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## Colonization of Jamaican bromeliads by *Tropocyclops jamaicensis* n. sp. (Crustacea: Copepoda: Cyclopoida)

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**Abstract.** *Tropocyclops jamaicensis* n. sp. is the most numerous copepod and frequently the most numerous metazoan of phytotelmata in leaf axils of terrestrial bromeliads of the Cockpit Country, Jamaica. Distinctive apomorphies of this species, particularly the naked pediger 5 and the 2 setae on leg 5, necessitate emending the diagnosis of the genus *Tropocyclops*. *Tropocyclops jamaicensis* occurred in 63% of bromeliads sampled, but the next most numerous copepod, *Ectocyclops phaleratus*, occurred in 17.5%. In colonization experiments, *T. jamaicensis*, along with ostracodes and chironomid and mosquito larvae, invaded some plants within 2 to 5 weeks. After 13 weeks, 8 of 10 plants harbored populations of this copepod.

*Additional key words:* ecology, phytotelmata, taxonomy, Antilles

Phytotelmata are liquid secretions or precipitation stored in plants or plant structures, forming a temporary or permanent pool (Varga 1928). Phytotelmata can be found in tree holes, flowers of *Heliconia* spp., or leaf axils, for example (Fish 1983). Especially in bromeliads, the establishment of phytotelmata is fostered by a leaf arrangement that causes rainwater to be funneled toward the leaf axils (“tank bromeliads”, Smith 1989). Accumulated leaf litter derived from the canopy may build up a detritus layer or “benthic zone”, and visible water can be considered as a “pelagic zone” in these aquatic microcosms (Janetzky & Vareschi 1993).

Copepods are commonly found in both terrestrial and arboreal bromeliads, and there are several reports from bromeliads in the Antilles. Laessle (1961) listed *Ectocyclops phaleratus* KOCH 1838, *Elaphoidella sewelli* (CHAPPUIS 1928), and *Tropocyclops prasinus* cf. *mexicanus* KIEFER 1938 in Jamaica. Maguire (1970) recorded *Bryocyclops anninae* (MENZEL 1925), *Bryocyclops chappuisi* KIEFER 1928, *E. sewelli*, and *Phyllognathopus viguieri* (MAUPAS 1892) in Puerto Rico. Reid (1993) described *Fimbricyclops jimhensoni* from Puerto Rico.

The aim of this article is to provide results of experiments on the capacity of a new species of *Tropocyclops* to colonize phytotelmata of bromeliads in Ja-

maica, as well as to describe the species. Because the new species displays several unique apomorphies, we propose an emended diagnosis for the genus *Tropocyclops*.

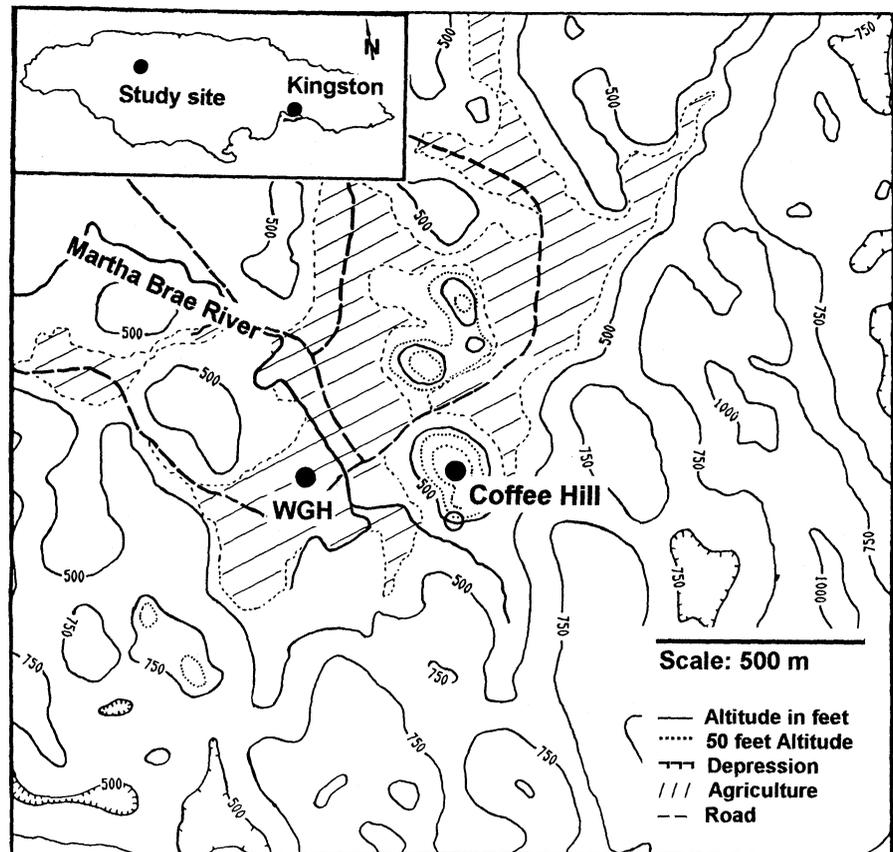
### Study Site

The study site was located at the northern rim of the Cockpit Country, Trelawny Parish, Jamaica (18°21'N, 77°39'W, altitude about 100–300 m) (Fig. 1). The local topography developed from limestone eroded by rainfall and underground drainage to form more or less conical hills separated by depressions (doline, “cockpits”) and small valleys. The dominant vegetation is “wet limestone forest” (precipitation 1900–3800 mm/year) including terrestrial bromeliads in the understory, mainly *Aechmea paniculigera* (SWARTZ) GRISEBACH 1864 and *Hohenbergia* spp. (Asprey & Robbins 1953; Proctor 1986; Janetzky & Vareschi 1993).

### Methods

Temperature, pH values, and electrical conductivity in rainwater, throughfall, and phytotelmata were measured with temperature-compensated instruments (Wissenschaftlich-Technische Werkstätten pH 91 and LF 92). Differences between paired values of pH and conductivity for rainwater and throughfall were tested for significance by a 2-sided U-test. Differences between paired mean values of pH and conductivity in

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**Fig. 1.** Map of Jamaica showing the study site and the location of Coffee Hill and Windsor Green House field station (WGH).

bromeliads and throughfall or in groups of different bromeliads were tested for significance by H-test.

Invertebrate populations in bromeliads were sampled October 1992–July 1993, February–May 1994, and March–May 1995. Samples were taken by first removing accumulated leaf litter from the phytotelmata and carefully washing it, saving the washings, then collecting the liquid with a 100-ml syringe. Drained leaf axils were rinsed with water to collect remaining material. The samples were sieved through a 108- $\mu$ m mesh sieve and fixed with formalin to approximately 5% final concentration. The samples were hand-sorted in the laboratory using a stereomicroscope, and the specimens were transferred to 70% ethanol.

For morphological examination, copepod specimens were temporarily mounted in glycerin or lactic acid, or permanently in commercial polyvinyl lactophenol with chlorazol black E stain. Structures were drawn using a Wild M30 microscope fitted with a drawing tube, at magnifications of 600 $\times$  or 1000 $\times$  (the latter with an oil immersion lens). Type specimens were deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington

(USNM), and the Museum für Naturkunde, Berlin (ZMB).

For colonization experiments (February 1994–March 1995), 10 plants growing on Coffee Hill—6 *Aechmea paniculigera* (denoted Ap1–6) and 4 *Hohenbergia* spp. (denoted H1–4)—were randomly chosen. All phytotelmata of each bromeliad were sampled (9–11 February 1994) as described above. After they were washed out, the bromeliads were treated with 70% ethanol for 30–45 minutes to avoid possible survival of resting eggs or animals hidden at the bottom of the leaf axils. They were then rinsed and refilled with filtered river water (pH 7.5, conductivity 336  $\mu$ S/cm). All material from each plant was treated as one sample, which was fixed and sorted as described above in order to determine the faunal assemblages present before beginning the experiment. During the experiment, 30-ml subsamples in 2 different leaf axils of each bromeliad were taken at least biweekly and examined for possible arrival of invertebrates. After 5 weeks (18 March 1994) and 13 weeks (13 May 1994), phytotelmata of 2 leaf axils of each bromeliad were completely sampled as described above for a more detailed survey. After approximately 13 months (7,8

March 1995), all phytotelmata of each bromeliad were sampled, and the results were combined.

The total amount of water stored per plant averaged 1008 ml (range 100–2500 ml) in Ap1–6 at the start and 633 ml (range 50–2100 ml) at the end. The H1–4 plants contained a mean of 313 ml (range 100–550 ml) at the start and 458 ml (range 330–850 ml) at the end. The results for the faunal assemblages (Table 3) were not standardized to an equal amount of water.

### Taxonomic Account

Family Cyclopidae BURMEISTER 1834

Subfamily Eucyclopinæ KIEFER 1927

*Tropocyclops* KIEFER 1927, 1931, char. emend.

**Diagnosis.** Body with broad prosome and narrow urosome. Pediger 5 usually with transverse fringe of hairlike setules on each side, except lacking such a fringe in *T. jamaicensis* n. sp. Seminal receptacle of female with anterior expansion usually T-shaped, lateral arms narrow or broad, and posterior part usually Y-shaped, except tripartite in *T. jamaicensis*. Anal operculum convex or triangular. Caudal ramus short (about 1.2–4 times longer than broad), without ornamentation except small spines at bases of some setae. Middle terminal caudal setae with uniform fine plumage. Antennule long, reaching past pediger 2 or longer; composed of 12 articles, with long setae on articles 1 and 4; articles 10–12 each with narrow longitudinal hyaline membrane. Antenna of 4 articles, basipodite bearing 1 or 2 setae on anterodistal corner; seta on posterodistal corner (representing exopodite) always present. Swimming legs 1–4 with rami each of 3 articles, exopodite articles 1–3 of legs 1–4 with identical setation of 1,1,5 setae respectively, endopodite article 1 with 1 medial seta, article 2 with 2 medial setae, article 3 of legs 1–4 respectively with 6 setae plus spine, 5 setae + spine, 5 setae + spine, and 3 setae (2 medial + 1 lateral) + 1 or 2 terminal spines. (Exceptions: *T. mellanbyi* ONABAMIRO 1952, with only 4 medial setae on leg 1 endopodite article 3, rather than the normal 5; *T. jamaicensis* n. sp., lacking seta on medial margin of leg 4 exopodite article 1). Medial terminal spine of leg 4 endopodite article 3 always longer than length of article. Reported spine formulas 3,4,4,3 (“*quaterni*”-group of Kiefer 1931), 3,4,3,3 (“*terni*”-group of Kiefer 1931), 3,3,3,3, or 2,3,3,3. Leg 5 consisting of 1 broad free article bearing 1 lateral and 1 terminal seta, plus 1 medial spiniform seta, except *T. jamaicensis* n. sp. lacking lateral seta.

Male: Antennule with slender setiform aesthetascs, difficult to distinguish from setae; at least 1 such aesthetasc on article 1, distribution of aesthetascs on remaining articles uncertain. Leg 6 consisting of broad

subtriangular plate with 1 lateral seta, 1 terminal seta, and 1 medial spiniform seta.

Many species deeply colored purple, green, blue, or tan in body tissues, not in integument. In all species for which the behavior has been observed, the animals swim on their backs, with the urosome flexed ventrally.

**Type species.** *Cyclops prasinus* FISCHER 1860, by original designation (Kiefer 1927).

### *Tropocyclops jamaicensis* n. sp.

**Synonymy.** *Tropocyclops prasinus* (FISCHER 1860).—Laessle 1961: 510, 511, Table 4.—Frank 1983: 126. *Tropocyclops prasinus* cf. *mexicanus* (KIEFER 1938).—Laessle 1961: 504.

**Holotype.** ♀, dissected on 1 slide, USNM 264195; allotype ♂, dissected on 1 slide, USNM 264196. **Paratypes.** ♀, dissected on 1 slide, USNM 264197; 100+, ♀♀, ♂♂, and copepodids, USNM 264198, all from Sample CH-KA4/Z, phytotelmata, 27.8° C, pH 5.3, conductivity 82.2 µS/cm, 23 March 1993. 100+, Sample C4I, mixed from several phytotelmata of bromeliad *Aechmea paniculigera*, March 1994, USNM 264199. 160+, Sample CHKA3/Misch, from *A. paniculigera*, 27.8° C, pH 4.6, conductivity 34.2 µS/cm, 23 March 1994, USNM 264200. 9, Sample CHKH1/Z, from bromeliad *Hohenbergia inermis*, 24.9° C, pH 4.6, conductivity 34.2 µS/cm, 13 May 1994, USNM 264201. 100+, Sample C4I, mixed from several phytotelmata of *A. paniculigera*, March 1994; 160+, Sample CHKA3/Misch, from *A. paniculigera*, 27.8° C, pH 4.6, conductivity 34.2 µS/cm, 23 March 1994; and 9, Sample CHKH1/Z, from *H. inermis*, 24.9° C, pH 4.6, conductivity 34.2 µS/cm, 13 May 1994, all ZMB 27138. All samples collected by W. Janetzky. 4 ♀♀, mounted on 1 slide in glycerin jelly, Sample 67-IN-C, bromeliad, Hardwar Gap, St. Andrew, Jamaica, 23 August 1952, USNM 264244. 1 ♀, Sample 70-A-C, bromeliad near Christiana, Manchester, Jamaica, 29 August 1952, USNM 264245. Both samples collected by A. M. Laessle. Undissected specimens preserved in 70% ethanol. Additional, non-paratype specimens in collection of W. Janetzky.

**Additional observations.** In both sexes, body tissues without color in specimens in ethanol. Behavior of living animals not observed.

**Etymology.** The species name is given for the island where the species was found.

### Females

Length of holotype in glycerin, not including caudal setae, 0.424 mm; lengths of 10 paratypes from same sample 0.420–0.440 mm (median = 0.424 mm).

Body widest at midlength of cephalosome in dorsal

view (Fig. 2a). Lateral margins of pedigers 3 and 4 produced posteriorly over pediger 5 (first urosomite). Body surface and posterior margins of prosomites and pediger 5 smooth. Pediger 5 without ornament except usual dorsal pair of hairlike sensilla. Genital double somite (Fig. 2a,b) about 1.3 times broader than long, broadest at anterior third. Seminal receptacle with T-shaped anterior part, lateral arms of "T" posteriorly curved; broad lateral canals; and tripartite posterior expansion; copulatory pore small, pore-canal unsclerotized. Posterior margin of genital double somite and next 2 urosomites with finely serrate hyaline membrane. Urosomite 4 with 3 dorsal hairlike sensilla. Anal somite (Fig. 2a,b) with row of small unsocketed spines along ventral margin above caudal ramus; anal operculum weakly crescentic. Caudal rami (Fig. 2a,b) about 2 times longer than broad, ornamented only with 1 or 2 small unsocketed spines anterior to insertion of lateral terminal seta. All caudal setae finely plumed. Lateral seta inserted slightly posterior to midlength of ramus. Dorsal seta inserted at about posterior 2/3, its length about 2.5 times length of ramus. Lateralmost (outer) and medialmost (inner) terminal setae about equal in length, lateralmost seta slightly longer (e.g., Fig. 1a) or slightly shorter (e.g., Fig. 1b) than medialmost seta in different specimens. Middle terminal setae lacking proximal breaking planes.

Antennule (Fig. 2a,c,d) reaching end of pediger 2, composed of 12 articles and with narrow longitudinal hyaline membrane on articles 10–12; this membrane smooth except finely serrate proximal to lateral seta on article 12. Armament of antennule articles 1–12 respectively: 8 setae (s) + ventral row of small unsocketed spines, 4s, 2s, 6s, 3s, 1s + spine, 3s, 2s, 2s + aesthetasc, 2s, 2s + aesthetasc, 7s (1 medial and 6 terminal including tiny hairlike seta) + aesthetasc. Aesthetasc of article 9 about 1/2 length of adjacent seta, aesthetasc of article 11 similar in length to adjacent seta. Aesthetasc of article 12 short, hyaline, basally fused with adjacent seta.

Antenna (Fig. 3a–c) with basis bearing 2 setae on anterodistal angle, plus seta representing exopod on posterodistal angle. Endopodite articles 1–3 with 1, 9, and 7 setae respectively. Frontal side of basis with 3 diagonal rows of broad unsocketed spines, 2 rows of small unsocketed spines, and 1 row of long hairlike unsocketed spines on proximal part; caudal side with scattered rows and irregular groups of unsocketed spines of different sizes, most spines tiny. First article of endopodite lacking ornament except few tiny unsocketed spines along posterior margin.

Labrum (Fig. 3d,e) with 10 teeth on margin between lateral corners, and groups of hairlike unsocketed spines on anterior and posterior surfaces.

Mandible (Fig. 3f) with reduced palp bearing 2 long plumose setae and 1 tiny naked seta.

Maxillule (Fig. 3g), precoxal arthrite with 3 strong terminal teeth and 8 spines and setae, next proximal-most seta stout and thickly plumed. Maxillular palp with usual structure for family, with 4 setae on proximal article and 3 setae on distal article.

Maxilla (Fig. 3h) of 5 articles as usual in family. Claw of article 3 (basis) with row of strong teeth along middle of inner margin, and row of smaller teeth along distal third of outer margin. Article 4 (endopod article 1) with 2 strong spiniform setae; article 5 (endopod article 2) with 1 strong spiniform seta and 2 slender setae.

Maxilliped (Fig. 3i) of 4 articles, bearing 3, 2, 1, and 3 setae respectively; articles 2 and 3 each with unsocketed spines on surface.

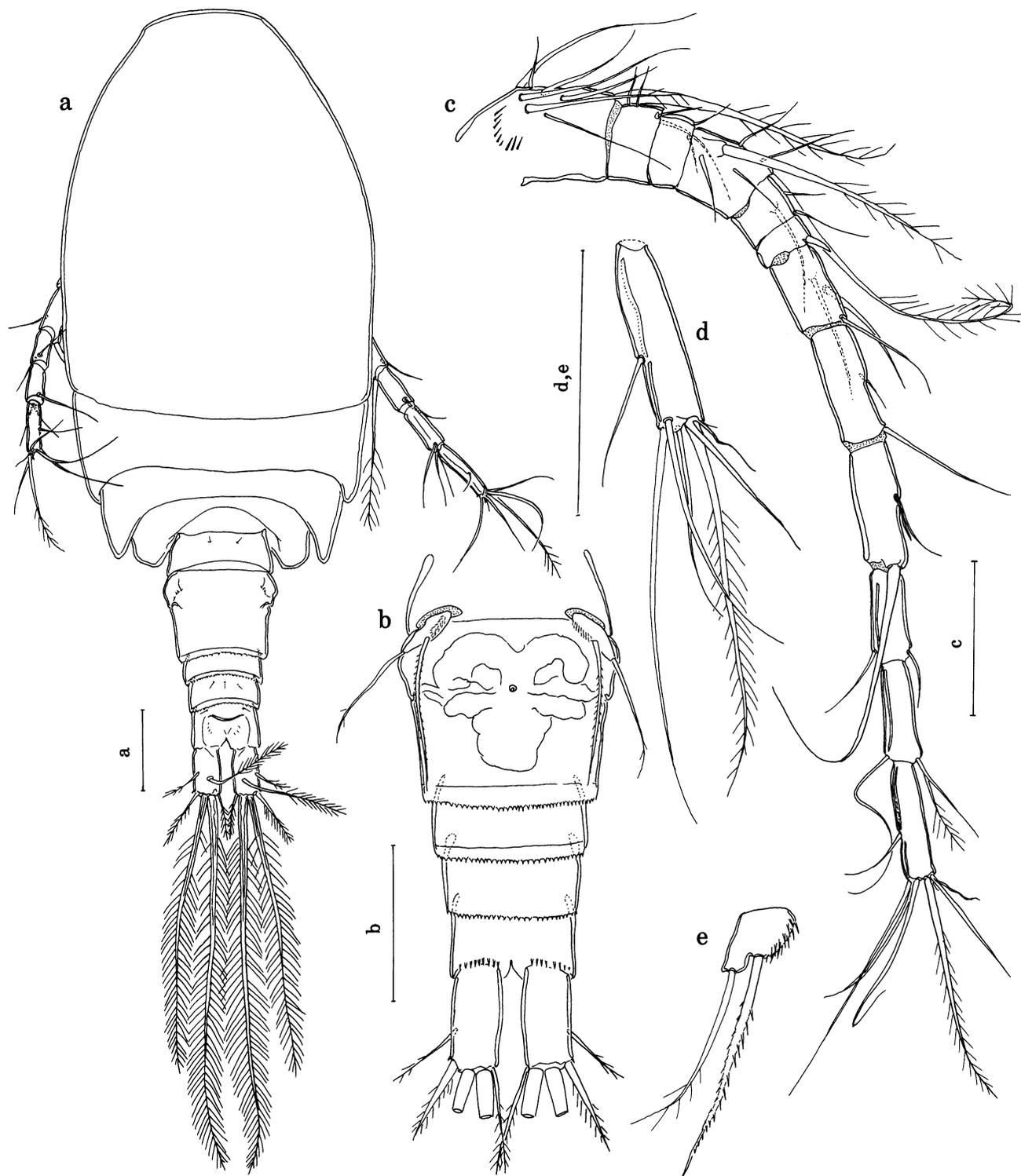
Legs 1–4 (Figs. 3j, 4) with rami each of 3 articles, major armament as in Table 1. Spine formula (number of spines on distalmost exopodite article of legs 1–4 respectively) 3,4,3,3. Basis of leg 1 lacking seta on medial expansion. Leg 4 exopodite article 1 lacking seta on medial margin. Frontal surface of coupler of leg 1 and frontal and caudal surfaces of couplers of legs 2–4 ornamented with rows or groups of unsocketed spines (Figs. 3j, 4). Coupler of leg 4 with 2 tiny unsocketed spines on free margin, in addition to ornamentation on frontal and caudal surfaces.

Leg 4 coxa with 2 transverse rows of unsocketed spines on caudal surface and 1 row on frontal surface. Basis with 3–5 stiff unsocketed spines on medial expansion (ornamentation at corresponding locations of legs 1–3 consisting of fringe of fine hairlike spines). Endopodite article 3 directed medially to a greater or lesser extent in nearly all specimens examined; this article 2.4–2.7 times longer than broad, medial terminal spine about 1.6–1.8 times longer than article, lateral terminal spine about 0.9–1.0 times length of article. Lateral terminal spine about 1/4–1/2 width of medial terminal spine at base, both spines finely serrate distally.

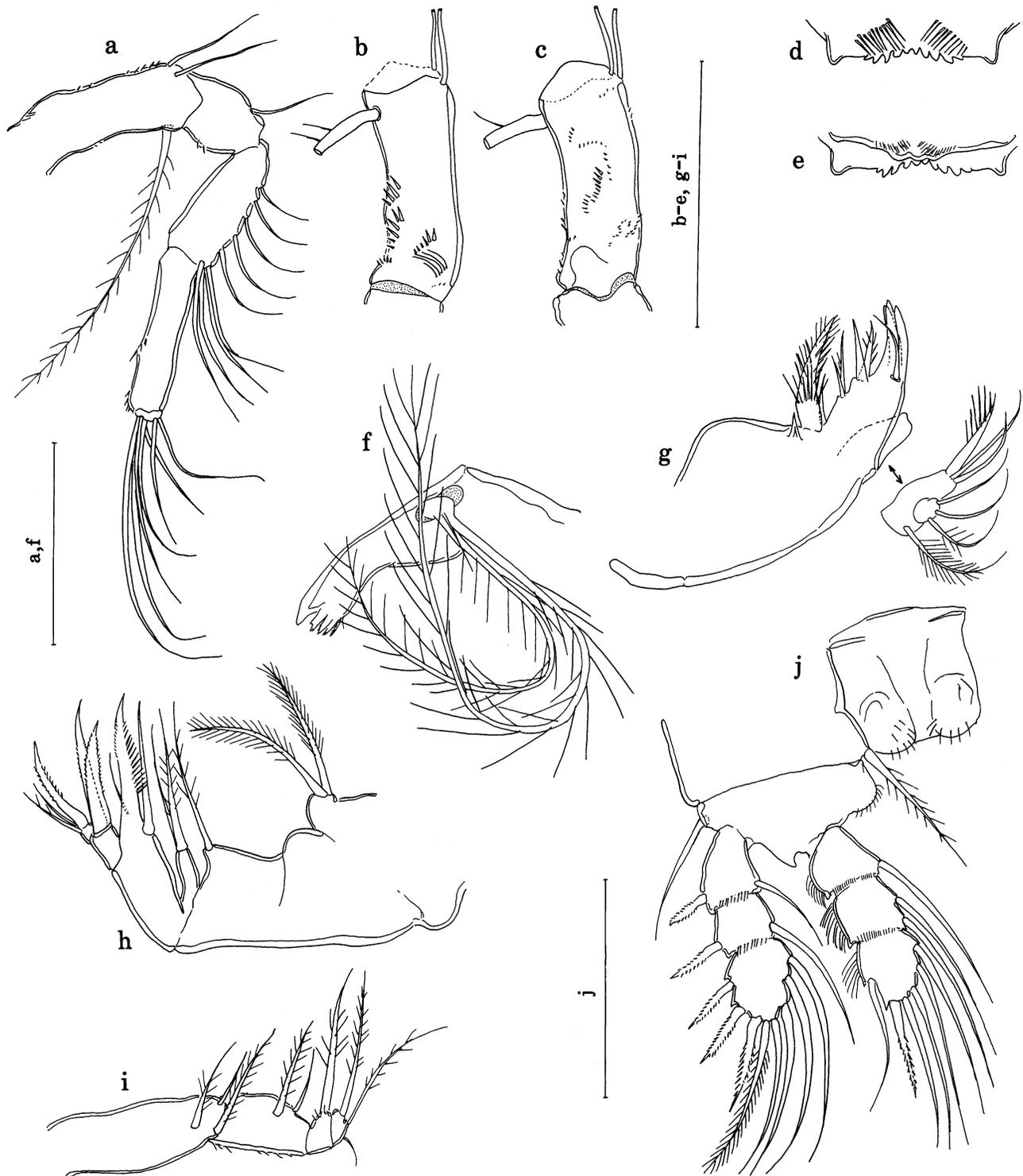
Leg 5 (Fig. 2b,e) consisting of 1 broad article bearing long, sparsely plumed terminal seta and long medial serrate spiniform seta. Surface ornamentation consisting of tiny unsocketed spines along medial surface proximal to medial spiniform seta.

Leg 6 (Fig. 2a) consisting of small plate bearing small dorsal seta and 2 tiny lateral spines.

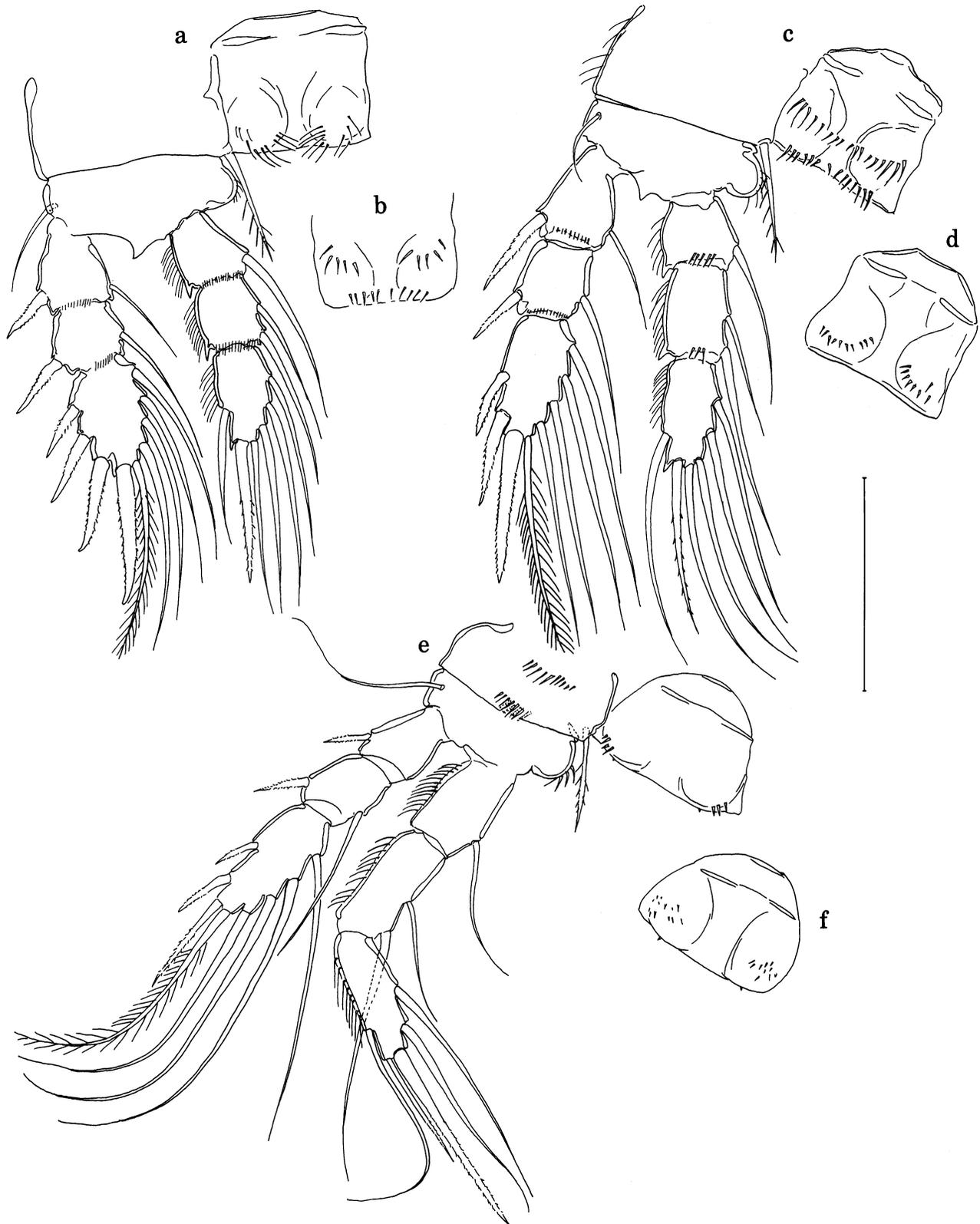
Paired egg sacs carried dorsolaterally. Each sac with 3–6 eggs in specimens from the Cockpit Country; in specimens from St. Andrew, each sac with 1 or 2 large eggs. Otherwise, specimens from St. Andrew and Hardwar Gap congruent in all respects with specimens from the Cockpit Country.



**Fig. 2.** *Tropocyclops jamaicensis* n. sp., female; a, c–e, holotype, USNM 264195, b, paratype, USNM 264197. a. habitus, dorsal; b. urosome, ventral; c. antennule; d. antennule article 12; e. leg 5. Scale bars, 50  $\mu$ m.



**Fig. 3.** *Tropocyclops jamaicensis* n. sp., female; a, d–i, holotype, USNM 264195, b, c, paratype, USNM 264197. a. antenna, caudal side; b. antenna basis, frontal side; c. antenna basis, caudal side; d. labrum, frontal side; e. labrum, caudal side; f. mandible; g. maxillule and palp; h. maxilla; i. maxilliped; j. leg 1 and coupler, frontal. Scale bars, 50  $\mu$ m.



**Fig. 4.** *Tropocyclops jamaicensis* n. sp., female; holotype, USNM 264195. **a.** leg 2 and coupler, frontal; **b.** leg 2 coupler, caudal; **c.** leg 3 and coupler, caudal; **d.** leg 3 coupler, frontal; **e.** leg 4 and coupler, caudal; **f.** leg 4 coupler, frontal. Scale bar, 50  $\mu$ m.

**Table 1.** Major armament of legs 1–4 of *Tropocyclops jamaicensis* n. sp. (Roman numerals indicate spiniform setae, Arabic numerals indicate setae).

	Coxa	Basis	Exopodite			Endopodite		
			1	2	3	1	2	3
Leg 1	0–1	0–0	I–1	I–1	III, 2, 3	0–1	0–2	1, I+1, 3
Leg 2	0–1	0–0	I–1	I–1	III, I+1, 4	0–1	0–2	1, I+1, 3
Leg 3	0–1	0–0	I–1	I–1	II, I+1, 4	0–1	0–2	1, I+1, 3
Leg 4	0–1	0–0	I–0	I–1	II, I+1, 4	0–1	0–2	1, II, 2

## Males

Length of allotype 0.412 mm; lengths of paratypes from same sample 0.404–0.432 mm (median = 0.420 mm). Body and appendages as in female except for normal dimorphism.

Antennule (Fig. 5a,b) geniculate, of 16 articles, article 9 reduced and telescoped under article 8 in some specimens including allotype, articles 4–6 partly fused, former articles 16 and 17 completely fused. Article 1 with 4 short rows of small unsocketed spines, 8 setae, and 1 long slender setiform aesthetasc. Similarly formed slender, socketed setiform structures, possibly aesthetascs, also present on articles 2, 3, 4, and 13 at locations corresponding to putative aesthetascs in other *Tropocyclops* (as illustrated by Gurney 1933). Article 9 without aesthetasc or seta. Articles 8 and 10–13 each with stout spiniform seta, setae on articles 10, 11, and 13 each with 1 or 2 rows of spinules, setae on articles 8 and 12 naked.

Leg 6 (Fig. 5c) consisting of broad subquadrate plate with medial spiniform seta reaching past succeeding 2 urosomites, and 2 lateral setae of which lateralmost seta is longest. Surface ornament consisting of tiny unsocketed spines along medial margin, and 2 tiny spines proximal to insertion of medial spiniform seta.

## Results of Colonization Experiments

The limnological characteristics of phytotelmata used for colonization experiments were influenced by rainwater and especially throughfall collected in the leaf axils. This was demonstrated by measurements of pH and conductivity (Table 2). The mean pH of precipitation differed significantly ( $P < 0.01$ ) from that of throughfall in both 1994 and 1995. The conductivity of precipitation and throughfall was significantly different only in 1995 (82.0 vs. 71.2  $\mu\text{S}/\text{cm}$  respectively;  $P < 0.01$ ).

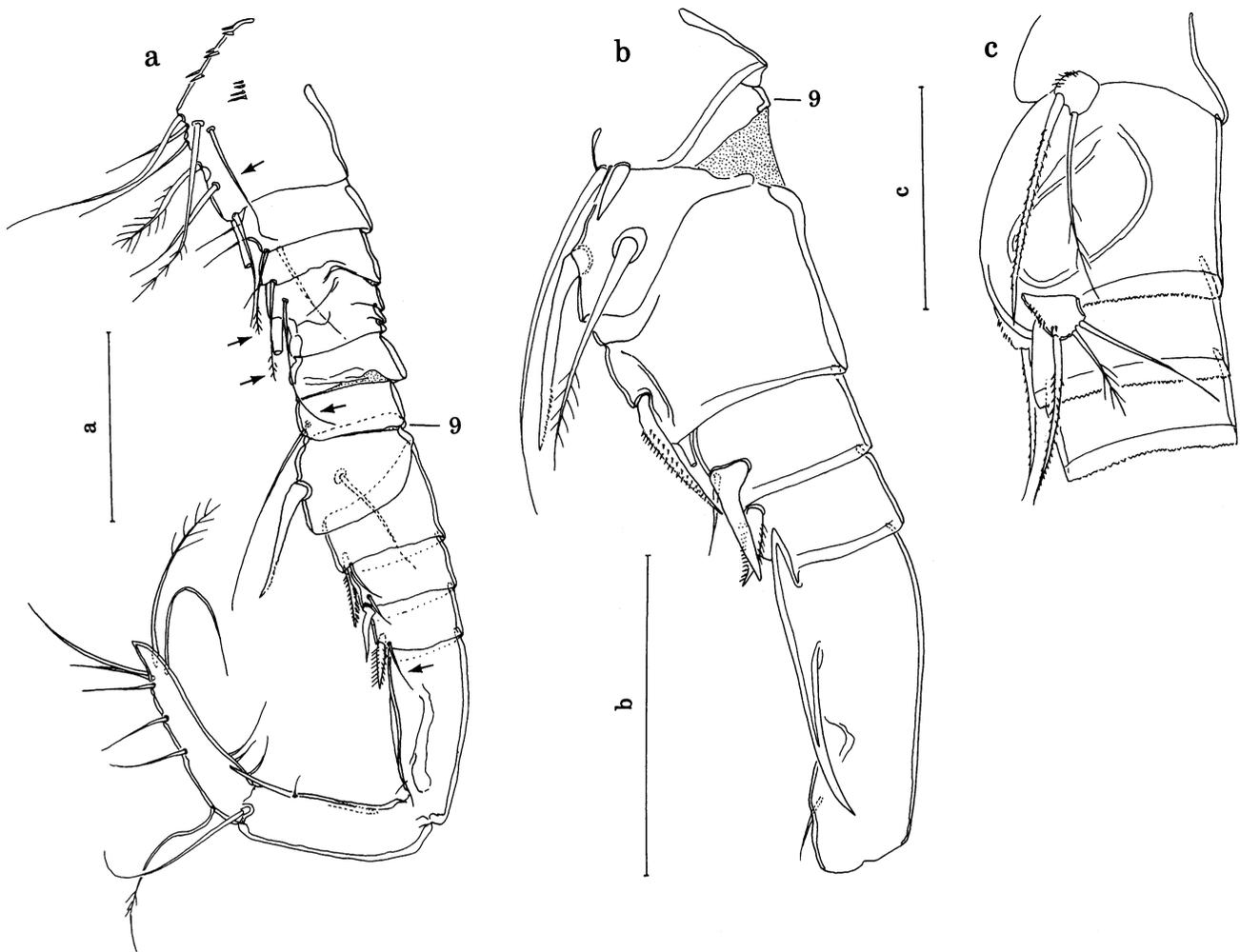
Conductivity measured in 1994 and 1995 for throughfall and bromeliads (Ap1–6, H1–4, and controls) showed no significant variations. Regarding pH values, only those measured for throughfall in 1994 and in bromeliads used as controls (6.3 and 5.3 re-

spectively;  $P < 0.01$ ) differed significantly. At the start of the colonization experiments in February 1994, plants Ap1–6, H1–4, and the controls were uniform with respect to pH and conductivity (no significant difference,  $P < 0.01$ ). When the experiments were completed in March 1995, the only significant difference was between pH values of phytotelmata in *Hohenbergia* spp. (H1–4) and the control plants (6.2 and 5.3 respectively,  $P < 0.01$ ).

The aquatic fauna of phytotelmata of bromeliads growing on Coffee Hill consisted of oligochaetes, crustaceans, and insect larvae. In terms of genera represented, insects, especially chironomids appeared to be most diverse, although taxonomic determination even to genus level was hindered by a lack of keys. In terms of abundance of individuals, cyclopoid copepods were dominant.

Cyclopoid copepods occurred in 126 of 200 samples taken between 1992 and 1994, including samples from the colonization experiments. *Tropocyclops jamaicensis* and *Ectocyclops phaleratus* were the only cyclopoid species found, the former being the dominant (more numerous). *Tropocyclops jamaicensis* was present in 125 samples with a mean of 158 individuals each (SD=320, range 1–2473). Variability among samples was high: in 96 samples, fewer than 100 individuals were found, but in only 5 samples, more than 500 specimens were counted. In contrast, *E. phaleratus* occurred in only 35 samples with a mean of 14 individuals (SD=27, range 1–132). In most samples (26), fewer than 10 individuals of *E. phaleratus* were found, whereas in 7 samples up to 30 specimens were counted, and in 2 samples, 99 and 132 individuals occurred. In most samples (34), *E. phaleratus* was found together with *T. jamaicensis*, but because samples from different phytotelmata of one bromeliad were combined, it is not known whether the species co-occur in the same phytotelm. When visible water bodies (pelagic zone) and the sediment layer (benthic zone) of phytotelmata were sampled separately, individuals of both species were found primarily in the water sample.

Harpacticoid copepods, mostly *Phyllognathopus viquierei*, occurred in 5 samples with 1 or 2 individuals



**Fig. 5.** *Tropocyclops jamaicensis* n. sp., male; a, c, allotype, USNM 264196, b, paratype, USNM 264198. **a.** antennule (not all setae indicated; probable aesthetascs indicated by arrows, see text); **b.** antennule articles 8–14; **c.** legs 5 and 6. Scale bars, 50  $\mu$ m.

each. A single individual of *P. viguieri* was found in plant H4 at the end of the colonization experiment, but is not listed in Table 3.

Prior to the start of the colonization experiments in 1994, the fauna in bromeliads Ap1–6 and H1–4 was composed mainly of ostracodes, *Tropocyclops jamaicensis*, and chironomids (Table 3A). These groups comprised respectively 20.8, 38.5, and 32% of the fauna in Ap1–6, and 10.5, 12.7, and 50% in H1–4. *Ectocyclops phaleratus* occurred only in Ap1–6, with 1.7% of the total fauna. The ostracodes were mainly Cypridae, of which 2 species are yet to be determined. Chironomid larvae were represented by the genera *Chironomus*, *Monopelopia*, and *Polypedilum* in descending order of abundance. *Tropocyclops jamaicensis* occurred in 9 of the 10 bromeliads; in contrast, *Ectocyclops phaleratus* was found in only 2.

Two weeks after the experiments started, *T. jama-*

*icensis* was found in 1 plant (Ap1), but in that plant the second observation of copepods was 6 weeks later (week 8). In plant Ap6, cyclopoids were found in samples taken after 3, 5, and 8 weeks, but not in between. A similar pattern was found for all plants investigated, that is, copepods did not occur in every sample after the date of first colonization. The discontinuity in copepod records might be attributed to the limited sample size and the fact that different phytotelmata of each plant were sampled sequentially. Different phytotelmata even in the same bromeliad apparently form distinct habitats with their own “history” in the establishment of aquatic communities.

At the more thorough 5-week sampling, ostracodes were found in phytotelmata of 3 bromeliads (Ap1–3). Adults of *Tropocyclops jamaicensis* occurred in 3 plants, and together with nauplii and copepodids in 5 (Ap1, Ap6, H1, H2, H4). Chironomid larvae occurred

**Table 2.** Measurements of pH and electrical conductivity ( $\mu\text{S}/\text{cm}$ ) in precipitation (rain), throughfall, and phytotelmata of bromeliads.

	pH				Conductivity ( $\mu\text{S}/\text{cm}$ )			
	Mean	SD	Range	N	Mean	SD	Range	N
Precipitation								
2 May 1994	5.5	0.6	4.5–6.6	33	40.1	29.5	6.1–112	30
3 May 1995	5.6	0.4	4.9–6.6	24	32.4	27.6	94–114	20
Throughfall								
2 May 1994	6.3	0.5	5.0–7.0	24	82.0 <sup>a</sup>	78.8 <sup>a</sup>	18.1–275	19
3 May 1995	6.3	0.7	5.4–7.8	27	71.2	43.0	19.7–194	27
Phytotelmata								
In experimental bromeliads:								
Ap1–6, 1994	5.6	1.0	3.9–6.8	19	119	89.9	11.9–263	16
Ap1–6, 1995	5.6	0.7	4.4–6.7	20	76.5	56.1	11.5–192	20
H1–4, 1994	5.7	0.9	4.5–6.5	7	160	120	48.1–321	4
H1–4, 1995	6.2	0.5	5.5–6.7	7	116	105	41.3–342	7
In control bromeliads	5.3	0.7	4.0–6.3	22	90.0	84.3	19.1–324	20

<sup>a</sup> Not including exceptionally high values (330, 380, 493  $\mu\text{S}/\text{cm}$ ).

in 8 bromeliads (all except H2 and H3). At 13 weeks after initiation (13 May 1994, Table 3B) the fauna was still depauperate compared to assemblages before the start of the experiments. Ostracodes occurred in 6 plants, adult cyclopoids in 8 (1 additional bromeliad contained nauplii only), and chironomid larvae in 9. Regarding cyclopoids, *T. jamaicensis* was found in 8 bromeliads and *E. phaleratus* in only 1 (Ap4). Larvae of *Aedes (Howardina) grabhami* were found in 6 of the 10 plants.

After a year (Table 3C), roughly the complete range of aquatic organisms originally observed in the bromeliads had returned. Despite the fact that all plants were manipulated in the same manner under the same environmental conditions, the community structure varied between individual plants, in terms of species numbers as well as numbers of individuals. However, *Tropocyclops jamaicensis* occurred in all the plants, with a mean of 484 individuals per plant. The highest number of individuals of this species (2473) occurred in Ap6, which stored about 2100 ml water. Only 1 specimen was found in H2, which stored 350 ml; and in Ap2, 72 individuals were counted in a total of 50 ml water. A possible correlation between water volume and number of individuals was not tested statistically, but other factors than size of phytotelmata seem to influence species abundance. *Ectocyclops phaleratus* was found in some bromeliads, but in lower numbers than *T. jamaicensis*. The mean number of individuals per plant was 20, and the plant with the highest number was Ap5 with 132.

Cyclopoid copepods in general were faunal domi-

nants in terms of individual numbers at the end of the experiments. *Tropocyclops jamaicensis* comprised 66.5% of the community in *Aechmea paniculigera* and 53.2% in *Hohenbergia* spp. *Ectocyclops phaleratus* constituted only 2.7% and 2.4%, respectively. In contrast to the copepods, ostracodes were less abundant in *Aechmea* than at the start of the experiments, decreasing from 20.8% to 5.6% of individuals. Ostracodes were slightly more abundant in *Hohenbergia*, increasing from 10.5% to 12.8%. In *Hohenbergia*, species belonging to Cypridae were replaced by *Metacypris* sp. The percentage of chironomid larvae, one of the major taxa in bromeliads, decreased in both plant species, in *Aechmea* from 32% to 18.1%, and in *Hohenbergia* from 50% to 22.8%. There was also a notable change in the composition of chironomid genera: at the start, *Chironomus anonymus* dominated, but after the experimental manipulation *Monopelopia* and *Polydillum* were present in higher numbers than *Chironomus*. In comparing faunal assemblages by percent, the high proportion of cyclopoid copepods should be borne in mind.

## Discussion

### Taxonomic relationships

The new species resembles other members of the genus *Tropocyclops* in respect to general body shape, the T-shaped anterior expansion of the seminal receptacle, the long slender antennule composed of 12 articles in the female and 16 articles in the male (the latter with slender setiform aesthetascs), the articula-

tion and general armament of the swimming legs, and the leg 5 consisting of a single plate with long setae. Additionally, the pattern of unsocketed spines on the surface of the antenna basipodite resembles the simplified eucyclopine patterns of *Tropocyclops prasinus* and *T. confinis* (KIEFER 1930) (Fiers & Van de Velde 1984). *Tropocyclops jamaicensis* differs from other congeners in its elaborately formed seminal receptacle, especially the broad lateral expansions and tripartite posterior expansion, and in 3 striking apomorphies: the naked pediger 5, the lack of a seta on the medial margin of leg 4 exopodite article 1, and the lack of the lateral seta of leg 5. Systematic relationships within *Tropocyclops* are unclear, because the genus has not been revised since Kiefer's (1931) effort. The spine formula of 3,4,3,3 in *T. jamaicensis* is that of members of Kiefer's *terni*-group (Kiefer 1931).

The present systematic concept of the family Cyclopidae is based primarily on the leg 5 structure and the number of its setae and/or spines. The subfamily Eucyclopininae is defined by possession of 3 setae or spines on the terminal (or only) article of this leg. Genera with 2 or fewer setae or spines at this location have usually been considered members of the subfamily Cyclopininae. Difficulties with this simple scheme were recognized early (e.g., Gurney 1933) and continue unresolved (Reid 1993). We now know of 2 species in which the leg 5 structure is not as conservative as had been supposed. One, *Austriocyclops vindobonae* KIEFER 1964, was originally assigned to the subfamily Cyclopininae on the basis of the extremely reduced leg 5, which consists of 1 or 2 short setae carried on a tiny, fused or even absent article. But Pospisil (1994) recently reported his discovery of the male and described the structure of its geniculate antennule, which bears the club-shaped aesthetascs that are typical of species of *Eucyclops* and several other genera of the Eucyclopininae, but which do not occur in the Cyclopininae. Aesthetascs are socketed sensory organs that may be modified setae and are short and club-shaped, long and cylindrical, or setiform. Pospisil (1994) argued that the possession of club-shaped aesthetascs justifies transfer of *A. vindobonae* to the subfamily Eucyclopininae, in spite of the extremely reduced fifth leg and its setae. *Tropocyclops jamaicensis* constitutes the second known case of reduction of the number of fifth leg setae in Eucyclopininae.

The systematics of the family Cyclopidae, especially the subfamilies Eucyclopininae and Cyclopininae, require analysis by modern methods. Neither subfamily has good defining synapomorphies, and the simple delimitation according to fifth leg structure appears increasingly inadequate. Other lines of investigation, such as comparative developmental patterns of articulation of

the swimming legs, have suggested that these subfamilies are polyphyletic (F.D. Ferrari, pers. comm. to JWR, 1995).

Most species of *Tropocyclops* are planktonic and epibenthic in ponds and lakes. The only other member of the genus known to inhabit phytotelmata is *T. schubarti* (KIEFER 1935), which has been recorded from bromeliads of the Brazilian Atlantic coastal rainforest (Kiefer 1935; Herbst 1959). From bromeliads in the same region, Hadel & Carvalho (1988) reported an unidentified species of *Tropocyclops*, possibly *schubarti*. The record by Laessle (1961) of *Tropocyclops prasinus* cf. *mexicanus* from Jamaican bromeliads refers to *T. jamaicensis*, as we found by inspection of Laessle's specimens. We have recorded *T. prasinus* from the Salt Spring River in the Black River Morass area of Jamaica (1 ♀ and 1 ♂ collected by WJ on 22 March 1994; USNM 264229), but have not found it in bromeliads. Nor have we found *T. jamaicensis* outside bromeliads, in the collections from surface water habitats made by one of us (WJ) in Jamaica.

Cyclopoids inhabiting benthic, interstitial, or otherwise spatially restricted habitats including phytotelmata may show reductions in the size, number of articles, and number of setae and spines of the mouthparts and swimming legs (Pesce & Galassi 1985, 1987; Reid 1991a; Pesca 1994; Reid & Strayer 1994). Although loss of 1 of the 2 setae on the anterodistal corner of the basis of the antenna has been reported for 3 planktonic species of *Tropocyclops* (Reid 1991a,b), in *T. jamaicensis* the full complement of antennal setae is present and the exopodite-seta is not reduced in length. Nor is there any reduction in the mouthparts or in the structure and setation of the swimming legs, except for the absence of a seta on the leg 4 exopodite article 3. We cannot suggest a possible mechanical gain in the lack of this seta. The most obvious structural difference in *T. jamaicensis*, the loss of the outermost seta of leg 5, may serve to streamline the animal in the spatially restricted bromeliad habitat.

The leg 4 endopodite article 3 of *T. jamaicensis* is bent inward to a degree not found in congeners, although in some this article is directed slightly inward, e.g., illustrations of *T. breviramatus* by Hsiao (1950), *T. polkianus* by Einsle (1971), and *T. pseudoparvus* by Dussart & Fernando (1986). It may be that this angled carriage of the endopodite serves to increase the prehensile capability of the leg in adhering to surfaces within the bromeliad. We have not yet observed the swimming or resting behavior of living animals.

Reid (1993) noted that cyclopoids inhabiting phytotelmata and living in other non-planktonic situations are likely to be unusually well-ornamented on the body or parts of the swimming legs, particularly the cou-

**Table 3.** Fauna of individual plants of bromeliad species *Aechmea paniculigera* (Ap1–6) and *Hohenbergia* spp. (H1–4). A. Before start of colonization experiments (9–11 February 1994), fauna in all phytotelmata of each whole plant. B. At 13 weeks after start of colonization experiments (13 May 1994), fauna found in subsamples: phytotelmata of 2 leaf axils of each plant. C. At 13 months after start of colonization experiments (7, 8 March 1995), fauna in all phytotelmata of each whole plant.

Fauna	A. Before experiments (whole plants)									
	Ap1	Ap2	Ap3	Ap4	Ap5	Ap6	H1	H2	H3	H4
Clitellata: Oligochaeta										
Lumbriculidae:										
<i>Lumbriculus</i> sp.	1	2	—	1	—	9	—	—	—	—
Naididae:										
<i>Aulophorus</i> cf. <i>superterrenus</i>	—	—	—	—	—	—	—	—	—	—
Tubificidae sp.	1	—	—	—	—	—	—	—	—	—
Crustacea: Ostracoda										
Cypridae sp.	30	45	234	1	284	3	8	3	—	22
Cytheridae: <i>Metacypris</i> sp.	12	1	—	1	—	—	1	—	—	—
Crustacea: Copepoda										
Cyclopidae:										
<i>Ectocyclops phaleratus</i>	30	—	—	—	—	20	—	—	—	—
<i>Tropocyclops jamaicensis</i>	443	28	78	212	10	362	33	2	—	6
Insecta: Odonata										
Coenagrionidae:										
<i>Diceratobasis macrogaster</i>	1	—	1	16	3	13	3	4	1	6
Insecta: Coleoptera										
Dytiscidae:										
<i>Desmopachria</i> sp.	—	—	—	—	—	—	1	—	—	—
Helodidae:										
<i>Cyphon</i> sp.	—	—	—	—	33	12	22	8	22	10
Insecta: Diptera										
Psychodidae sp.										
Ceratopogonidae sp.	—	—	—	—	—	—	1	—	—	—
Culicidae:										
<i>Aedes</i> ( <i>Howardina</i> ) <i>grabhami</i>	—	—	1	5	35	14	6	—	—	3
<i>Aedes</i> ( <i>Howardina</i> ) <i>walkeri</i>	—	—	—	9	—	1	—	—	—	—
Chironomidae:										
<i>Chironomus anonymus</i>	2	26	1	92	253	244	27	12	11	35
<i>Monopelopia</i> sp.	—	—	—	97	107	73	34	1	42	—
<i>Polypedilum</i> cf. <i>tritum</i>	—	—	35	12	—	—	—	—	—	—
Syrphidae:										
<i>Eristalis</i> sp.	—	—	—	1	—	—	—	—	—	—
Suborder Brachycera sp., larvae	—	—	35	12	—	—	—	—	—	—

plers. Reid suggested that extra ornamentation (spines and hairs) may help prevent attachment of detritus and epizoites. In support of this hypothesis, in *T. jamaicensis* the couplers of all 4 swimming legs are well ornamented. *Tropocyclops schubarti* also has long hairs along the free margins and rows of tiny spines on the surface of the couplers of legs 2–4 (Reid 1991b). However, 2 planktonic congeners, *T. prasinus* as redescribed from Japan by Ueda et al. (in press),

and *T. prasinus* aff. *aztequei* LINDBERG 1955 as described by Suárez-Morales et al. (1996), have equally elaborate coupler ornamentation. Although coupler ornamentation is less well-developed in other planktonic congeners (e.g., Boxshall & Braide 1991; Reid 1991a,b), there appears to be no clear correlation with habitat. Also, if extra body ornamentation were advantageous in the phytotelmic habitat, one would expect that the lateral fringe of pediger 5 would have been

**Table 3.** Extended.

B. 13 weeks (subsamples)										C. 13 months (whole plants)									
Ap1	Ap2	Ap3	Ap4	Ap5	Ap6	H1	H2	H3	H4	Ap1	Ap2	Ap3	Ap4	Ap5	Ap6	H1	H2	H3	H4
—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	5	2	15	2
—	—	—	—	—	—	—	—	—	—	—	—	1	44	2	—	—	—	—	1
—	—	11	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
3	7	25	—	—	1	9	—	—	1	2	—	—	—	—	311	—	5	5	35
—	—	—	—	—	—	—	—	—	—	—	—	—	30	4	—	—	10	113	—
—	—	—	14	—	—	—	—	—	—	17	18	—	—	132	—	7	—	6	19
14	25	10	—	29	26	30	8	—	7	156	72	255	471	709	2,473	275	1	267	155
—	—	2	1	2	1	1	—	—	1	—	2	19	24	18	26	4	—	4	6
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	1	—	—	—	—	—	1	1	5	4	4	—	—	10
—	—	—	—	—	—	—	—	—	—	—	—	—	6	29	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	21
—	3	1	—	4	17	11	—	—	9	17	8	11	6	17	121	9	9	3	2
—	—	—	—	—	—	—	—	—	1	4	—	—	3	11	1	—	—	4	—
1	4	2	5	60	20	30	9	—	16	49	—	21	49	37	72	—	—	17	4
—	—	—	1	7	4	3	—	—	1	15	7	55	79	152	158	—	—	26	51
—	—	—	—	—	—	—	—	—	—	46	6	49	73	160	89	—	65	44	92
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	24	—	—	6	—	36	—	—	—	8

retained in *T. jamaicensis*. This hypothesis, then, seems to be poorly supported by present evidence.

**Environmental conditions and colonization**

Rainwater is altered when passing through the canopy, because of leaching of components such as dust on plant surfaces (e.g., Bruijnzeel 1991). Throughfall and stemflow enriched by leaching influence phyto-

telmic environmental conditions and may contribute nutrients to both the bromeliads and the aquatic communities of their phytotelmata. Leaf litter accumulated in phytotelmata also influences the physical, chemical, and biological characteristics of phytotelmata, such as the oxygen balance (Laessle 1961; Diesel 1992; Janetzky & Vareschi 1993).

In phytotelmata of the experimental and control bromeliads, mean pH values were between 5.3 and 6.2.

In the bromeliads studied by Laessle (1961), pH values were often considerably below 4.0, and higher values were often correlated with the presence of calcareous fragments such as snail shells. Our results for conductivity varied between 11.9 and 324  $\mu\text{S}/\text{cm}$ , with lower readings usual in phytotelmata with little accumulated organic detritus. Increased conductivity was related to the amount of accumulated leaf litter and possibly also to leachates from this organic material.

Differences between precipitation and throughfall may occur because of leaching of soluble compounds into rainfall passing through the canopy. The lack of differences between throughfall and phytotelmata in most cases, and the eventual dilution of the river water used to refill bromeliads for the experiments imply that throughfall influences conditions in the phytotelmata. Exceptional differences in pH of throughfall and phytotelmata, or between different bromeliads, reveal the influence of accumulated leaf litter. Rylov (1948) showed that at least some cyclopoids are restricted to neutral or acidic conditions. Changes in environmental conditions may prevent species from colonizing newly formed habitats. However, the lack of differences in pH, except in H1–4 and controls in 1995, and in conductivity in bromeliads at the beginning and end of the experiments, provides evidence that differences in faunal assemblages might be caused by other factors, such as the amount of debris accumulated in phytotelmata, or the degree of insolation.

The amount of accumulated leaf litter may influence the species composition in phytotelmata. Cyclopoid copepods and larvae of the culicids *Aedes (Howardina) grabhami* and the less common *Aedes (Howardina) walkeri* occurred in the open water (pelagic zone) of the Jamaican phytotelmata. Benthic organisms associated with the leaf litter include harpacticoid copepods (e.g., *Phyllognathopus viguieri*), ostracodes (e.g., *Metacypris* sp.), oligochaetes, and some insect larvae (e.g., *Chironomus anonymus*, *Monopelopia* sp.). Laessle (1961) showed that *Chironomus* spp. occurred in sun-exposed phytotelmata with algae and little detritus, whereas *Cyphon* spp. were found in shaded phytotelmata with abundant detritus.

Maguire (1963, 1971) described colonization as a process of interlinked events including dispersal, arrival, and establishment of species. Maguire listed several important mechanisms of dispersal: (1) air currents or rain transporting disseminules of small aquatic organisms, (2) flight of winged organisms, and (3) phoresy. Micro-organisms especially may colonize through air currents (Maguire 1963; Krügel 1993), but active colonization seems to be the major mechanism for dispersal of larger organisms (Krügel 1993). Examples of phoresy were given by Maguire (1963), Maguire &

Belk (1967), and Seidel (1989). With these considerations in mind, animals such as snails visiting the bromeliads were checked, but no evidence of transport of aquatic organisms, especially copepods, by these visitors was found. Plastic jars placed at the study site have shown no sign of colonization by copepods; therefore we discount the likelihood of wind transport of resting eggs or other disseminules. The question of the means used by the copepods to colonize the manipulated bromeliads and their phytotelmata remains open.

Most of the colonizing groups, including *Tropocyclops jamaicensis*, required several months to re-establish stable populations in the phytotelmata following the experimental elimination. This length of time may be due to the need to build up organic matter to provide a sufficient food supply. Even at the end of the colonization experiments, water was visible and only small amounts of debris occurred at the bottom of each phytotelm. In contrast, in phytotelmata of bromeliads in their natural state, the water is often covered with leaf litter derived from the canopy. The lack of organic matter could have led to strong competition between arriving organisms, especially planktonic copepods and culicid larvae, and may have led to failure of some early colonies.

The random nature of the colonization process, by whatever means, is indicated by the variations between plants in community structure, that is, in species composition and numbers of individuals, even after a full year. The differences in community structure might also be correlated with the amount of leaf litter stored in phytotelmata.

It is clear that *Tropocyclops jamaicensis* is a rapid colonizer and dominant organism of phytotelmata in the terrestrial bromeliads of Jamaica. The rate of spread of this copepod into the experimental plants was comparable to that of the larvae of flying insects, especially chironomids and culicids. However it arrives in the plants, *T. jamaicensis* apparently has a high reproductive capacity. Approximately 8 eggs (4 per sac) were produced by females over an interval of 2 or 3 days; in comparison, females of *E. phaleratus* carried only 2 eggs. This difference may partly account for the greater abundance of *T. jamaicensis*.

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