

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/289677653>

# A new genus of the Clausidiidae (Copepoda: Poecilostomatoida) associated with a polychaete from Korea, with discussion of the taxonomic status of *Hersiliodes* Canu, 1888

Article in *Proceedings of the Biological Society of Washington* · June 2004

CITATIONS

8

READS

70

2 authors, including:



**Il-Hoi Kim**

Gangneung-Wonju National University

120 PUBLICATIONS 787 CITATIONS

[SEE PROFILE](#)

## A new genus of the Clausidiidae (Copepoda: Poecilostomatoida) associated with a polychaete from Korea, with discussion of the taxonomic status of *Hersiliodes* Canu, 1888

Ju-shey Ho and Il-Hoi Kim

(JSH) Department of Biological Sciences, California State University, Long Beach, California  
90840-3702, U.S.A., e-mail: jsho@csulb.edu;

(IHK) Department of Biology, Kangreung National University, Kangreung, Kangwondo, 210-702,  
Korea, e-mail: ihkim@kangnung.ac.kr

**Abstract.**—A new genus and new species of the Clausidiidae (Copepoda: Poecilostomatoida), *Hemadona clavicrura*, is described based on the specimens obtained from the washings of the polychaete, *Dasybranchus caudatus* Grube, collected from Namhae-do Island in Korea. The new genus is characteristic in having (1) the 3rd segment of the antenna drawn out to form a sharp claw, (2) a 3-segmented maxilliped in female, and (3) an armature formula of II-4 on the third endopodal segment of leg 1. Phylogenetic analysis on the genera of the Clausidiidae shows that *Hersiliodes* can not be relegated to a synonym of *Hemicyclops* as proposed in the recent past. It is a sister-taxon with the new genus, *Hemadoma*, and separated from *Hemicyclops* in having a 6-segmented antennule, an armature formula of II,4 on the distal segment of the endopod of leg 1, and a medial protrusion on the proximal segment of the male maxilliped. Interestingly, the phylogenetic analysis shows also that the three genera (*Conchylurus*, *Leptinogaster*, and *Pholadicola*) living in bivalve mollusks are monophyletic.

Poecilostome copepods of the family Clausidiidae are known to live largely in symbiosis with various marine invertebrates, such as alcyonarians, polychaetes, mollusks, and callianassid crustaceans. Currently, the family comprises nearly 80 species in 9 genera. One of its genera, *Hersiliodes* Canu, 1888, living in association with polychaetes and bivalves, has been considered almost impossible to separate from *Hemicyclops* Boeck, 1872 by Bocquet et al. (1963) and Vervoort & Ramirez (1966). Furthermore, Gooding (1963) as well as Humes & Huys (1992) had even advocated the doubtfulness of keeping the genus *Hersiliodes* as a valid taxon in the Clausidiidae. Nevertheless, in his book on the copepods associated with the marine invertebrates of the British Isles, Gotto (1993) treated *Hersiliodes* as a valid genus of the

Clausidiidae and, furthermore, in their report on a new species of *Hersiliodes* from Korea, Kim & Stock (1996) alleged that the genus differs from *Hemicyclops* in bearing a 6-segmented (instead of 7-segmented) antennule and an armature formula of II,4 (instead of I,5) on the third endopodal segment of leg 1. However, it should be pointed out that the former character state is also found in one (out of 38) species of *Hemicyclops* and the latter, in all nine species of *Conchylurus*.

Recently, one of us (IHK) discovered, during his general survey of the symbiotic copepods on Namhae-do Island in Korea Strait, a new genus and species of clausidiid associated with a polychaete. The new form carries, interestingly, some characteristic features of both *Conchylurus* and *Hersiliodes*. Thus, in this paper, in addition to de-

scribing this new clausidiid, a phylogenetic analysis of the ten genera of the Clausidiidae will be conducted to investigate the taxonomic status of the genus *Hersiliodes*.

### Materials and Methods

The polychaetes, *Dasybranchus caudatus* Grube (Capitellidae), were dug out from the mud flat and were placed in a plastic bag and fixed with 70% ethanol. Back at the laboratory, water was added into the bag containing the worm fixed in alcohol and then shaken hard to dislodge the copepods. The water together with the sediment and debris were examined under a dissection microscope for associated copepods. The copepods were removed and preserved in 70% ethanol. In studying the preserved copepods, the specimens were cleared in lactic acid, dissected on a wooden slide (Humes & Gooding 1964), and examined under a compound microscope. All drawings were made with the aid of a *camera lucida*. For formula of armature, "A" represents aesthete; Roman numeral, spine; and Arabic numeral, seta.

Seven genera were recognized by Humes & Huys (1996) in the family Clausidiidae. They are *Hemicyclops* Boeck, 1873; *Clausidium* Kossmann, 1874; *Hippomolgus* G. O. Sars, 1917; *Leptinogaster* Pelseneer, 1929; *Conchylurus* Bocquet & Stock, 1957; *Doviella* Rocha, 1986; and *Hyphalion* Humes, 1987. However, several changes have been made since then; two new genera (*Foliomolgus* Kim and *Pholadicola* Ho & Wardle) were added, respectively, by Kim (2001) and Ho & Wardle (1992), *Hersiliodes* Canu, 1888 was suggested to be resurrected by Kim & Stock (1996), and *Doviella* was relegated to a synonym of a clausiid genus by Ho & Kim (in press). Thus, including a new genus to be described below, there are now 10 genera in the Clausidiidae to be considered.

The data used in the character analysis to prepare for construction of a matrix were taken from the type species of each of the

10 clausidiid genera. Since Ho's (1992) phylogenetic analysis of the Poecilostomatoidea shows that Erebonasteridae Humes, 1987 occurs in sister-taxa relationship with a monophyletic clade comprising Clausidiidae + (Oncaeidae + Paralubbockiidae), Erebonasteridae was accordingly employed as an outgroup to polarize the 14 characters selected and also to root the cladogram(s) in reconstruction of the phylogeny. Although *Centobnaster* Huys & Boxshall, 1990 is generally considered the most primitive erebonasterid copepod (Huys & Boxshall 1990), some features in *Tychidion* Humes, 1973 were found to be even more primitive. Therefore, both *Centobnaster* and *Tychidion* were used as outgroup in the polarization of the selected characters shown in Appendix A. Also, in coding multistate characters, when a transformation series containing a single basal bifurcation (dichotomous transformation) was encountered, the method of "internal rooting" proposed by O'Grady & Deets (1987) was employed. In this case, as shown in Characters 3, 4 and 8 in Appendix B, the coding of "0" indicates apomorphy, not plesiomorphy.

The computer program HENNIG86 Version 1.5 (Farris 1988) was employed to analyze the phylogenetic relationships among the genera of the Clausidiidae. The command "ie\*" (implicit enumeration) was used to produce multiple, shortest trees through performance of exhaustive search and use all available tree space to find all shortest trees. In order to avoid predetermination of the topology of the resultant cladogram(s), all multistate characters were changed to nonadditive (unordered) before employing the command to reconstruct the phylogeny.

### Description

Order Poecilostomatoidea Thorell, 1859

Family Clausidiidae Embleton, 1901

*Hemadona*, new genus

*Diagnosis*.—Body elongate, 9-segmented in female and 10-segmented in male.

First pediger fused to cephalosome. Antennule short, 6-segmented, with 2nd and 3rd segments incompletely separated. Antenna 4-segmented, with 3rd segment (middle segment of endopod) drawn out into a large claw, distal segment tipped with 7 elements. Labrum well-developed. Mandible tipped with 2 large spiniform elements and 2 setae. Paragnath a lobe with spinules. Maxillule bilobate distally, both lobes tipped with setae. Maxilla 2-segmented, with armature formula of 2, 4. Maxilliped 3-segmented in female and 4-segmented in male; proximal segment in male with medial outgrowth. Legs 1–4 biramous with 3-segmented rami; armature formulae generally as in *Hemicyclops*, except 3rd segment of leg 1 endopod with II,4 and 3rd segment of leg 4 exopod with III,I,5. Leg 5 2-segmented, armature formula as in *Hemicyclops*. Basal segment of leg 5 in male fused to pediger. Leg 6 in male a single seta on genital operculum. Caudal ramus with usual 6 elements. Egg sac elongate, multiseriate.

*Etymology*.—The generic name *Hemadona* is an anagram of the island Namhae-do located in the Korean Strait from where the new genus was discovered. Gender feminine.

*Type species*.—*Hemadona clavicurura* new species.

***Hemadona clavicurura*, new species**

Figs. 1–3

*Material examined*.—3 ♀♀ and 7 ♂♂ collected from washings of *Dasybranchus caudatus* Grube collected from intertidal mud flat on Namhae-do Island (34°49'N 128°03'E) in Korea Strait on 22 July 2001. Holotype ♀ (USNM 1013731), allotype ♂ (USNM 1013732), and 6 paratypes (USNM 1013733, including 1 ♀ and 5 ♂♂) are deposited in the U.S. National Museum of Natural History in Washington, D.C. Dissected paratypes (1 ♀ and 1 ♂) are kept in the author's (IHK) collection.

*Female*.—Body (Fig. 1A) elongate, 6.34 mm long (excluding setae on caudal rami).

Cephalothorax semicircular and containing 1st pediger. Second pediger widest of body, 1.04 mm; width of 3rd and 4th pedigers decreasing only slightly from that of 2nd pediger. Urosome 5-segmented, 2.37 times longer than prosome. Genital double somite longer than wide, 877 × 693 μm, with aliform dorsolateral protrusion in anterior half of somite covering area of egg sac attachment (Fig. 1A). Abdomen 3-segmented, with all segments longer than wide, 833 × 553 μm, 798 × 508 μm, and 880 × 430 μm. Caudal ramus (Fig. 1C) 4.44 times longer than wide (720 × 162 μm), armed with 1 short, outer seta at about midlength of lateral margin, 1 short, medial, subterminal seta, and 2 short and 2 long terminal setae; longest terminal seta (830 μm) 1.15 times as long as ramus. Egg sac greatly elongated (7.05 mm), longer than body and cylindrical.

Rostrum subquadrate in dorsal view, produced forward, and well demarcated from cephalothorax (Fig. 1A). Antennule (Fig. 1B) short and robust, 6-segmented; formula of armature: 5, 16, 10, 4, 2 + A, and 7 + A. Antenna (Fig. 1C) 4-segmented; first segment (coxobasis) longer than wide, with long outer-distal seta; second segment (1st endopodal segment) shorter than proximal segment, with small subterminal seta; third segment (2nd endopodal segments) drawn out into a large uncinatate claw, with basal patch of spinules on outer surface and 2 unequal setae plus 1 blunt tip, bent, spiniform seta bearing terminal row of spinules on medial margin; terminal segment 2.75 times longer than wide, tipped with 3 unequal setae and 4 spiniform setae structured as that one on 3rd segment. Labrum (Fig. 1D) well-developed, with submarginal, inner, central process, and 2 disjunct, marginal rows of spinules on either side of this process. Gnathobase of mandible (Fig. 1E) armed terminally with 1 stout, pinnate element, 1 stout, spinulose element, and 1 pinnate and 1 naked setae. Paragnath (Fig. 1F) an obtuse lobe fringed with spinules on distal margin. Maxillule (Fig. 1G) bilobate,

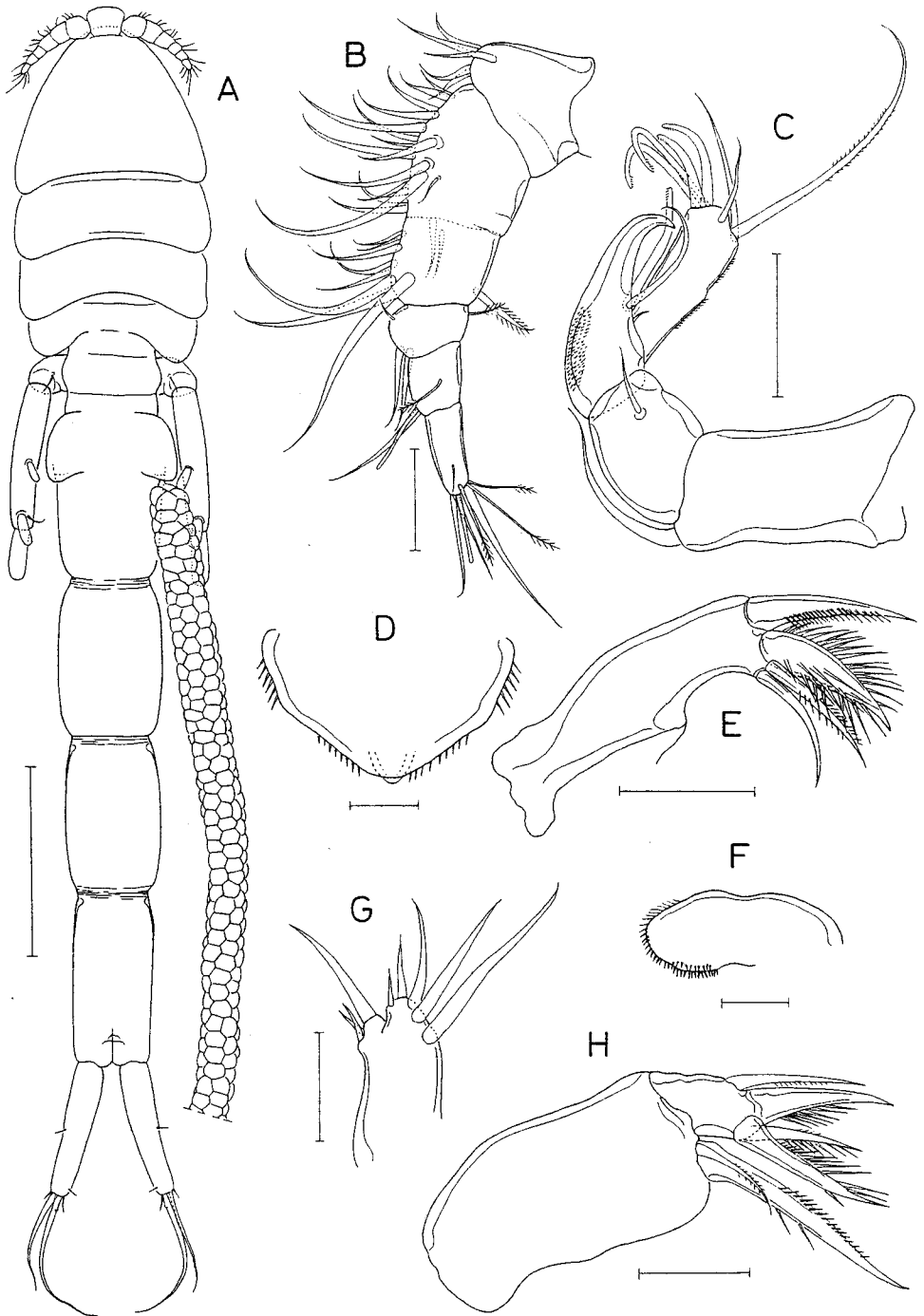


Fig. 1. *Hemadona clavicurura*, new genus, new species, female. A, habitus, dorsal; B, antennule; C, antenna; D, labrum; E, mandible; F, paragnath; G, maxillule; H, maxilla. Scale bars: A, 1 mm; B, C, 0.02 mm; D, F, 0.02 mm; E, G, H, 0.05 mm.

small outer lobe tipped with 1 long and 2 short setae and larger inner lobe with 5 unequal setae. Maxilla (Fig. 1H) 2-segmented; robust proximal segment (syncoxa) armed with 1 large spiniform and 1 small pinnate setae; distal segment (allobasis) tipped with 2 spiniform elements bearing spinules on one side and 2 pinnate setae. Maxilliped (Fig. 2A) 3-segmented; proximal segment (syncoxa) with 2 unequal medial setae; middle segment (basis) greatly expanded laterally and carrying 2 unequal medial setae; terminal segment (endopod) tiny, bearing 1 spiniform and 2 setiform elements.

Legs 1–4 (Figs. 2B–D, 3A) biramous, with 3-segmented rami. Formula of spines and setae as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	1–I	I–0; I–1; III,I,4	0–1; 0–1; II,4
Leg 2	0–I	1–0	I–0; I–1; III,I,5	0–1; 0–2; II,I,3
Leg 3	0–I	1–0	I–0; I–1; III,I,5	0–1; 0–2; II,II,2
Leg 4	0–1	1–0	I–0; I–1; III,I,5	0–1; 0–2; II,II,1

Outer surface of all segments on rami fringed with spinules. Outer spines on all legs club-shaped, with swollen tip covered with fine denticles. Leg 5 (Fig. 3B) 2-segmented; proximal segment small, carrying simple, outer seta; distal segment elongate, about 4 times longer than wide ( $750 \times 187 \mu\text{m}$ ), armed with 3 club-like spines and 1 thin, simple seta.

*Male*.—Body (Fig. 3C) elongate as in female, 3.40 mm long (excluding setae on caudal rami). Cephalothorax semi-ellipsoid shaped and containing 1st pediger. Second pediger widest of body,  $532 \mu\text{m}$  wide; width of 3rd and 4th pedigers decreasing only slightly from that of 2nd pediger. Urosome 6-segmented, 1.51 times longer than prosome. Ventrally, proximal segment of leg 5 indistinctly separated from its pediger (Fig. 3D). Genital somite slightly longer than wide,  $310 \times 300 \mu\text{m}$ ; genital operculum (Fig. 3D) small. Abdomen 4-segment-

ed, with following measurements (proceeding from anterior to posterior):  $295 \times 282 \mu\text{m}$ ,  $366 \times 275 \mu\text{m}$ ,  $317 \times 254 \mu\text{m}$ , and  $423 \times 246 \mu\text{m}$ . Caudal ramus 4.08 times longer than wide ( $408 \times 100 \mu\text{m}$ ) and armed as in female. Maxilliped (Fig. 3E) 4-segmented; proximal segment (syncoxa) with large, medial protrusion tipped with 3 sharp tines; second segment (basis) largest, armed with small patch of subterminal denticles on lateral surface, a seta in distomedial corner followed by a row of spinules on medial margin; third segment (1st endopodal segment) smallest and naked; distal segment (2nd endopodal segment) drawn out into a long claw with accessory tine and 2 simple setae on medial surface of basal region.

*Etymology*.—The species name is a combination of Latin, *clava* (= a club) and *crus* or *cruris* (= leg), alluding to the club-shaped outer and terminal spines on all five pairs of legs.

*Remarks*.—The general appearance of *Hemadona clavocrura* resembles the species of *Conchylurus* in having an elongated (non-cycloform) body. They are further alike in having a 6-segmented antennule, an armature formula of II,4 on the terminal segment of the endopod of leg 1, and a prominent medial, basal protuberance on the proximal segment (syncoxa) of the male maxilliped. These four features are also shared with *Hersiliodes*. However, *H. clavocrura* cannot be placed in *Conchylurus* due to the presence of the following character states: (1) the hook on the 3rd segment of the antenna is completely fused to its segment proper, (2) the gnathobase of the mandible carries four (instead of three) terminal elements, (3) the proximal segment (syncoxa) of the maxilla bearing two (instead of none) elements at outer-distal corner, and (4) the maxilliped in female is 3-segmented (instead of 2-segmented). Moreover, 10 species of *Conchylurus* are known and, unlike *H. clavocrura* living in association with polychaetes, they were all

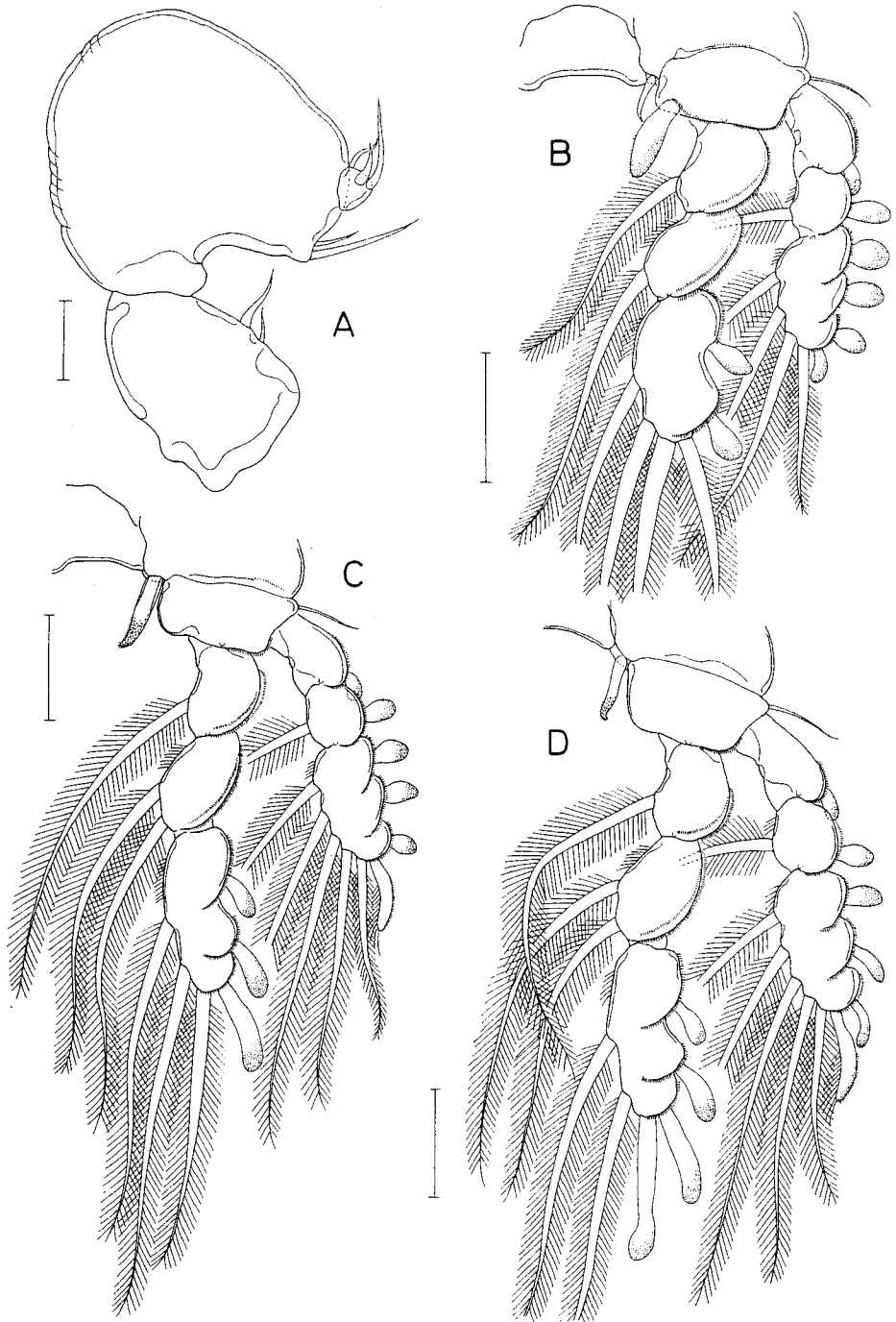


Fig. 2. *Hemadona clavicurura*, new genus, new species, female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3. Scale bars: A, 0.05 mm; B-D, 0.2 mm.

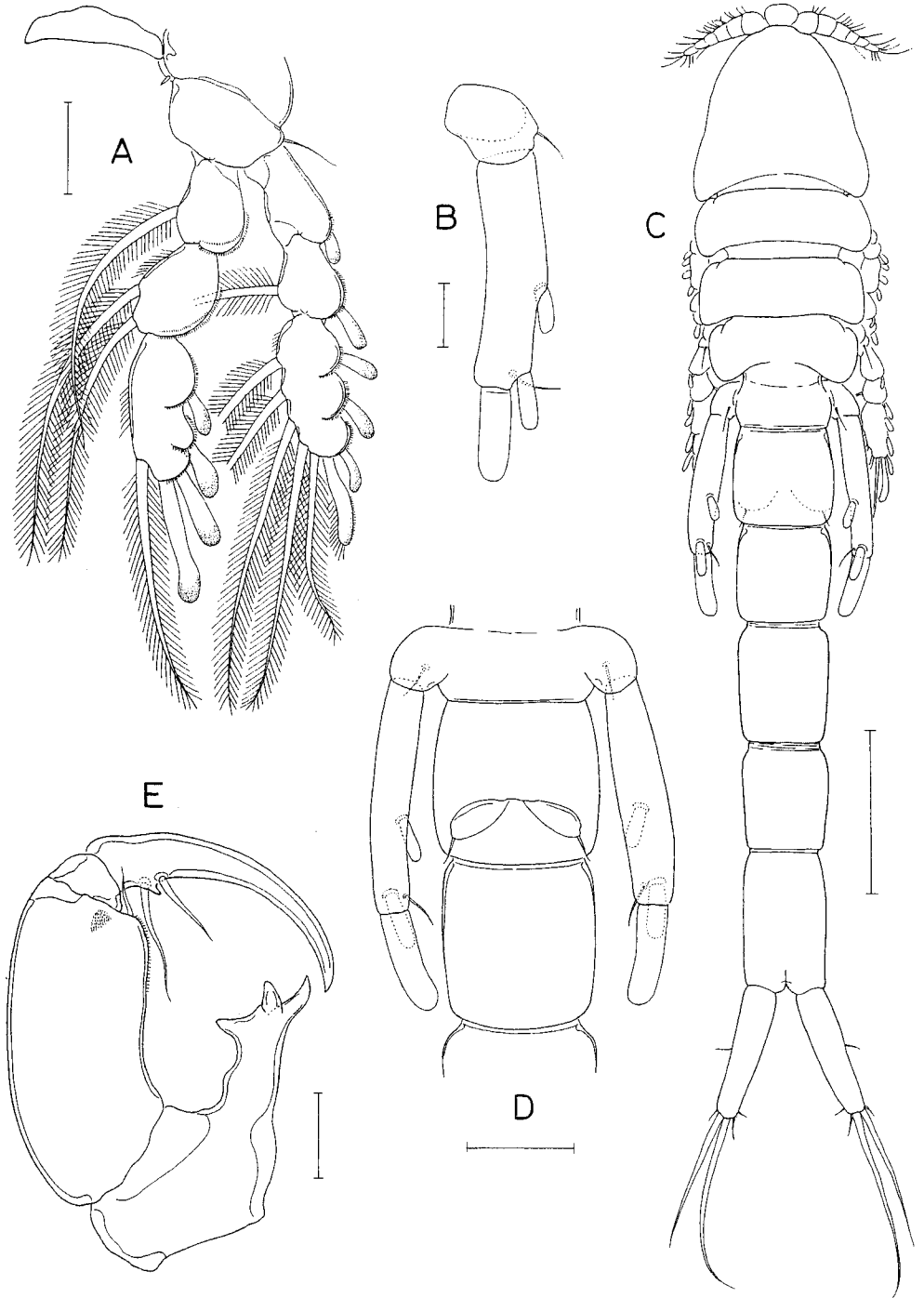
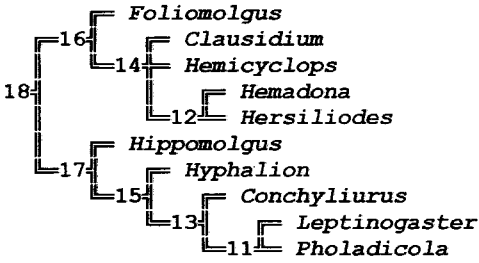


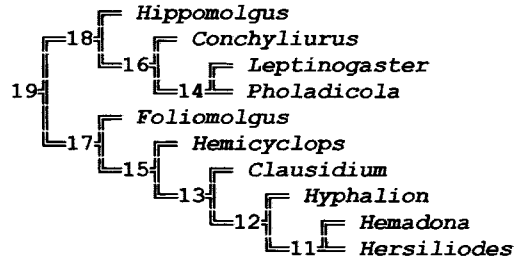
Fig. 3. *Hemadona clavicurura*, new genus, new species. Female: A, leg 4; B, leg 5. Male: C, habitus, dorsal; D, first three somites of urosome, ventral; E, maxilliped. Scale bars: A, B, D, 0.2 mm; C, 0.5 mm; E, 0.05 mm.



## Tree 1



## Tree 7



## Tree 9

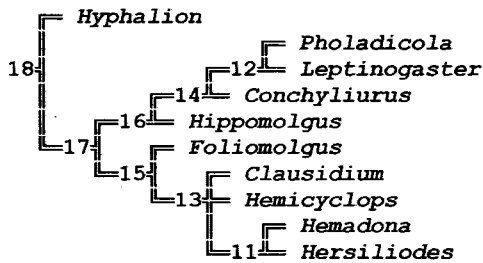


Fig. 4. Clausidiid phylogeny produced through analysis of nonadditive (unordered) coding. Showing three representatives from three patterns of phylograms. (Other 15 phylograms are available from JSH upon request.)

reported from the mantle cavities of the bivalve mollusks.

Of the four differences mentioned above between *H. clavicurura* and *Conchyliurus*, only items (1) and (4) also apply to the distinction between it and *Hersiliodes*. So far two species of *Hersiliodes* are known from either a polychaete (Bocquet et al. 1963) or a bivalve (Kim & Stock 1996). Thus, it seems *Hemadona* is closer to *Hersiliodes* than to *Conchyliurus*.

In general, *H. clavicurura* is most characteristic in having an unusually long urosome (2.37 times longer than its prosome) and club-shaped outer and/or terminal spines on all five pairs of legs.

## Phylogenetic Analysis

A total of 18 equally parsimonious trees (cladograms, phylograms) were obtained with a length of 37 steps, a consistency index (CI) of 64 and a retention index of 62.

A close comparison of these 18 trees shows that there are three patterns of tree according to the grouping of the 10 genera. In Pattern I, as Tree 1 in Fig. 4, the 10 genera are separated into two clades, with one clade (Clade 16) containing *Clausidium*, *Foliomolgus*, *Hemadona*, *Hemicyclops*, and *Hersiliodes* and the other clade (Clade 17), *Conchyliurus*, *Hippomolgus*, *Hyphalion*, *Leptinogaster*, and *Pholadicola*. There are 10 phylograms belonging to this category—Tree 1, 2, 3, 4, 5, 6, 11, 12, 13 and 14 (authors' enumeration; unpublished data). Phylograms in Pattern II, as Tree 9 in Fig. 4, have *Hyphalion* set aside on a clade of its own and the remaining nine genera divided into two groups, with *Clausidium*, *Foliomolgus*, *Hemadona*, *Hemicyclops*, and *Hersiliodes* in one clade (Clade 15) and *Conchyliurus*, *Hippomolgus*, *Leptinogaster*, and *Pholadicola* in the other clade (Clade 16). There are six phylograms belonging to

this category—Tree 8, 9, 10, 16, 17 and 18 (authors' enumeration; unpublished data). One of the two remaining phylograms, Tree 7, belonging to Pattern III, is shown in Fig. 4. It has the 10 clausidiid genera divided into two groups, with one comprising *Conchylurus*, *Hippomolgus*, *Leptinogaster*, and *Pholadicola* and another one, *Clausidium*, *Foliomolgus*, *Hemadona*, *Hemicyclops*, *Hyphalion* and *Hersiliodes*.

The difference among the three patterns mentioned above is chiefly due to the inconsistent positions of *Hyphalion*. In Pattern I (see Tree 1 in Fig. 4), it is a member of the group comprising *Conchylurus*, *Hippomolgus*, *Leptinogaster*, and *Pholadicola*; in Pattern II (see Tree 9 in Fig. 4) it is by itself; and in Pattern III (see Tree 7 in Fig. 4) it is a member of the group comprising *Clausidium*, *Foliomolgus*, *Hemadona*, *Hemicyclops*, *Hyphalion* and *Hersiliodes*, which is entirely different from the one that it is affiliated with in Pattern I.

There are two monophyletic taxa that maintain identical relationships in all 18 phylograms. They are *Hemadona* + *Hersiliodes* and *Conchylurus* + (*Pholadicola* + *Leptinogaster*). The former two genera are held together by sharing characters 1 (with 6-segmented antennule), 12 (proximal segment of male maxilliped with medial protrusion) and 13 (with an armature formula of II,4 on distal segment of leg 1 endopod), and the latter three genera, by sharing characters 3 (with 2 elements on 3rd segment of antenna), 5 (mandible tipped with 3 elements) and 10 (with 3-segmented maxilliped in female). It is noteworthy that both *Hemadona* and *Hersiliodes* are characteristic in having a 6-segmented antennule (Character 1). They were not placed in the same group (clade) with *Conchylurus* + *Leptinogaster* + *Pholadicola* on any of the 18 phylograms. In other words, the two constant monophyletic taxa are remotely related. It is interesting to point out that the latter three genera comprise parasites of bivalve mollusks, while species of *Pholadicola* inhabit in the host's intestine, and

those of *Conchylurus* and *Leptinogaster* are found in the host's mantle cavities.

Five of the 18 obtained phylograms contain a clade with trichotomy, three of these phylograms (Trees 1, 5 and 12) are in Category I and the other two (Trees 9 and 17), in Category II. *Hemicyclops* appears as one of the three terminal clades in all five phylograms showing trichotomy. In four of these five phylograms, i.e., Trees 1, 5, 12 and 9, the branch embracing *Hemadona* + *Hersiliodes* appears as another terminal clade, with either *Clausidium* or *Foliomolgus* as the third terminal clade. In addition, Trees 2 and 13 in Category I have a topology showing *Hemicyclops* in a sister-taxon relationship with *Hemadona* + *Hersiliodes*. These six phylograms indicate that both *Hemadona* and *Hersiliodes* are closely affiliated with *Hemicyclops*. However, since none of the 18 phylogram shows *Hersiliodes* in a sister-taxa relationship with *Hemicyclops*, the former, accordingly, cannot be relegated to a synonym of the latter. Thus, the present phylogenetic analysis supports Kim and Stock's (1996) notion that *Hersiliodes* is a valid genus in the Clausidiidae and cannot be synonymized with *Hemicyclops*.

#### Key to the Genera of the Clausidiidae

A key to the genera of the Clausidiidae was provided by Humes and Huys (1992). Since only six of the ten genera currently recognized were dealt with in that key, a new key is provided below.

1. Formula of armature on terminal segment of leg 1 endopod I,5 . . . . . 2
  - Formula of armature on terminal segment of leg 1 endopod otherwise . . . . . 5
2. Antenna 3-segmented . . . . . *Hyphalion*
  - Antenna 4-segmented . . . . . 3
3. Maxilliped in female 4-segmented . . . . . *Hemicyclops*
  - Maxilliped in female reduced or absent . . . . . 4
4. Antennule 7-segmented; 3rd segment of antenna with 4 elements . . . . . *Foliomolgus*
  - Antennule 6-segmented; 3rd segment of antenna with 2 elements . . . . . *Leptinogaster*

5. Endopods of legs 1–4 with sucking discs; middle exopodal segment of leg 1 without inner seta . . . . . *Clausidium*
- No sucking discs on legs; middle exopodal segment of leg 1 with inner seta . . . . . 6
6. Proximal segment of maxilla armed with setae . . . . . 7
- Proximal segment of maxilla unarmed . . . . . 8
7. Maxilliped in female 4-segmented and well-developed; armature formula for terminal segment of leg 1 exopod II, I, 5 . . . . . *Hersiliodes*
- Maxilliped in female 3-segmented and reduced; armature formula for terminal segment of leg 1 exopod III, I, 5 . . . . . *Hemadona*
8. Armature formula for terminal segment of female leg 1 endopod II, 4 . . . . . *Conchylurus*
- Armature formula for terminal segment of female leg 1 endopod otherwise . . . . . 9
9. Maxilliped in female rudimentary . . . . . *Pholadicola*
- Maxilliped in female well developed, at least 3-segmented . . . . . *Hippomolgus*

### Acknowledgment

Studies on this project were aided by a grant from the Paramitas Foundation to the senior author (JSH) and from the Korea Science and Engineering Foundation (2000-1-20200-003-3) to the junior author (IHK).

### Literature Cited

- Bocquet, C., J. H. Stock, & G. Kleeton. 1963. Copépodes parasites d'invertébrés des côtes de la Manche. X. Cyclopoïdes poecilostomes associés aux Annélides polychètes dans la région de Roscoff.—Archives de Zoologie expérimentale et générale 102 (Notes et Revue 1):20–40.
- Farris, J. S. 1988. Hennig86 Reference, Version 1.5.—Published by the author, Port Jefferson, New York, 18 pp.
- Gooding, R. U. 1963. External morphology and classification of marine poecilostome copepods belonging to the families Clausidiidae, Clausiidae, Nereicolidae, Eunicicolidae, Synaptiphilidae, Catiniidae, Anomopsyllidae, and Echiurophiliidae.—Unpublished Ph.D. thesis, University of Washington, Seattle, 276 pp.
- Gotto, V. 1993. Commensal and parasitic copepods associated with marine invertebrates (and whales).—The Linnean Society (London), 264 pp.
- Ho, J.-s. 1992. Phylogeny of Poecilostomatoida: a major order of symbiotic copepods.—Bulletin of Plankton Society of Japan, Special Volume Pp. 25–48.
- , & I.-H. Kim. (2003). New clausiid copepods (Poecilostomatoida) associated with polychaetes of Korea, with cladistic analysis of the family Clausiidae.—Journal of Crustacean Biology 22:568–581.
- , & W. J. Wardle. 1992. *Pholadicola intestinalis*, new genus and species, a clausioid copepod parasitic in a deep-burrowing clam from Texas.—Bulletin of Marine Science 51:37–44.
- Humes, A. G., & R. U. Gooding. 1964. A method for studying the external anatomy of copepods.—Crustaceana 6:238–240.
- , & R. Huys. 1992. Copepoda (Poecilostomatoida and Siphonostomatoida) from deep-sea hydrothermal vent areas off British Columbia, including *Amphicrossus altalis*, a new species of Erebonasteridae, with notes on the taxonomic position of the genus *Tychidion* Humes.—Canadian Journal of Zoology 70:1369–1380.
- Huys, R., & G. A. Boxshall. 1990. Discovery of *Centobnaster humesi*, new genus, new species (Erebonasteridae), the most primitive poecilostomatoid copepod known, in New Caledonian deep waters.—Journal of Crustacean Biology 10:504–519.
- Kim, I.-H. 2001. *Foliomolgus cucullus*, a new genus and species of Clausidiidae (Crustacea: Copepoda: Poecilostomatoida) associated with a polychaete in Korea.—Proceedings of the Biological Society of Washington 114:660–666.
- , & J. H. Stock. 1996. A new species of Clausidiidae (Copepoda, Poecilostomatoida) associated with the bivalve *Ruditapes philippinarum* in Korea. Cahiers de Biologie marine 14:1–6.
- O'Grady, R. T., & G. B. Deets. 1987. Coding multistate characters, with special reference to the use of parasites as characters of their hosts.—Systematic Zoology 36:268–279.
- Vervoort, W., & F. Ramirez. 1966. *Hemicyclops thalassius* nov. spec. (Copepoda, Cyclopoida) from Mar del Plata, with revisionary notes on the family Clausidiidae.—Zoologische Mededelingen (Leiden) 41:195–220.

Appendix 1.—Characters and character states used in the phylogenetic analysis of the Clausidiidae. Numbers in parentheses denote the numerical coding of the character states. Coding in Characters 3, 4, and 8 employed “internal rooting” proposed by O’Grady & Deets (1987). *Centobnaster* and *Tychidion* were utilized as the outgroup in polarization of the character state transformations.

01	3rd and 4th segments of antennule separated (0) or fused (1)
02	Aesthetasc on antepenultimate segment of antennule absent (0) or present (1)
03	3rd segment of antenna with 3 elements (1), 4 elements (0) or 2 elements (2)
04	Terminal segment of antenna with 6 elements (1), 7 elements (0), 5 elements (2) or 4 elements (3)
05	Mandible tipped with 4 elements (0) or 3 elements (1)
06	Inner lobe of maxillule carrying 2 elements (0) or 3 elements (1)
07	Outer lobe of maxillule carrying 3 elements (0) or 4 elements (1)
08	Proximal segment of maxilla without seta (0), with 1 seta (1), 2 setae (2) or 3 setae (3)
09	Distal segment of maxilla with 4 elements (0), 3 elements (1), 2 elements (2) or 1 element (3)
10	Maxilliped in female 4-segmented (0), 3-segmented (1), 2-segmented (2) or absent (3)
11	Proximal segment of female maxilliped with 2 setae (0), 1 seta (1) or none (2)
12	Proximal segment of male maxilliped without protrusion (0) or with medial protrusion (1)
13	Distal segment of endopod on leg 1 with an armature formula of I, 5 (0) or II, 4 (1)
14	Distal segment of exopod on leg 4 with an armature formula of II, I, 5 (0) or III, I, 5 (1)

Appendix 2.—Data matrix of 14 characters and their states in ten genera of Clausidiidae as used in the cladistic (phylogenetic) analysis. The question mark “?” indicates an unknown state. Due to the application of “internal rooting” (O’Grady & Deets, 1987) those characters coded with “1” in the outgroup are treated as plesiomorphic and “0” in the ingroup, apomorphic.

Genus (OTU)	Characters													
	1		5		10		14							
Outgroup	0	0	1	1	0	0	0	1	0	0	0	0	0	0
<i>Clausidium</i>	0	0	0	0	1	1	1	3	0	0	0	0	?	0
<i>Conchylurus</i>	1	1	2	0	1	1	1	0	0	2	1	1	1	1
<i>Foliomolgus</i>	0	1	0	0	0	1	1	1	1	3	?	0	0	0
<i>Hemadona</i>	1	0	0	0	0	1	1	2	0	1	0	1	1	1
<i>Hemicyclops</i>	0	1	0	0	0	1	1	2	0	0	0	0	0	0
<i>Hersiliodes</i>	1	1	0	0	0	1	1	2	0	0	0	1	1	0
<i>Hippomolgus</i>	1	1	1	0	0	1	1	0	0	0	1	?	0	0
<i>Hyphalion</i>	1	0	?	?	0	?	?	1	0	2	2	0	0	0
<i>Leptinogaster</i>	1	1	2	2	1	0	0	0	2	3	?	0	0	0
<i>Pholadicola</i>	1	0	2	3	1	0	0	0	3	3	?	0	?	?