ZOOLOGICAL SCIENCE **29**: 127–133 (2012)

# A New Species of *Paramacrochiron* (Copepoda: Cyclopoida: Macrochironidae) Associated with the Rhizostome Medusa *Rhopilema hispidum* Collected from the Gulf of Thailand, with a Phylogenetic Analysis of the Family Macrochironidae

**Susumu Ohtsuka[1]*, Geoffrey A. Boxshall[2], and Khwanruan Srinui[3]**

[1]*Takehara Marine Science Station, Setouchi Field Science Center, Graduate School of Biosphere Science,*
*Hiroshima University, 5-8-1 Minato-machi, Takehara, Hiroshima 725-0024, Japan*
[2]*Department of Zoology, The Natural History Museum, Cromwell Road,*
*London SW7 5BD, United Kingdom*
[3]*Institute of Marine Science, Burapha University,*
*Bangsaen, Chon Buri, Thailand 20131*

***Paramacrochiron thailandicum* n. sp. (Copepoda: Cyclopoida: Macrochironidae) is described from the rhizostome medusa *Rhopilema hispidum* occurring in the Gulf of Thailand. The new species is distinguishable from other congeners mainly by detailed features of the fourth legs and the urosome in both sexes. Copepodid and adult stages of the genus *Paramacrochiron* seem to be host-specific to rhizostome medusae, but may spend periods free in the plankton or benthos during the absence of the host. A cladistic analysis shows that the Macrochironidae comprises two main lineages. *Paramacrochiron* is recovered as a monophyletic group, located on one lineage together with *Pseudomacrochiron*, which appears as a paraphyletic taxon with the limited character set used. The other main lineage comprises the genera *Macrochiron* and *Sewellochiron*, but the sole species of the latter genus, *Sewellochiron fidens*, is nested within *Macrochiron*. This analysis provides little support for maintaining *Sewellochiron* as a separate genus.**

**Key words:** copepod, rhizostome medusa, *Paramacrochiron*, phylogeny, *Rhopilema hispidum*, symbiont

## INTRODUCTION

A wide variety of symbioses exists between jellyfish and invertebrates/vertebrates, ranging from phoresy through parasitism and commensalism to mutualism (Ohtsuka et al., 2009, 2010). Some cyclopoid and harpacticoid copepods live in association with scyphomedusae in tropical and subtropical waters of the world (Humes, 1953, 1969, 1970, 1985; Reddiah, 1968, 1969; Boxshall and Halsey, 2004; Browne and Kingsford, 2005). During our survey of the edible rhizostome medusae of Indonesia and Thailand, an undescribed species of the cyclopoid copepod genus *Paramacrochiron* Sewell, 1949 (family Macrochironidae) was discovered from the rhizostome medusa *Rhopilema hispidum* (Vanhöffen, 1888) in the Gulf of Thailand, and is described herein. Copepods in the genus seem to be closely associated with rhizostome medusae occurring in the tropical and subtropical waters of the Indo-West Pacific and its species consume mucus released from the medusae (Humes, 1969, 1970; Browne and Kingsford, 2005). Members of *Paramacrochiron* have been only rarely reported as free living within plankton communities (Thompson and Scott, 1903; Sewell, 1949; Wilson, 1950; Browne and Kingsford, 2005; Mulyadi, 2005). Including the present new species, the genus *Paramacrochiron* now accommodates eight species: *P. maximum* Thompson and Scott, 1903, *P. pacificum* Wilson, 1950, *P. ennorense* Reddiah, 1968, *R. sewelli* Reddiah, 1968, *P. rhizostomae* Reddiah, 1968, *P. japonicum* Humes, 1970, *P. amboinense* Mulyadi, 2005, and *P. thailandicum* n. sp. described herein.

The family Macrochironidae is composed of four genera: *Macrochiron* Brady, 1872, *Paramacrochiron*, *Pseudomacrochiron* Reddiah, 1969, and *Sewellochiron* Humes, 1969. All genera are associated with marine invertebrates (Boxshall and Halsey, 2004). In this study, we performed a preliminary cladistic analysis for the family to verify the generic placement of the new species, to test the validity of the genera, and to identify any general patterns in host utilization.

## MATERIALS AND METHODS

Three individuals of the host rhizostome *Rhopilema hispidum* (bell diameter 34.5, 39.0, 46.5 cm) were collected from off Laem Phak Bia (13°1.69′ N, 100°5.2′ E) on 19 October 2010 on the coast of the Gulf of Thailand. A scoop-net with 50-cm diameter and 2-mm mesh size was deployed from fishing boats. Each of the medusae was put into a plastic bag and cooled with ice cubes in cooler boxes. In the laboratory the medusae were washed using filtered seawater and the supernatant washings were then filtered through a sieve of 2-mm mesh size. Another species of rhizostome,

---

* Corresponding author. Tel. : +81-846-22-2362;
Fax : +81-846-23-0038;
E-mail : ohtsuka@hiroshima-u.ac.jp

doi:10.2108/zsj.29.127

*Lobonemoides robustus* Stiasny, 1920, was also collected off Laem Phak Bia and examined, but no copepods were associated with it.

The type specimens are deposited at the Kitakyushu Museum of Natural History and Human History, Japan (KMNH IvR).

The cladistic analysis was conducted using PAUP version 4.0b10 (Swofford, 2001) on a matrix comprising 13 characters and 27 taxa (Table 1). *Contomolgus lokobeensis* Humes and Stock, 1973 was used as the outgroup: it is a member of the family Rhynchomolgidae, which was identified as the plesiomorphic sister-group to the lineage containing the Macrochironidae in the analysis of Humes and Boxshall (1996). Two described species of *Paramacrochiron*, and one each of *Pseudomacrochiron* and *Macrochiron* were omitted from the analysis because they were either inadequately described or known from only one sex. The characters and states are listed in Table 2: characters were scored 0, 1, 2 or "?" for missing characters. A heuristic search was performed and all characters were treated as unordered.

**Table 1.** Characters and character states used in cladistic analysis.

1. Rostrum: tapering or rounded (0), terminating in needle-like point (1)
2. Antenna segmentation: 4-segmented (0), 3-segmented (with second and third endopodal segments fused) (1)
3. Main claw of antenna: long and unornamented (0), long ornamented with denticles (1), short, strongly recurved (2)
4. Secondary claw on antenna: long and weakly curved (0), absent (1)
5. Maxilla claw: inner concave margin smooth or with row of tiny denticles (0), inner with single, usually conspicuous tooth on concave margin (1)
6. Form of female maxilliped: subchelate, with basis typically shorter and more robust than syncoxa (0), elongate with slender basis (1)
7. Female maxilliped: basis endopod articulation expressed (0), basis and endopod fused (1)
8. Female maxilliped, number of terminal elements: 4 (0), 3 (1)
9. Leg 4 endopod, inner seta derived from first endopodal segment: present (0), absent (1)
10. Leg 4 third exopodal segment, proximal outer margin spine: present (total 3 spines) (0), absent (total 2 spines) (1)
11. Leg 4 endopod: articulation between first and second ancestral segments expressed (0), endopod with marginal notch marking plane of non-expressed articulation between first and second segments (1), lacking marginal notch (2)
12. Leg 4 endopod, distal corners of segment: rounded or with slight points (0), drawn out into long pointed processes (1)
13. Male maxilliped claw: tapering to simple tip (0), with expanded crest unilaterally at tip (1)

**Table 2.** Character states for Macrochironidae. Characters were scored 0, 1, 2 or "?" for missing characters.

| Taxon\Character No. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Contomolgus lokobeensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Macrochiron angulare* | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Macrochiron anomalum* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Macrochiron cheliferum* | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 |
| *Macrochiron echinicolum* | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Macrochiron fucicolum* | 1 | 1 | 1 | 0 | ? | 0 | 0 | ? | 1 | 1 | 1 | 0 | ? |
| *Macrochiron hudsoni* | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | ? |
| *Macrochiron lobatum* | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *Macrochiron lytocarpi* | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| *Macrochiron mutatum* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| *Macrochiron rostratum* | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Macrochiron sargassi* | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Macrochiron valgum* | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Macrochiron vervoorti* | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 |
| *Paramacrochiron amboinense* | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 |
| *Paramacrochiron ennorense* | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 |
| *Paramacrochiron japonicum* | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 |
| *Paramacrochiron sewelli* | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 |
| *Paramacrochiron rhizostomae* | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 |
| *Paramacrochiron thailandicum* | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 |
| *Pseudomacrochiron fucicolum* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 |
| *Pseudomacrochiron ornatum* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 |
| *Pseudomacrochiron parvum* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | ? |
| *Pseudomacrochiron pocilloporae* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Pseudomacrochiron stocki* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Pseudomacrochiron urosternum* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| *Sewellochiron fidens* | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |

## TAXONOMY

### Subclass Copepoda Milne-Edwards, 1840
### Order Cyclopoida Burmeister, 1834
### Family Macrochironidae Humes and Boxshall, 1996
### Genus *Paramacrochiron* Sewell, 1949
### *Paramacrochiron thailandicum* n. sp.
### (Figs. 1–3)

*Types*. Holotype, 1♀, whole specimen, 2.65 mm in body length, associated with *Rhopilema hispidum* collected from off Laem Phak Bia, Gulf of Thailand (KMNH IvR 500,514). Paratypes: 6♀♀, whole specimens, 2.30–2.79 mm (KMNH IvR 500,515–500,520); 1♀, dissected and mounted on five glass slides, 2.63 mm (KMNH IvR 500,521); 16♂♂, whole specimens, 1.88–2.37 mm (KMNH IvR 500,522–500,537); 1 ♂, dissected and mounted on four glass slides, 2.21 mm (KMNH IvR 500,538); collection site as for the holotype.

*Body length.* Female 2.30–2.79 mm (mean ± standard deviation = 2.51 ± 0.03 mm, *N* = 8). Male 1.88–2.37 mm (mean ± standard deviation = 2.11 ± 0.02 mm, *N* = 17).

*Description of female*. Body (Fig. 1A) cyclopiform. Cephalosome almost completely fused to first pedigerous somite with weak suture line dorsally and laterally. Rostrum (Fig. 1B) protruding ventroposteriorly into smoothly round process. Labrum (Fig. 1C) bilobed, shallowly concave midway along posterior margin. Second pedigerous somite separate from first; third pedigerous somite constricted anteriorly; fourth pedigerous somite produced posterolaterally into rounded lobe reaching beyond fifth pedigerous somite. Urosome 5-segmented; fifth pedigerous somite small, wider than long; genital double-somite 1.5 times wider than long, swollen anterolaterally; ratio of lengths of genital double-somite and free abdominal somites (two postgenital and anal) 2.0: 1.0: 1.0: 1.7. Caudal rami (Fig. 1D) symmetrical, 3.8 times longer than wide; caudal setae III and VI plumose basally; minute prominence at base of seta VI.

Antennule (Fig. 1E) 7-segmented; armature elements as follows: first–4 setae, second–13, third–6, fourth–3, fifth–4+ae, sixth–2+ae, seventh–7+ae; second segment with sclerotized ridge running length of segment; terminal seta and aesthetasc fused at base. Antenna (Fig. 1F) stout, 4-segmented; first and second segments each bearing one minute seta anteriorly; third segment small, with three setae of unequal length; fourth segment with heavily sclerotized, smoothly curved claw and six setae. Mandible (Fig. 1G) with spinular row and spinulose seta proximally; terminal, slender part bipinnate. Maxillule (Fig. 1H) with four unequal setae terminally, one of which clearly spinulose. Maxilla (Fig. 1I) with first segment unarmed; second segment triangular, with one naked and one spinulose seta and smoothly curved, spinulose lash terminally. Maxilliped (Fig. 1J) with first segment unarmed; second segment swollen midway, with 2 minute, spinulose setae not reaching posterior end of seg-

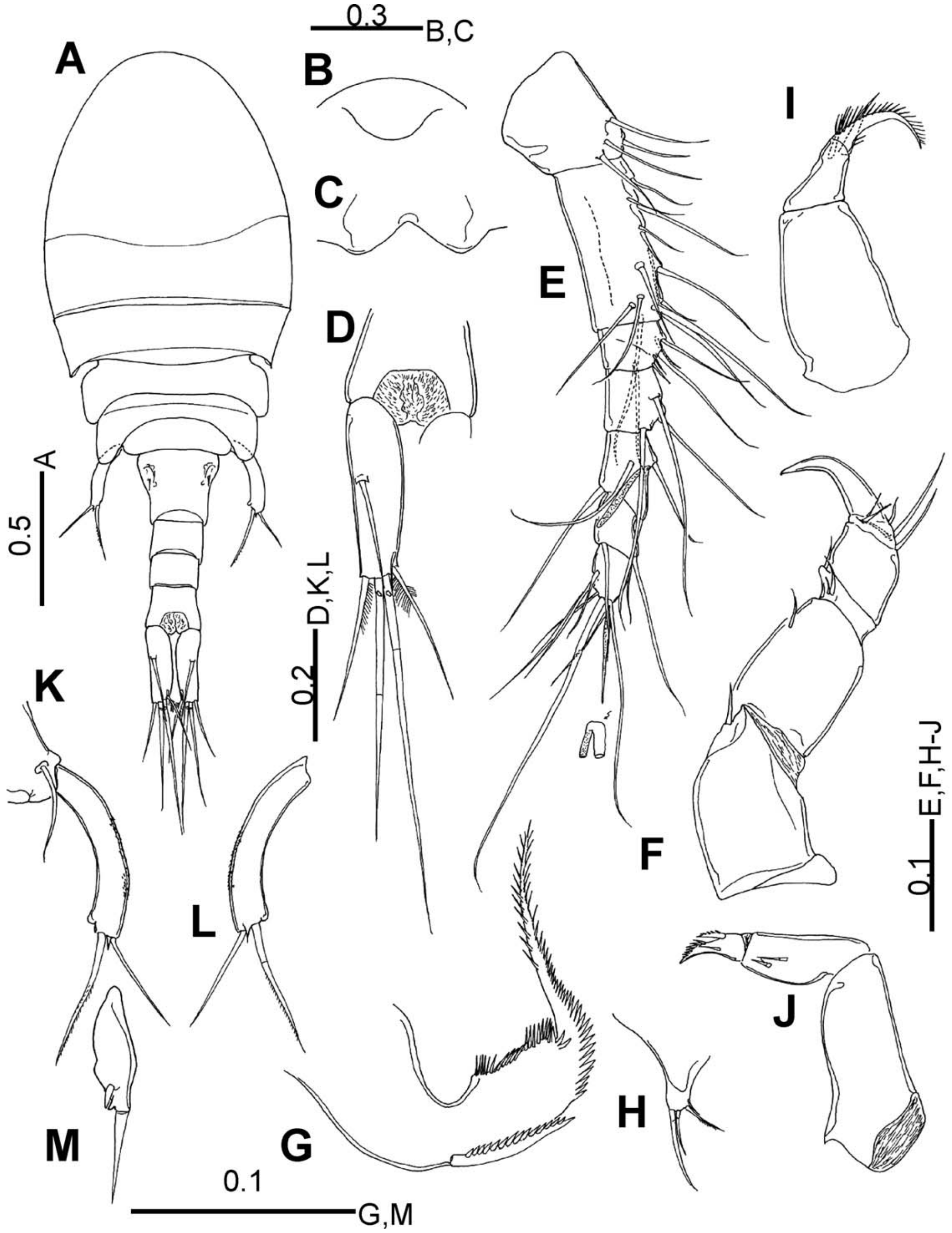

**Fig. 1.** *Paramacrochiron thailandicum* n. sp., female (paratype, KMNH IvR 500,521). **(A)** habitus, dorsal view; **(B)** rostrum; **(C)** labrum; **(D)** left caudal ramus and anal somite, dorsal view; **(E)** antennule; **(F)** antenna; **(G)** mandible; **(H)** maxillule; **(I)** maxilla; **(J)** maxilliped; **(K)** right leg 5, dorsal surface; **(L)** right leg 5, ventral surface; **(M)** left leg 6. Scales in mm.

ment; third segment small, bearing one naked and one spinulose seta, and spinulose process terminally.

Legs 1–4 (Fig. 2A–D) each biramous with 3-segmented rami except for 1-segmented endopod of leg 4; inner coxal setae of all legs plumose; basis furnished with tuft of fine setules along inner margin and triangular process near base of exopod; outer basal setae of legs finely serrated. Endopod of leg 4 (Fig. 2D) reaching mid-length of third exopodal segment; 2 terminal setae unequal in length; serrated process present at base of inner seta. Leg 5 (Fig. 1K, L) composed of basal segment incorporated into somite bearing one dorsal seta and free exopodal segment; free segment curved inward, with fine spinules along outer posterior half of length; inner terminal portion with rounded inner process and pointed terminal process; inner spinulose seta longer than outer naked seta, reaching slightly beyond first abdom-

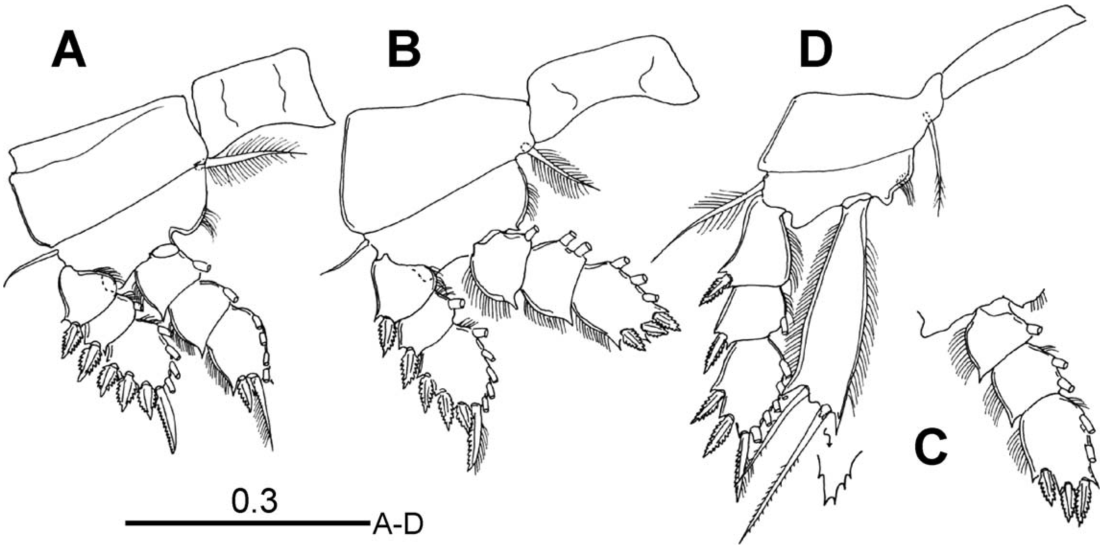

**Fig. 2.** *Paramacrochiron thailandicum* n. sp., female (paratype, KMNH IvR 500,521). **(A)** leg 1, posterior surface; **(B)** leg 2, posterior surface; **(C)** endopod of leg 3, posterior surface; **(D)** leg 4, posterior surface. Scales in mm.

inal somite. Leg 6 (Fig. 1M) consisting of genital flap bearing two naked elements and minute prominence between them.

*Description of male*. Body (Fig. 3A) similar to, but more slender than, that of female. Caudal rami (Fig. 3B) relatively shorter than those of female. Genital somite swollen; ratio of lengths of genital, three abdominal and anal somites 3.3: 1.0: 1.0: 1.0: 1.5.

Antennule (Fig. 3C) similar to that of female except for presence of aesthetasc on second and fourth segments. Antenna (Fig. 3D), mandible, maxillule and maxilla similar to those of female. Maxilliped (Fig. 3E) well-developed, 4-segmented; first and third segments unarmed; second segment long, bearing row of spinules along nearly entire inner margin and two unequal setae in middle; fourth segment represented by drawn-out claw curved smoothly inward, with one minute and one spiniform element basally.

Legs 1–4 similar to those of female except for endopod of leg 4 (Fig. 3F, G) reaching midpoint of third exopodal segment; endopod variable in ornamentation with or without outer subterminal, acutely pointed prominence; fusion line visible in some endopods (Fig. 3G). Leg 5 (Fig. 3H) consisting of basal part representing incorporated protopodal segment, bearing dorsal seta, and free exopodal segment with two setae terminally. Leg 6 (Fig. 3I) composed of genital flap bearing two nearly equal setae and minute prominence at inner distal corner.

*Variation*. The endopods of legs 4 of the male exhibit variability. A minute prominence on the outer margin of the left endopod of leg 4 can be present or absent.

*Remarks*. Among its seven congeners, the new species most closely resembles *Paramacrochiron japonicum* Humes, 1970, found associated with a rhizostome in Japan. However, it can be distinguished from the latter by: (1) the length ratio of the genital double-somite and postgenital somites of the female 2.0: 1.0: 1.0: 1.7 (2.7: 1.4: 1.0: 1.6 in *P. japonicum*); (2) the length ratio of the genital somite and postgenital somites of the male 3.3: 1.0: 1.0: 1.0: 1.5 (4.6: 1.4: 1.3: 1.0: 1.5 in *P. japonicum*); (3) female leg 5 nearly reaching the end of the genital double-somite (mid-point of the genital double-somite); (4) the posterior margin of the labrum shallowly concave at midpoint (deeply concave); (5) two setae on the second segment of the female maxilliped short, not reaching to the terminal end of the segment (long, reaching to or beyond the terminal end); (6) the presence of minute spinules along the outer margin of the free segment of leg 5; (7) lack of an proximal aesthetasc on the second segment of the male antennule (present); (8) proximal spinules along the anterior margin of the second segment of the male maxilliped larger than in *P. japonicum*; (9) the endopod of male leg 4 reaching midpoint of the third exopodal segment (not reaching the distal end of the second exopodal segment).

The new species is also similar to *P. amboinense* Mulyadi, 2005 found from a plankton sample in Indonesia. However it can be readily differentiated from the latter by: (1) the caudal ramus is much more slender (3.8 times as long as wide) (2.4 times in *P. amboinense*); (2) length ratio of the genital double-somite and postgenital somites 2.0: 1.0: 1.0: 1.7 (2.3: 1.4: 1.0: 2.5); (3) female leg 5 ornamented with spinules along the outer margin (unornamented). The female of the new species also has larger female body size (ca. 2.5 mm) compared to 2.38 mm in *P. amboinense*, but this may not be significant, as the body length of the new species ranges from 2.30 to 2.79 mm.

The present new species is readily distinguishable from the remaining six congeners by differences in the proportional lengths of the urosome somites and by detailed features of the antennae, female maxillipeds, endopods of legs 1 and 4, and leg 5. Unfortunately ovigerous females of the new species were not found in the present study, but the shape of egg-sacs is also species-specific (see Humes, 1970).

Early and late copepodid stages of *P. thailandicum* were also found associated with *Rhopilema hispidum* in the Gulf of Thailand (present study). In addition to *P. thailandicum* other symbionts were collected from the host medusa *R. hispidum*. The ophiuroid *Ophiocnemis marmorata* (Lamarck, 1816) and

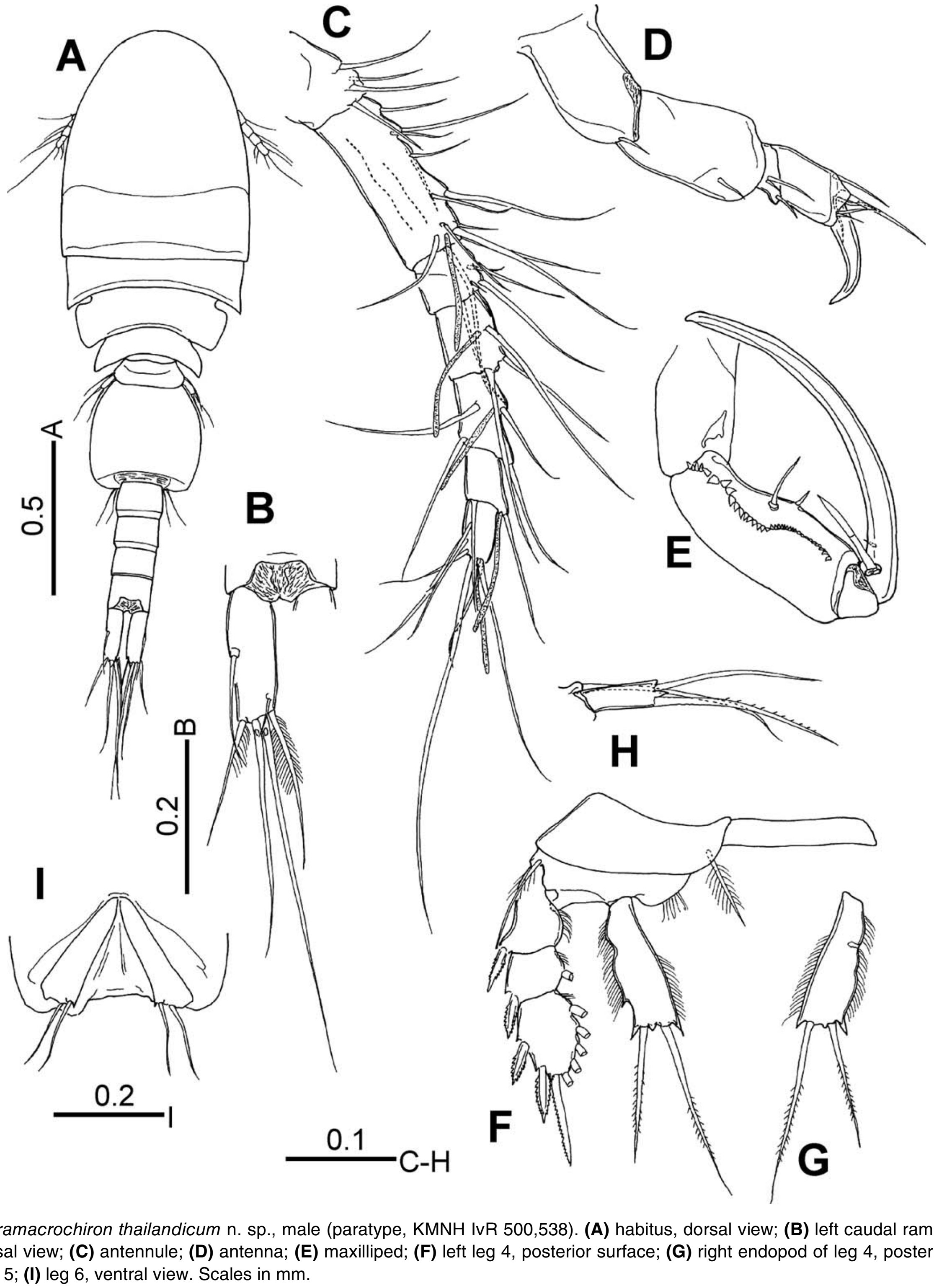

**Fig. 3.** *Paramacrochiron thailandicum* n. sp., male (paratype, KMNH IvR 500,538). **(A)** habitus, dorsal view; **(B)** left caudal ramus and anal somite, dorsal view; **(C)** antennule; **(D)** antenna; **(E)** maxilliped; **(F)** left leg 4, posterior surface; **(G)** right endopod of leg 4, posterior surface.; **(H)** right leg 5; **(I)** leg 6, ventral view. Scales in mm.

the caridean shrimp *Latreutes* sp. were found on the oral arms of the medusae, and juveniles of shrimp scad *Alepes djedaba* (Forsskål, 1775) were found schooling around the medusae.

*Etymology*. The specific name of the new species is derived from its locality (Latin *thailandicus*).

## PHYLOGENY

The heuristic analysis yielded 41 trees (length 31) from which the strict and 50% consensus trees were calculated. Given the low number of characters (13) relative to the number of included taxa (27), the strict consensus tree (Fig. 4) is used here and our phylogenetic inferences should be regarded as preliminary. The analysis suggests that the Macrochironidae comprises two main lineages, each containing two of the four genera accepted as valid by Humes and Boxshall (1996). *Paramacrochiron* is recovered as a monophyletic group and the new species is confirmed as a member of the genus. On this lineage together with *Paramacrochiron* are the species of *Pseudomacrochiron*; however, this genus appears only as a paraphyletic taxon. Given the relatively small numbers of characters (13) used in the matrix compared to the number of taxa (27 species), we propose to retain *Pseudomacrochiron* until a more comprehensive analysis can be performed. The second main lineage comprises the type genus *Macrochiron* and the monotypic *Sewellochiron*. However, the sole species of *Sewellochiron, S. fidens* Humes, 1969, is nested within *Macrochiron* (Fig. 4), occurring on a small lineage together with *M*. *echinicolum* Humes and Stock, 1973 and *M. sargassi* Sars, 1916. This analysis provides little support for retaining *Sewellochiron* as a separate genus.

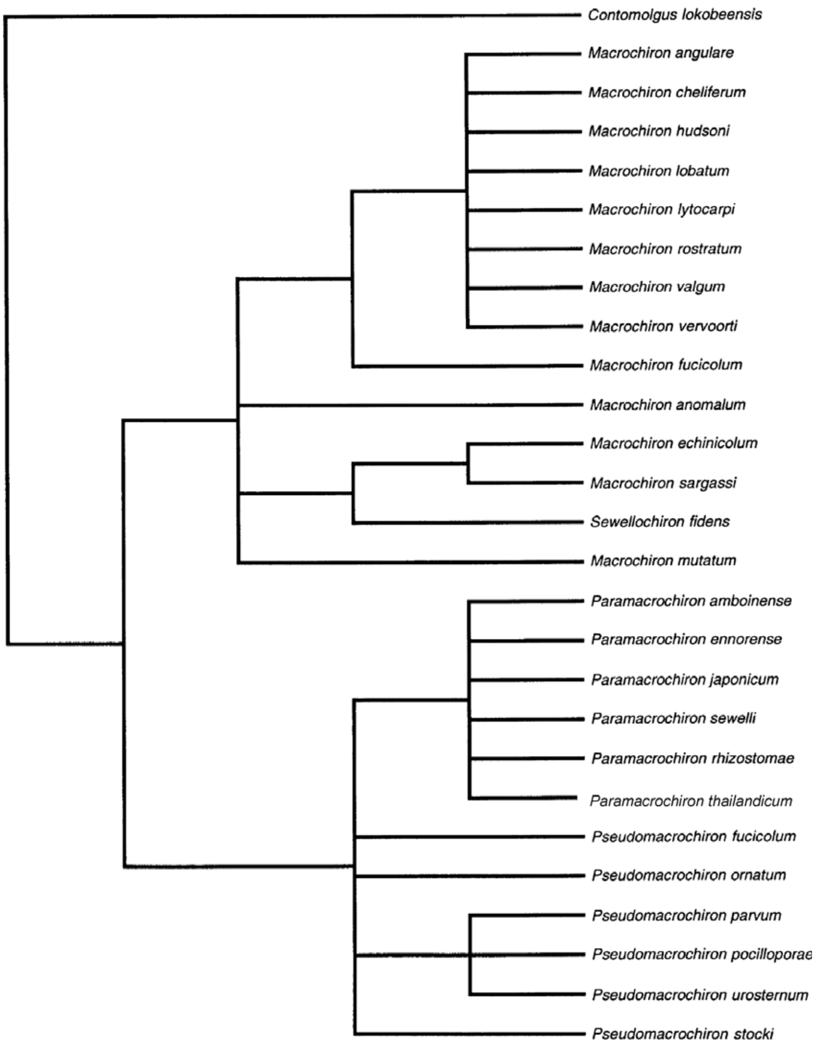

**Fig. 4.** Strict consensus tree of the family Macrochironidae.

**Table 3.** Host and locality of *Paramacrochiron*.

| Species | Host | Locality | Reference |
|---|---|---|---|
| *Paramacrochiron maximum* (Thompson & Scott, 1903) | *Catostylus mosaicus* | New South Wales, Australia | Browne and Kingsford (2005) |
| *Paramacrochiron pacificum* Wilson, 1950 | – | off Luzon, Philippines | Wilson (1950) |
| *Paramacrochiron ennorense* Reddiah, 1968 | Unidentified medusae | Madras, India | Reddiah (1968) |
| *Paramacrochiron sewelli* Reddiah, 1968 | *Lychnorhiza malayensis* | Madras, India | Reddiah (1968) |
| *Paramacrochiron rhizostomae* Reddiah, 1968 | *Rhizostoma* sp. | Gulf of Manaar, India | Reddiah (1968) |
| *Paramacrochiron japonicum* Humes, 1970 | *Thysanostoma thysanura* | Shirahama, Japan | Humes (1970) |
| *Paramacrochiron amboinense* Mulyadi, 2005 | – | Ambon Bay, Indonesia | Mulyadi (2005) |
| *Paramacrochiron thailandicum* n. sp. | *Rhopilema hispidum* | Gulf of Thailand, Thailand | present study |

## DISCUSSION

Host specificity and locality data for species of the genus *Paramacrochiron* of the family Macrochironidae are summarized in Table 3. This genus appears to be host-specific to scyphomedusae, in particular, to rhizostome medusae occurring in tropical and subtropical waters of the world. Since these copepods were usually collected from washings of medusae (Reddiah, 1968; present study), the attachment sites on the hosts were often not specified. However, *Paramacrochiron maximum* inhabits the oral arms and gastric cirri of the rhizostome *Catostylus mosaicus* (Quoy and Gaimard, 1824) (Browne and Kingsford, 2005). Methods of collection and the morphological similarities between these copepods suggest that they are all essentially ectoparasites on the outer surface of the host medusae, as for *P. maximum*. In macrochironid genera other than *Paramacrochiron*, only *Sewellochiron* is associated with a rhizostome, *Cassiopea xamachana* Bigelow, 1892 (Humes, 1970). Species of *Macrochiron* and *Pseudomacrochiron* have been reported from semaeostome medusae, hydrozoans and other invertebrates (Boxshall and Halsey, 2004). There is a single anomalous report of *Paramacrochiron sewelli* from the gills of a teleost fish, *Trachurus trachurus* (Linnaeus, 1758) (Avdeev, 1975).

The life cycle of these medusa-associated macrochironid copepods is still unknown. Not only adults but also copepodid stages of *Paramacrochiron* are found from the host medusae (Reddiah, 1968; Browne and Kingsford, 2005; present study). In addition, adults and/or copepodid stages of three species of *Paramacrochiron* were also collected from plankton (Thompson and Scott, 1903; Wilson, 1950; Browne and Kingsford, 2005; Mulyadi, 2005). Abundances of *Paramacrochiron maximum* on the host rhizostome *Catostylus mosaicus* and in plankton samples in Australian waters were compared by Browne and Kingsford (2005) who found that adults and copepodid stages occurred mainly on the oral arms of the medusae and the maximum abundance was 5,675 individuals per medusa. In contrast, in planktonic samples the density of the copepods was at most 0.9 and 0.3 individuals per $m^3$ inside and outside the aggregation of the medusae, respectively. We infer that these planktonic forms had become detached from the host medusae by accident.

The seasonal occurrence of host medusae in the water column is usually restricted. For example, jellyfish fisheries (target species: *Rhopilema hispidum*, *Lobonemoides robustus*) in the Gulf of Thailand are restricted to the period from August to November (Nishikawa et al., unpub. data). It is possible that *P. thailandicum* spend a part of its life cycle free in planktonic and/or benthic mode during periods when the medusae are absent from the water column. Browne and Kingsford (2005) supposed that *P. maximum* was present in very low densities in the water column during such periods and restores its association with any available medusae, such as *Catostylus mosaicus*, when it becomes available. Since other macrochironid genera such as *Pseudomacrochiron* are found not only as commensals on host medusae but also as free-living forms in the plankton (Krishnaswamy, 1952; Reddiah, 1969; Morris, 1973; Boxshall and Halsey, 2004), such a life cycle as proposed for *Paramacrochiron* may be applicable to these copepods.

Many kinds of planktonic and benthic animals such as fish juveniles, shrimps, crabs and ophiuroids are associated with edible rhizostome medusae in addition to commensals like *Paramacrochiron* (Ohtsuka et al., 2009, 2010; present study). Jellyfish fisheries intensively carried out in southeastern Asian countries and China (Omori and Nakano, 2001; Nishikawa et al., 2008) might hinder recruitment and dispersal of these animals (Ohtsuka et al., 2010). According to Omori and Nakano (2001), the average catch of edible rhizostomes in these areas attains 321,000 ton in wet weight. Nishikawa et al. (2008) also estimated the catch of rhizostomes (mainly *Rhopilema hispidum*) in northern Vietnam during a fishing season as about 800,000 to 1,200,000 individuals. Considering such large catches of edible jellyfishes, it seems likely that the population dynamics of the associates, as well as the hosts, are impacted by the pressure of the fisheries.

## ACKNOWLEDGMENTS

We would like to express our sincere thanks to Drs. Jun Nishikawa and Hiroshi Miyake for their cooperation at sea. This study was partially supported by grant-in-aid from the Japan Society of Promotion for Science (bilateral cooperation between Japan and Indonesia in 2008–2010; No. 20380110).

## REFERENCES

Avdeev GV (1975) The first case of discovery of Lichomologidae member (Copepoda, Cyclopoida) on a vertebrate animal from the region of Sri Lanka. Parazitologiya 9: 201–204 (in Russian with English summary)

Boxshall GA, Halsey SH (2004) An Introduction to Copepod Diversity. Ray Society, London

Browne JG, Kingsford MJ (2005) A commensal relationship between the scyphozoan medusae *Catostylus mosaicus* and the copepod *Paramacrochiron maximum*. Mar Biol 146: 1157–1168

Humes AG (1953) Two new semiparasitic harpacticoid copepods from the coast of New Hampshire. J Washington Acad Sci 43: 360–373

Humes AG (1969) A cyclopoid copepod, *Sewellochiron fidens* n. gen., n. sp., associated with a medusa in Puerto Rico. Beaufortia 16: 171–183

Humes AG (1970) *Paramacrochiron japonicum* n. sp., a cyclopoid copepod associated with a medusa in Japan. Publ Seto Mar Biol Lab 18: 223–232

Humes AG (1985) Cnidarians and copepods: a success story. Trans Am Microsc Soc 104: 313–320

Humes AG, Boxshall GA (1996) A revision of the lichomolgoid complex (Copepoda: Poecilostomatoida), with the recognition of six new families. J Nat Hist 30: 175–227

Krishnaswamy S (1952) Some new species of copepods from Madras coast. Rec Ind Mus 49: 321–336

Morris B (1973) Two new species of *Macrochiron* Brady, 1872, and a new record for *Pseudomacrochiron parvum* (A. Scott, 1909) in the Northwest Atlantic (Copepoda, Cyclopoida). Crustaceana 24: 51–71

Mulyadi (2005) Two new species of *Hemicyclops* (Copepoda, Clausiidae) and a new species of *Paramacrochiron* (Copepoda, Macrochironidae) from Indonesian waters. Crustaceana 78: 917–929

Nishikawa J, Thu NT, Ha TM, Thu PT (2008) Jellyfish fisheries in northern Vietnam. Plankton Benthos Res 3: 227–234

Ohtsuka S, Koike K, Lindsay D, Nishikawa J, Miyake H, Kawahara M, et al. (2009) Symbionts of marine medusae and ctenophores. Plankton Benthos Res 4: 1–13

Ohtsuka S, Kondo Y, Sakai Y, Shimazu T, Shimomura M, Komai T, et al. (2010) In-situ observations of symbionts on medusae occurring in Japan, Thailand, Indonesia and Malaysia. Bull Hiroshima Univ Mum 2: 9–18

Omori M, Nakano E (2001) Jellyfish fisheries in southeastern Asia. Hydrobiologia 451: 19–26

Reddiah K (1968) Three new species of *Paramacrochiron* (Lichomolgidae) associated with medusae. Crustaceana, Suppl 1: 193–209

Reddiah K (1969) *Pseudomacrochiron stocki* n. g., n. sp., a cyclopoid copepod associated with a medusa. Crustaceana 16: 43–50

Sewell RBS (1949) The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida. John Murray Exped 1933–34, Sci Rept 9: 17–199

Swofford DL (2001) Phylogenetic Analysis Using Parsimony (*and other methods). Ver. 4.0b. Sinauer Associates, Sunderland, MA

Thompson IC, Scott A (1903) Report on the Copepoda collected by Professor Herdman, at Ceylon, in 1902. Rept Govt Ceylon Pearl Oyster Fish. Gulf of Manaar, 1, Suppl Rept 7: 227–307

Wilson CB (1950) Copepods gathered by the United States Fisheries Steamer "Albatross" from 1887–1909, chiefly in the Pacific Ocean. Bull US Nat Mum 100: 141–441

(Received June 2, 2011 / Accepted August 16, 2011)