A new species of *Tomlinsonia* Turquier, 1985 (Crustacea, Cirripedia, Trypetesidae) in hermit crab shells from the Philippines, and a new parasite species of *Hemioniscus* Buchholz, 1866 (Crustacea, Isopoda, Hemioniscidae)

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Williams J. D. & Boyko C. B. 2006. — A new species of *Tomlinsonia* Turquier, 1985 (Crustacea, Cirripedia, Trypetesidae) in hermit crab shells from the Philippines, and a new parasite species of *Hemioniscus* Buchholz, 1866 (Crustacea, Isopoda, Hemioniscidae). *Zoosystema* 28 (2): 285-305.

ABSTRACT
Over 950 hermit crabs from coral reef habitats in the Philippines were collected during 1997 and 1999 and examined for burrowing barnacles. Among these specimens, a new species of *Tomlinsonia* was found and is described as *T. mclaughlinae* n. sp. The barnacle was associated with approximately 3% of the shells inhabited by three hermit crab species of the genus *Calcinus*; maximally one female/male barnacle pair was found per shell. Females of *T. mclaughlinae* n. sp. reach lengths of over 8 mm and produce a burrow on the columella that extends toward the apex of the shell. Males are small (0.4-0.7 mm), boot-shaped, and found attached to females below the mantle aperture. The species can be differentiated from *T. asymetrica* of Madagascar based on proportions of terminal cirri segments, shape of the labrum, and mouthpart morphology. Among the 31 specimens of *T. mclaughlinae* n. sp. examined, three were parasitized by two to six males and/or juvenile females of a new species of cryptoniscoid isopod, described as *Hemioniscus pagurophilus* n. sp. Males of this species can be differentiated from *Hemioniscus balani balani* Buchholz, 1866 and *H. balani japonica* Ogawa & Matsuzaki, 1985 based on coxal plate dentition and shape of the ventral median lobe between the first pair of pleopods. Description of the new isopod parasite requires modification in diagnoses of *Hemioniscus* and Hemioniscidae; a review of the nine species of epicarideans that parasitize barnacles distributed among three families is provided. This is the first report of a species of *Tomlinsonia* in the northern hemisphere, of males in the genus, and the first identified cryptoniscoid isopod parasitizing acrothoracican barnacles. The feeding biology and potential for trypetesids to be egg predators of host hermit crabs is discussed.

KEY WORDS
Crustacea, Cirripedia, *Tomlinsonia*, Isopoda, *Hemioniscus*, barnacle, hermit crabs, symbionts, parasites, new species.

RÉSUMÉ

Description d'une nouvelle espèce de Tomlinsonia *Turquier, 1985 (Crustacea, Cirripedia, Trypetesidae) récoltée dans des coquilles de bernard-l'ermite des Philippines et d'une nouvelle espèce parasite d'*Hemioniscus *Buchholz, 1886 (Crustacea, Isopoda, Hemioniscidae).*

Plus de 950 bernard-l'ermite des fonds coralliens des Philippines ont été examinés de 1997 à 1999 à la recherche de balanes fouisseurs. Parmi les spécimens récoltés, une espèce nouvelle de *Tomlinsonia* a été découverte et est décrite ici sous le nom de *T. mclaughlinae* n. sp. Ce balane était associé avec 3 % environ des coquilles habitées par trois espèces de bernard-l'ermite du genre *Calcinus* ; au maximum une paire femelle/mâle a été trouvée par coquille. Les femelles de *T. mclaughlinae* n. sp. atteignent des tailles dépassant 8 mm et forment, sur la columelle, un terrier qui s'étend vers l'apex de la coquille. Les mâles sont petits (0,4-0,7 mm), en forme de chaussure, et se trouvent attachés à la femelle sous la lèvre du manteau. L'espèce peut être distinguée de *T. asymetrica* de Madagascar en se basant sur les proportions des segments des cirri terminaux, la forme du labrum et la morphologie des pièces buccales. Parmi les 31 spécimens de *T. mclaughlinae* n. sp. examinés, trois étaient parasités par des mâles au nombre de deux à six et/ou des femelles juvéniles d'une espèce nouvelle d'un isopode cryptonicien, décrit comme *Hemioniscus pagurophilus* n. sp. Les mâles de cette espèce peuvent être distingués de ceux d'*Hemioniscus balani balani* Buchholz, 1866 en se basant sur la dentition de la plaque coxale et la forme du lobe médian ventral se trouvant entre les premiers pléopodes. La description du nouvel isopode parasite implique la modification des diagnoses du genre *Hemioniscus* et de la famille Hemioniscidae ; les neuf espèces d'épicarides, réparties dans trois familles, qui parasitent les balanes, sont passées en revue. C'est la première fois que des mâles du genre *Tomlinsonia* sont examinés et c'est également la première fois que des balanes acrothoraciques, parasités par des isopodes cryptoniciens, sont observés.

MOTS CLÉS
Crustacea,
Cirripedia,
Tomlinsonia,
Isopoda,
Hemioniscus,
balanes,
bernard-l'ermite,
symbiontes,
parasites,
espèces nouvelles.

INTRODUCTION

In the central Philippines, we recently discovered a species of burrowing trypetesid barnacle of the genus *Tomlinsonia* Turquier, 1985 in shells occupied by three species of *Calcinus* Dana, 1851 hermit crabs from the shallow subtidal zone of coral reef habitats. These specimens can clearly be placed in *Tomlinsonia*, rather than *Trypetesa* Norman, 1903 (the only other genus in this family), as they have protuberant "cushions" on the distal inner margin of all three pairs of terminal cirri, rather than only on the first two pairs as in *Trypetesa* (see Turquier & Carton 1976). They also bear distinctly asymmetrical opercular bars (apertural lips), as opposed to the subequal opercular bars of *Trypetesa* spp. These specimens differ in several aspects from *Tomlinsonia asymetrica* (Turquier & Carton, 1976) from Madagascar, the only previously known species of the genus, and are described herein as a new species. Five of the Philippine specimens have associated dwarf males and this is the first report of males for *Tomlinsonia*.

Three female specimens of this new *Tomlinsonia* have the mantle cavity containing two to six cryptoniscoid isopods. Although the first report of cryptoniscoid isopods parasitizing acrothoracican barnacles was given by Turquier (1987, on

Lithoglyptes stirni Turquier, 1987), those specimens were then only tentatively identified as perhaps belonging to a new genus near *Hemioniscus* Buchholz, 1866 or *Scalpelloniscus* Grygier, 1981, and have never been subsequently fully identified or described. Identification of isopods that parasitize other crustaceans (known either as Epicaridea or Bopyroidea) can be a challenge as older descriptions are often lacking in key morphological details and many type specimens have been lost. These problems are particularly apparent when dealing with those epicarideans that parasitize barnacles, as most of the key morphological characters used to delimit species (and even genera and families) are found in the neotenous males that are externally indistinguishable from the cryptoniscid larvae. Historically, however, authors have focused on describing the highly reduced, sac-like females and only superficially describing the males. Only relatively recently has there been a concerted effort to describe males at the level of detail needed to identify species and attempt to define genera on morphological characters rather than on an artificial framework of host specificity (e.g., Nielsen & Strömberg 1965, 1973a, b). Identification of the Philippine cryptoniscoid parasites required a review of the nine species of epicarideans that parasitize barnacles distributed among three families: Hemioniscidae (six species on pedunculate and sessile Thoracica), Crinoniscidae (one species on sessile Thoracica), and Cryptoniscidae (two species of *Liriopsis* on Rhizocephala and two species of *Scalpelloniscus* on scalpellid Thoracica), as well as the monotypic genus *Gorgoniscus* Grygier, 1981 (family *incertae sedis*) from ascothoracicans. Based on this review, we conclude that the Philippine cryptoniscoids from *Tomlinsonia* belong to an undescribed species of the genus *Hemioniscus*, but that both *Hemioniscus* and Hemioniscidae require some modification in diagnoses to accommodate the new species.

METHODS

Hermit crabs inhabiting gastropod shells were collected shallow subtidally (< 5 m) in Aklan, Bataan, and Oriental Mindoro provinces of the Philippines from June to August 1997 and January to April 1999 (Williams 2002: fig. 1). Hermit crabs were removed from shells after cracking with a mortar and pestle constructed of galvanized steel pipe (60 mm in diameter) and the shield length (SL) of host hermit crabs was measured using a vernier caliper or stage micrometer to the nearest 0.1 mm. Isopod size is given as total body length (anterior margin of head to posterior margin of pleotelson). Maximal length and width of complete barnacles were measured.

For SEM, fixed specimens were dehydrated in an ascending ethanol series followed by four changes of 100% ethanol. Drying was completed with a Samdri 795 Critical Point Drier. Dried specimens were mounted on an aluminum stub, coated with gold (EMS-550 Sputter coater), and viewed with a Hitachi S-2460N SEM. Type specimens are deposited in the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, Singapore (ZRC) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM). Higher level classification follows Martin & Davis (2001).

The simple, bifid and multifid projections on the inner and outer surfaces of the opercular bars have been variously referred to as spines (Turquier 1978), denticules (Watling 1989), scales (Kolbasov 1999) and teeth (Smyth 1986). It is not clear if these structures are all modified setae with individual sockets or non-articulated cuticular extensions (homologous with spines or scales as defined by Watling 1989). However, they are definitely not "teeth" in any sense and we use the terminology of Watling (1989) to describe them.

In the text we use the term "male" to refer to any cryptoniscid isopod not clearly in the process of metamorphosis into the definitive female phase. It is not possible to distinguish larvae from males or even immature females at early stages of development and it is possible that at least one individual in each batch will become a female, but we cannot demonstrate this point through external examination of specimens.

SYSTEMATICS

Infraclass CIRRIPEDIA Burmeister, 1834
Superorder ACROTHORACICA Gruvel, 1905
Order APYGOPHORA Berndt, 1907
Family TRYPETESIDAE Stebbing, 1910
Genus *Tomlinsonia* Turquier, 1985

Tomlinsonia mclaughlinae n. sp.
(Figs 1-6)

TYPE MATERIAL. — **Philippines.** Boracay, Rocky Beach, 11°57'N, 121°56'E, from shell of *Drupella cornus* (Röding, 1798) inhabited by ovigerous ♀ *Calcinus gaimardii* (H. Milne Edwards, 1848) (3.4 mm SL), 13.IV.1999, ovigerous ♀ holotype 8.15 mm max. length, 4.3 mm max. width (USNM 1084093), ♂ allotype 0.71 mm (USNM 1084094). — Puerto Galera, Big Lalaguna Beach, 13°30'N, 120°57'E, from shell of *Peristernia incarnata* (Kiener, 1840) inhabited by ovigerous ♀ *C. gaimardii* (3.8 mm SL), 21.VII.1997, 1 ♀ paratype with *Hemioniscus* (USNM 1084095); from shell of *Drupella cornus* inhabited by ovigerous ♀ *Calcinus minutus* Buitendijk, 1937, 31.VII.1997, 1 ♀ paratype (USNM 1084096). — Puerto Galera, Coco Beach, 13°30'N, 120°56'E, from shell of *D. cornus* inhabited by ovigerous ♀ *C. gaimardii*, 12.I.1999, 1 ♀ paratype (USNM 1084165; mantle on one SEM stub, cirri on separate SEM stub). — Puerto Galera, Bayanan and Haligi Beaches, 13°29'N, 120°53'E, from shell of *D. cornus* inhabited by ovigerous ♀ *C. gaimardii*, 13.I.1999, 1 ♀ paratype (ZRC 2006.0001). — Bataan, Mabayo, 14°44'N, 120°16'E, from shell of *Drupa grossularia* Röding, 1798 inhabited by ovigerous ♀ *C. minutus* (2.85 mm SL), 21.II.1999, 1 ovigerous ♀ paratype (ZRC 2006.0002); from unidentified gastropod shell inhabited by ♀ *C. minutus* (2.25 mm SL), 21.II.1999, 1 ♀ paratype (ZRC 2006.0003); from shell of *Morula granulata* (Duclos, 1832) inhabited by ♀ *C. minutus* (2.2 mm SL), 21.II.1999, 1 ♀ paratype (ZRC 2006.0004); from shell of *D. grossularia* inhabited by ♀ *C. minutus* (3.0 mm SL), 21.II.1999, 1 ♀ paratype (USNM 1084097); from shell of *Cantharus undosus* (Linnaeus, 1758) inhabited by ♀ *C. gaimardii* (3.02 mm SL), 21.II.1999, 1 ♀ paratype (ZRC 2006.0005); from unidentified gastropod shell inhabited by ovigerous ♀ *C. minutus* (2.18 mm SL), 21.II.1999, 1 ♀ paratype (USNM 1084098); from unidentified gastropod shell inhabited by ovigerous ♀ *C. minutus* (2.82 mm SL), 21.II.1999, 1 ♀ paratype (USNM 1084099); from unidentified gastropod shell inhabited by ♀ *C. gaimardii* (1.69 mm SL), 21.II.1999, 1 ♀ paratype (USNM 1084100); from unidentified gastropod shell inhabited by ♀ *C. gaimardii* (2.34 mm SL), 21.II.1999, 1 ♀ paratype (USNM 1084101); from unidentified gastropod shell inhabited by ♀ *C. minutus* (2.98 mm SL), 21.II.1999, 1 ♀ paratype (USNM 1084102); from unidentified gastropod shell inhabited by ovigerous ♀ *C. minutus* (2.42 mm SL), 21.II.1999, 1 ♀ paratype, 1 ♂ paratype (USNM 1084103); from unidentified gastropod shell inhabited by ovigerous ♀ *C. gaimardii* (3.31 mm SL), 21.II.1999, 1 ♀ paratype (USNM 1084104; mouthparts on SEM stub); from unidentified gastropod shell inhabited by ovigerous ♀ *C. minutus* (2.9 mm SL), 21.II.1999, 1 ovigerous ♀ paratype 5.90 mm (USNM 1084105); from unidentified gastropod shell inhabited by ovigerous ♀ *C. minutus* (2.54 mm SL), 21.II.1999, 1 ♀ paratype 5.9 mm max. length (USNM 1084106; mouthparts on SEM stub); from unidentified gastropod shell inhabited by ♀ *C. minutus* (2.58 mm SL), 21.II.1999, 1 ♀ paratype 3.69 mm max. length, 2.07 mm max. width, 1 ♂ paratype 0.50 mm (USNM 1084107). — Boracay, Rocky Beach, 11°57'N, 121°56'E, from shell of *D. cornus* inhabited by ♂ *C. gaimardii* (2.9 mm SL), 12.IV.1999, 1 ♀ paratype (USNM 1084108), 1 ♂ paratype 0.68 mm (USNM 1084109); from shell of *D. cornus* inhabited by ♀ *C. gaimardii* (3.85 mm SL), 12.IV.1999, 1 ♀ paratype (USNM 1084110); from shell of *Drupella rugosa* (Born, 1778) inhabited by ovigerous ♀ *C. gaimardii* (3.5 mm SL), 15.IV.1999, 1 ♀ paratype (USNM 1084111); from shell of *D. rugosa* inhabited by ♀ *C. minutus* (3.85 mm SL), 15.IV.1999, 1 ♀ paratype (USNM 1084112); from shell of *D. cornus* inhabited by ovigerous ♀ *C. gaimardii* (3.7 mm SL), 15.IV.1999, 1 ovigerous ♀ paratype (USNM 1084113). — Bataan, Morong, 14°41'N, 120°16'E, from shell of *C. undosus* inhabited by ♀ *C. gaimardii*, 25.IV.1999, 1 ♀ paratype with *Hemioniscus* (USNM 1084114); from unidentified gastropod shell inhabited by ♀ *C. minutus* (3.0 mm SL), 25.IV.1999, 1 ♀ paratype (USNM 1084115); from unidentified gastropod shell inhabited by ♀ *C. minutus* (3.25 mm SL), 25.IV.1999, 1 ♀ paratype (USNM 1084116); from shell of *D. grossularia* inhabited by ovigerous ♀ *C. gaimardii* (3.6 mm SL), 25.IV.1999, 1 ♀ paratype (USNM 1084117); from shell of *C. undosus* inhabited by ♀ *C. gaimardii* (5.2 mm SL), 25.IV.1999, 1 ♀ paratype with *Hemioniscus* (USNM 1084118).

ADDITIONAL MATERIAL EXAMINED. — **Philippines.** Bataan, Morong, 14°41'N, 120°16'E, from unidentified gastropod shell inhabited by ♀ *Calcinus latens* (Randall, 1839) (2.2 mm SL), 28.II.1999, ♀ (JDW personal collection). — Bataan, Mabayo, 14°44'N, 120°16'E, from unidentified gastropod shell inhabited by ovigerous ♀ *C. minutus* (1.75 mm SL), 21.II.1999, 1 ovigerous ♀ (JDW personal collection).

ETYMOLOGY. — In honor of Patsy A. McLaughlin for her many years in pursuit of new and interesting taxa of hermit crabs, as well as for her gracious help in identifying specimens for those in need, including both of the present authors – for which we are grateful.

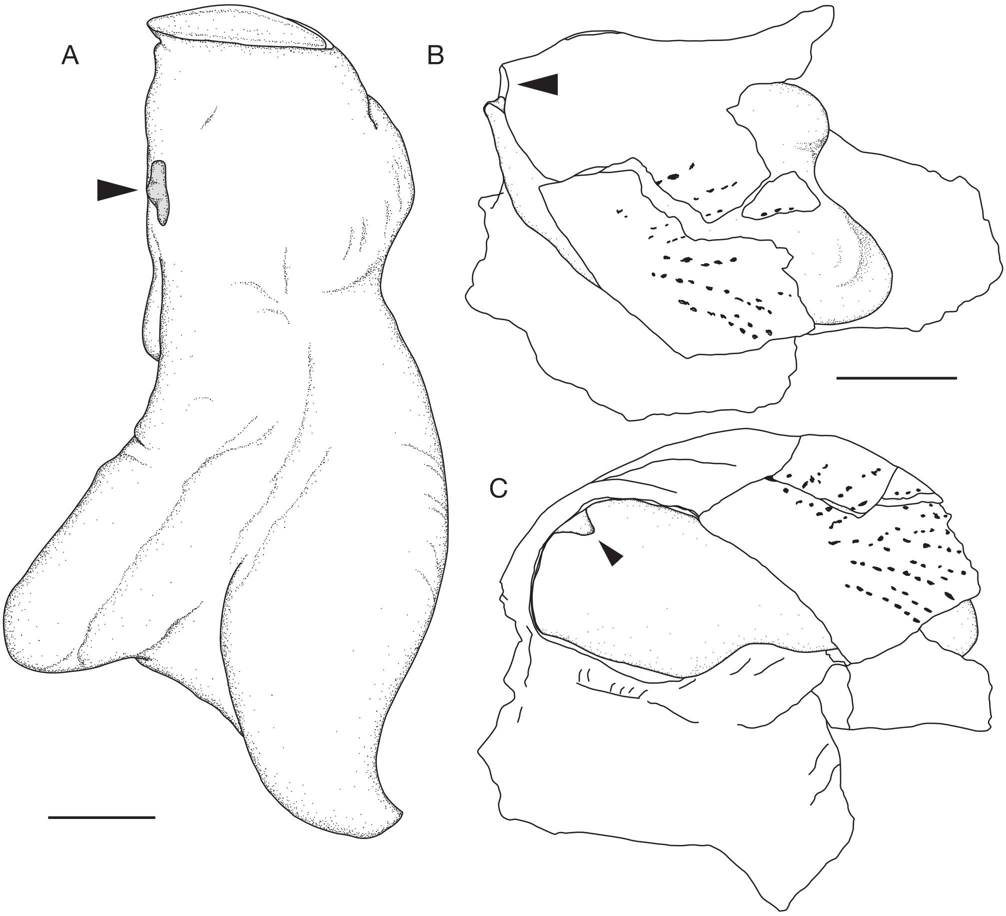

Fig. 1. — *Tomlinsonia mclaughlinae* n. sp.: **A**, holotype ♀ 8.15 mm (USNM 1084093), entire female removed from shell of *Drupella cornus*, female viewed from right side showing flattened distal margin of right opercular bar, position of male (in gray) shown by arrowhead; **B**, **C**, paratype ♀ 3.69 mm (USNM 1084107); **B**, female in shell cracked to expose body of barnacle, aperture of barnacle burrow on columella shown by arrowhead; **C**, left side of specimen in B, showing thin opercular bar with "notch" indicated by arrowhead (striae extending toward apex shown by dark dotted lines in B and C). Scale bars: 1 mm.

Distribution. — Found in shells of *Calcinus* spp. hermit crabs from Aklan, Bataan, and Oriental Mindoro provinces in the central Philippines; shallow subtidally (< 5 m).

Diagnosis. — Female: mantle laterally compressed, muscular, oriented ventrally to aperture, conforming to spiral of the columella, body bluntly rounded at distal end toward apex or with short lobes; chitinous attachment disc with minute tubercles. Left opercular bar thin with notch on ventral side, dorsal side with shallow, rounded indentation; right opercular bar thick with flattened distal margin bordered by raised ridges along length. Opercular bar outer surfaces with dense horizontal rows of variously shaped denticules. Labrum ends of distal margin strongly produced, one broad and rounded distally and one narrow and tapered distally, medial margin subquadrate. Mandible strongly recurved. Maxilla I with acute upper spine and smaller proximo-ventral spine. Maxilla II an ovate plate with sparsely distributed stub setae. Cirrus I endopod and exopod of about 1/2 length protopod. Three pairs of terminal cirri uniramous with four segments; basal segment elongate, tubular, reaching to near end of second segment; second segment approximately as broad as basal segment but about 1/2 as long with protuberant "cushion" on distal inner surface, ridges on cushion with numerous regular rows of blade-like denticules; third segment narrower

than basal or second, approximately as long as basal segment; fourth segment narrower than third, tapering distally, terminating in pair of bifid hooks and superior short recurved spine.
Male: if present, one male per female, attached below mantle aperture. Form of stout boot with dorsal surface nearly straight, anteroventral surface domed and separated from posterodorsal surface by rounded concave area of nearly 90°, all corners rounded, ventral and posterior extensions of body subequal in length, anterolateral corner low.

Description

Female (Figs 1; 2A-C, E; 3-6)

Maximal length 8.15 mm, maximal width (holotype) 4.3 mm (Fig. 1A). Mantle (*sensu* Kolbasov & Newman 2005) laterally compressed, perpendicular to the surface of gastropod shell (Figs 1; 2A, C). Flattened part of mantle ("disc") dorsoventrally compressed, parallel to surface of gastropod shell (Figs 1; 2A, B). Chitinous attachment disc regularly rounded, oval, or irregular, depending on size of barnacle; in some larger specimens disc extends as a spiral covering the barnacle body that is exposed in this region, conforming to the shape of the shell (Fig. 2B, C), chitinous disc covered with minute tubercles. Disc lying in a plane perpendicular to sides of mantle and attaching upper part of animal with cement to wall of burrow along columella in position that orifice leads directly into mantle cavity (Fig. 2A). Aperture on columella of shell approximately straight to slightly curved, tapered slit-like opening 5.5 mm in length and 0.9 mm in width at widest point in holotype, tapering to thin extension (peduncular slit) oriented toward apex of shell (Fig. 2A, E).

Mantle muscular, oriented ventrally to aperture, extending toward apex of shell, conforming to spiral of the columella, in larger specimens extending into the shell whorls, body bluntly rounded at distal end toward apex or with short lobes corresponding to shell whorls in larger individuals, burrow position shown by striae in thin layer of shell overlaying barnacle (Figs 1B, C; 2A). Orifice of mantle a narrow fissure-like opening about 1/4 length of barnacle, tapering to thin opening on ventral end with round opening at dorsal end (Fig. 2C). Left opercular bar thin with abrupt rounded end on ventral side giving the appearance of a notch, dorsal side with shallow, rounded indentation preceding connection with right opercular bar (Figs 1C; 3J, K); right opercular bar thick with flattened distal margin bordered by raised ridges along length (Figs 1A; 2C; 3A, B); right opercular bar approximately 1/3 longer than left opercular bar. Left opercular bar outer surface with dense horizontal rows of ovate denticules (some with bifid or trifid tips) (Figs 3J, L; 4E), row of long simple setae on upper margin (Fig. 3J, L), distal portion of denticule row presenting sparser area of short multifid star-shaped denticules and fewer, shorter simple setae (Fig. 3J, M); sloping region of mantle distal to notch in opercular bar with sparse area of multifid denticules similar to those seen in Figure 3M but with slightly longer shafts (Fig. 3J, N). Left opercular bar inner surface with small inner ridge bordered by dense rows of variously simple to multifid finger-like denticules, tapering towards region of mouth cirri (Fig. 3K, P), small area distal to ridge with sparse field of star-shaped multifid short denticules (Fig. 3K, O), small field of long plumose setae ventral to inner ridge (Fig. 3K; similar to those in Figure 3H on inner surface of right opercular bar), area dorsal to mouth cirri with sparse field of elongate variously simple to multifid denticules and few long simple setae (Fig. 3K, Q). Right opercular bar outer surface with sparse irregular field of simple tear-drop-shaped denticules ventral to dorsal margin and long simple setae on edge (Fig. 3A, D), below opercular bar edge dense rows of simple tear-drop-shaped denticules (Fig. 3A, C), denticules appear flat viewed head-on but are curved in lateral view (Fig. 3E). Right opercular bar inner surface with strong ridge bordered by dense rows of large multifid, foot-shaped denticules (with up to seven denticular blades), field of denticules tapering towards mouth cirri (Figs 3B, G; 4D), area dorsal to mouth cirri region with sparse rows of ovate denticules (Fig. 3B, F), distal margin with thin sparse rows of ovate denticules, mostly with bifid tips and interspersed with few short simple setae (Fig. 3B, I), area ventral to inner ridge with field of long plumose setae (Fig. 3B, H).

Labrum very large, inner edge partially covered by minute denticules and row of long setae proximal to margin along whole length of labrum, ends of

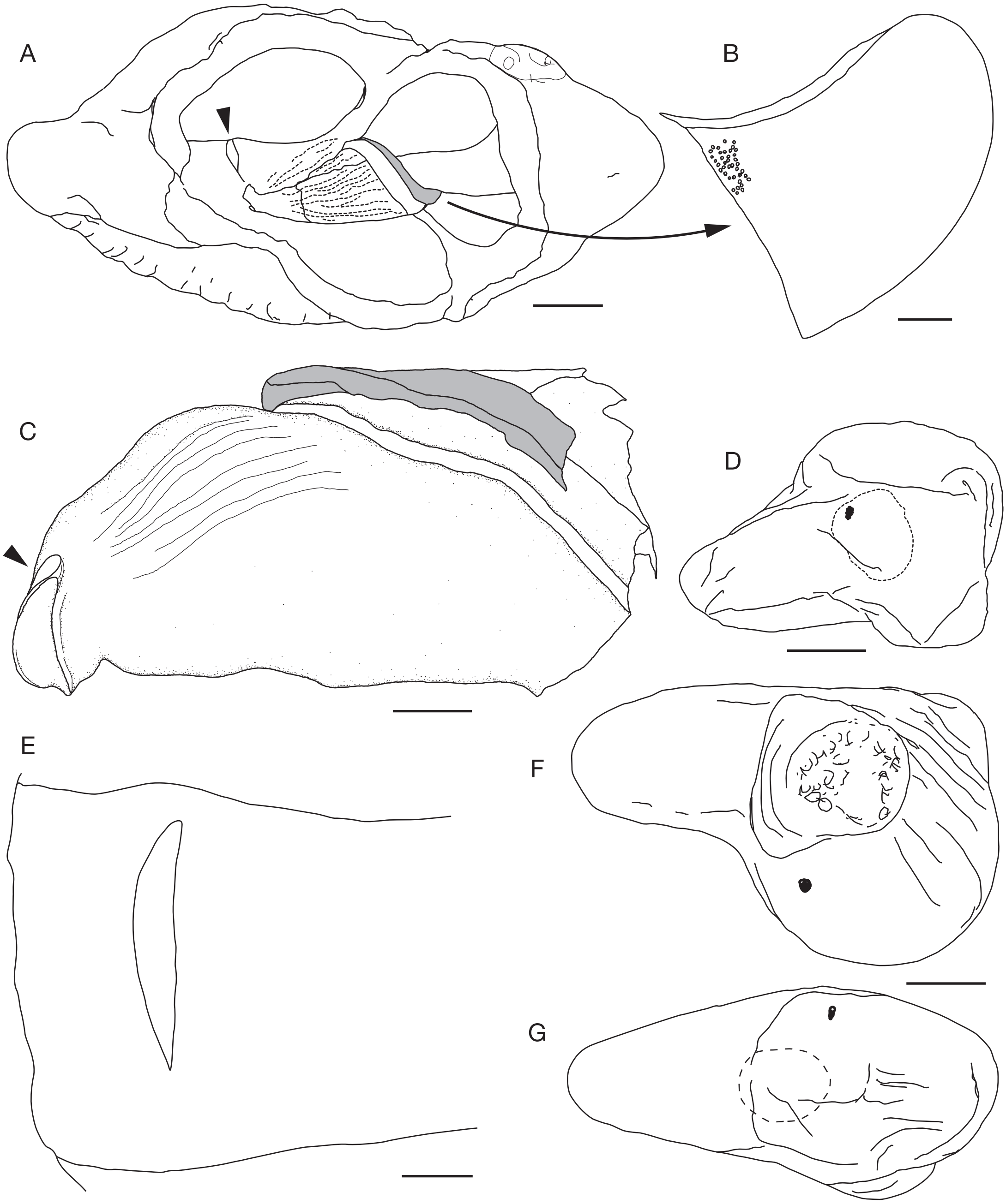

FIG. 2. — *Tomlinsonia mclaughlinae* n. sp.: **A**-**C**, paratype ♀ 5.90 mm (USNM 1084105); **A**, shell of *Drupella cornus* cut away to show barnacle *in situ*, view of columella with aperture (arrowhead) and striae extending toward apex of shell, chitinous attachment disc shown in gray; **B**, distal end of chitinous attachment disc covering body of barnacle toward apex of shell, minute tubercles that cover entire disc are only drawn in the upper-left portion; **C**, female removed from shell shown in A, viewed from right side in same orientation as in A (arrow shows rounded dorsal side of mantle orifice), chitinous attachment disc (in gray) is slightly lifted off of barnacle, distal portion of body not drawn; **D**, paratype ♂ 0.50 mm (USNM 1084107), lateral view; **E**, paratype ♀ (USNM 1084102), aperture on columella of unidentified gastropod shell; **F**, **G**, paratype ♂ 0.68 mm (USNM 1084109); **F**, lateral view; **G**, dorsal view. Scale bars: A, 2.0 mm; B, D, F, G, 125 µm; C, E, 500 µm.

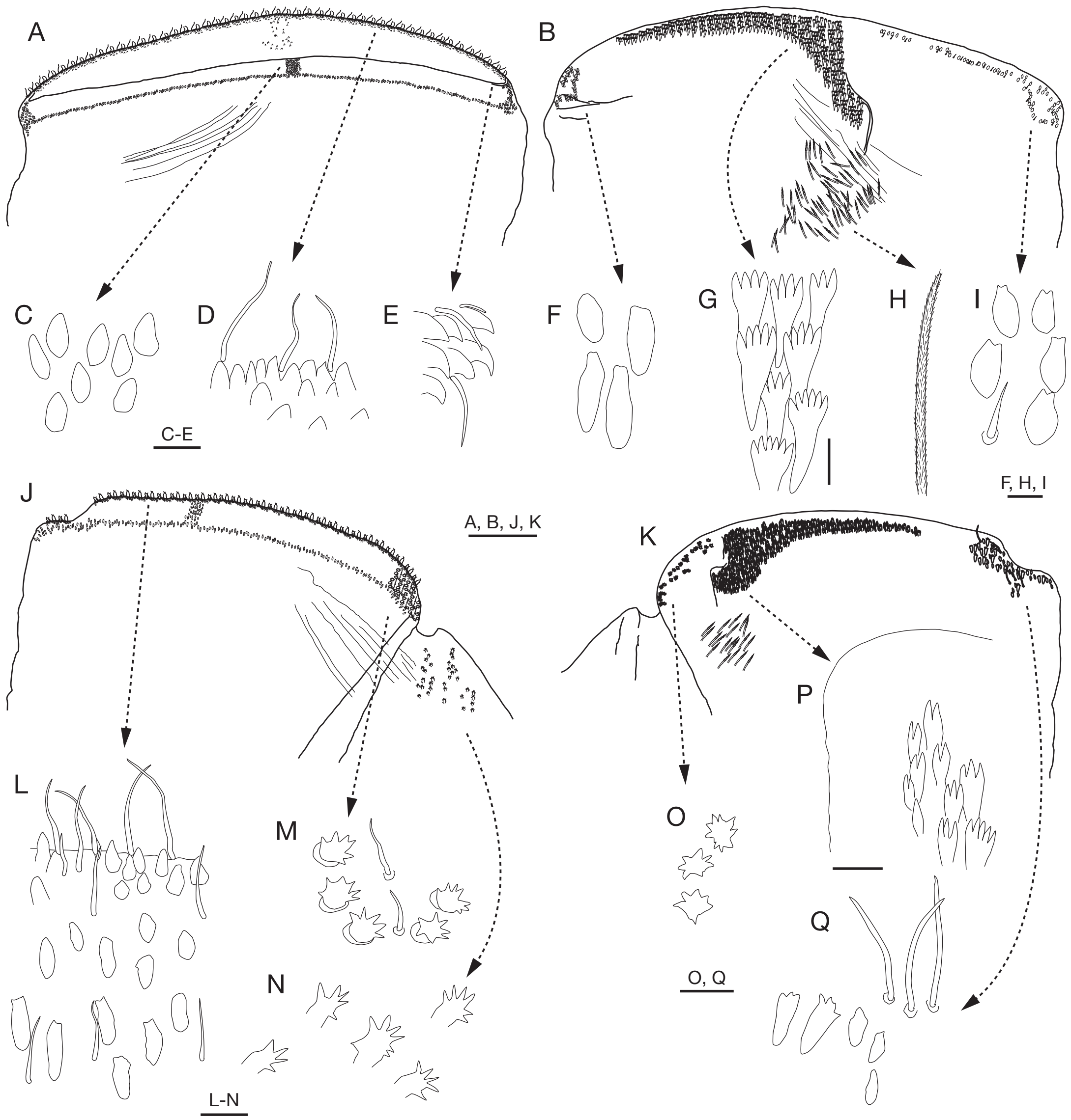

FIG. 3. — *Tomlinsonia mclaughlinae* n. sp., paratype ♀ (USNM 1084097) (note: only selected patches of denticules shown in A, B, J, K): **A**, right opercular bar, lateral outer view; **B**, right opercular bar, lateral inner view; **C**, denticules on outside of right opercular bar, apical view; **D**, denticules and setae on distal edge of right opercular bar; **E**, denticules and setae on outside of right opercular bar, lateral view; **F**, denticules on inside of right opercular bar, apical view; **G**, multifid denticules on inside of right opercular bar and along inner ridge, apical view; **H**, plumose seta on inside of right opercular bar; **I**, denticules on inside of right opercular bar, apical view; **J**, left opercular bar, lateral outer view; **K**, right opercular bar, lateral inner view; **L**, denticules and setae on edge of left opercular bar; **M**, multifid denticules and setae on outside of left opercular bar, lateral view; **N**, multifid denticules on inside of left opercular bar, apical view; **O**, denticules on inside of left opercular bar, apical view; **P**, denticules along inner ridge (curved line) of right opercular bar, apical view; **Q**, denticules and setae on inside of left opercular bar, apical view. Scale bars: A, B, J, K, 250 µm; C-F, H, I, L-N, 6.25 µm; G, O-Q, 12.5 µm.

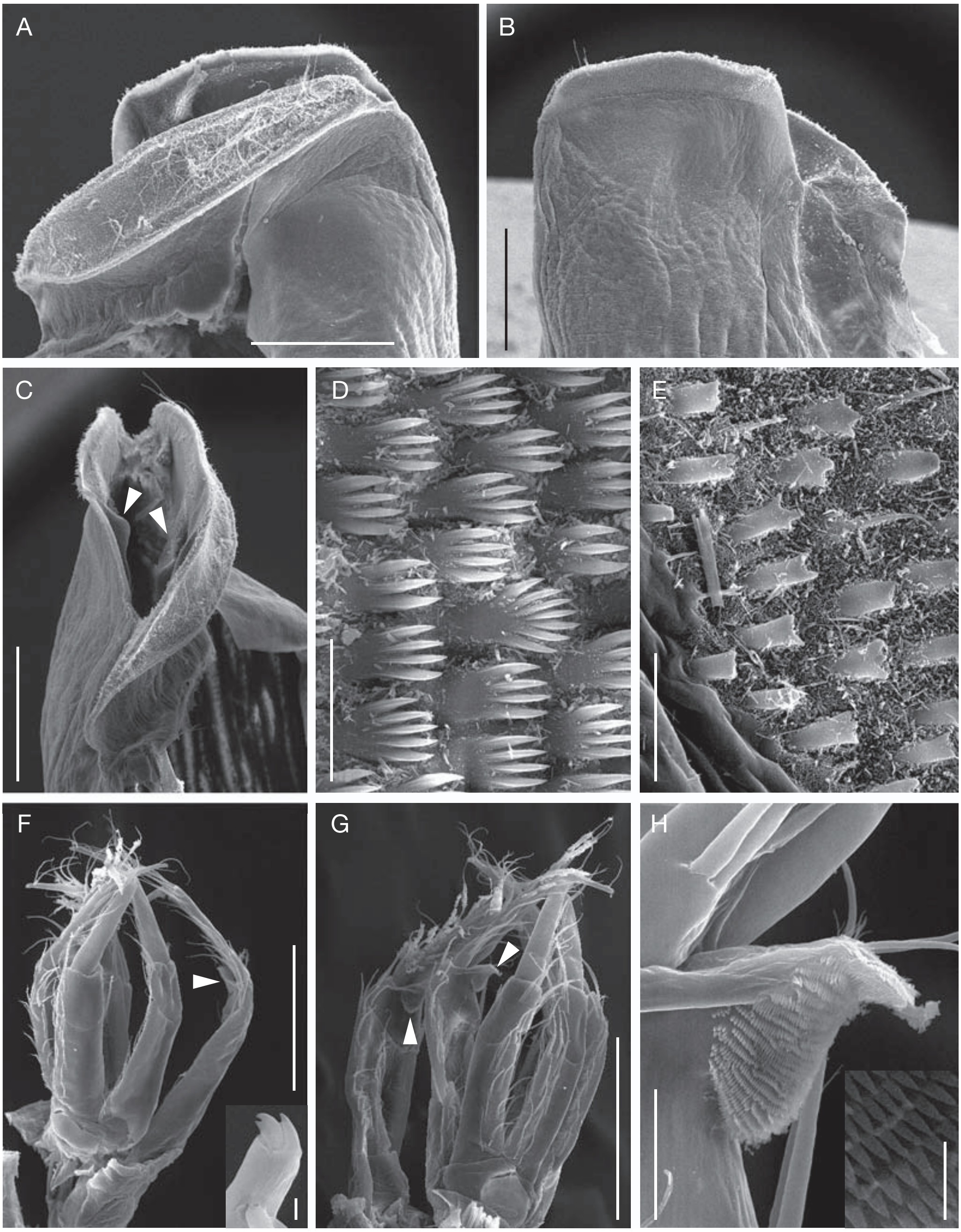

FIG. 4. — *Tomlinsonia mclaughlinae* n. sp., paratype ♀ (USNM 1084165), scanning electron micrographs: **A**, right opercular bar, lateral outer view; **B**, left opercular bar, lateral outer view; **C**, mantle aperture, ventral view (arrowheads show inner ridges); **D**, multifid denticules on inside of right opercular bar and along inner ridge, apical view; **E**, denticules and setae on outside of left opercular bar, lateral view; **F**, terminal cirri, lateral view, arrowhead shows position of cirral "cushion" (inset shows terminal view of cirrus); **G**, terminal cirri, lateral view, arrowheads show position of cirral "cushions"; **H**, terminal cirral "cushion" (inset shows denticules of "cushion"). Scale bars: A-C, 500 µm; D, E, H, 20 µm; F, G, 200 µm; insets of F, H, 2.5 µm.

distal margin of labrum unequal but both strongly produced, one broad and rounded distally and one narrow and tapered distally (Figs 5C; 6B), both with groups of typically three short simple setae (Fig. 5C inset), medial margin subquadrate (Figs 5C; 6B). Mandible strongly recurved, distally as acute projection, no accessory spines (Figs 5D; 6C). Maxilla I smaller than mandible with acute upper spine and smaller proximoventral spine (Figs 5E; 6C), with rows of five or six tapered denticules along inner margin (Fig. 6E). Maxilla II (maxillule) an ovate plate with rows of tiny setae on mesiodistal edge and a strong stout seta near mediomesial edge (Figs 5E; 6C), with sparsely distributed stub setae, more abundant at the base (Fig. 6D).

Four pairs of cirri. Cirrus I (mouth cirrus) biramous; protopod elongate and tubular, naked; endopod and exopod of about 1/2 length of protopod; exopod bearing more long plumose setae on surface and tip than endopod (Figs 5B; 6A, B). Three pairs of terminal cirri (IV-VI) widely separated from mouth cirrus, uniramous with four segments (Figs 4F, G; 5A); basal segment elongate, tubular, with row of long setae along inner surface, reaching to near end of second segment; second segment approximately as broad as basal segment but only about 1/2 as long, with protuberant "cushion" on distal inner surface (Fig. 4H), ridges on cushion with numerous regular rows of small tapered, bladelike denticules (Fig. 4H and inset); third segment narrower than basal or second, approximately as long as basal segment, narrow setae along lateral margins; fourth segment narrower than third, tapering distally, terminating in pair of bifid hooks and single superior short recurved spine (Figs 4F inset; 5A inset, bottom) (one specimen with three bifid hooks plus superior spine, see Fig. 5A inset, top), two very long setae positioned subterminally.

Male (Figs 1A; 2D, F, G)

Length 0.71 mm (allotype). One male present maximally per female, attached below mantle aperture of female (Fig. 1A). Form of stout boot with dorsal surface nearly straight, anteroventral surface domed and separated from posterodorsal surface by rounded concave area of nearly 90°, all corners rounded, both ventral and posterior extensions of body subequal in length (Fig. 2D, F), anterolateral corner low and rounded. Lateral surface with distinct median bulge (Fig. 2G). Penis not observed. Ganglion on vesicular seminalis connected by nerve to small dark eyespot (Fig. 2D, F, G).

Remarks

Tomlinsonia Turquier, 1985 was proposed for the preoccupied genus name *Alcippoides* Turquier & Carton, 1976 (*non* Strand, 1928) (see Turquier 1985; Tomlinson 1987), and the type species is still known from only a single female specimen. The form of the protuberant "cushion" or "button" on the second segment of cirri IV-VI of female trypetesid specimens has been described as "transversely wrinkled by fine, distinctly crenated ridges of unknown function" (Nilsson-Cantell 1978). In fact, these "wrinkles" are composed of regular rows of minute tapered and bladelike denticules and possibly serve a function in feeding (Fig. 3H). As indicated by Turquier & Carton (1976), these "cushions" were suggested to be vestigial endopodites (Darwin 1851), although the complexity of the denticules on the surfaces does not fit well with a vestigial designation.

Males of *Tomlinsonia mclaughlinae* n. sp. differ markedly from those reported for *Trypetesa* species in that their sides form a vaguely equilateral triangle with one concave margin and lack either the elongated penis containing lobe of *Trypetesa lampas* (Hancock, 1849), *Trypetesa habei* Utinomi, 1962, and *Trypetesa spinulosa* Turquier, 1976 or the deeply concave margins of *Trypetesa nassarioides* Turquier, 1967. The male of *Trypetesa lateralis* Tomlinson, 1953 has never been figured or adequately described but was said by Tomlinson (1953, 1969) to lack a penis. Although we have found no evidence of a penis in *Tomlinsonia mclaughlinae* n. sp., we have only seen five specimens. The apparent absence of a penis is not likely due to immaturity of the specimens (they lack the antennules which are characteristic of immature males) (see Turquier 1971). However, the majority of males in many acrothoracican species may appear to lack penes as these organs can develop relatively late in the life of the male (Tomlinson 1969). Only after examination of large series of males, as done by Tomlinson (1969) for *Trypetesa lateralis*, should

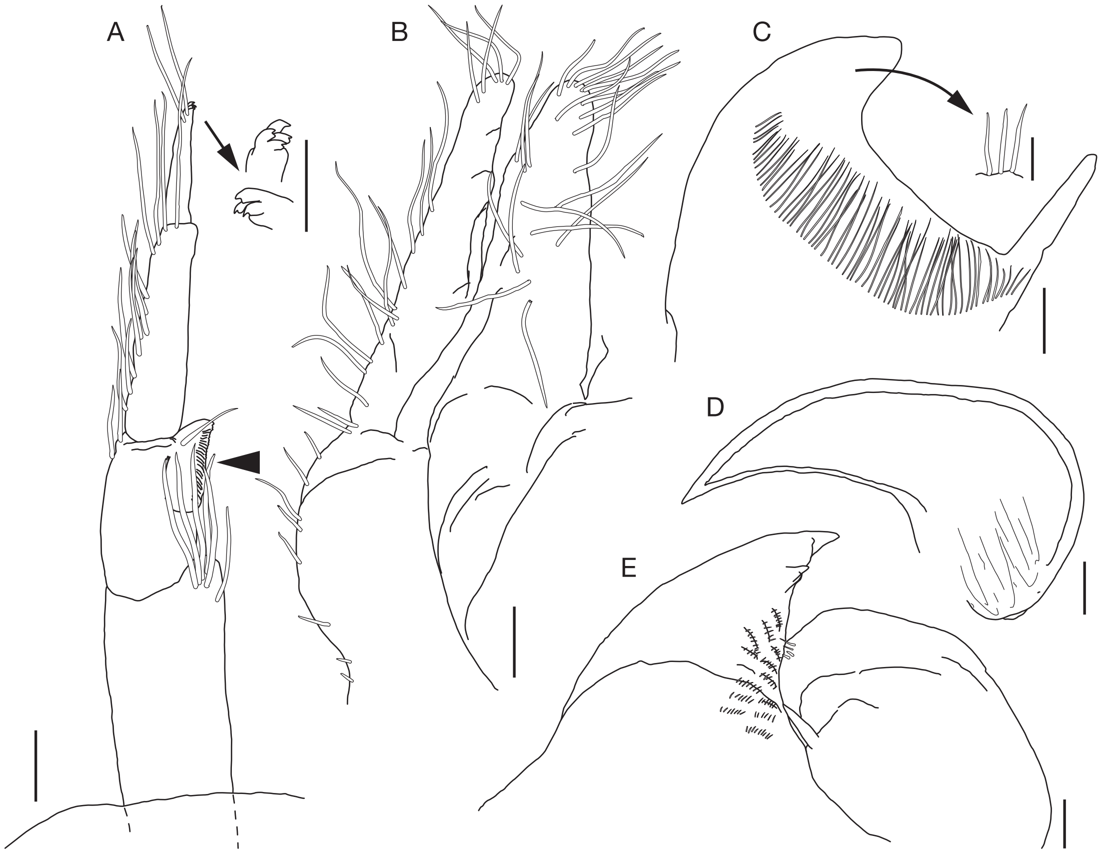

FIG. 5. — *Tomlinsonia mclaughlinae* n. sp.: **A**, paratype ♀ (USNM 1084097), terminal cirrus, lateral view, arrowhead shows position of cirral "cushion" (inset shows two views of terminal hooks); **B**, paratype ♀ (USNM 1084112), mouth cirri, lateral view (note: plumose nature of setae not shown); **C**-**E**, paratype ♀ (USNM 1084097); **C**, labrum, lateral view (inset shows short setae that cover extensions of labrum); **D**, mandible; **E**, maxilla I and maxilla II. Scale bars: A, B, 50 µm; C, 125 µm; D, 25 µm; E, 12.5 µm; insets of A, C, 6.25 µm.

any conclusions about presence or absence of penes in acrothoracican species be made.

The only acrothoracican previously reported from the Philippines was *Trypetesa lampas* (Rosell 1981). Study of Rosell's (1981) description and illustration leaves no doubt that he was dealing with a *Trypetesa* species, but his description could apply to any species in the genus and the illustrations, particularly of the mandible, strongly suggest that this was not *T. lampas*, but perhaps an undescribed species. The so-called "caudal appendage" cited by Rosell (1981) is the sixth pair of terminal cirri; there are no caudal appendages (= furca) on apygophoran acrothoracicans.

The present finding of a *Tomlinsonia* species in the Philippines extends the distribution of the genus considerably from the type locality of *T. asymetrica* in Madagascar and represents the first report of this genus in the northern hemisphere. Such an amphitropical distribution is also seen in *Trypetesa* and may reflect a relictual distribution of the entire family (cf. Newman 1979).

The proportions of the terminal cirri segments in *Tomlinsonia mclaughlinae* n. sp. are quite different from those reported in *T. asymetrica*. In *T. mclaughlinae* n. sp. the first two segments are subequal in width and the distal two segments are much thinner, while the first and third segments are nearly as long as each other with the second and fourth segments being approximately 1/2 the length of first and third. In *T. asymetrica*, the first three segments are all about as wide and as long as each other, while only the fourth segment is shorter (although not 1/2 as long) and thinner. The existence of a pair of bifid terminal hooks and superior spine (Fig. 5A) has not been previously reported in trypetesids.

The shape of the labrum differs between the two species of *Tomlinsonia* with *T. asymetrica* having a gently rounded medial margin between the terminal produced lobes while the same area in *T. mclaughlinae* n. sp. is subquadrate. In *T. asymetrica* the thinner terminal lobe is longer than the broader lobe, whereas in *T. mclaughlinae* n. sp. the broader lobe nearly extends as far as the thinner one.

There are also some differences between the mouthparts of the two *Tomlinsonia* species. The mandible of *T. mclaughlinae* n. sp. is more acutely tapered than that of *T. asymetrica* and lacks the distal small spine; maxilla II of *T. mclaughlinae* n. sp. is also more acutely tapered than that of *T. asymetrica*, while the maxilla I is more regularly ovate and possesses a stout inner setae that is lacking in *T. asymetrica*.

It is difficult to compare the various denticules on the inner and outer opercular bars of *T. mclaughlinae* n. sp. with those of *T. asymetrica*, as Turquier & Carton (1976) described and figured only those from certain portions of the opercular bars. However, the basic form of ovate denticules with simple to multifid tips can be seen in both species. The dense rows of denticules found on the inner opercular bars dorsal to the ridges are similar to those reported for *Trypetesa spinulosa* Turquier, 1976 (see Turquier 1978: pl. 3, fig. 4) but are more densely packed and with typically four or five denticular blades on a single shaft as compared to typically two or three in *T. spinulosa*.

Ecology

The prevalence of *Tomlinsonia mclaughlinae* n. sp. ranged from 0.45 to 7.94% in the samples from the Philippines (overall prevalence = 3.2%, n = 981 hermit crabs collected during 1997 and 1999). The species is known to be associated with the three most common species of hermit crabs (*Calcinus gaimardii* [n = 14], *C. latens* [n = 16], and *C. minutus* [n = 1]) from the coral reef areas sampled in the Philippines (Williams 2002). Of the 31 *Tomlinsonia mclaughlinae* n. sp. specimens examined all but one was found associated with female hermit crabs; 15 of these females were ovigerous (50%). Although the sex-ratios of the hermit crabs did not significantly differ from 50:50 (χ^2 [n = 325] = 1.63, P = 0.2, df = 1], the distribution of the barnacles among the two most common hermit crabs was significantly different than predicted values (χ^2 [n = 14] = 10.29, P = 0.001, df = 1; this and previous χ^2 test based on a subset of the 1999 collections for which the sex of all hermit crabs was recorded). *Tomlinsonia mclaughlinae* n. sp. has been found in six species of gastropod shells (most commonly *Drupella cornus*). No shells were found to harbor more than one *Tomlinsonia* individual, although other species of boring barnacles (such as members of the genera *Trypestesa* and *Weltneria* Berndt, 1907) were found in the same shells as those occupied by *T. mclaughlinae* n. sp. The position of the barnacle in the columella and general body shape of *T. mclaughlinae* n. sp. are similar to that of *T. asymetrica* and *Trypetesa nassarioides* Turquier, 1967 in conforming to the helical spiral of the columella. The aperture of *T. mclaughlinae* n. sp. is oriented so that the ventral, tapered end of the slit is facing the apex of the gastropod shells, often too far inside the shell to be detected until cracked. *Tomlinsonia mclaughlinae* n. sp. is apparently an obligate commensal of hermit crabs and is the seventh known species of extant trypetesid associated with hermit crab hosts (Williams & McDermott 2004). Additional trypetesids are known from the fossil record based on their borings in shells (Lambers & Boekschoten 1986; Baluk & Radwánski 1991).

The feeding biology of *Tomlinsonia* and *Trypetesa* remains largely unknown. Tomlinson (1987) suggested the reduced cirri of the barnacles could not be extended outside the aperture and were only used for feeding on small particles brought in by pumping action of the thorax. However, Williams (1999, 2002) reported that an unidentified species of the genus *Trypetesa* was found to ingest the eggs or developing embryos of host hermit crabs from the

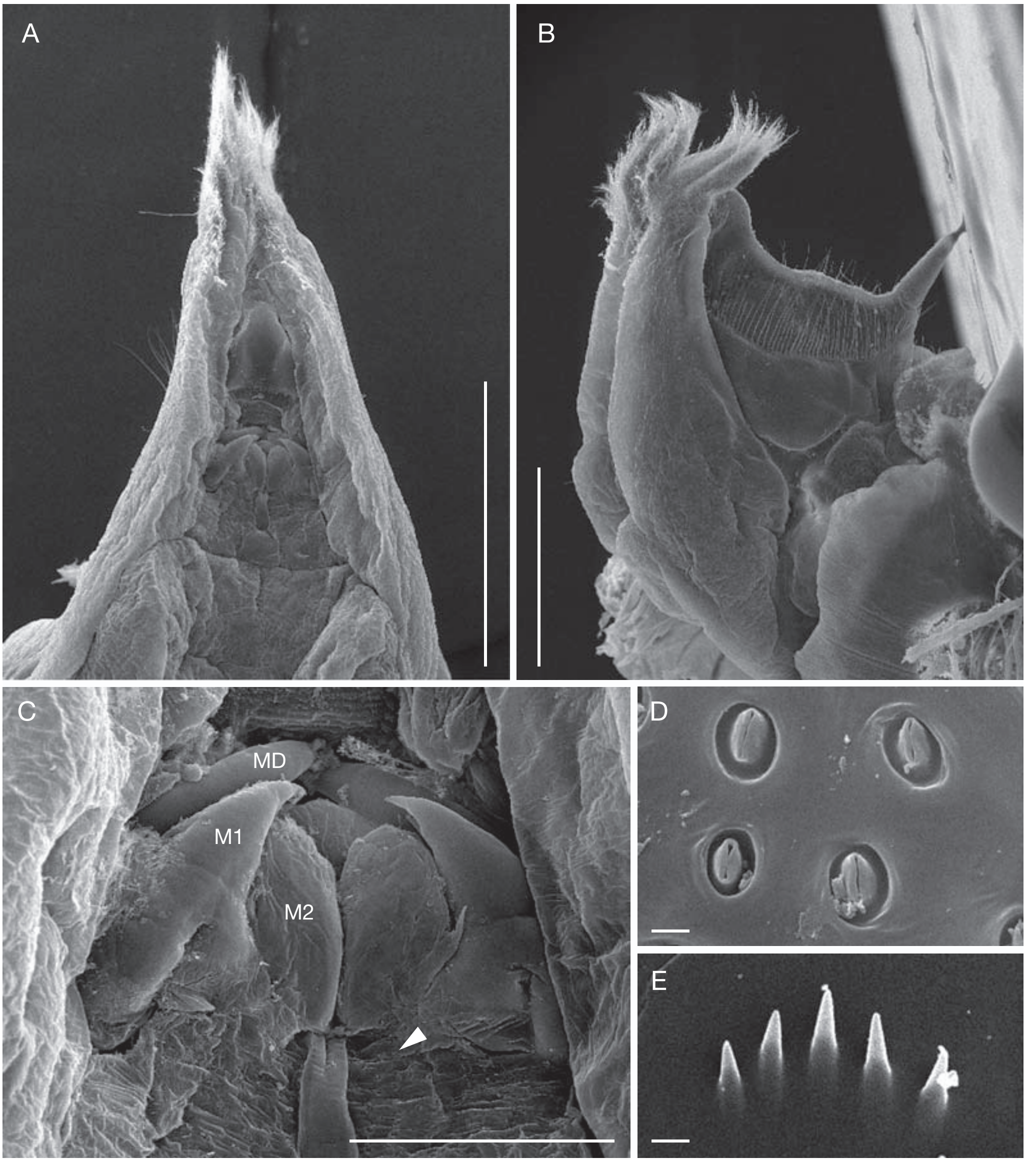

FIG. 6. — *Tomlinsonia mclaughlinae* n. sp., scanning electron micrographs: **A**-**C**, paratype ♀ (USNM 1084104); **A**, mouth cirri and mouthparts, dorsal view; **B**, mouth cirri and labrum, lateral view; **C**, maxillae and mandibles, position of stub setae at base of maxillae II shown by arrowhead; **D**, **E**, paratype ♀ 5.9 mm (USNM 1084106); **D**, stub setae; **E**, denticules of maxilla II. Abbreviations: **MD**, mandible; **M1**, maxilla I; **M2**, maxilla II. Scale bars: A, B, 500 µm; C, 100 µm; D, 5 µm; E, 2.5 µm.

Philippines. Based on its position within the shell and proximity to eggs or embryos attached to the pleopods of host hermit crabs (similar to that seen in *Trypetesa* sp. from the Philippines), *Tomlinsonia mclaughlinae* n. sp. may also be an egg predator. Among the present samples of *T. mclaughlinae* n. sp. there is no direct evidence (e.g., egg corions from host hermit crabs identified within the stomach of the barnacles) for this behavior. However, the body of some specimens contained material that was the same coloration as host hermit crab eggs and the barnacles were found predominately with female hermit crabs. Since gonadal tissue of the barnacles could be confused with ingested eggs or embryos of the hosts, histological examination of newly collected specimens needs to be completed to determine if the new species is an egg predator. The barnacles might also gain food in the form of dropped food particles by the crab, materials brought in by the respiratory currents, and/or fecal material of the crab (Baluk & Radwánski 1991; Williams & McDermott 2004), or even the consumption of other symbionts or their offspring in gastropod shells inhabited by hermit crabs. Although egg predation would in large part explain the blind gut of trypetesids, how they are able to capture host eggs and what they feed on while inhabiting shells with male hermit crabs remains unknown.

Tomlinsonia mclaughlinae n. sp. produce fairly large broods of eggs (estimated at *c.* 100+ eggs) that are 186 ± 5 µm in length and 145 ± 7 µm in width (n = 10). The eggs appear to hatch as nauplii as evidenced by this stage found in the mantle cavity of some specimens of *Tomlinsonia mclaughlinae* n. sp.

Order ISOPODA Latreille, 1817
Suborder EPICARIDEA Latreille, 1831
Superfamily CRYPTONISCOIDEA Kossmann, 1880
Family HEMIONISCIDAE Bonnier, 1900
Genus *Hemioniscus* Buchholz, 1866

Hemioniscus pagurophilus n. sp.
(Figs 7-9)

TYPE MATERIAL. — **Philippines.** Bataan, Morong, 14°41'N, 120°16'E, in *Tomlinsonia mclaughlinae* n. sp. from shell of *Cantharus undosus* inhabited by ♀ *Calcinus gaimardii*, 25.IV.1999, ♂ holotype 1.0 mm (USNM 1084119), 1 ♂ paratype (ZRC 2006.0006); in *Tomlinsonia mclaughlinae* n. sp. from shell of *C. undosus* inhabited by ♀ *C. gaimardii*, 25.IV.1999, 5 ♂♂ paratypes (USNM 1084120). — Oriental Mindoro, Puerto Galera, Big Lalaguna Beach, 13°30'N, 120°57'E, in *Tomlinsonia mclaughlinae* n. sp. from shell of *Peristernia incarnata* inhabited by ovigerous ♀ *C. gaimardii* (3.8 mm SL), 21.VII.1997, immature ♀ allotype 0.9 mm (USNM 1084121), 2 immature ♀♀ paratypes (USNM 1084122), 2 ♂♂ paratypes 0.86 mm (USNM 1084123; 1 on SEM stub, 1 in alcohol).

ADDITIONAL MATERIAL EXAMINED. — **Philippines.** Bataan, Morong, 14°41'N, 120°16'E, in *Tomlinsonia mclaughlinae* n. sp. from shell of *Cantharus undosus* inhabited by ♀ *Calcinus gaimardii*, 25.IV.1999, 1 ♂ (JDW personal collection).

ETYMOLOGY. — From the Greek, *pagouros* (= kind of crab) and *philos* (= who loves), latinized as *pagurophilus*, and meaning lover of hermit crabs. The name refers to the role played by the isopod in sterilizing the cirripede and therefore helping hermit crabs by avoiding weakening of their shells by the barnacle and for the inordinate fondness for paguroids by Patsy A. McLaughlin, the best friend a hermit ever had.

DISTRIBUTION. — Found in the mantle cavity of *Tomlinsonia mclaughlinae* n. sp., in shells of *Calcinus gaimardii* hermit crabs from Bataan and Oriental Mindoro provinces, central Philippines; shallow subtidally (< 5 m).

DIAGNOSIS. — Male: cuticular surface with distinct striations, prominent on coxal plates. Head widest at posterolateral junction with pereomere 1, eyes present. Antennule of three articles, basal article with seven teeth and cuticular scale-like ridges, article 1 overlapping basal article of antenna. Antennae of nine articles, articles 1-3 cylindrical with cuticular ridges; flagellar articles much narrower than peduncular articles, proximal flagellar article longest, flagellar articles 2-5 of approximately equal length. Oral cone anteriorly directed. Pereomeres 5 and 6 broadest. Body pigmentation lacking. Pereomeres with entire coxal plates. Pereopods 1 and 2 stout, gnathopodal, with dactyli entire; propodus smooth; ventral surfaces of carpus and merus with large flat cuticular ridges. Pereopods 3-7 ambulatory, smooth; dactyli long, straight, slender, smooth margins, with ventral setal comb, tip hooked with long (pereopods 3-5) or short (pereopods 6, 7) seta at base of hooked tip; propodi straight, medially inflated (pereopods 3-5 broader than 6 and 7), with ventral setal comb. Pleon with five pleopods. Ventral abdominal lobe between first pair of pleopods with two lateral projections and median smooth concave margin. Pleotelson quadrangular, endopods approximately twice as long as exopods.
Immature female with posterior four pleon segments fused with lateral undulations.

DESCRIPTION

Male (Figs 7A, B, D; 8; 9)

Length 1.00 mm, maximum width 0.33 mm at pereomere 4, head length 0.12 mm, pleon length 0.44 mm (holotype); body tear-drop-shaped

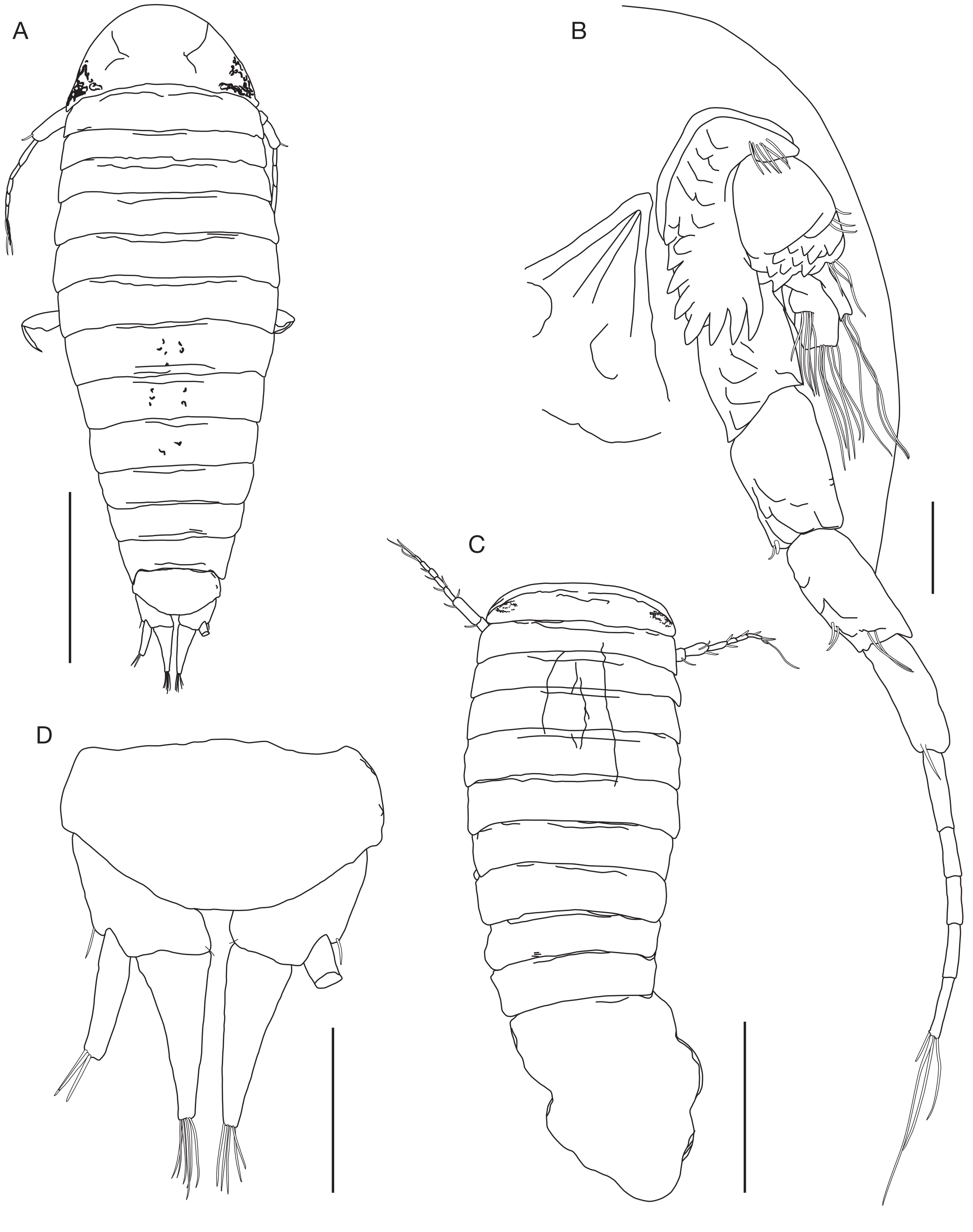

FIG. 7. — *Hemioniscus pagurophilus* n. sp.: **A**, **B**, holotype ♂ 1.0 mm (USNM 1084119); **A**, male dorsal view; **B**, left antenna, antennule and oral cone; **C**, allotype ♀ 0.90 mm (USNM 1084121), immature female dorsal view; **D**, holotype ♂ 1.0 mm (USNM 1084119), pleotelson, dorsal view. Scale bars: A-C, 250 µm; D, 50 µm.

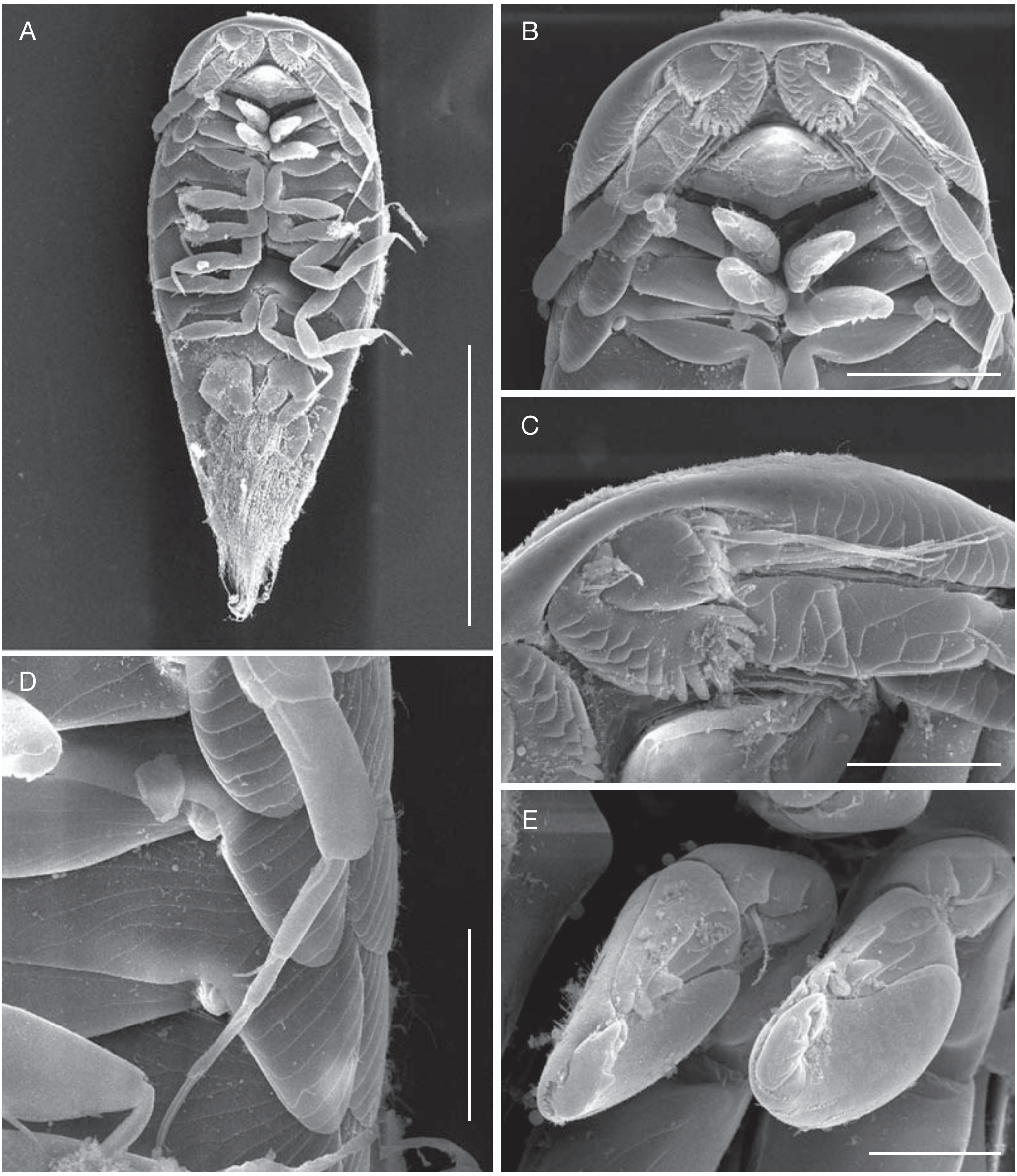

FIG. 8. — *Hemioniscus pagurophilus* n. sp., paratype ♂ 0.86 mm (USNM 1084123), scanning electron micrographs: **A**, male ventral view; **B**, anterior end, ventral view; **C**, left antennule and base of antenna; **D**, coxal plates of pereomeres 1-3, right side; **E**, right pereopods 1 and 2. Scale bars: A, 400 µm; B, 100 µm; C, D, 50 µm; E, 20 µm.

(Figs 7A; 8A). Cuticular surface with distinct striations, prominent on coxal plates (Fig. 8C, D).

Head anterior margin ovate, posterior margin concave, widest at posterolateral junction with pereomere 1 (Fig. 7A). Eyes diffuse, moderately large (approximately 40 µm in maximal length) located proximolaterally, eyes with irregular pigment most prominent around laterally directed edge (Fig. 7A). Antennule of three articles (Figs 7B; 8B, C), first (basal) article with seven teeth approximately three times longer than broad, cuticular scale-like ridges present, most prominent on mesial margin, proximolateral lobe distally tapered with group of setae along sinuous cuticular ridge; article 1 slightly overlapping basal article of antenna, article 2 with cuticular scale-like ridges along distal margin, 4-6 setae on distal margin, article 3 with two flagella and bundle of aesthetascs (Figs 7B; 8C). Antennae of nine articles (four peduncular and five flagellar) (Fig. 7B); articles 1-3 cylindrical with cuticular scale-like ridges (Fig. 8C); flagellar articles much narrower than peduncular articles, each with a terminal seta, proximal flagellar article longest, flagellar articles 2-5 of approximately equal length, article 5 with four distal setae (Fig. 7B). Oral cone anteriorly directed (Figs 7B; 8B).

Pereomeres 5 and 6 broadest, tapering anteriorly and posteriorly. Body pigmentation lacking. Pereomeres with entire (not toothed) coxal plates 1-7 (Fig. 8B, D). Pereopods 1 and 2 short and stout, gnathopodal with dactyli entire (non-bifid) and having few large cuticular scale-like ridges and rows of minute setae on dorsal edge (Fig. 8E); propodus smooth with few rows of short setae distodorsally, rows of minute setae along distal edge of propodus around joint with dactylus, with setae along edge apposed to dactylus; ventral surfaces of carpus and merus with large flat cuticular scale-like ridges and few long setae (Fig. 8E). Pereopods 3-7 ambulatory, smooth; dactyli long, straight, slender, smooth margins, with ventral setal comb, tip hooked via ventral indentation of margin with long (pereopods 3-5) or short (pereopods 6, 7) seta at base of hooked tip (Fig. 9A, B); propodi straight, medially inflated (pereopods 3-5 broader than 6 and 7), with ventral setal comb and one large stout ventral seta approximately 1/2 (pereopods 3-5) or 1/3 (pereopods 6 and 7) from distal margin and second single smaller seta near junction with dactylus (Fig. 9B); carpi of pereopods 3-7 with one stout terminal ventral seta; meri with one thin terminal ventral seta.

Pleon with five pleopods composed of basis (sympod), exopod, and endopod (Fig. 9C). Sympods with two medially directed setae bearing 3-branched tips, endopods and exopods with plumose setae (five setae each on pleopod 1, three setae on endopod of pleopod 5), with laterally directed seta shorter than other setae on exopod. Ventral abdominal lobe between first pair of pleopods with two lateral projections and median smooth concave margin

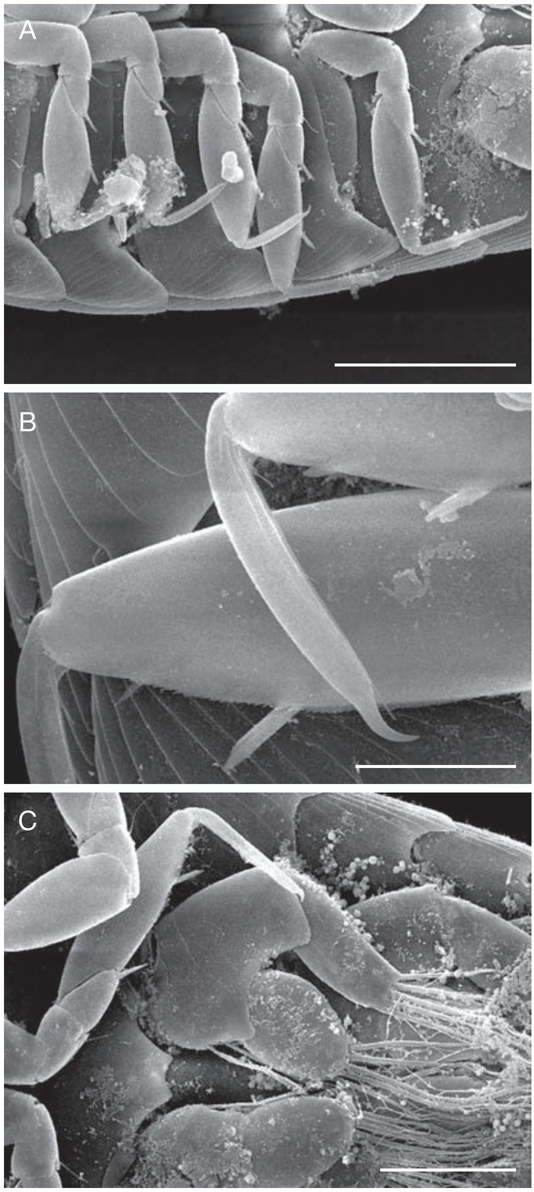

FIG. 9. — *Hemioniscus pagurophilus* n. sp., paratype ♂ 0.86 mm (USNM 1084123), scanning electron micrographs: **A**, right pereopods 3-7; **B**, propodi and dactyli of right pereopods 5 and 6; **C**, left pleopod 1. Scale bars: A, 100 µm; B, 20 µm; C, 50 µm.

(Fig. 9C). Pleotelson quadrangular, endopods approximately twice as long as exopods, basis with one distolateral seta, endopods and exopods with terminal setae (Fig. 7D).

Immature female (Fig. 7C)
Maximal body length 0.90 mm, maximal width 0.31 mm at segment 4, pleon length 0.32 mm. Similar to male in dorsal aspect, except for fused posterior four pleon segments appearing as an irregular sac posteriorly on the body and with lateral undulations indicating position of pleomeres (Fig. 7C).

REMARKS
Identification of this material was hampered by the confused taxonomy of cryptoniscid isopods in general and that of barnacle parasites in particular (e.g., Nielsen & Strömberg 1965, 1973b). The following comparisons with all other species of cryptoniscoids known to parasitize barnacles were necessary to reach our conclusions.

Cryptothir Dana, 1852 (*incertae sedis*): the type species, *C. minutus* Dana, 1852, was incompletely described and figured (Dana 1852, 1855) from an Indo-West Pacific barnacle of the genus *Creusia* (material lost). It may be synonymous with *Hemioniscus* or at least belong to the Hemioniscidae (in which case the family would have to be called Cryptothiridae). However, as noted by Grygier (1993), it is probably best to leave *Cryptothir* as *incertae sedis* until such time as additional material can be examined.

Liriopsis Schultz *in* Müller, 1864 (Cryptoniscidae): the new material shows no resemblance to either *Liriopsis pygmaea* (Rathke, 1843) or *L. monophthalma* Fraisse, 1878. The most obvious difference is that the females of the new species are only posteriorly degenerated, while those of *Liriopsis* spp. are unsegmented and form a double lobed shape. Males of the new species have only moderately long dactyli on pereopods 6 and 7, whereas those of *Liriopsis* spp. are exceedingly long and thin.

Hemioniscus Buchholz, 1866 (Hemioniscidae): the males of the new species are similar to those of the type species *Hemioniscus balani balani* Buchholz, 1866 (see Goudeau 1967, 1970), but differ in that the coxal plates of *H. balani balani* have seven or eight teeth on the first plate, and four or five on posterior plates, while the new species has no teeth on any of the coxal plates. Other differences include strong cuticular striations on the anterolateral expansion of the basal antennule segment (weakly striated in *H. balani balani*), considerably shorter distal teeth on the basal antennular article in *H. pagurophilus* n. sp., medially inflated propodi on pereopods 3-5 (distally inflated in *H. balani balani*), pronounced indentation on the ventral margin near the tip of dactyli (no such indentation in *H. balani balani*), and ventral median lobe between first pair of pleopods with concave margin (trilobed in *H. balani balani*). Shared characters between *H. balani balani* and *H. pagurophilus* include: moderate striation of the dorsal cuticle, seven teeth on the basal article of the antennule (occasionally eight in *H. balani balani*), cuticular ridges on the second article of the antennule, moderate setation on the terminal article of the antennule, eyes present, cuticular ridges on the dactyli of the first two pereopods, and moderate dorsal expansion of the meri of the pereopods. The development of the females is essentially identical to that seen in *H. balani balani*. All of the differences cited above between *H. pagurophilus* n. sp. and *H. balani balani* are also true when comparing *H. pagurophilus* n. sp. and *H. balani japonica* Ogawa & Matsuzaki, 1985. The description of *H. balani japonica* is somewhat difficult to interpret, the line drawings are poor and Ogawa & Matsuzaki only compared their material with older descriptions of *H. balani balani* (e.g., Buchholz 1866; Sars 1899) and not with the more detailed studies (e.g., Goudeau 1967, 1970). Many of the purported distinguishing morphological characters between the subspecies (Ogawa & Matsuzaki 1985: table 1) do not allow for differentiation, as their information for variation in *H. balani balani* is incomplete. The two taxa do show quite different coxal plate formulae, and this suggests that they represent distinct species rather than subspecies. However, in the absence of specimens of *H. balani japonica*, we are unwilling to make any definite opinion on the matter and retain the two taxa as subspecies for the present. The only other species ever placed in this genus was *H. socialis* Pérez, 1900, which is now considered a synonym of *H. balani balani* (Caullery 1908). This genus is the type of Hemioniscidae Bonnier, 1900.

Leponiscus Giard, 1887 (Hemioniscidae): Giard (1887) did not select a type species from the two he included in this genus. *Leponiscus anatifae* Giard, 1887 was described by reference to the figures of the unnamed taxon reported by Hesse (1867), and is an available name; *L. pollicipedis* Giard, 1887 was accompanied by neither description nor illustration and is a *nomen nudum*. The type species of the genus must therefore be *L. anatifae*. Unfortunately, the figures of Hesse (1867) show no clear characters to distinguish *L. anatifae* from *Hemioniscus* spp. and *Leponiscus* must be considered *inquirenda* within the Hemioniscidae. Gruvel (1901) described the only other species of *Leponiscus*, *L. alepadis*, but it differs markedly from *L. anatifae* and appears to belong in the Crinoniscidae (see below). Gruvel (1902) also cited "*Leponiscus hessei* Giard" but as Giard never mentioned such a name, it is presumed that *L. hessei* is a lapsus for *L. pollicipedis*, which was not cited by Gruvel (1901, 1902). The conclusions of Bocquet-Védrine & Bocquet (1972) that *Leponiscus* Giard, 1887 is a *nomen nudum*, and that the taxon is valid from Gruvel (1901) (with *L. alepadis* as the type species) are clearly incorrect as one of the originally included species in *Leponiscus* Giard, 1887 is an available name. However, their statement that *L. alepadis* is actually allied to *Crinoniscus* was correct, and their suggestion that *Leponiscus* Giard, 1887 may be identical to *Hemioniscus* is a reasonable hypothesis, albeit an untestable one in the absence of lepadid cryptoniscid parasite material.

Crinoniscus Bonnier, 1900 (Crinoniscidae): the new material does not resemble the type and sole species *Crinoniscus equitans* (Pérez, 1900), the only species currently placed in the family (Pérez 1900a, b). Males of *C. equitans* lack teeth on the basal segment of the antennule and females metamorphose into a cross-shaped incubatory pouch. *Leponiscus alepadis* Gruvel, 1901 appears more closely related to *Crinoniscus* than either *Leponiscus* or *Hemioniscus* as the males also lack teeth on the basal antennular segment, and the females show complete metamorphosis. However, the female body shape of *L. alepadis* resembles an ovoid sac with small lobes at the corners, rather than the elongate cross of *Crinoniscus* suggesting that *L. alepadis* is not congeneric with *C. equitans* and requires its own genus (Boyko & Williams pers. obs.). Such action is outside the scope of this work.

Gorgoniscus Grygier, 1981 (unplaced): males of the new material differ from males of sole species of *Gorgoniscus*, *G. incisodactylus* Grygier, 1981, in the following: basal article of antennule with seven teeth (five in *G. incisodactylus*) and tapered proximolateral lobe (lobe lacking in *G. incisodactylus*), moderate cuticular striations on whole body (dense cuticular striations on head and first pereomere in *G. incisodactylus*), and dactyli of pereopods 6 and 7 with smooth margins (notched in *G. incisodactylus*). Females of *G. incisodactylus* are globose and lack most appendages and an obvious head, whereas immature females of the new species retain the anterior portion of the body as recognizably isopod-like. Grygier (1981) left *Gorgoniscus* unplaced as to family, suggesting that a new family might be required for it. This genus still remains unplaced, and no further specimens have been reported.

Scalpelloniscus Grygier, 1981 (?Hemioniscidae): males of both *S. penicillatus* Grygier, 1981, and *S. binoculis* (Menzies & George, 1972) differ from the new material in having toothed coxal plate formulae similar to that seen in *H. balani balani*, more setae on the third articles of the antennules, lack of cuticular ridges on the second article of the antennules, strongly dorsally inflated meri on the pereopods, and lack of eyes. Mature females of *Scalpelloniscus* are unknown. Based on the current classification scheme, *Scalpelloniscus* appears to belong to the Hemioniscidae rather than the Cryptoniscidae, but all the families of Cryptoniscoidea need clearer diagnoses and mature females are needed for *Scalpelloniscus* to determine the degree and form of their metamorphosis.

In conclusion, examination of the new species of cryptoniscid from the *Tomlinsonia* hosts indicates that they are best placed in the Hemioniscidae, and are rather close to *Hemioniscus balani balani*. There are at least as many differences between our Philippine material and *H. balani balani* as between *Hemioniscus* and *Scalpelloniscus*. However rather than erect a new genus for this new species, we have conservatively placed it within *Hemioniscus* as the males share many characters with those of the type species, and differ most obviously only in the dentition of the coxal plates, a variable feature in other cryptoniscoid families as currently defined. The females of *H. balani balani* and

H. pagurophilus n. sp. have very similar development with nearly identical degeneration of the posterior segments into an irregularly shaped incubatory pouch, while retaining the anterior segments in unmodified form. In order to include the new species in *Hemioniscus*, it becomes necessary to modify Nielsen & Strömberg's (1973b) definition of Hemioniscidae as follows: dorsal cuticular ridges relatively prominent; eyes present; basal segment of antennule with seven or eight teeth on distal margin; oral cone anteriorly directed; coxal plates with or without toothed ventral margins; posterior margin of pleotelson entire; parasitic on cirripedes. This definition is acknowledged to be a temporary one, as it is certain that future phylogenetic analyses of cryptoniscoid isopods will result in rearrangement of genera based on shared derived characters rather than shared host taxa.

ECOLOGY

Of the 31 potential host barnacles examined during 1997 and 1999, three were found to harbor *Hemioniscus pagurophilus* n. sp. (total prevalence = 9.7%); numbers of isopods within the mantle cavity of the hosts ranged from two to six. Interestingly, numerous specimens of an unidentified species of *Trypetesa* from the same localities were not found parasitized by *H. pagurophilus* n. sp.

Acknowledgements

Our thanks to Drs Jens Høeg (University of Copenhagen), William Newman (Scripps Institute of Oceanography, USA) and Roland Bourdon (France) for very helpful comments on the manuscript. Financial support from Hofstra University to JDW is greatly appreciated.

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Submitted on 14 October 2005;
accepted on 20 January 2006.