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NEW CLAUSIID COPEPODS (POECILOSTOMATOIDA) ASSOCIATED WITH POLYCHAETES OF KOREA, WITH CLADISTIC ANALYSIS OF THE FAMILY CLAUSIIDAE

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ABSTRACT

Two new species of the Family Clausiidae, *Likroclausia namhaensis* n. gen. and n. sp. and *Rhodinicola laticauda* n. sp., were described from washings of polychaetes collected from an intertidal mud flat on Namhae Island in the Korea Strait and from an intertidal sandstone in Kyokpo in the Yellow Sea, respectively. The host of the former species is *Dasybranchus caudatus* Grube, but that of the latter is unidentified. Cladistic analysis of the family indicated that the 20 clausiid species should be kept in six groups, with *Pontoclausia*-group containing five species (*antiqua*, *lobata*, *prima*, *tomis*, *wilsoni*); *Likroclausia*-group, one species (*namhaensis*); *Rhodinicola*-group, three species (*gibbosa, elongata, laticauda*); *Mesnilia*-group, two species (*cluthae, martinensis*); *Clausia*-group, seven species (*bacescui*, *curticaudatum*, *lubbocki*, *mirabilis*, *rugosum*, *thomassini*, *uniseta*); and *Pseudoclausia*-group, two species (*giesbrechti*, *longiseta*). Each group is a monophyletic entity identified with one or more synapomorphies. Whilst the taxonomical status of the genera *Indoclausia*, *Megaclausia*, *Pherma*, and *Seridium* are unclear, it is unequivocal that the following four genera should be treated as valid taxa in the Clausiidae in addition to *Clausia*: *Mesnilia*, *Pontoclausia*, *Pseudoclausia*, and *Rhodinicola*. Also, both *Doviella prima* Rocha, 1986, and *Clausia wilsoni* Gooding, 1963, are transferred to *Pontoclausia*. *Rhodinicola thomassini* Laubier, 1970, should be transferred to *Clausia* for the time being.

Copepods of the family Clausiidae are essentially living in symbiosis with the polychaetes (O'Reilly, 1995; Kim, 2001). Although the name "Familie Clausiidae" appeared in the 19th century (Giesbrecht, 1895: 226), the definition of the family was not formally given until 1955 when Wilson and Illg gave an emended diagnosis of the Clausiidae. Only six species in five genera (*Clausia*, *Mesnilia*, *Rhodinicola*, *Seridium*, *Teredicola*) were recognized. Although 12 genera have been "put forward as tentative clausiids" (O'Reilly, 1995: 57), through the works of Gooding (1963), Stock (1968, 1979), and Ho (1984), by the time O'Reilly (1995) reported a new genus and new species of clausiid (*Megaclausia mirabilis*) from the maldanid polychaetes obtained in the Firth of Forth off the coast of Scotland, only seven genera (*Clausia*, *Indoclausia*, *Mesnilia*, *Pontoclausia*, *Pseudoclausia*, *Rhodinicola*, *Stockia*) were recognized as valid in the family.

In his work on the "Nereicoliform Group" of copepods associated with various marine invertebrates, Gooding (1963) adopted an 'inclusive concept' and placed all species of *Mesnilia*, *Pontoclausia*, and *Pseudoclausia* under the genus *Clausia* without retaining the component groupings at a subgeneric level. This 'inclusive concept' was not followed by O'Reilly (1995), because he argued that Bocquet and Stock's (1963) report of a true male of *Pseudoclausia giesbrechti* "undermined Gooding's hypothesis" (O'Reilly, 1995: 57). Nevertheless, recently, when Kim (2000: 379) reported some new poecilostome copepods from Korea, he resurrected Gooding's (1963) 'inclusive concept' for the treatment of the clausiids, because "the degree of leg simplification, a traditional diagnostic character for distinguishing genera, is not clear-cut among genera but reveals a morphocline" (Kim, 2001: 222). In this paper, in addition to describing two more new species of clausiids from Korea, we apply a cladistic approach to investigate whether the trend in leg simplification is applicable to the classification of the clausiid copepods.

MATERIALS AND METHODS

Polychaetes dug out from the mud flat or sandstone were placed in a plastic bag with one species per bag and fixed with alcohol. Back in the laboratory, water was added to the bag containing the worm fixed in alcohol, which was 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% alcohol. In studying the preserved copepods, specimens were cleared in lactic acid, dissected on a wooden slide (Humes and Gooding, 1964), and examined under a compound microscope. All drawings were made with the aid of a *camera lucida*. For seta formulae, "A" represents aesthete; Roman numerals, spines; and Arabic numerals, setae.

The computer program HENNIG86 Version 1.5 (Farris 1988) was employed to analyze the phylogenetic relationships between the species of Clausiidae. The commands "mhennig*" and "bb*" were used to produce multiple, shortest trees through performance of extended branch swapping.

TAXONOMY

Family Clausiidae Giesbrecht, 1895

Likroclausia, new genus

Diagnosis.—Female body cyclopiform, with lateral part of tergum of 2nd–4th pedigers protruded posterolaterally into antler-like process. Urosome 6-segmented. Antennule 6-segmented, with aesthete on segments 4–6. Antenna 3-segmented, with 4 terminal claws. Mandible tipped with 1 element. Maxillule with anteriorly protruded spinulose lobe, 3 outer setae and no inner seta. Maxilla 2-segmented, with sigmoid distal segment. Female maxilliped 2-segmented. Legs 1–4 biramous, with 3-segmented rami, except endopod of leg 1, which is 2-segmented and uncinate. Leg 5 2-segmented, armature 1-0; 4. Female leg 6 represented by 2 setae in egg sac attachment area.

Gender.—Feminine.

Type species.—*Likroclausia namhaensis*, new genus and new species.

Etymology.—The generic name is a combination of "*likros*" (= antler in Greek) and "*clausia*" (type genus of the Clausiidae), alluding to the antler-like processes on the terga of 2nd, 3rd, and 4th pedigers. The species name is derived from the name of the type locality, Namhae Island, in the Korea Strait.

Likroclausia namhaensis, new species

Figs. 1–4

Material Examined.—8 ♀♀ and 8 copepodids collected from washings of *Dasybranchus caudatus* Grube collected from intertidal mud flat in Namhae Island (34°49′N 128°03′E) in Korea Strait on 22 July 2001. Holotype ♀ (USNM 1009439) and 13 paratypes (including 6 ♀♀ and 7 copepodid V ♀♀) (USNM 1009440) are deposited in the U.S. National Museum of Natural History, Smithsonian Institution, in Washington, D.C. Dissected paratypes (1 ♀ and 1 copepodid V ♀ are kept in the second author's (IHK) collection.

Female.—Body (Fig. 1A) cyclopiform, 3.18 mm long (excluding setae on caudal rami). Cephalothorax semicircular, with 6 short sensilla on lateral surface and 1 long sensillum at tip of protruded posterolateral corner. Lateral area of tergum of 2nd and 3rd pedigers produced posterolaterally into large antler-like process, bearing 2 short sensilla on lateral surface, 2 at terminal end, and 1 longer one at tip of inner basal protrusion. Antler-like process on 4th pediger with 2 short sensilla at terminal end and 1 long sensillum on each short protrusion located on inner and outer surface. Urosome (Fig. 1B) 6-segmented. Genital double-somite wider than long, 300 × 615 µm, with dorsal conical protrusion near area of egg sac attachment. Abdomen (Fig. 1C) 4-segmented, reducing in size posteriorly and bearing transverse row of setules on ventral surface of 1st, 2nd, and 3rd somites and 2 patches of denticles on either side of ventral surface of 4th (anal) somite. Caudal ramus (Fig. 1C) 4.84 times longer than wide (310 × 64 µm), distal edge on ventral surface fringed with spinules; ramus proper armed with 1 median dorsal seta, and 4 short and 1 long terminal seta; longest terminal seta 3 times as long as ramus. Egg sac (not drawn, readily disintegrates in lactic acid) elliptical, flat, arranged in 2 layers, and wedged between antler-like process of 4th pediger and urosome.

Rostum truncate anteriorly but fused to cephalothorax and represented only by faint outline posteriorly (Fig. 2A). Antennule (Fig. 1D) slender and 6-segmented; armature formula: 4, 14, 10, 4+A, 2+A, and 7+A. Aesthetes extremely slender, hardly distinguishable from setae. Antenna (Fig. 1E) slender as in antennule and 3-segmented; first segment (coxobasis) with middle region of outer margin fringed with a row of spinules and armed with 1 distal-inner seta; second segment (1st endopodal segment) with longitudinal patch of spinules; third segment (fused 2nd and 3rd endopodal segments) 6.67 times as long as wide (240 × 36 µm) and armed

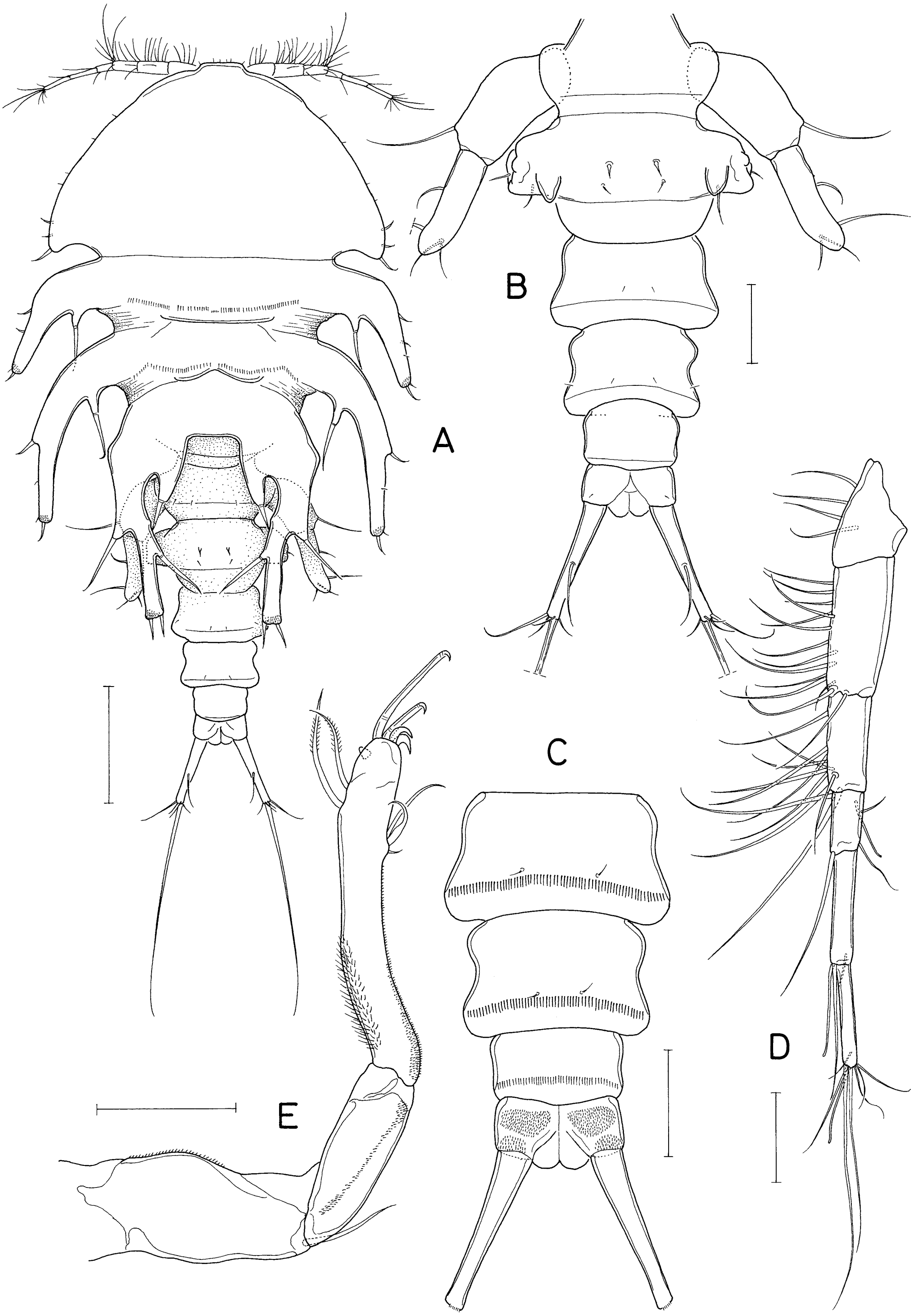

Fig. 1. *Likroclausia namhaensis* n. gen. and n. sp., female. A, habitus, dorsal; B, urosome, dorsal; C, abdomen, ventral; D, antennule; E, antenna. Scale bars: A = 0.5 mm; B, C = 0.2 mm; D, E = 0.1 mm.

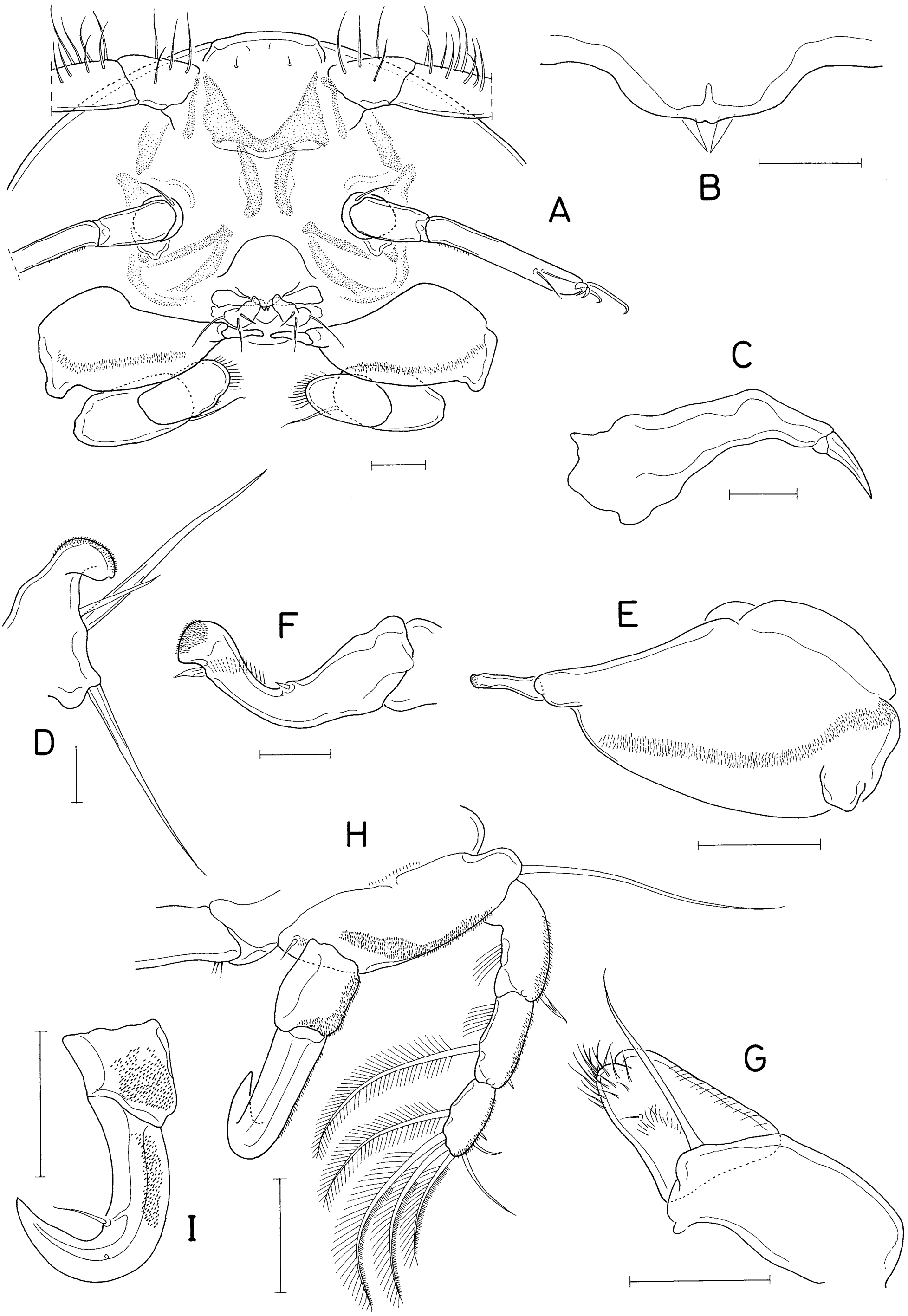

Fig. 2. *Likroclausia namhaensis* n. gen. and n. sp., female. A, rostral and oral areas, ventral; B, labrum, ventral; C, mandible; D, maxillule; E, maxilla; F, distal segment of maxilla; G, maxilliped; H, leg 1; I, endopod of leg 1. Scale bars: A, E, G–I = 0.1 mm; B = 50 μm; C, D, F = 20 μm.

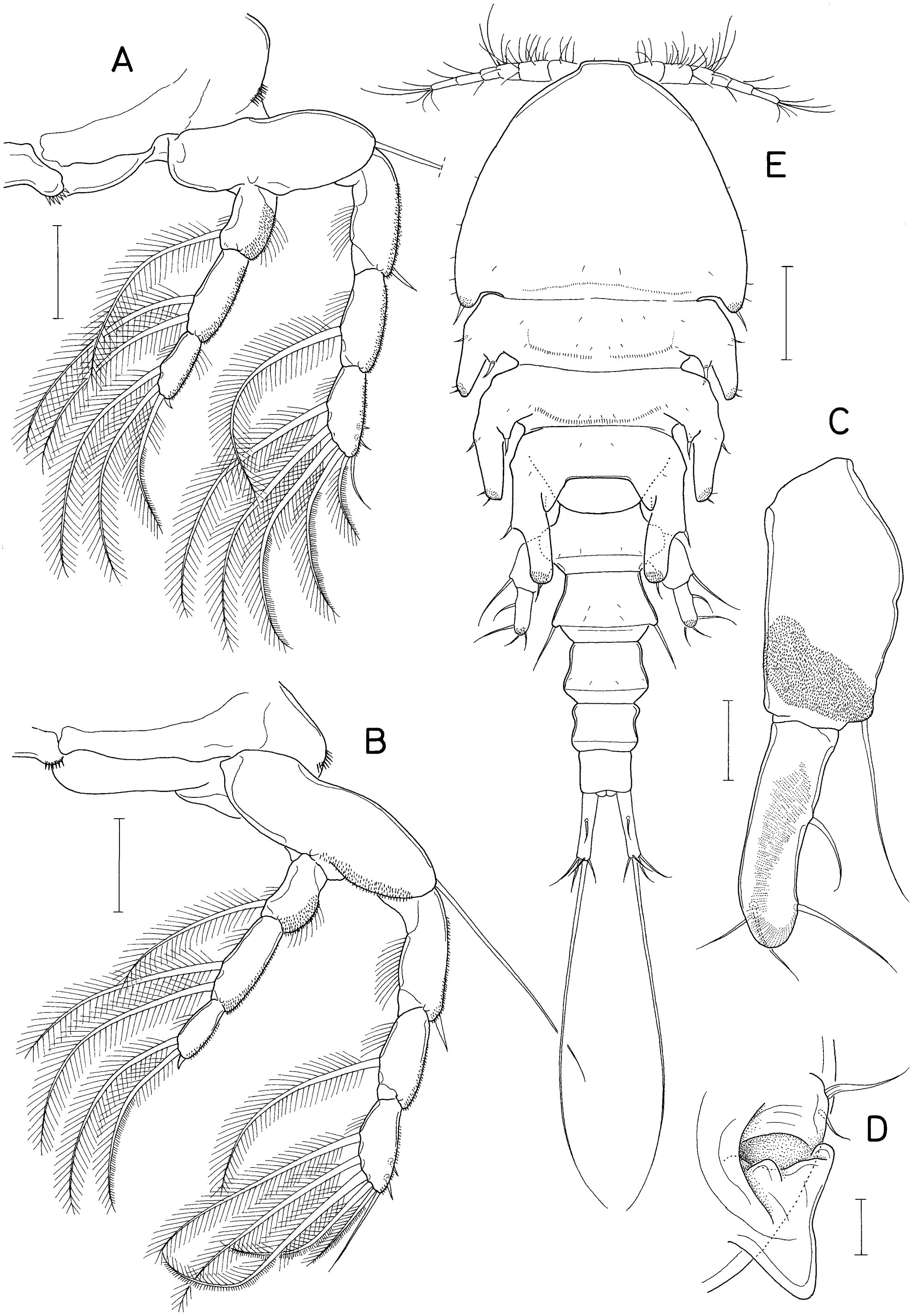

Fig. 3. *Likroclausia namhaensis* n. gen. and n. sp., female. A, leg 2; B, leg 4; C, leg 5; D, area of egg sac attachment; E, habitus of copepodid V. Scale bars: A–C = 0.1 mm; D = 20 μm; E = 0.2 mm.

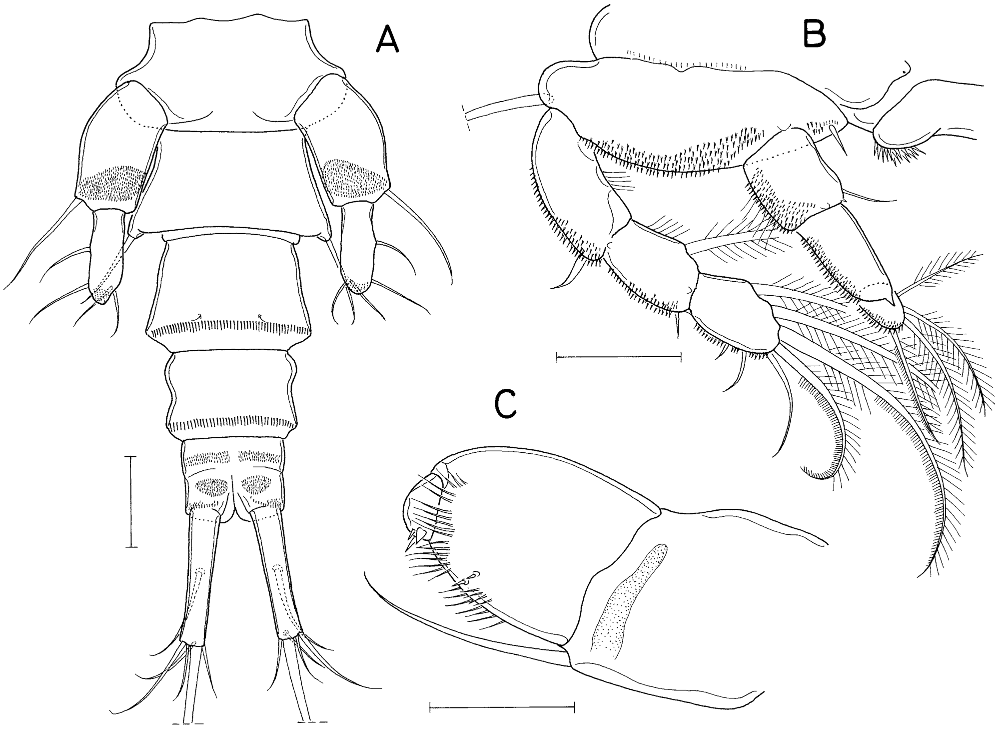

Fig. 4. *Likroclausia namhaensis* n. gen. and n. sp., female copepodid V. A, urosome, ventral; B, leg 1; C, maxilliped. Scale bars: A = 0.1 mm; B, C = 50 µm.

with spinules on 2/3 of proximal inner margin and setules on proximal half of outer margin; distally with 3 setae, 2 pectinate setae on outer margin, 1 small subterminal knob, and 4 unequal, terminal, spines with bent tip. Labrum small, covering only tips of mandible; with 2 spiniform, marginal processes in central region (Fig. 2B). Mandible (Fig. 2C) small, gnathobase armed terminally with smooth but sharply pointed process. Maxillule (Fig. 2D) bilobate, small outer lobe tipped with long seta and longer inner lobe with spinulation at tip and 2 unequal setae at base. Maxilla (Fig. 2E) 2-segmented; robust proximal segment armed with long patch of spinules on posteroventral surface, sigmoid distal segment (Fig. 2F) armed with 2 setae, row of setules between these two setae, and patch of spinules at tip. Maxilliped (Fig. 2G) 2-segmented; proximal segment (syncoxa) with long medial-terminal seta; distal segment (basis) slightly bipartite distally, with fine setules in middle region of inner surface and coarse setules at tip of inner lobe.

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

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	1–1	I–0; 1–1; 3,4	0–0; 0–1
Leg 2	0–0	1–0	I–0; 0–1; 3,5	0–1; 0–2; I,3
Leg 3	0–0	1–0	I–0; 0–1; 3,5	0–1; 0–2; I,3
Leg 4	0–0	1–0	I–0; 0–1; 2,6	0–1; 0–2; I,2

Outer surface of all leg segments covered with spinules. Coxa of leg 1 with loose row of spinules on ventral surface, basis bearing a long and dense patch of spinules. Coxa of legs 2, 3, and 4 each with short row of spinules at outer-distal corner; basis of legs 2 and 3 without spinules, that of leg 4 bearing long patch of marginal spinules between bases of rami. Distal segment of endopod of leg 1 (Fig. 2I) modified into a strong, curved, sharp process. Leg 5 (Fig. 3C) 2-segmented; formula of armature 1-0; 4. Leg 6 represented by 2 setae in egg sac attachment area (Fig. 3D).

Male.—Unknown.

Female Copepodid V.—Body (Fig. 3E) 1.71 mm long (excluding setae on caudal rami) and 625 µm wide (across cephalothorax). Antler-like tergal processes on 2nd, 3rd, and 4th pedigers generally as in those of adult. Urosome (Fig. 4A) 5-segmented, with 3 somites in abdominal region. Appendages as those of adult except for maxilliped and leg 1. Maxilliped (Fig. 4C) 3-segmented; proximal segment (syncoxa) with long medial-terminal seta; middle segment (basis) with coarse setules on medial and distal margin and 2 small medial setae; distal segment (endopod) small, carrying 3 small, spiniform elements on medial surface. Leg 1 (Fig. 4B) biramous with 3-segmented rami. Exopod as in adult but endopod different in having 1 inner seta on proximal segment, no seta on middle segment, and 4 (2 inner and 2 terminal) setae on distal segment; distal part of middle segment protruded into short process on ventral surface.

Remarks.—The most remarkable feature of the present species is the possession of a pair of antler-like lateral processes on the tergum of pedigers 2, 3, and 4. Although a similar process is known for some harpacticoids, like Ancorabolidae and Cerviniidae, it is new for the poecilostomatoid copepods. Furthermore, while the terminal armature of the antenna and structure of the mandible, maxillule, and maxilla are of typical form found in the Clausiidae, the 2-segmented maxilliped and the uncinate endopod of leg 1 are unique. Thus, a new genus was proposed for this new form of the clausiid copepods obtained from the washings of *Dasybranchus* polychaetes.

Rhodinicola Levinsen, 1878
Rhodinicola laticauda, new species
Figs. 5–7

Material Examined.—1 ♀ in the washings of an unidentified polychaete collected from intertidal sandstone in Kyokpo (34°49′N 128°03′E), Korea, in the Yellow Sea on 8 April 2001. Holotype (with antennule, antenna, maxilla, and legs 1–5 on left side removed for close study) has been deposited in U.S. National Museum, Smithsonian Institution, in Washington, D.C. (USNM 1009441).

Female.—Body (Fig. 5A) elongate and broad throughout, 1.22 mm long (excluding setae on caudal rami) and 357 μm wide (across 2nd pediger). Cephalothorax shield like, 288 × 350 μm, and with protruded rostral area. Metasomal somites short and wide, at least 4 times wider than long. Urosome 6-segmented, except for anal somite (135 × 238 μm), all other somites more than twice as wide as long. Caudal ramus longer than wide, 58 × 38 μm, and carrying 5 (2 outer, 1 dorsal, and 2 terminal) short setae and 1 long terminal seta 4.31 times longer than ramus. Egg sac unknown.

Rostrum (Fig. 5B) truncate anteriorly but fused to cephalothorax and leaving behind only faint outline posteriorly. Antennule (Fig. 5C) 6-segmented; formula of armature: 4, 13, 9, 4, 2 + A, and 7 + A. Antenna (Fig. 5D) stocky, 3-segmented, and profusely armed with spinules as shown in Fig. 5D; proximal segment (coxobasis) with bilaterally pectinate spiniform seta on distal-inner corner; middle segment (1st endopodal segment) without seta; terminal segment (fused 2nd and 3rd endopodal segments) armed with 4 unequal, terminal, hooked spines, 2 subterminal, bipectinate, long, outer setae and 2 subterminal, short, inner setae. Labrum small, covering only tips of mandible (Fig. 6A). Mandible (Fig. 6B) small, gnathobase armed subterminally with short, smooth, spiniform process and terminally with long process with spinules on distal inner margin. Maxillule (Fig. 6C) a thumb-like process covered with denticles and bearing 3 setae on outer surface and 1 seta at base of inner surface. Maxilla 2-segmented, largest oral appendage (Fig. 6A), greatly inflated basal segment covered with large patch of denticles on ventral surface; terminal segment (Fig. 6D) subquadrate, with patch of spinules on dorsal margin, seta on posterior surface, fine denticles on distal surface. Maxilliped reduced (Fig. 6A) and 2-segmented (Fig. 6E); proximal segment (coxobasis) with 2 setae on medial margin and row of coarse spiniform elements on anterior margin; distal segment (endopod) produced into spiniform process armed with 2 unequal setae at base.

Legs 1–4 (Figs. 6F, G, 7B, C) biramous, with 3-segmented rami. Formula of spines and setae as follows:

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

Outer surface of all leg segments covered with spinules. Coxa of all legs with row of spinules on outer-distal margin. Basis of all legs with row of spinules on posterior margin, that of leg 1 with additional row on ventral surface. Endopod of right leg 2 (Fig. 7A) abnormal, with much-reduced 2 distal segments and lacking spine and setae. Leg 5 (Fig. 6H) 2-segmented; proximal segment (100 × 93 μm) enlarged

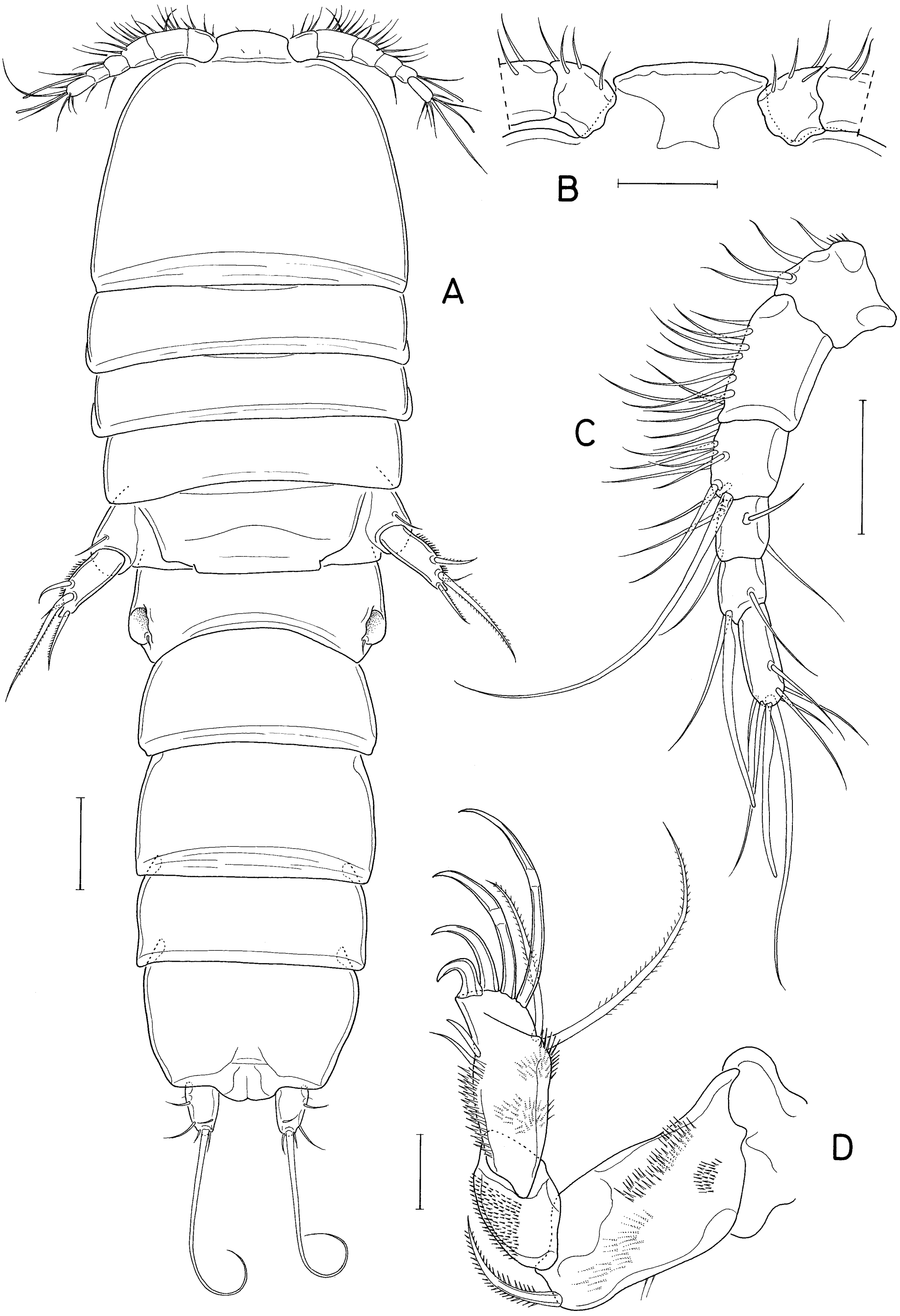

Fig. 5. *Rhodinicola laticauda* n. sp., female. A, habitus, dorsal; B, rostral area, ventral; C, antennule; D, antenna. Scale bars: A = 0.1 mm; B, C = 50 μm; D = 20 μm.

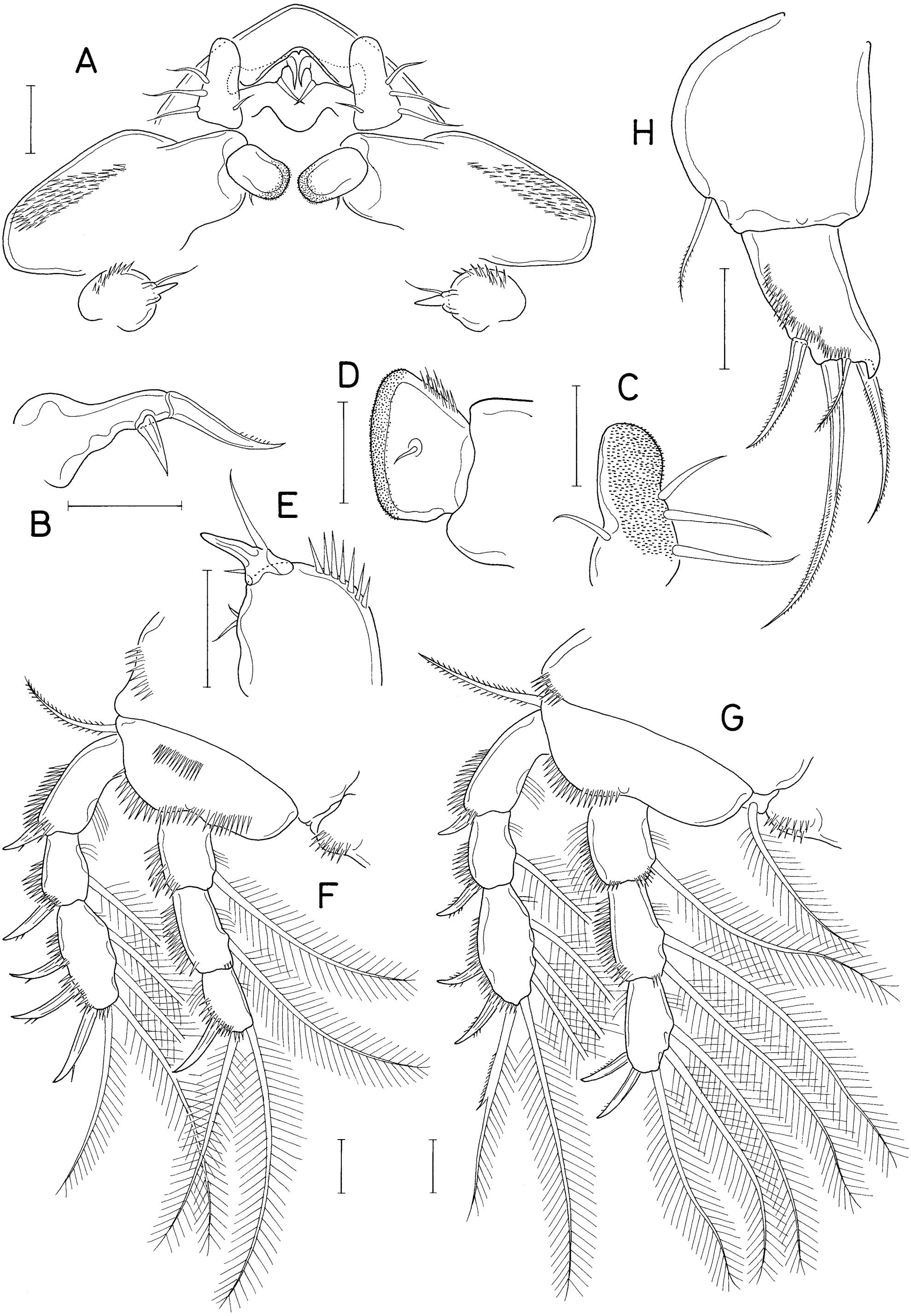

Fig. 6. *Rhodinicola laticauda* n. sp., female. A, oral area, ventral; B, mandible; C, maxillule; D, terminal segment of maxilla; E, maxilliped; F, leg 1; G, leg 2; H, leg 5. Scale bars: A–G = 20 μm, H = 50 μm.

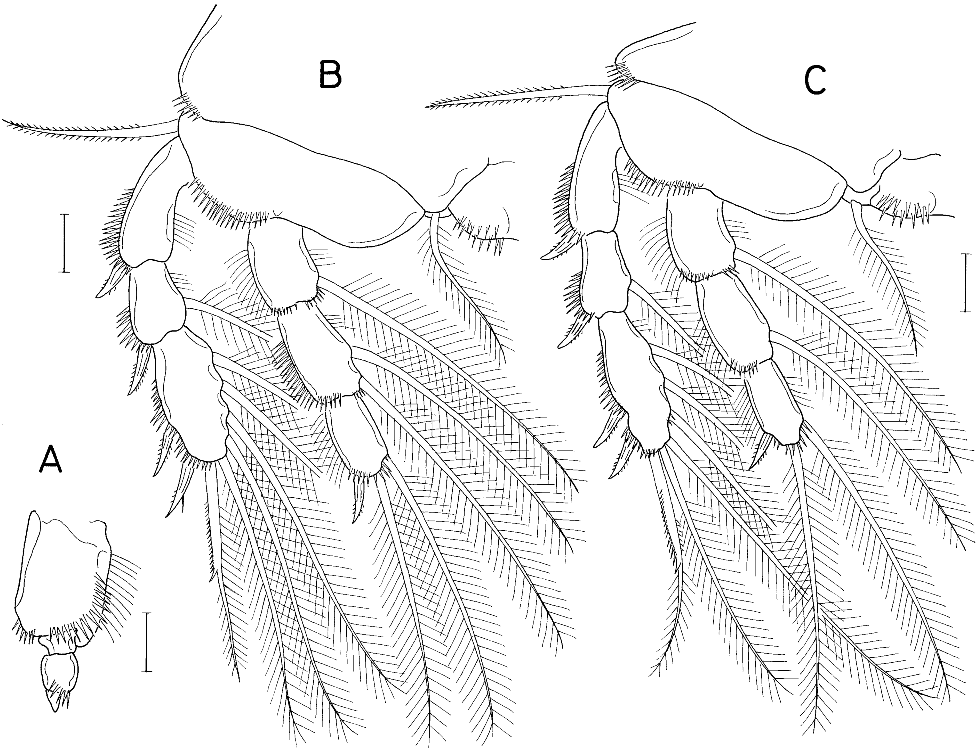

Fig. 7. *Rhodinicola laticauda* n. sp., female. A, abnormal endopod of leg 2; B, leg 3; C, leg 4. Scale bars: A–C = 20 μm.

laterally and without ornamentation; distal segment (78 × 45 μm) smaller, with hooked inner-distal corner and rows of spinules on outer margin, formula of armature 1-0; 4. Leg 6 represented by seta in egg sac attachment area (Fig. 5A).

Male.—Unknown.

Etymology.—The specific name is from the Latin "*latus*" (= broad) and "*cauda*" (= tail), referring to the unusually broad somites in the abdomen.

Remarks.—Although four species of clausiids are currently accepted in the genus *Rhodinicola* (O'Reilly 1995: 58), two of them, *Rhodinicola rugosa* (Giesbrecht) and *Rhodinicola thomassini* Laubier, should be removed, because they do not have 3-segmented rami on both exopod and endopod of legs 1 through 4. The former species was originally described by Giesbrecht (1895) and placed in a new genus *Seridium*, but it was later transferred to *Rhodinicola* by Bresciani (1964) because of the finding of their fundamental similarities in the cephalic appendages.

According to Bresciani's (1964) work on the other two species of *Rhodinicola*, *R. elongata* Levinsen, 1878, and *R. gibbosa* Bresciani, 1964, the present species is attributable to *Rhodinicola* because it shares with them the following characteristic features: (1) elongated body, (2) 3-segmented rami on legs 1–4, and (3) absence of an inner element (spine or seta) on the basis of leg 1. However, it differs from them in (1) lacking papilliform spine on the basal segment of the antennule, (2) with a subterminal spine on the mandible, (3) with thumb-like spinulose projection on the maxillule, (4) with much reduced maxilliped, and (5) much smaller caudal ramus (in comparison with anal somite).

CHARACTER ANALYSIS

In spite of arguments on the generic attribution of the clausiids (Gooding, 1963; O'Reilly, 1995; Kim, 2000, 2001), placement of the 21 species (including the above two newly described species) of poecilostome copepods in the Clausiidae is considered valid. As shown in Table 1, those 21 species of clausiids were proposed by their original authors in 12 genera. In the following, *Stockia indica* Sebastian and

Table 1. Poecilostome copepods considered valid in the Clausiidae.

Clausia antiqua Kim, 2001	*Pontoclausia tomis* Băcescu and Por, 1959
Clausia cluthae T. and A. Scott 1986	*Pherma curticaudatum* Wilson, 1923
Clausia lobata Kim, 2000	*Pseudoclausia giesbrechti* Bocquet and Stock, 1960
Clausia lubbockii Claparède, 1863	*Pseudoclausia longiseta* Bocquet and Stock, 1963
Clausia uniseta Bocquet and Stock, 1960	*Rhodinicola elongata* Levinsen, 1878
Clausia wilsoni Gooding, 1963	*Rhodinicola gibbosa* Bresciani, 1964
Doviella prima Rocha, 1986	*Rhodinicola laticauda* n. sp.
Indoclausia bacescui Sebatian and Pillai, 1974	*Rhodinicola thomassini* Laubier, 1970
Likroclausia namhaensis n. gen. and n. sp.	*Seridium rugosum* Giesbrecht, 1895
Mesnilia martinensis Canu, 1898	*Stockia indica* Sebastian and Pillai, 1974
Megaclausia mirabilis O'Reilly, 1995	

Pillai, 1974, will be removed from the prescribed analysis because only the male is known of that Indian clausiid, and, as in other symbiotic copepods, the taxonomy of Clausiidae is primarily based on the female characteristics. Furthermore, because specimens of the reported clausiid species are not all available for us to conduct a reexamination, we can use only the published information to compile data for character analysis. We opted to use only the thoracic legs in our analysis for the phylogenetic groupings of the clausiid copepods, because, in general, the thoracic legs of copepods are much easier to study than the cephalic appendages; information about legs found in the literature must be more reliable than those of other appendages.

In order to perform an unbiased analysis, each clausiid species listed in Table 1 is identified from this point on by its specific epithet only. Also, because more than half (11/20) of the clausiids have unknown males, the characters and character states to be analyzed are restricted to the female only. The characters selected for the analysis of phylogenetic relationships are listed in Appendix I with the code for each state indicated in parentheses. Based on Ho's (1984) phylogenetic analysis of the nereicoliform copepods, *Synaptiphilus* Canu and Cuénot, 1892, was selected as the outgroup to polarize the character states listed in Appendix I. Altogether 19 apomorphic states are recognized, and the coding for each of the 20 clausiid species is given in Appendix II. It is from this list an input file was created to conduct the cladistic analysis.

CLADISTIC ANALYSIS

In employing the computer program HENNIG86 to perform the cladistic analysis, the algorithm "mhennig*" was used first to construct initial cladogram(s) and save all shortest trees (cladograms) after running a limited branch-swapping. Six such trees were produced. Then, with the application of "bb*" command, those six initial trees were used to perform extended branch-swapping to produce multiple shortest trees. As a result of this combined algorithm, a total of 23 equally parsimonious trees were generated, with a length of 31 steps, a consistency index (CI) of 61, and a retention index (RI) of 90. In order to find whether any monophyletic clades persisted in those 23 trees obtained, the Strict (Nelson) Consensus Tree was calculated.

The consensus tree (Fig. 8) shows that the 20 species can be divided into six groups, with each representing a monophyletic clade and defined by one or more synapomorphies. The synapomorphies at each node are given in the caption for Fig. 8.

The basal two nodes, Node 25 and Node 24, are defined by the two apomorphic states of character 1. Group I, consisting of five species (*antiqua*, *lobata*, *prima*, *tomis*, *wilsoni*), is separated from the rest of the clausiids by maintaining the plesiomorphic state of character 1 (with posteromedial spine on the basis of leg 1) and Group II, comprising a single species (*namhaensis*), by having the apomorphic state of 1(1) (with a seta instead of spine). Thus, at Node 24, the synapomorphy is a further derived state of character 1 [1(2)] where the medial element on the basis of leg 1 is absent.

The next two nodes, Node 23 and Node 22, are defined by the apomorphic states of segmentation on the rami. Group III, comprising three species (*gibbosa*, *elongata*, *laticauda*), is separated by maintaining the plesiomorphic state of characters 7 (with 3-segmented endopod on leg 3) and 9 (with 3-segmented endopod on leg 4), and Group IV, consisting of two species (*cluthae*, *martinensis*), by keeping the plesiomorphic state of characters 2 (3-segmented

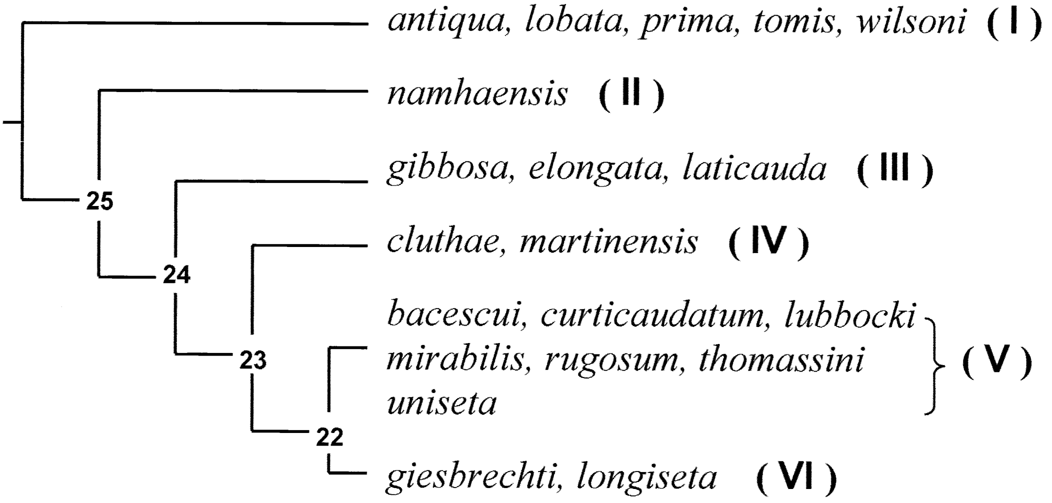

Fig. 8. A cladogram modified from the consensus tree of Clausiidae produced through analysis of the thoracic legs. Roman numerals on the right of taxa indicate the Group. Synapomorphies at each node (branch) are: 1(1) at Node 25; 1(2) at Node 24; 7(3) and 9(3) at Node 23; and 2(1), 3(1), 4(1), 5(1), 6(1), and 8 (2) at Node 22.

exopod on leg 1), 3 (3-segmented endopod on leg 1), 4 (3-segmented exopod on leg 2), 5 (3-segmented endopod on leg 2), 6 (3-segmented exopod on leg 3), and 8 (3-segmented exopod on leg 4). The terminal cohort, Group VI, comprising two species (*giesbrechti*, *longiseta*), is separated from the largest group, Group V, consisting of seven species (*bacescui*, *curticaudatum*, *lubbocki*, *mirabilis*, *rugosum*, *thomassini*, *uniseta*), by the reversal of characters 2 and 4 to the plesiomorphic states and gaining further apomorphic states for characters 6 [6(2)] and 8 [8(3)].

DISCUSSION

There is no doubt that the armature of podomeres in the clausiids must contain powerful information useful in the operation of cladistic analysis. However, without the chance of examining the specimen(s) of each of the 20 species and knowing information in the literature is not always reliable, it is difficult, if not impossible, to interpret certain patterns of armature transformation on a given podomere. Therefore, only the changes of the number of segments on a ramus in question are considered in the present cladistic analysis.

The result of our cladistic analysis indicates that creation of a new genus to accommodate *namhaensis* is justified. Its uniqueness is not only found in the possession of a naked seta on the posteromedial surface of the basis of leg 1 [1(1)], but also the antler-like projections on the pedigers 2 through 4 and the conversion of a ramus (leg 1 endopod) into a prehensile structure (see Figs. 2H, I). Interestingly, the latter unique character, though for the clausiids, is also found in some harpacticoid copepods, e.g., antler-like projections in Cerviniidae, and a prehensile endopod in Laophontidae.

Group I contains by far the most primitive clausiids. In addition to carrying a spine on the posteromedial surface of the basis of leg 1 (as in the outgroup *Synaptiphilus*), the leg rami are all 3-segmented, except for *lobata* which has 2-segmented rami on leg 4. With the general resemblance of cephalic appendages among the five species of this group, it is suggested to call this group *Pontoclausia*, which is the oldest genus name used for one of the component species *tomis* by Băcescu and Por (1959). Thus, the new names for the other four species will be *P. antiqua* (Kim, 2001), *P. lobata* (Kim, 2000), *P. prima* (Rocha, 1986), and *P. wilsoni* (Gooding, 1963).

It is interesting to point out that the three species in Group III are, as in *Pontoclausia* and *Likroclausia*, also characteristic in retaining 3-segmented rami on all of their thoracic legs. However, the three species (*gibbosa*, *elongata*, *laticauda*) are clustered together because of the absence of an element on the posteromedial surface of the basis of leg 1. This is the main reason for placing *laticauda* in the genus *Rhodinicola*. Whilst *gibbosa* and *elongata* are closer to each other in carrying papilliform setae on the first one or two segments of the antennule, this is not the case in *laticauda*. However, because we had only one specimen, it is impossible to state with certainty that papilliform setae are truly lacking on the antennule of *R. laticauda*. With this cladistic analysis, it became clear that *Rhodinicola thomassini* Laubier, 1970, needs to be removed from *Rhodinicola*, because it has 2-segmented (instead of 3-segmented) rami on all legs except for the endopods of legs 3 and 4 that bear only one segment.

The remaining three groups, Groups IV, V, and VI, are monophyletic because of the absence of endopods on legs 3 (character 7) and 4 (character 9). The first group that diverged within this clade contains *cluthae* and *martinensis*. These two species are distinguished from the rest by maintaining 3-segmented condition in both rami of legs 1 and 2 and both exopods of legs 3 and 4. Both species were reported and placed in genus *Mesnilia* Canu, 1898. Thus, Group IV is identified with *Mesnilia* without problem. However, that is not the case for Group V.

The seven species in Group V were placed, respectively, in six genera (*Clausia*, *Indoclausia*, *Megaclausia*, *Pherma*, *Rhodinicola*, *Seridium*) by their original authors. In our cladistic analysis, the seven species were clustered together because of the sharing of the following synapomorphies: lacking posteromedial element on the basis of leg 1, and bearing 2-segmented rami on legs 1 and 2. Thus, differences among them are chiefly found in the structure and/or absence of ramus on legs 3 and 4. Because their cephalic and oral appendages also show certain differences, this group must comprise more than one genus. However, clarification of this group will have to wait until reexamination of the specimen(s) of each species. It is interesting to point out that although Gooding (1959, fig. 12) suspected that there was a posteromedial spine on the basis of leg 1 basis of *Pherma curticaudatum*, based on our cladistic analysis, that cannot be the case.

Group VI is in sister-taxa relationship with Group V. It is distinguished from the latter by the reversal of characters 2 and 4 to the plesiomorphic state and by gaining further apomorphic states for characters 6 (with 1-segmented exopod on leg 3) and 8 (absence of exopod on leg 4). Thus, Bocquet and Stock's (1963) proposal of creating *Pseudoclausia* to accommodate *longiseta* and transfer into it Giesbrecht's (1893) "*Clausia lubbocki*" (renamed *Pseudoclausia giesbrechti*) is supported. Accordingly, Group VI can be considered as representing the genus *Pseudoclausia*.

CONCLUSION

It is clear from Fig. 8 that the results of our cladistic analysis do not support Gooding's (1963) "inclusive concept" on the treatment of the clausiid species. Whilst the taxonomical status of the genera *Indoclausia*, *Megaclausia*, *Pherma*, and *Seridium* are unclear, it is unequivocal to treat each of the following four genera as a valid taxon in addition to *Clausia*: *Mesnilia*, *Pontoclausia*, *Pseudoclausia*, and *Rhodinicola*. The results also show that both *Doviella prima* Rocha, 1986, and *Clausia wilsoni* Gooding, 1963, are to be transferred to *Pontoclausia*, and *Rhodinicola thomassini* Laubier, 1970, to *Clausia* for the time being.

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Appendix I. Characters and character states used in the cladistic analysis of Clausiidae, including the two new species. Numbers in parentheses denote the numerical coding of the character states.

1 Medial element on posterior margin of leg 1 basis: a spine (0), a seta (1), or absent (2)
2 Exopod of leg 1: 3-segmented (0) or 2-segmented (1)
3 Endopod of leg 1: 3-segmented (0), 2-segmented (1), or 1-segmented (2)
4 Exopod of leg 2: 3-segmented (0) or 2-segmented (1)
5 Endopod of leg 2: 3-segmented (0), 2-segmented (1), or 1-segmented (2)
6 Exopod of leg 3: 3-segmented (0), 2-segmented (1), or 1-segmented (2)
7 Endopod of leg 3: 3-segmented (0), 2-segmented (1), 1-segmented (2), or absent (3)
8 Exopod of leg 4: 3-segmented (0), 2-segmented (1), 1-segmented (2), or absent (3)
9 Endopod of leg 4: 3-segmented (0), 2-segmented (1), 1-segmented (2), or absent (3)

Appendix II. Data matrix of nine characters and their states in 20 species of Clausiidae as used in the cladistic (phylogenetic) analysis. "?" indicates an unknown state.

	Characters								
Species of Clausiidae	1	2	3	4	5	6	7	8	9
antiqua	0	0	0	0	0	0	0	0	0
bacescui	2	1	1	1	1	2	3	2	3
cluthae	2	0	0	0	0	0	3	0	3
curticaudatum	0	1	1	1	1	1	1	3	3
elongata	2	0	0	0	0	0	0	0	0
gibbosa	2	0	0	0	0	0	0	0	0
giesbrechti	2	0	1	0	1	2	3	3	3
laticauda	2	0	0	0	0	0	0	0	0
lobata	0	0	0	0	0	0	0	1	1
longiseta	2	0	1	0	1	2	3	3	3
lubbocki	2	1	1	1	1	2	3	3	3
martinensis	?	0	0	0	0	0	3	0	3
mirabilis	2	1	1	1	1	1	3	1	3
namhaensis	1	0	1	0	0	0	0	0	0
prima	0	0	0	0	0	0	0	0	0
rugosum	2	1	2	1	2	1	2	1	2
thomassini	2	1	1	1	1	1	2	1	2
tomis	0	0	0	0	0	0	0	0	0
uniseta	2	1	1	1	1	2	3	3	3
wilsoni	0	0	0	0	0	0	0	0	0