounds.

On the south coast of Papua New Guinea, Lowry collected specimens of *M. commensalis* from 5m in Bootless Bay, on the gorgonian *Melithaea* sp., while in the Madang Lagoon, no specimens of *M. commensalis* were taken from any gorgonians in depths less than 25m. In the shallower waters of the Madang Lagoon (less than 3 m), amphipods were lacking from the same gorgonian species on which they occurred in large numbers below 25 m. This pattern may reflect depth preference by the amphipods, reduced browsing activity by fish at the depth where most commensal occurrences were noted (25 m), or some other unknown factor. Browsing rates and activities of reef fish are most intense in the shallower portions of the reef, dropping off significantly below 10 m (Hay, 1991). The apparent contrast in depth distribution does not appear to be host-limited since there are abundant gorgonian host species throughout the range of *M. commensalis.* Another contrast between Bootless Bay and Madang specimens of *M. commensalis* are the differences in color of the amphipods. Lowry reported specimens to mimic the host in color (red) making them difficult to see, whereas Madang specimens are creamy white and readily distinguishable to the observer against the background color of the host. Gorgonian hosts in Madang waters are red to brownish yellow on the surface, but appear black at depth due to light attenuation.

Spatial refuges from predation have been demonstrated for amphipods living in proximity to chemical defended or unpalatable organisms (Hay and Duffy, 1990). Gorgonians, and a variety of other benthic invertebrates, have been reported to possess a rich suite of active chemical compounds (Norris and Fenical, 1985; Paul, 1992). While a chemically defended spatial refuge of *M. commensalis* is not demonstrated with the present data, further investigations may illuminate the circumstances surrounding the apparent obligate association of *M. commensalis* with its particular gorgonian hosts. The presence of the amphipods may also elicit production of mucus or other chemical derivatives by the host that render the gorgonian unpalatable to predators. Production of mucus-bound chemicals could also serve as a food source for amphipods which have the ability to behaviorally sequester toxic compounds found in algae (Hay et al., 1988).

Acknowledgments

The author thanks Dr. J. K. Lowry for the opportunity to let J. L. Barnard examine specimens of *Maxillipius commensalis* at the Australian Museum. Dr. M. Jebb, former Director of the Christensen Research Institute (CRI) at Madang, provided excellent field and laboratory facilities. Funds for field work were supplied by grants from the National Geographic Society (3723-87 and 4421-90), and the National Science Foundation (DEB-89-15688) to the author. Dr. F. M. Bayer of the National Museum of Natural History, Smithsonian Institution, graciously identified the gorgonians. L. B. Lutz, Vicksburg, Mississippi, inked the pencil drawings.

This was the last field project J. L. Barnard participated in before his death in August, 1991. His unbridled enthusiasm and excitement while working with live amphipods will be fondly remembered.

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