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PHOLADICOLA INTESTINALIS, NEW GENUS AND SPECIES, A CLAUSIDIID COPEPOD PARASITIC IN A DEEP-BURROWING CLAM FROM TEXAS

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ABSTRACT

Pholadicola intestinalis is described based on specimens taken from the intestine of the deep-burrowing pholad clam, *Cyrtopleura costata* (Linné, 1758), collected in the Galveston Bay Estuary, Texas. The new form is closely affiliated with *Leptinogaster*; however, it can be distinguished from this and other genera of Clausidiidae by having (1) a modified body, (2) both caudal ramus and leg 5 modified into a fleshy process, (3) a ventrally located attachment area for the egg sac, (4) the absence of the maxilliped in the female (represented by a small sclerite) and (5) structurally reduced spines and setae on all legs. This is the first record of a clausidiid copepod living as an internal parasite.

Until the discovery of the family Erebonasteridae from deep-sea hydrothermal vents (Humes, 1987), copepods of the family Clausidiidae were considered to be the most primitive forms of the order Poecilostomatoida (Gooding, 1963; Ho, 1984). The primitiveness of the Clausidiidae is chiefly exhibited in the structure of the antenna (being 4-segmented) and legs (with 3-segmented rami in legs 1 to 4, and with 2 free segments in leg 5), and in the armature of the mandible (tipped with 2 or 3 accessory elements) and leg 1 (with an inner spine on the basis). In the present paper, we describe an unusual clausidiid that exhibits many derived character states, but at the same time retains all of the above-mentioned primitive features of the family.

Although clausidiids, particularly members of the genus *Hemicyclops*, are occasionally found in plankton samples, they are generally regarded as a family of symbiotic copepods living in close association with various marine invertebrates, including sponges, alcyonarians, scleractinians, polychaetes, sipunculans, echiurans, vestimentiferans, gastropods, bivalves, and crustaceans (Ho, 1991). The new clausidiid described in the present report is remarkable in that it is an intestinal parasite of the angelwing clam, *Cyrtopleura costata* (Linné, 1758). *C. costata* is a deep-burrowing pholad inhabiting sand-mud substrates from New England to Brazil (Abbott, 1974). This clam is common along the shores of the lower part of the Galveston Bay Estuary in intertidal mud flats adjacent to *Spartina* marshes. Only clams (*C. costata*) from this part of the Texas coast have been examined for the present study.

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MATERIALS AND METHODS

Specimens of the host clam, *Cyrtopleura costata*, were collected from intertidal mudflats by shovel from waters ranging in salinity from 16 to 32‰. The shell length of each specimen was measured to the nearest millimeter along the anterior-posterior axis. The viscera of each clam were removed from the shell, rinsed externally with 25‰ sterile seawater and serially sectioned at 3- to 4-mm intervals. Sections of viscera were isolated individually in 25‰ seawater and examined microscopically against a dark background for the presence of copepod parasites.

Copepods were removed by pipette and stored in 70% alcohol. Of the 47 specimens of clams examined between 18 December 1989 and 3 February 1991, copepod parasites were found in the digestive tracts of 28 clams (60% incidence of infection). The number of intestinal parasites in infected clams ranged from 1 to 16, with an average of 3 specimens per infected host.

Of the 83 specimens of new parasites encountered, only 7 were male; 5 of the 76 females were in the 5th copepodid stage and another 2 in the 4th copepodid stage. The copepods were cleared and measured in lactic acid. The wooden-slide method developed by Humes and Gooding (1964) was employed to study the morphology of the copepods. All drawings were made with the aid of a camera lucida. Holotype female (USNM 254508), allotype male (USNM 254509), and 15 paratypes (USNM 254510; 10 females and 5 males) have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

We studied the clams (*Cyrtopleura costata*) for parasites that ranged in size (shell length) from 68 to 125 mm, with an average length of 100 mm. The 28 infected clams ranged in length from 76 to 121 mm with a mean length of 103.5 mm. The sex ratio of the 47 clams examined was 17 males to 30 females (1 to 1.8). That of clams infected with the copepod parasite was 11 males to 17 females (1 to 1.6).

Pholadicola new genus

Diagnosis.—Clausidiidae. Body modified. Urosome indistinctly 5-segmented in female, 6-segmented in male. Caudal ramus fleshy, elongated. Antennule 6-segmented. Antenna 4-segmented, third segment with large outer claw and terminal segment, 3 terminal claws. Labrum with pointed posteroventral edge. Mandible with spinulose process and 2 pectinate plates. Maxillule with 5 setae. Maxilla 2-segmented, terminal segment claw-like and bearing 1 seta. Maxilliped absent in female, 4-segmented in male. Legs 1–4 biramous with 3-segmented rami. Leg 5 fleshy, elongate; unsegmented in female, 2-segmented in male.

Type Species.—*Pholadicola intestinalis* new species.

Etymology.—The generic name is a combination of "Pholad," the common name of the family to which the host clam belongs, and the Latin "cola" (=to dwell).

Pholadicola intestinalis new species
Figures 1A–L, 2A–I, 3A–H

Female.—Body (Fig. 1A) elongate and modified, 3.02–4.18 mm in length. Somites of prosome about equal in width. Urosome indistinctly 5-segmented. Fifth pediger about as wide as previous pedigers but genital complex and abdominal somites distinctly narrower. Anal somite about one-third length of first abdominal somite. Attachment area of egg sac (Fig. 1B) located in anterior region of genital complex on ventrolateral surface. Caudal ramus modified into fleshy process carrying 4 minute setae close to pointed tip (see enlarged part in Fig. 1A). Egg sac (Fig. 1A) long, with many rows of small eggs about 52 μm in diameter.

Rostral area (Fig. 1C) weakly developed. Patch of denticles on ventral surface of cephalosome posterolateral to bases of antennae (Fig. 1C). Antennule (Fig. 1D) indistinctly 6-segmented; armature on these segments: 5, 13, 9, 4, 2 + 1 aesthete, and 7 + 1 aesthete. Antenna (Fig. 1E) 4-segmented and strongly prehensile. First segment largest, with distal seta. Second segment with lateral seta just beyond midlength. Third segment with large terminal, denticulate, clawlike spine, small seta on subterminal papilla, and outer marginal row of denticles. Fourth segment smallest, tipped with 1 seta and 3 denticulate, clawlike spines.

Labrum (Fig. 1C) with medially pointed posteroventral edge. Mandible (Fig. 1F) tipped with 1 spinulose process and 2 pectinate plates. Maxillule (Fig. 1G) with 5 setae in 2 groups: 3 posterior and 2 terminal. Maxilla (Fig. 1H) large, 2-segmented; distal segment clawlike and bearing 1 seta. Maxilliped extremely reduced (represented by a small sclerite) or absent. Oral area with 2 pairs of fleshy lobes located between members of paired oral appendages (Fig. 1C).

Legs 1–4 (Fig. 1I, J, K, L) biramous with 3-segmented rami. Spines and setae

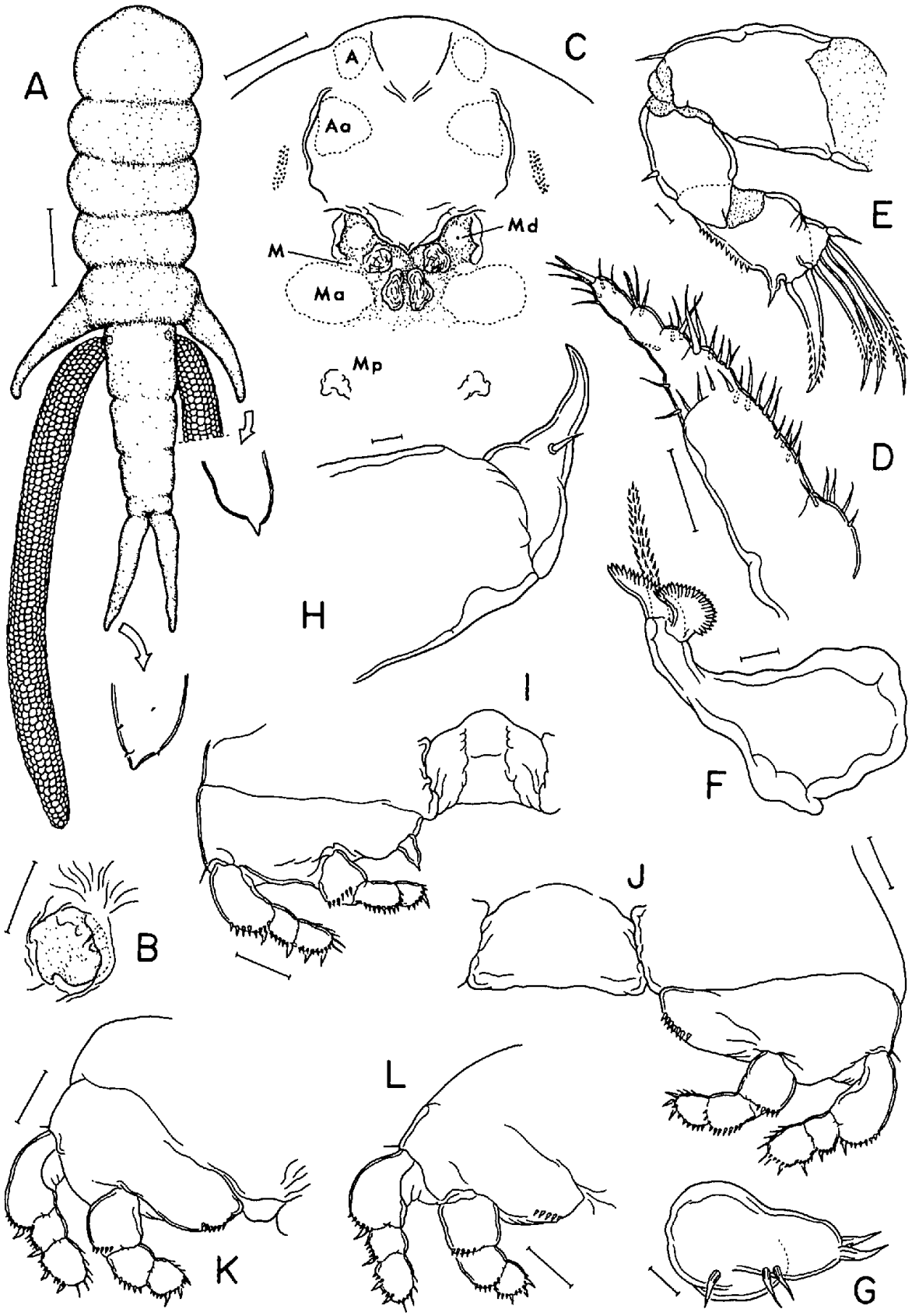

Figure 1. *Pholadicola intestinalis* new genus, new species. Female: A, habitus, dorsal; B, attachment area of egg sac, ventral; C, cephalothorax showing vestiges of maxillipeds (Mp), with antennules (A), antennae (Aa), mandibles (Md), maxillules (M), and maxilla (Ma) removed, ventral; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I, leg 1; J, leg 2; K, leg 3; L, leg 4. Scale bars: 0.5 mm in A; 0.05 mm in B, D, I–L; 0.1 mm in C; 0.01 mm in E–H.

on all rami greatly reduced. Armature (Roman numerals indicating spines, Arabic numerals representing setae) as follows:

Leg 1	Prp	0-0;	1-I	Exp	I-0;	I-0;	II, 5
				Enp	0-0;	0-0;	I
Leg 2	Prp	0-0;	1-0	Exp	I-0;	I-0;	II, 6
				Enp	0-0;	0-0;	III, 3
Leg 3	Prp	0-0;	1-0	Exp	I-0;	I-0;	II, 6
				Enp	0-0;	0-0;	III, 3
Leg 4	Prp	0-0;	1-0	Exp	I-0;	I-0;	II, 4
				Enp	0-0;	0-0;	III

Intercoxal plates weakly developed in leg 1 (Fig. 1I) and leg 2 (Fig. 1J), lacking entirely in leg 3 (Fig. 1K) and leg 4 (Fig. 1L). Leg 5 modified into large, fleshy process with terminal tooth (Fig. 1A). Leg 6 (Fig. 1B) represented by a small seta and knob in attachment area of egg sac.

Male.—Body (Fig. 2A) elongated with distinct segmentation, 2.41–3.56 mm in length. Cephalothorax with maximum width of 0.74–0.86 mm. Urosome (Fig. 2B) 6-segmented. Genital area (Fig. 2C) without seta or spine. Caudal ramus (Fig. 2D) modified into a long fleshy process, bearing 1 outer seta at midlength, 4 subterminal setae and 1 terminal blunt spine.

Rostrum, antennule, antenna, labrum, mandible, maxillule, maxilla, and 2 pairs of fleshy lobes in oral region as in female. Maxilliped (Fig. 2E) 4-segmented. First segment with 1 long inner seta. Second segment with medial surface having proximal protrusion bearing 2 small setae located between 2 patches of denticles. Third segment smallest, partly fused to fourth segment, which is a claw bearing 2 setae.

Legs 1–4 not as reduced as in female. Armature as follows:

Leg 1	Prp	0-0;	1-I	Exp	I-0;	I-1;	II, 5
				Enp	0-1;	0-1;	I, 5
Leg 2	Prp	0-0;	1-0	Exp	I-0;	I-1;	II, 6
				Enp	0-1;	0-2;	III, 3
Leg 3	Prp	0-0;	1-0	Exp	I-0;	I-1;	II, 6
				Enp	0-1;	0-2;	III, 3
Leg 4	Prp	0-0;	1-0	Exp	I-0;	I-1;	II, 5
				Enp	0-1;	0-1;	III, 2

Intercoxal plates of leg 1 (Fig. 2F) and leg 2 (Fig. 2G) with posteroventral corner protruded and bearing spinules. Leg 3 as in leg 2. Setae on rami of leg 4 (Fig. 2H) more reduced than those on previous 3 legs. Leg 5 (Fig. 2I) modified into fleshy process but, nevertheless, retaining 2-segmented appearance; each segment tipped with 1 seta. Leg 6 absent.

Fifth Female Copepodid.—Body (Fig. 3A) modified, measuring 2.38–2.67 mm in length. Urosome 5-segmented. Area of egg sac attachment not developed. Caudal ramus (Fig. 3C) armed as in fourth copepodid. Rostrum, antennule, antenna, labrum, mandible, maxillule, maxilla, 2 pairs of fleshy lobes in oral region, sclerite representing remnant of maxilliped, and legs 1–5 as in adult.

Fourth Female Copepodid.—Body (Fig. 3B) modified, measuring 1.37 and 1.41 mm in length. Cephalothorax relatively larger than succeeding metasomal somites.

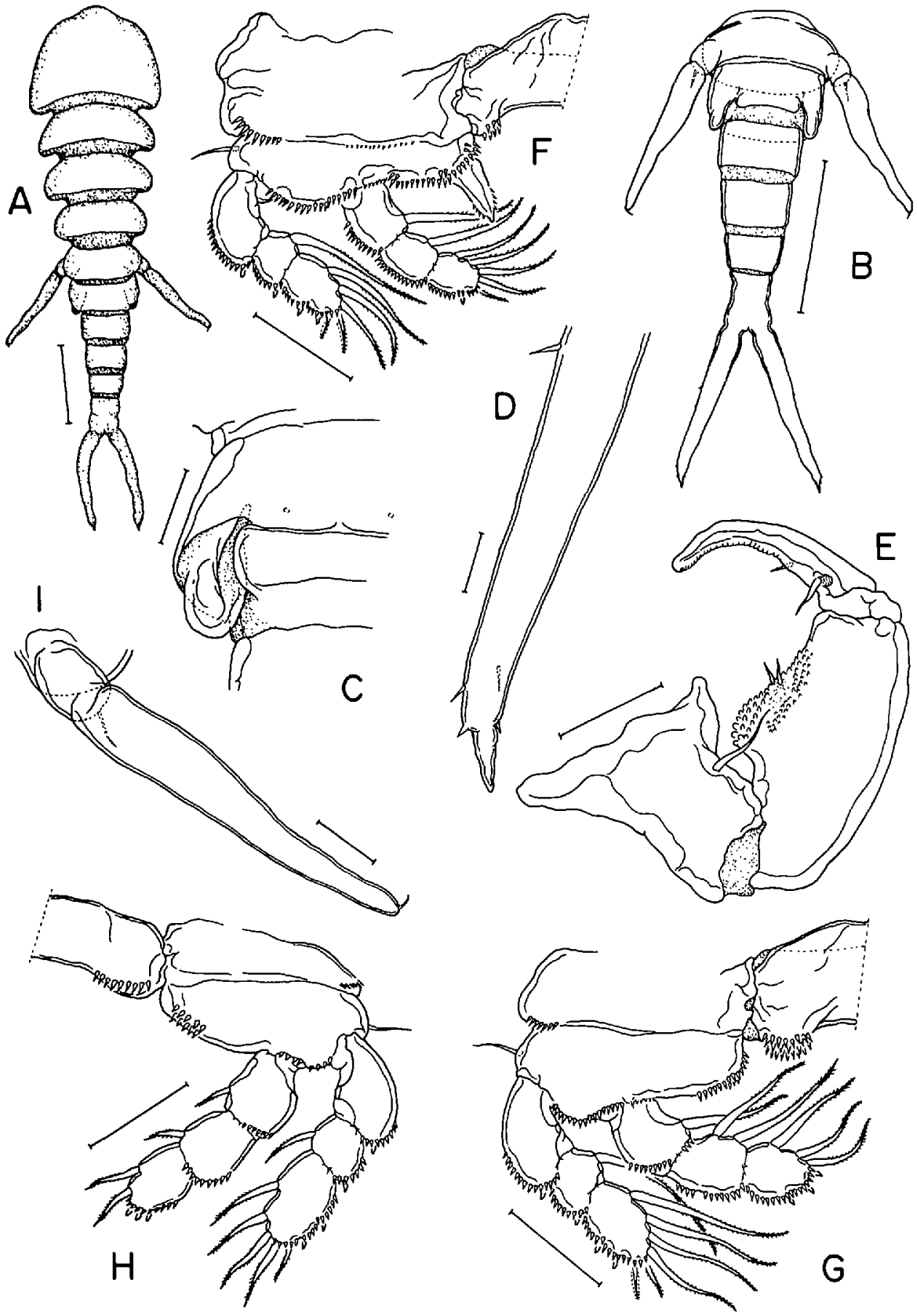

Figure 2. *Pholadicola intestinalis* new genus, new species. Male: A, habitus, dorsal; B, urosome, ventral; C, genital area, ventral; D, caudal ramus, ventral; E, maxilliped; F, leg 1; G, leg 2; H, leg 4; I, leg 5. Scale bars: 0.5 mm in A, B; 0.1 mm in C–I.

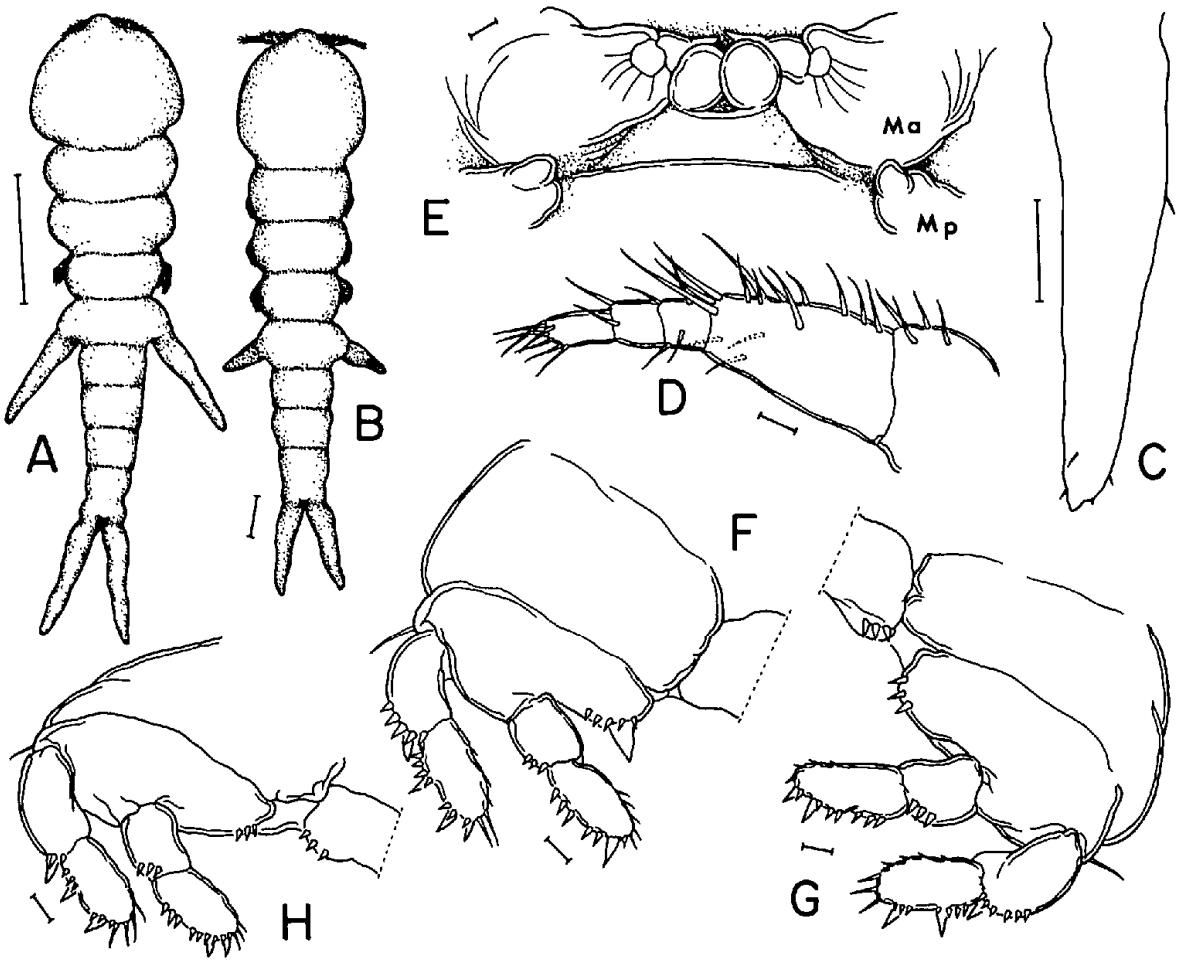

Figure 3. *Pholadicola intestinalis* new genus, new species. Female copepodids. Fifth copepodid: A, habitus, dorsal. Fourth copepodid: B, habitus, dorsal; C, caudal ramus, dorsal; D, antennule; E, postoral area showing maxillae (Ma) and rudimentary maxillipeds (Mp); F, leg 1; G, leg 2; H, leg 4. Scale bars: 0.5 mm in A, 0.1 mm in B, 0.05 mm in C, 0.01 mm in D–H.

Urosome 4-segmented. Caudal ramus (Fig. 2C) with 1 outer seta far separated from terminal armature of 4 setae and 1 conical knob. Rostrum, antenna, labrum, mandible, maxillule, maxilla, and 2 pairs of fleshy lobes in oral region as in fifth copepodid. Antennule (Fig. 3D) 5-segmented, armature on these segments: 4, 15, 4, 2, and 7. Maxilliped (Fig. 3E) extremely small, rudimentary, indistinctly 2-segmented. Legs 1–4 biramous with 2-segmented rami bearing reduced spines and setae. Armature as follows:

Leg 1	Prp	0-0;	1-I	Exp	I-0; III, 5
				Enp	0-0; I, 5
Leg 2	Prp	0-0;	1-0	Exp	I-0; II, 7
				Enp	0-0; II, 4
Leg 3	Prp	0-0;	1-0	Exp	I-0; II, 7
				Enp	0-0; II, 4
Leg 4	Prp	0-0;	1-0	Exp	I-0; II, 4
				Enp	0-0; II, 3

Intercoxal plate of leg 1 (Fig. 3F) without spines, but that of leg 2 (Fig. 3G) and leg 4 (Fig. 3H) bearing 3 spines on posteroventral corner. Leg 3 as in leg 2. Leg 5 (Fig. 3B) as in fifth copepodid, except shorter.

Etymology.—The specific epithet is from the Latin referring to the host organ (intestine) in which the new parasites were found.

Discussion

The 10 previously described genera of the Clausidiidae can be conveniently divided into two groups based on the number of antennular segments. The antennule is 7-segmented in *Clausidium* Embleton, *Hemicyclops* Boeck, and *Tychidion* Humes; and 6-segmented in *Conchyliurus* Bocquet and Stock, *Cotylomolgus* Humes and Ho, *Doviella* Rocha, *Hippomolgus* Sars, *Hyphalion* Humes, *Leptinogaster* Pelseneer, and *Myzomolgus* Bocquet and Stock. Having a 6-segmented antennule coupled with a maxilliped which is extremely reduced or lacking, the new genus *Pholadicola* seems to show a close affinity with *Cotylomolgus, Leptinogaster,* and *Myzomolgus* of the 6-segmented-antennule group. In lacking a sucker on the third segment of the antenna, *Pholadicola* can be considered most closely affiliated with *Leptinogaster,* since this sucker is present in both *Cotylomolgus* and *Myzomolgus.*

Currently, eight species of *Leptinogaster* are known, all of which have been reported as symbionts in the mantle cavity of bivalves. Causey (1953) found *L. major* (Williams) (listed as *Myicola major* Williams) from "*Pholas costata* L." [=*Cyrtopleura costata* (L.)] at Grant Isle, Louisiana and we have also found it in *Cyrtopleura costata* taken from the Galveston Bay Estuary. On five occasions we found *L. major* in the same host from which *P. intestinalis* was recovered. These two species are easily distinguished, since *P. intestinalis* has a modified body with large, fleshy caudal rami and leg 5, and with much reduced armature on legs 1–4. Besides, the body size differs greatly between the two cohabitants; an ovigerous *L. major* is only about the size of a *P. intestinalis* in its fourth copepodid stage.

According to Humes (1986), the fourth copepodid of *L. major* has, as described above for the same stage in *P. intestinalis,* a 4-segmented urosome, 5-segmented antennule, atrophied maxilliped, and 2-segmented rami in legs 1–4. The major difference between the two species at this stage is found, as in the adult, in the state of modification of the body, caudal ramus and leg 5. Therefore, the modification of the body and appendages in *P. intestinalis* must have occurred early in the copepodid stage.

In Poecilostomatoida the female copulatory pore and gonopore are generally found within a common genital aperture on the dorsolateral surface of the genital complex (genital double somite). However, these paired genital apertures are considered to have been ventrally located in the ancestral copepod (Boxshall et al., 1984) and it is only in the Order Poecilostomatoida that such an apomorphic dorsal migration is observed (Ho, 1990). Recently, Huys and Boxshall (1990) reported the discovery of the most primitive poecilostomatoid copepod yet known, *Centobnaster humesi,* collected from deep water (500 m) northeast of New Caledonia. One of the several primitive features of *C. humesi* enumerated by Huys and Boxshall is the location of the female genital openings. The copulatory pores of *C. humesi* are widely separated from their respective gonopores and are located in the midventral surface of the genital somite. In other words, in *C. humesi* the ancestral position of the copulatory pores is retained, while the gonopores have become shifted to an apomorphic dorsolateral position.

With regard to the position of female genital openings, *P. intestinalis* is even more primitive than *C. humesi.* Both copulatory pore and gonopore are located within a common aperture that is still situated on the ventral surface of the genital somite (Fig. 1A, B). This new information on the ventral location of the female

genital openings in primitive poecilostomatoids corroborates Ho's (1991) contention that the clade Paralubbockiidae-Oncaeidae-Clausidiidae-Erebonasteridae-Myicolidae contains the most primitive forms of Poecilostomatoida.

On three occasions during our study, a specimen of female *Mytilicola porrecta* Humes was found together with the new copepod in the host's intestine. This is a new record for *M. porrecta,* which is so far known only from Barataria Bay, Louisiana, in the ribbed mussel, *Geukensia demissa* (Dillwyn) (=*Modiolus demissus granosissimus* Sowerby), the hooked mussel, *Ischadium recurvum* (Rafinesque) (=*Mytilus recurvus* Rafinesque), an the northern quahog, *Mercenaria mercenaria* (Linné) [=*Venus mercenaria* (Linné)] (Humes, 1954). In one occasion, a 120-mm long clam was found to carry 2 *L. major* in the mantle cavity and 16 *P. intestinalis* plus 1 *M. porrecta* in its intestine.

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