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A new genus and species of nicothoid copepod (Crustacea: Copepoda: Siphonostomatoida) parasitic on the mysid *Siriella okadai* Ii from off Japan

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Abstract

Neomysidion rahotsu, a new genus and species of the siphonostomatoid family Nicothoidae Dana, 1849, is described from the marsupium of the mysid *Siriella okadai* Ii in the shallow waters of the Seto Inland Sea of Japan. This is the first record of nicothoids parasitic on mysids in Asian waters. The new genus is closely related to the three other mysid-infesting nicothoid genera, *Aspidoecia* Giard & Bonnier, 1889, *Mysidion* Hansen, 1897 and *Hansenulus* Heron & Damkaer, 1986, but is distinguishable by: the trunk of adult females being remarkably transformed at maturity; the male cephalosome covered with numerous rounded knobs posterodorsally; the absence of caudal rami in the female; three-segmented antennules in both sexes; two-segmented antenna in the male; remarkable sexual dimorphism in the maxillae; the presence of a pair of spinulate sclerites between the maxillae in both sexes; three-segmented maxillipeds in both sexes; the absence of legs 1 to 5 in the female; the presence of two pairs of legs in the male; and egg-sacs laid free.

Introduction

Mysids play an important role in linking lower and higher trophic levels in detritus and predation food chains of aquatic ecosystems (Mauchline, 1980). Mysid populations are regulated by various environmental and biological factors (cf. Mauchline, 1980). Daly & Damkaer (1986) revealed that an ectoparasitic nicothoid copepod that feeds voraciously on mysid eggs and embryos within the marsupium had a significant influence on the population dynamics of brackish mysids in the Columbia River estuary, USA. In addition to copepods, a wide variety of symbionts such as ciliates, ellobiopsids, hydrozoans, trematodes, cestodes, nematodes and epicaridean isopods are associated with mysids (Mauchline, 1980; Théodoridès, 1989; Ohtsuka et al., 2000). However, it is not clear to what degree these symbionts have an effect on their hosts.

During extensive investigation of parasites on zooplankters in Japanese waters (Ohtsuka et al., 2000, 2003, 2004a, 2005; Horiguchi & Ohtsuka, 2001; Hanamura & Ohtsuka, 2003; Shimomura et al., 2005) a new genus and species of nicothoid copepod (present study) and an undescribed species of the epicaridean isopod *Prodajus* Bonnier, 1903 (Shimomura et al., 2005) were found within the marsupium of the same mysid host *Siriella okadai* Ii in the Seto Inland Sea of Japan. Only three species of nicothoid copepods are known from Asian waters (Hansen, 1897; Yoo & Lim, 1996): *Sphaeronella chinensis* Hansen, 1897 from the amphipod *Corophium bonellii* Milne Edwards in Hong Kong; *S. calliopii* Hansen, 1897 from the amphipod *Calliopius laeviusculus* (Krøyer) in East Asia; and *S. squamosa* Yoo & Lim, 1996 from an ostracod in Korea. This is also the first record of nicothoids ectoparasitic on mysids in Asia. Three genera of the family Nicothoidae are known from mysids (Boxshall & Lincoln, 1983): *Mysidion* Hansen, 1897 (Norway, United Kingdom:

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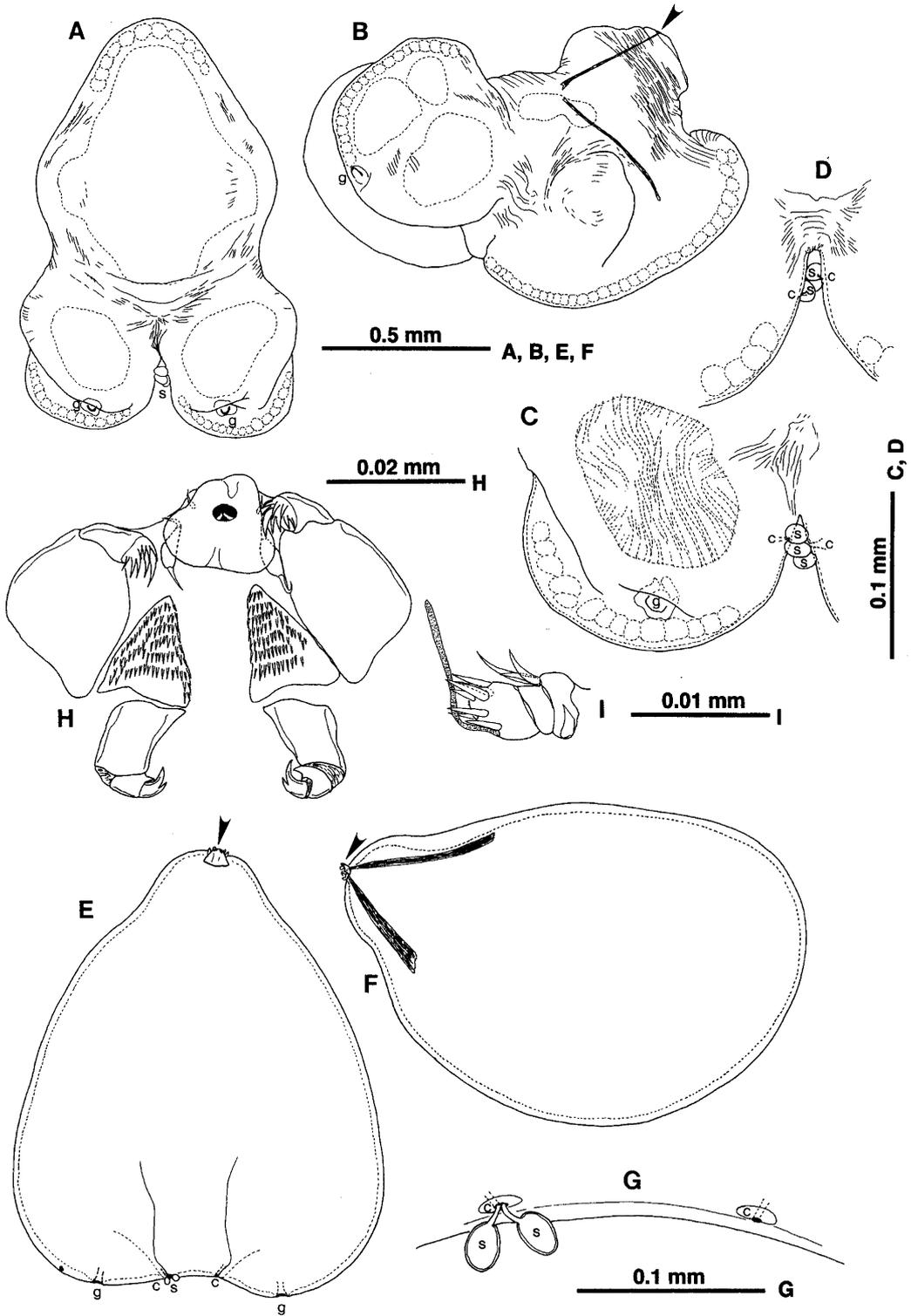


Figure 1. *Neomysidion rahotsu* n. g., n. sp., female, paratypes. A-D,H. Fully mature, ovigerous female; E-G,I. Non-ovigerous, developing female. A. Habitus, ventral view; B. Habitus, lateral view, position of cephalosome arrowed; C. Gonopore and copulatory pores, ventral view; D. Copulatory pores, dorsal view; E. Habitus, dorsal view, cephalosome arrowed; F. Habitus, lateral view, cephalosome arrowed; G. Copulatory pores, two spermatophores attached to left pore; H. Cephalosome, ventral view, antennules omitted; I. Antennule. Abbreviations: c, copulatory pore; g, gonopore; s, spermatophore.

Hansen, 1897; Mauchline, 1969), *Aspidoecia* Hansen, 1897 (Norway: Hansen, 1897) and *Hansenulus* Heron & Damkaer, 1986 (Northwestern North America: Heron & Damkaer, 1986). *Mysidion* and *Hansenulus* are ectoparasitic within the host marsupium, whereas *Aspidoecia* is located on the eyestalk or abdomen of its host (Hansen, 1897; Heron & Damkaer, 1986). Nicothoid copepods are suggested to be harmful to the host, devouring host eggs (Hansen, 1897; Bowman & Kornicker, 1967; Heron & Damkaer, 1986). The prevalence of the new nicothoid on *S. okadai* was relatively high during spring to summer (Naito, 2001; unpublished data). The present study describes the adults and copepodid stage of the new nicothoid copepod using both light and scanning electron microscopy. The biology and ecology of this new nicothoid will be dealt with in a forthcoming paper.

Materials and methods

The host mysid *Siriella okadai* was collected in the vicinity of Takehara, Hiroshima, in the central part

of the Seto Inland Sea of Japan (34°19'N, 132°55'E) during April to August 2003. Since the host mysid exhibits diel vertical migration occurring up near the surface only at night, collections were made along the surface during flood tides at night, using conical plankton nets (diameter 30 cm; mesh size 0.1 or 0.3 mm). Mature females of the mysid with a fully-developed marsupium were selected with wide-mouth pipettes and fixed in 10% neutralised formalin/seawater soon after capture. The parasitic copepods were carefully removed from within the host marsupium with fine needles and forceps under a dissecting microscope. Adult female parasites were sometimes accompanied by adult males and/or copepodids within the marsupium. A live adult female released a number of copepodids in the laboratory after capture. These stages were also observed with light and scanning electron microscopy. All drawings were made with the aid of a drawing apparatus attached to a differential interference contrast microscope (Nikon Optiphoto). Two adult females, one adult male, and one copepodid of the new parasite were also observed using a scanning electron microscope (Jeol T-20). In addition one adult female with spermatophores on the copulatory pores (21 April, 2004) was fixed with Bouin's solution, dehydrated in graded ethanol series and embedded in paraffin wax. Serial sections were stained with Mayer's haematoxylin and eosin in order to confirm the number of seminal receptacles.

The terminology follows Heron & Damkaer (1986) and Huys & Boxshall (1991). Type-specimens are deposited at the Kitakyushu

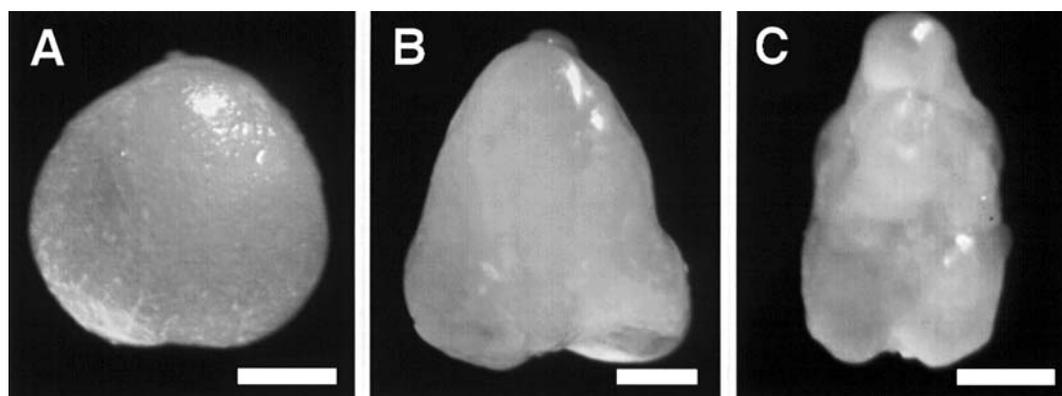


Figure 2. *Neomysidion rahotsu* n. g., n. sp., female, holotype (C) & paratypes (A,B). A,B. Developing female; C. Fully grown female. Scale-bar: 0.3 mm.

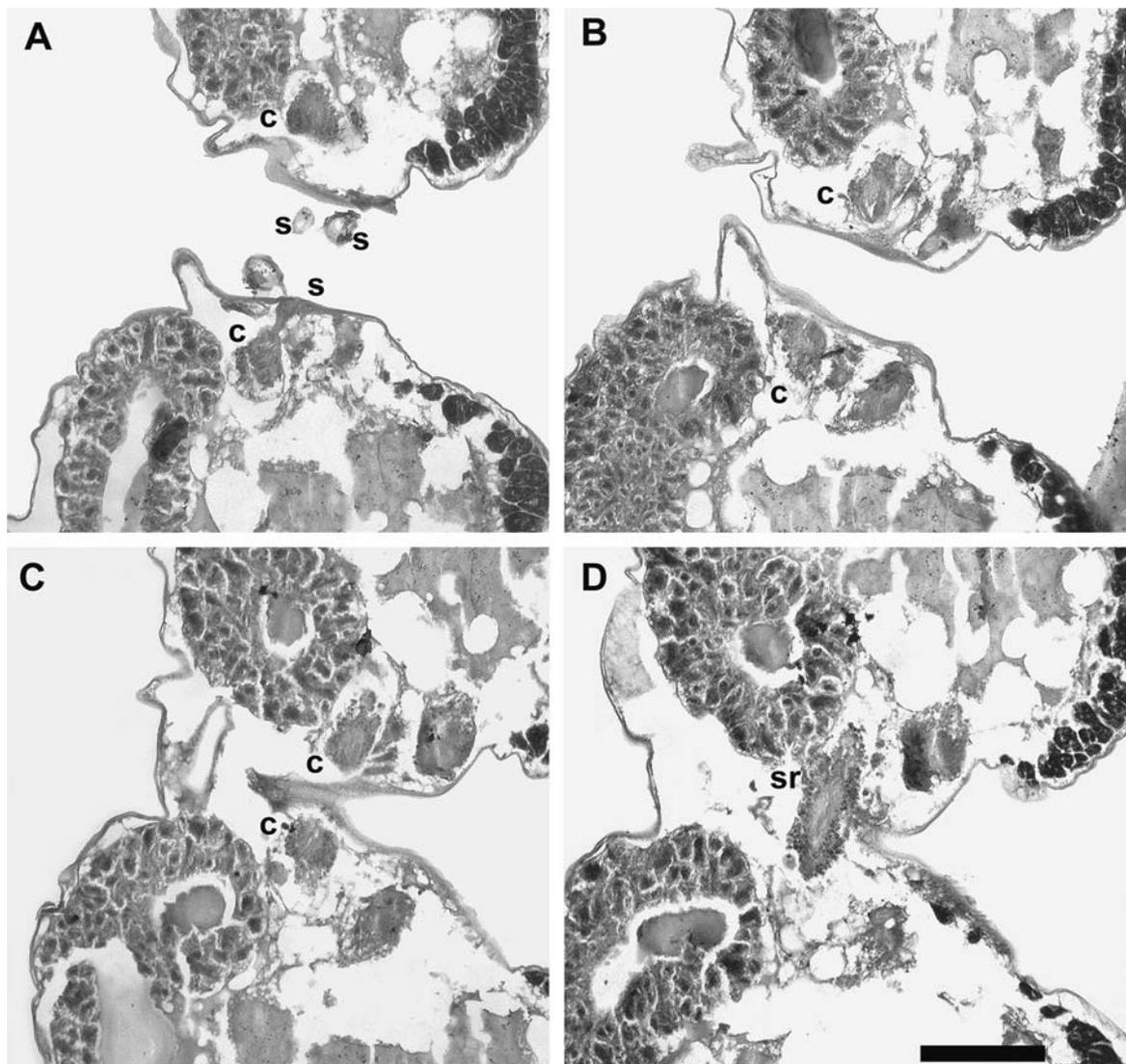


Figure 3. Serial sections of copulatory ducts and seminal receptacle of adult female *Neomysidion rahotsu* n. g., n. sp. A-D. Transverse sections of trunk from posterior (A) to anterior (D). Abbreviations: c, copulatory duct; s, spermatophore; sr, seminal receptacle. Scale-bar: 0.1 mm.

Museum of Natural History and Human History (KMNH IvR) and at the Natural History Museum, London (NHM).

Family Nicothoidae Dana, 1849
***Neomysidion* n. g.**

Diagnosis

Female. Body consisting of cephalosome and trunk; trunk variable according to state of maturity, almost ovoid or pyriform in young females to

quadrilobed in fully mature female with anterior part produced into rounded process; anterodorsal part of body expanded to form median lobe on which small cephalosome is located; middle part somewhat constricted; posterior part bilobed. Paired gonopores located separately at posterior end of each lobe; paired copulatory pores present between gonopores; seminal receptacle unpaired. Caudal rami absent. Antennule 3-segmented. Antenna represented by single seta. Maxillule with 2 setae. Maxilla 2-segmented; proximal segment (syncoxa) robust; distal segment with rake-like

structure terminally. Paired spinulate sclerites located between maxillae. Maxilliped 3-segmented; first segment (syncoxa) robust; second segment (basis) with inner projection; third segment (endopod) bifurcate at tip. Legs 1 to 5 absent.

Male. Body globular, somewhat depressed, distinctly divided into cephalosome and trunk. Cephalosome covered with rounded knobs posterodorsally; rostrum produced anteriorly into broad plate. Antennule 3-segmented. Antenna 2-segmented; first segment unarmed; second segment

bearing 2 terminal setae. Maxilla 2-segmented, chelate; proximal segment (syncoxa) produced posteriorly into triangular process; distal segment tapering distally. Paired spinulate sclerites present between maxillae. Maxilliped 3-segmented; first segment (syncoxa) longest, curved inward; second segment (basis) with pointed process at inner distal corner; third segment (endopod) claw-like, bifid at tip. Surface of trunk entirely covered with lamellar ornamentation; posteroventral part ornamented with comb-like plates; paired gonopores located

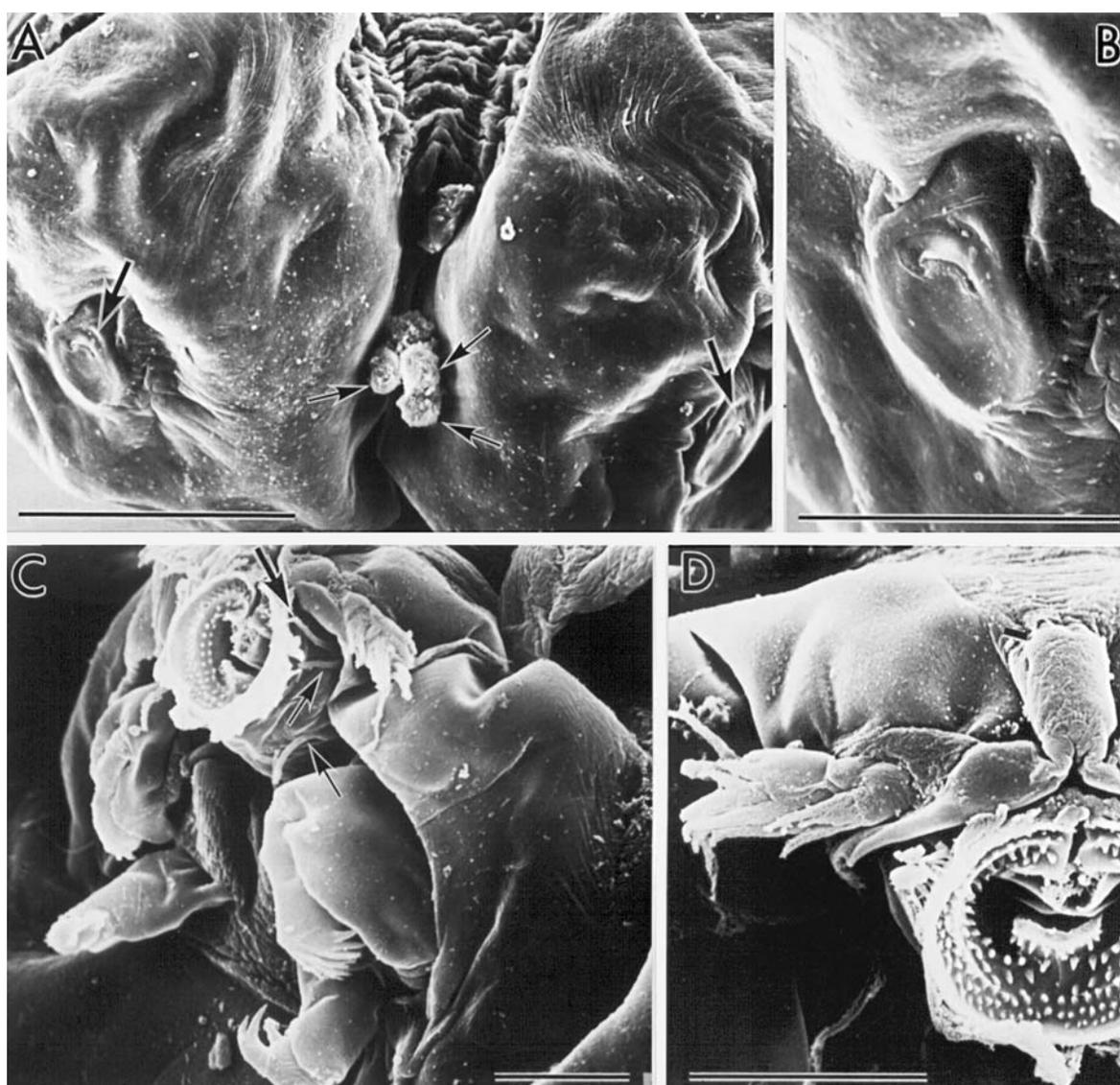


Figure 4. Scanning electron micrographs of *Neomysidion rahotsu* n. g., n. sp., female. A. Gonopores (indicated by large arrows) and spermatophores (by small arrows); B. Gonopore; C. Cephalosome, ventrolateral view, 1 antennary and 2 maxillular setae indicated by large and small arrows, respectively; D. Antennule and oral cone. *Scale-bars:* A, 0.2 mm; B, 0.1 mm; C-D, 10 μ m.

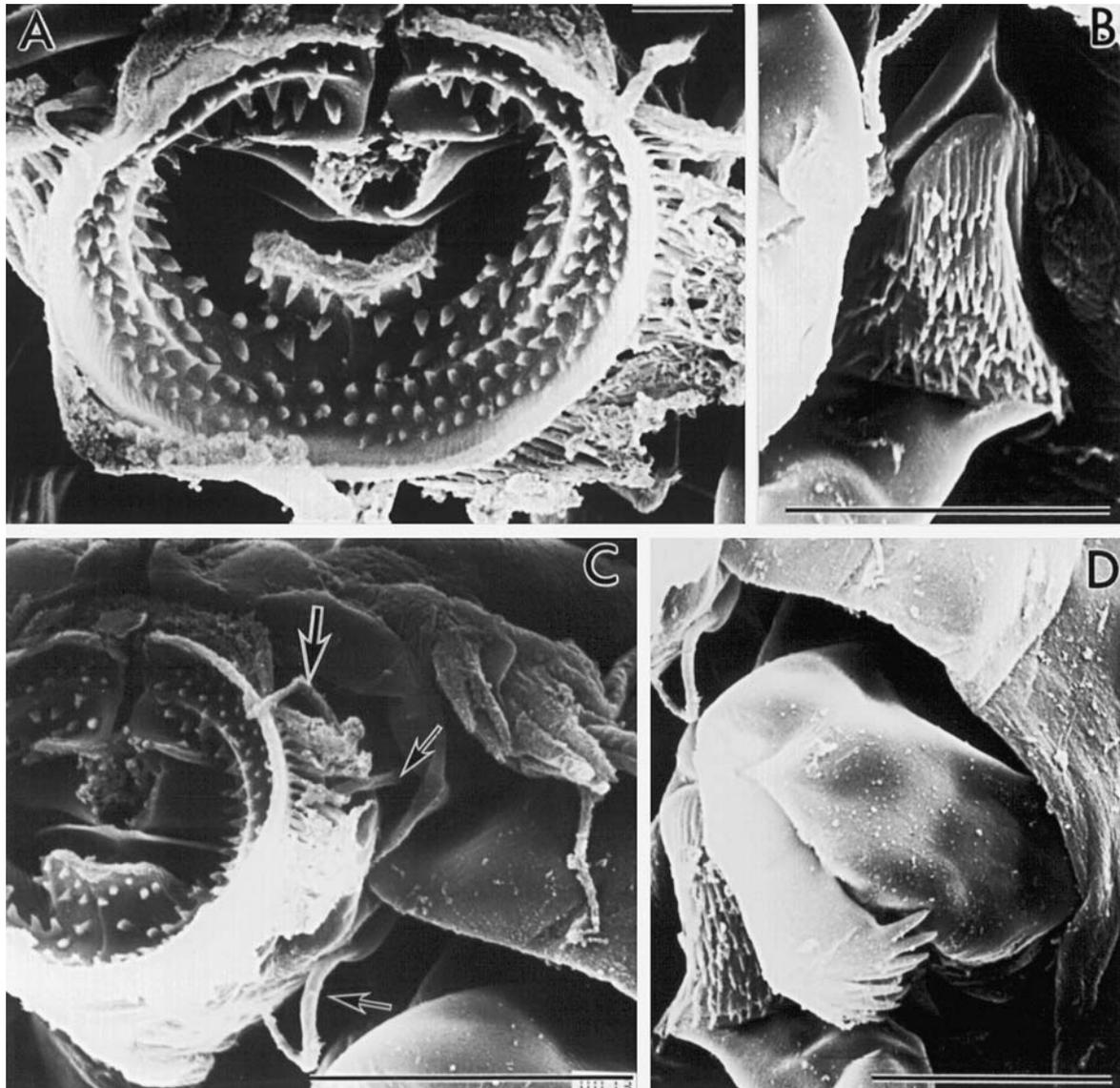


Figure 5. Scanning electron micrographs of *Neomysidion rahotsu* n. g., n. sp., female. A. Oral cone; B. Spinulate sclerite between maxillae; C. Antennule and oral cone, 1 antennary and 2 maxillary setae indicated by large and small arrows, respectively; D. Maxilla. Scale-bars: A,C, 2 μ m; B,D, 10 μ m.

dorsolaterally; legs 1 and 2 cylindrical, each bearing 2 terminal setae. Legs 3 to 5 absent. Caudal rami with 3 distal setae.

Copepodid. Body of typical nicothoid form with median pouch on ventral surface of cephalothorax. Cephalothorax longitudinally striated ventrolaterally. Urosome 3-segmented; first urosomite (= third pediger) with 2 pairs of unequal setae at distal corners; second urosomite constricted proximally; caudal ramus with 1 long

inner and 2 outer setae. Antennule 2-segmented, with extremely elongate aesthetasc on distal segment. Antenna 3-segmented; proximal 2 segments each bearing minute seta at distal corner; third segment with 3 short setae at tip. Maxilla 3-segmented; first segment robust, serrate along inner margin; third segment claw-like. Maxilliped 4-segmented; first segment elongate; third segment with inner setae; fourth segment forming long curved claw. Post-maxillipedal pouch

pointed posteriorly. Legs 1 and 2 consisting of protopod and 1-segmented rami; setal formula of exopods of both legs III, 1, 3; endopod of legs 1 and 2 with setal formula of I, 2, 4 and I, 2, 3, respectively. Leg 3 represented by 2 pairs of unequal setae.

Ectoparasitic in marsupium of mysids. Adult females with anterodorsal side positioned against anteroventral side of host mysid within marsupium; cephalosome reflexed dorsally. Males attached to inner surface of mysid marsupium or to adult female. Type-species *N. rahotsu* n. sp. (original designation).

Etymology. The new generic name is derived from the Greek neo, meaning new, and a closely related mysid-infesting genus *Mysidion*.

Remarks

In the Nicothoidae the new genus is assigned to the *Sphaeronella* group sensu Boxshall & Lincoln (1983) by virtue of having 3-segmented antennules and 3-segmented maxillipeds in the adult. In this group there are now only four genera in which paired gonopores of the female are positioned close together and are not surrounded by a common plate or chitinous framework: *Mysidion*, *Aspidoecia*, *Hansenulus* and *Neomysidion*. All are ectoparasites on mysids (Hansen, 1897; Heron & Damkaer, 1986; present study). The new genus is easily distinguished from these three existing genera by the combination of the following features: (1) the body of females remarkably transformed with maturity (unique to the new genus);

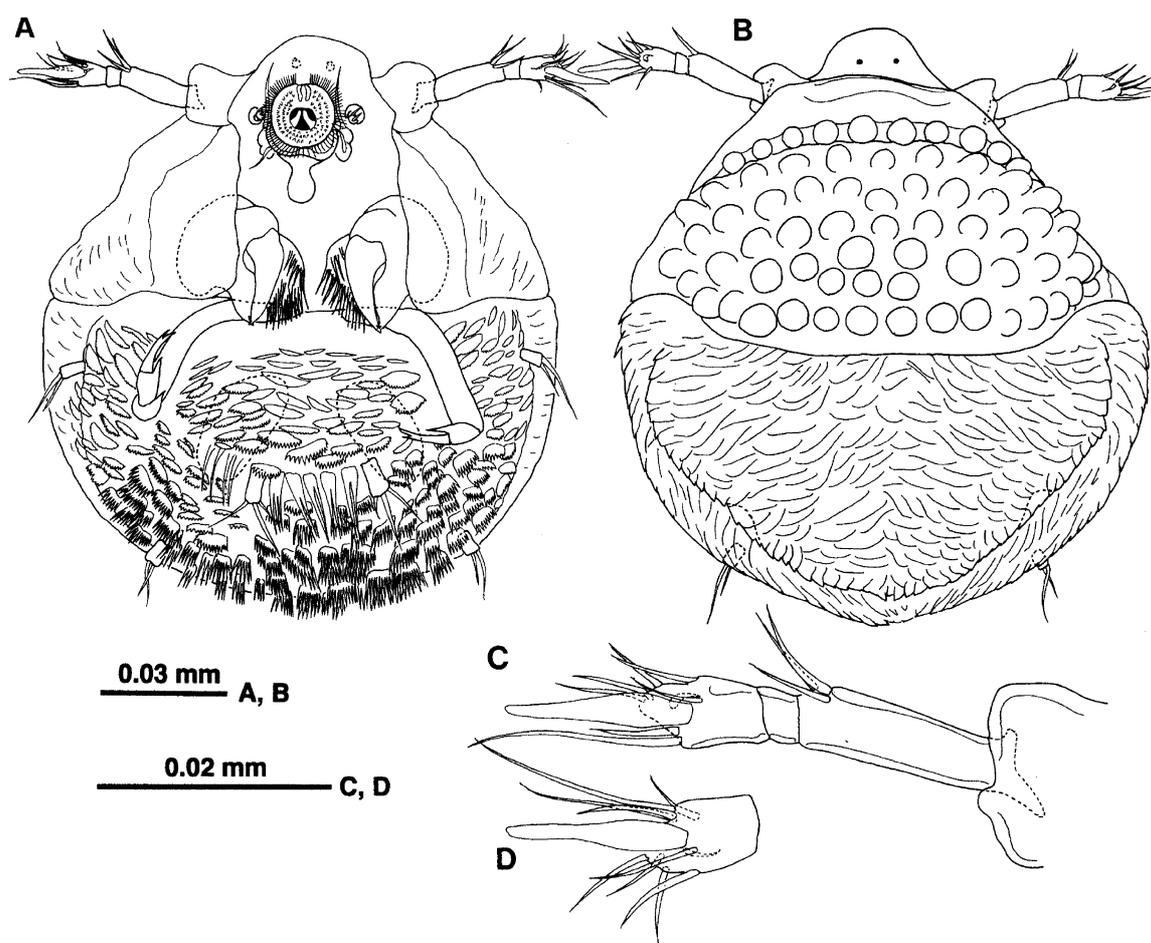


Figure 6. *Neomysidion rahotsu* n. g., n. sp., male, allotype. A. Habitus, ventral view; B. Habitus, dorsal view; C. Left antennule; D. Terminal segment of right antennule.

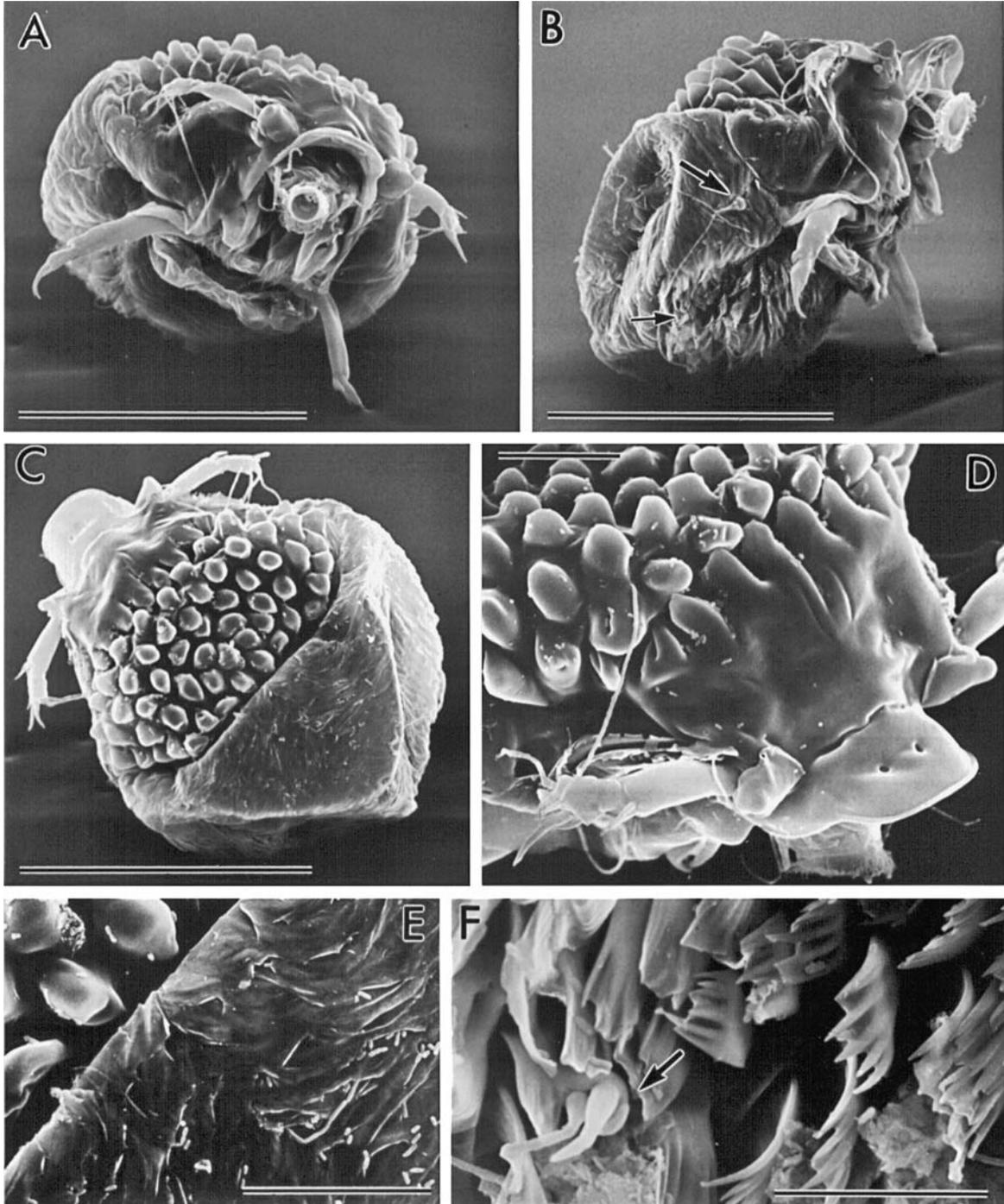


Figure 7. Scanning electron micrographs of *Neomysidion rahotsu* n. g., n. sp., male. A. Habitus, anteroventral view; B. Habitus, lateral view, legs 1 and 2 indicated by large and small arrows, respectively; C. Habitus, dorsal view; D. Cephalosome, dorsolateral view; E. Boundary between cephalosome and trunk, dorsal view; F. Trunk, lateral view showing leg 2 (arrowed). Scale-bars: A-C, 0.1 mm; D-E, 20 μ m; F, 10 μ m.

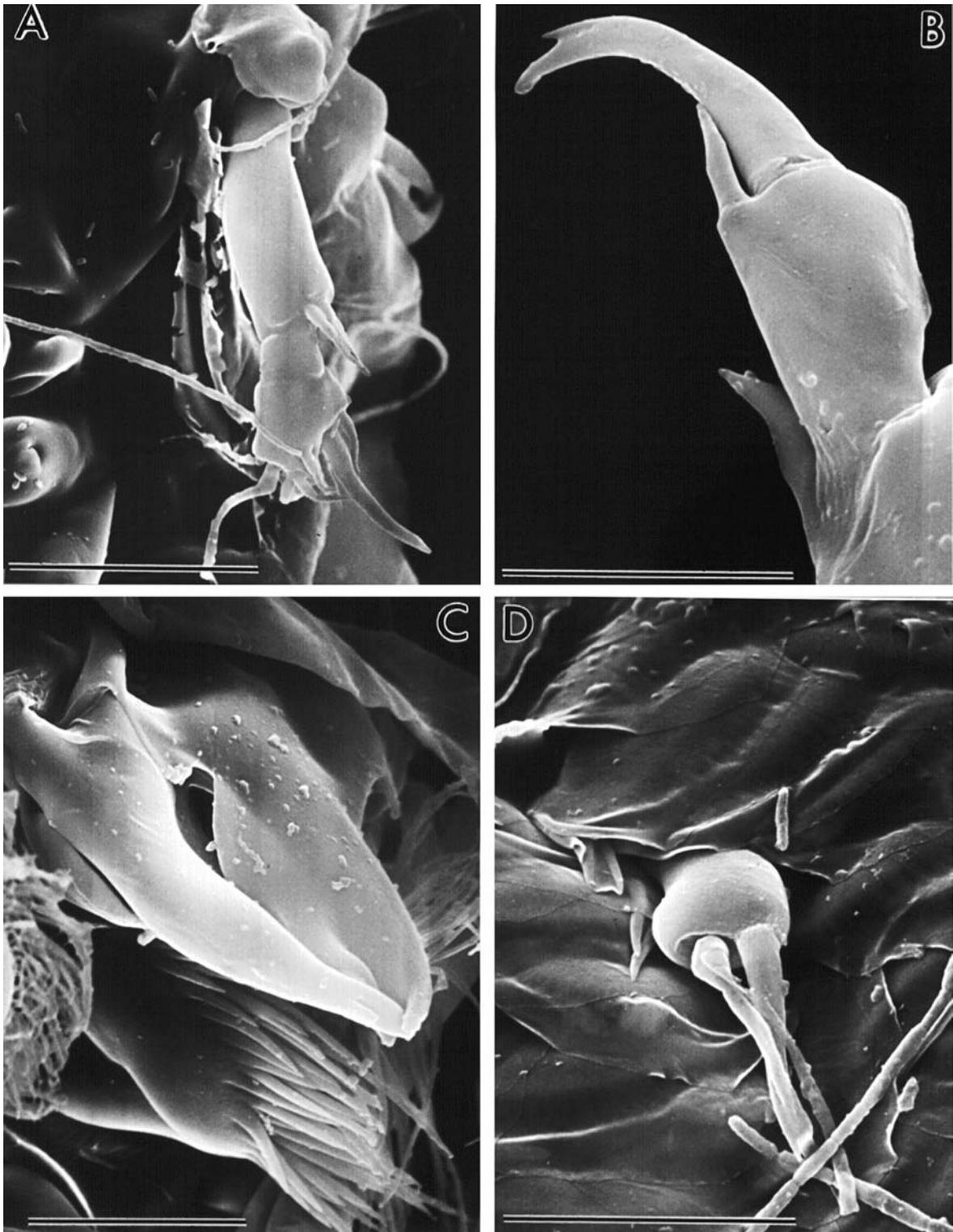


Figure 8. Scanning electron micrographs of *Neomysidion rahotsu* n. g., n. sp., male. A. Antennule; B. Terminal segments of maxilliped; C. Maxilla; D. Leg 1. Scale-bars: A, 20 μm ; B-D, 10 μm .

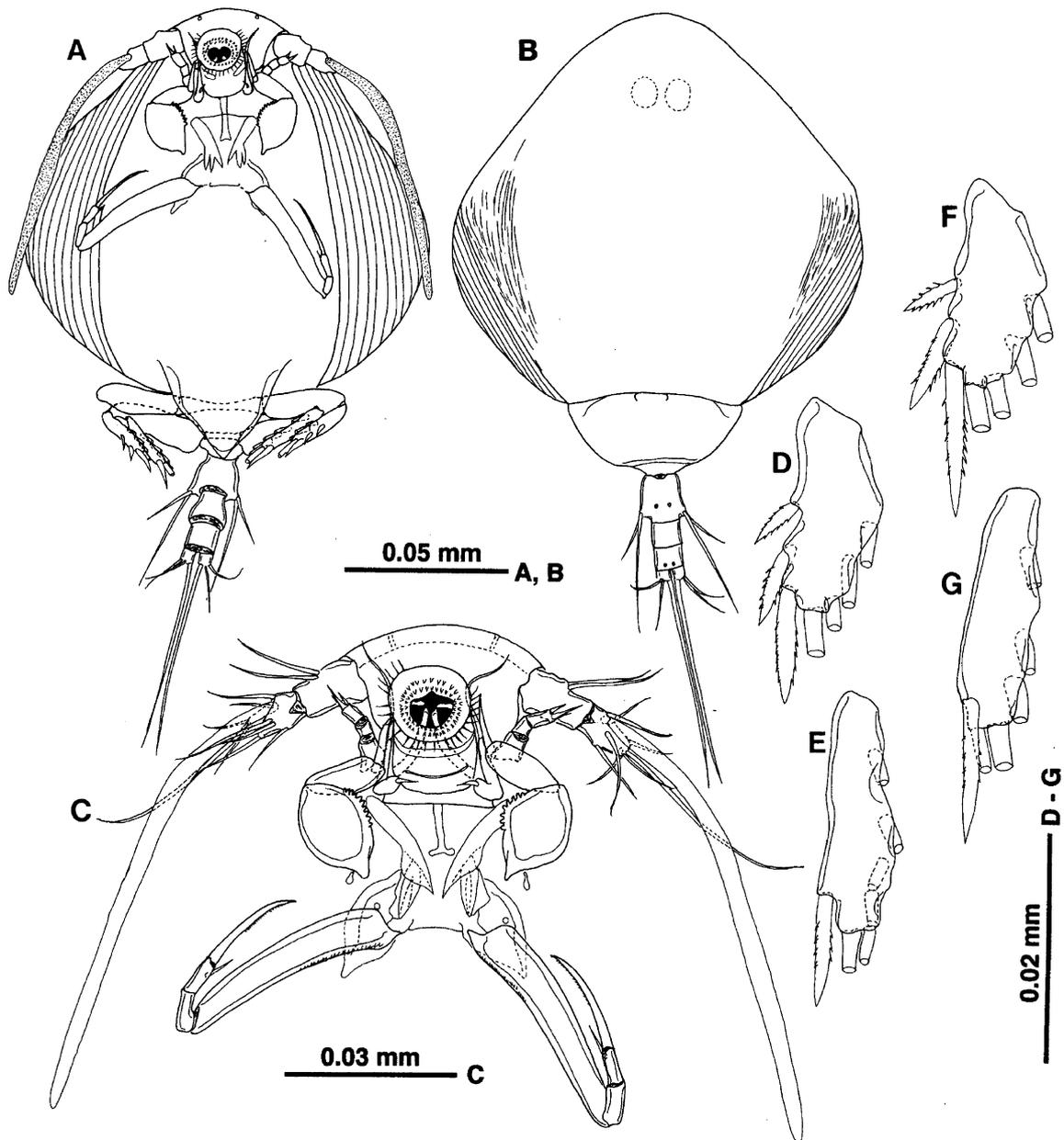


Figure 9. *Neomysidion rahotsu* n. g., n. sp., copepodid found from mysid marsupium, paratype. A. Habitus, ventral view, rami of right leg 1 and left leg 2 omitted; B. Habitus, dorsal view; C. Cephalosome, ventral view; D. Exopod of leg 1, anterior surface; E. Endopod of leg 1, anterior surface; F. Exopod of leg 2, anterior surface; G. Endopod of leg 2, anterior surface.

(2) the male cephalosome entirely covered with rounded knobs dorsally (unique to the new genus); (3) the absence of caudal rami in the female (present in *Hansenulus*); (4) 3-segmented antennules in both sexes (1- or 2-segmented in *Mysidion* and *Aspidoecia*); (5) 3-segmented antenna in the male (absent in *Mysidion* and *Aspidoecia*); (6)

remarkable sexual dimorphism in the maxillae (basically similar in the other genera); (7) rake-like, terminal segment of maxilla of the female (simply claw-like in the other genera); (8) the presence of spinulate sclerites between the maxillae (unique to the new genus); (9) the maxilliped 3-segmented in both sexes (4-segmented in both sexes of

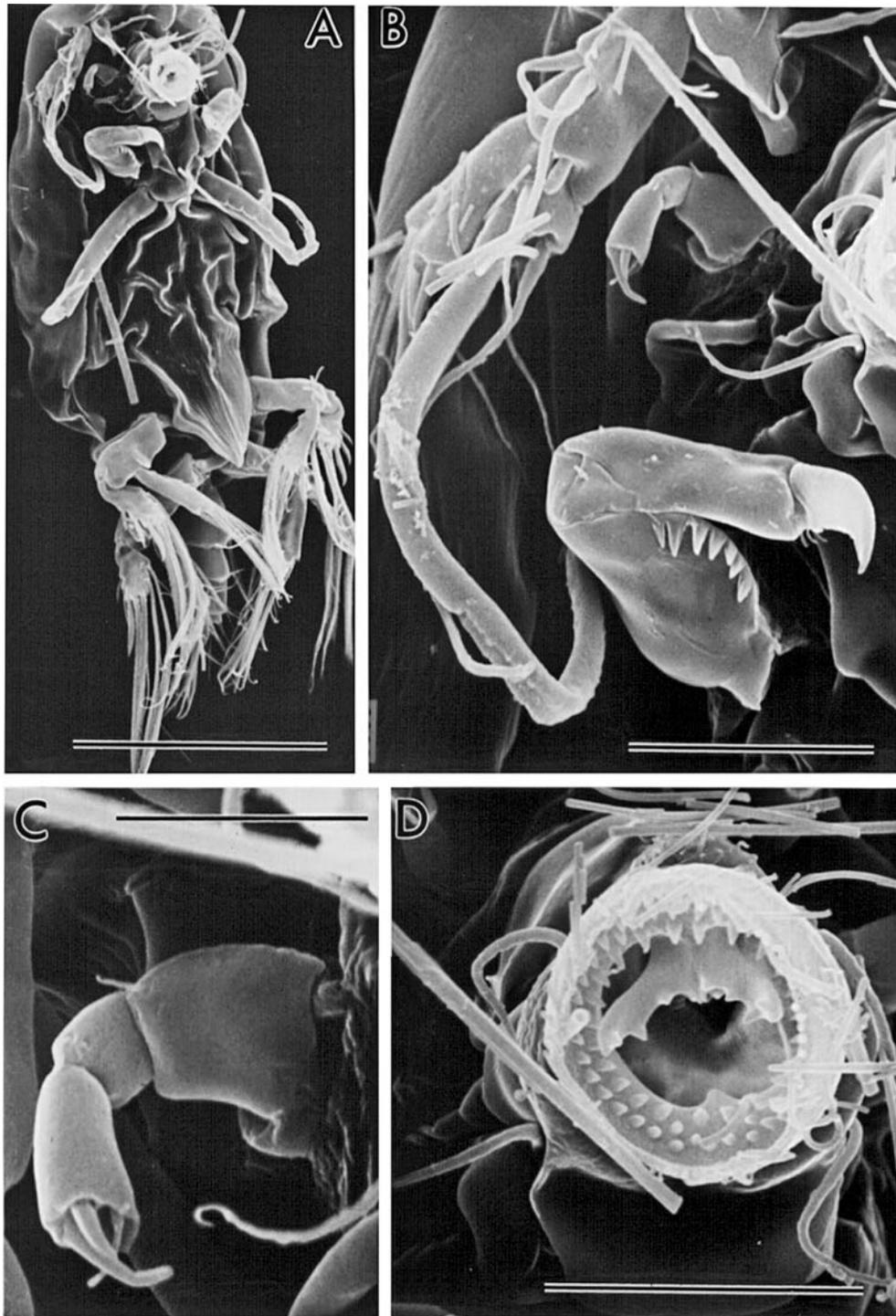


Figure 10. Scanning electron micrographs of *Neomysidion rahotsu* n. g., n. sp., copepodid just after release from egg-sac. A. Habitus, ventral view; B. Antennule to maxilla; C. Antenna; D. Oral cone. Scale-bars: A, 0.05 mm; B,D, 10 μ m; C, 5 μ m.

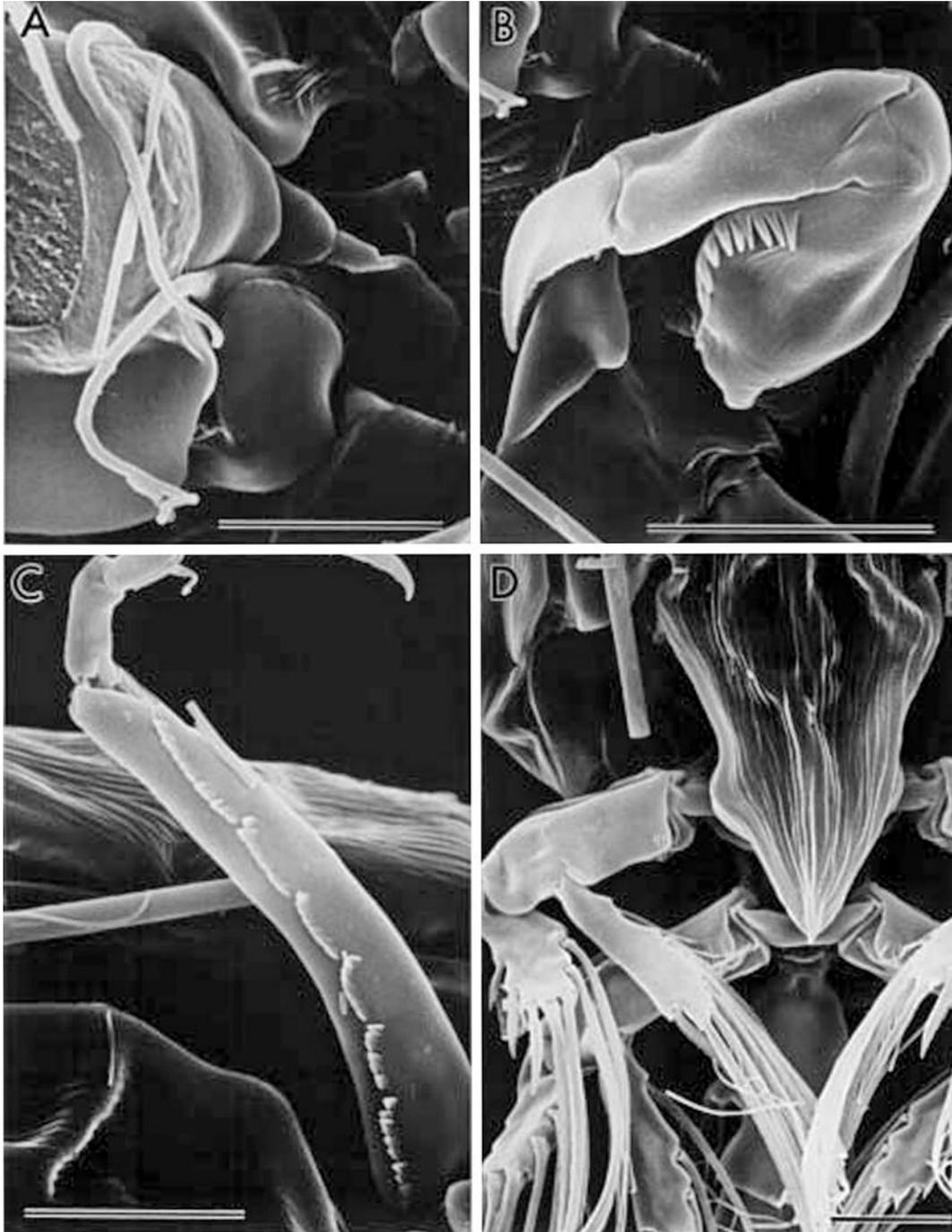


Figure 11. Scanning electron micrographs of *Neomysidion rahotsu* n. g., n. sp., copepodid just after release from egg-sac. A. Maxillule; B. Maxilla; C. Maxilliped; D. Postmaxillipedal pouch and legs 1 and 2. Scale-bars: A, 5 μ m; B-D, 10 μ m.

Hansenulus; absent in the female of *Aspidoecia*); (10) the absence of legs in the female (present in *Hansenulus*); (11) the presence of legs in the male (absent in *Mysidion* and *Aspidoecia*); and (12) egg-

sacs laid free (hinged from gonopores in *Mysidion* and *Aspidoecia*).

According to Heron & Damkaer (1986), the three mysid-infesting genera, *Aspidoecia*,

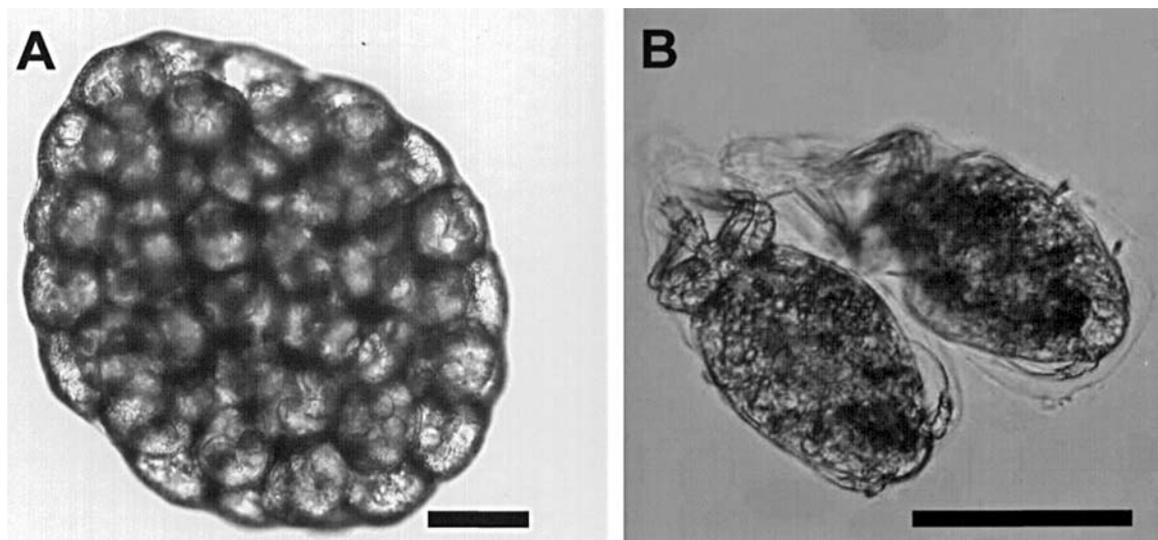


Figure 12. Egg-sac of *Neomysidion rahotsu* n. gen., n. sp. A. Egg-sac containing developing eggs; B. Detail of egg containing copepodid stage just before hatching. Scale-bars: 0.1 mm.

Hansenulus and *Mysidion*, each have a single seminal receptacle, whereas all other nicothoid genera have paired ones. A single receptacle is present in the new genus (see Figure 4).

Copepodid stages of the family Nicothoidae are frequently found on the host crustaceans. To date, this stage is known from the following ten genera: *Aspidoecia* (see Hansen, 1897); *Choniomyzon* Pillai, 1962 (see Bradford, 1975); *Choniorhiza* Boxshall & Lincoln, 1983 (see Boxshall & Lincoln, 1983); *Choniotoma* Hansen, 1886 (see Hansen, 1897); *Diexanthema* Ritchie, 1975 (see Ritchie, 1975); *Hansenulus* (see Heron & Damkaer, 1986); *Mysidion* (see Hansen, 1897); *Neomysidion* (present study); *Nicthoe* Audouin & Milne Edwards, 1826 (see Gurney, 1930); *Sphaeronella* Salensky, 1868 (see Bradford, 1975; Boxshall & Lincoln, 1983); *Sphaeronelloides* Bradford, 1975 (see Bradford, 1975); and *Sphaeronellopsis* Hansen, 1904 (see Bowman & Kornicker, 1967, 1968). Green (1959) reported the male of *Rhizorhina serolis* Green, 1959 which attached to the highly transformed female parasitic on the deep-sea isopod *Serolis bromleyana* Suhm. The general appearance of the male resembles the copepodid stages of other nicothoid genera, but spermatophores were formed within the body (see Green, 1959: figures 5, 6, Discussion).

In the *Sphaeronella* group *sensu* Boxshall & Lincoln (1983) with an at most 4-segmented

maxilliped in the adult, the copepodid stage is also characterised by the lower number of maxillipedal segments in comparison with those of other nicothoid genera (4- versus 5-segmented). The unique post-maxillipedal pouch of the nicothoid copepodids, whose function is still unknown, is found in both the *Rhizorhina* and *Sphaeronella* groups *sensu* Boxshall & Lincoln (1983).

Neomysidion rahotsu n. sp.

Material examined: 16♀♀, 14♂♂ & 2 copepodids, off Takehara, Hiroshima Prefecture, Japan (Seto Inland Sea of Japan), April to August 2003, 21 April 2004.

Type-material: All type-specimens collected from marsupium of host mysid *Siriella okadai* off Takehara, Hiroshima Prefecture, Japan (Seto Inland Sea of Japan). Holotype: ♀, whole specimen, 31 July 2003, KMNH IvR 500103. Allotype: ♂, mounted on glass slide, 26 June 2003, KMNH IvR 500104. Paratypes: ♀, cephalosome dissected and mounted on glass slide, 2 June 2003, KMNH IvR 500105; ♀, cephalosome dissected and mounted on glass slide, 26 June 2003, KMNH IvR 500106; 11♀♀ & 12♂♂, whole specimens, April to August 2003, NHM 2005.77–86; 1 copepodid, mounted on glass slide, 23 April 2003, KMNH IvR 500107.

Etymology. The new specific name *rahotsu* (Japanese, meaning grouped hairs of Buddha statue)

alludes to the uniquely arranged cephalic knobs on the dorsal side of the adult male.

Description (Figures 1–13)

Female. Body (Figures 1A,B,E,F, 2A–C) comprising cephalosome and trunk. Trunk shape remarkably variable with state of maturity; simply ovoid (mean body length 0.83 mm; mean body width 0.90 mm, N = 2) or pyriform (mean body length 1.36 mm; mean body width 1.06 mm, N = 3) in young females (Figures 1E,F, 2A,B) to quadrilobed (mean body length 1.10 mm; mean body width 0.72 mm, N = 8) in fully mature female (Figures 1A,B, 2C), with anteriorly protruded lobe, dorso-medial lobe on which cephalosome located (see Figures 1E,F, 4C) and paired posterior lobes. Paired gonopores (Figures 1A–C,E, 4A,B) located at end of each posterior lobe; paired copulatory pores (Figures 1C,D,E,G; 4A) present between gonopores; single seminal receptacle present (Figure 3). Caudal rami absent.

Cephalosome (Figures 1H, 4C) reflexed dorsally, somewhat sclerotised. Post-antennular appendages and oral cone enclosed by sclerotised lateral margins (see Figure 4C). Antennule (Figures 1I, 4C,D, 5C) short, 3-segmented posterodorsally, thick; setal formula 3, 0, 8 (?) + aesthetasc. Antenna (Figures 1H, 4C, 5C) represented by single seta located anterolateral to oral cone. Oral cone (Figures 1H, 4D, 5A,C) tipped with sucker of about 0.016 mm in diameter; inner surface of sucker ornamented with small, pointed denticles. Mandible (Figures 1H, 5A) stylet-like, contained within oral cone with only tip projecting from distal opening. Maxillule (Figures 1H, 4C, 5C) almost concealed between oral cone and sclerotised lateral margins, bearing 2 setae. Maxilla (Figures 1H, 4C, 5D) stout, 2-segmented; proximal segment (syncoxa) robust, triangular; distal segment shorter than proximal, directed posteriorly, and with rake-like structure terminally. Paired spinulate sclerites present on ventral cephalic surface between maxillae (Figures 1H, 4C, 5B,D). Maxilliped (Figures 1H, 4C) compact, 3-segmented; first segment (syncoxa) longer than second and third combined, unarmed; second segment (basis) short, bearing inner spiniform element at mid-length; third (endopod) curved inward, bifid at tip. Legs 1 to 5 absent.

Male. Body (Figures 6A,B, 7A–C) globular, somewhat dorsoventrally depressed, about 0.13–0.15 mm long (mean 0.14 mm, N = 13), almost as wide as long. Cephalosome distinctly separate from trunk (Figures 5A,B, 6B,C), ornamented with rounded, sclerotised protuberances dorsally except near anterior margin (Figures 6B, 7C,D); rostrum (Figures 6B, 7A–D) extended anteriorly as broad semi-circular plate, with paired integumental pores dorsally; frontal attachment filament absent. Trunk almost as long as cephalosome; ventral surface entirely covered with dense array of comb-like ornamentation platelets varying in shape along antero-posterior axis, with tines of combs longer towards posterior; large bifid spinular platelets present between caudal rami (Figures, 6A, 7B,F). Dorsal and lateral surfaces of trunk with thin lamellar markings (Figures 6B, 7B,E). Paired spermatophores located in middle of trunk of paratypic males (Figure 6A). Paired gonopores not clearly visible, but apparently located dorsolaterally, near leg 2 (dotted in Figure 6B). Caudal rami located ventromedially, cylindrical with 3 setae terminally. Anus not discernible.

Antennule (Figures 6A–D, 7A–D) 3-segmented; first segment longer than other segments combined, with 3 setae; second segment shortest, unarmed; third segment bearing 9 setae and 1 aesthetasc. Antenna (Figure 6A) reduced, 2-segmented; proximal segment tapered, unarmed; distal segment short, cylindrical, with 2 apical setae. Oral cone (Figures 6A, 7A,B) tipped with sucker frilled by fine setules around aperture margin; inner surface of sucker ornamented with acute denticles. Mandible (Figure 6A) stylet-like, contained within oral cone, only tip visible at distal opening. Maxillule (Figure 6A) bilobed; each lobe with apical seta. Maxilla (Figures 6A, 7A, 8C) chelate, 2-segmented; proximal segment (syncoxa) with outer process bifurcate at tip; distal segment smoothly curved, tapered distally. Paired spinulate sclerites present on ventral surface between maxillae (Figures 6A, 7A, 8C). Maxilliped (Figures 6A, 7A,B, 8B) distinctly 3-segmented; first segment (syncoxa) much longer than distal 2 segments combined, curved inward proximally, with acutely pointed process at inner distal corner; second segment (basis) with inner distal spine; third segment (endopod) forming curved claw with bifid tip. Legs 1 and 2

(Figures 6A,B, 7B,F, 8D) unisegmented, cylindrical, each with 2 setae at tip.

Copepodid. Body (Figures 9A,B, 10A) 0.17 mm in length, lacking frontal attachment filament. Prosome (Figures 9A,B) consisting of expanded cephalothorax and 1 free pedigerous somite. Cephalosome of individuals taken from mysid marsupium (Figure 9A,B) more swollen laterally than individuals just after release from egg-sac (see Figure 10A), globular; pleural area striated longitudinally; naupliar eyes present (Figure 9B); postmaxillipedal pouch (Figures 9A, 10A, 11D) triangular, extends to anterior margin of first urosomite. Second free pedigerous somite with anterodorsal knob. Urosome (Figure 9A,B) 3-segmented; first urosomite (= third pedigerous somite) longest, with dorsal seta of leg 3 about twice as long as ventral seta, reaches beyond caudal rami, and with paired integumental pores dorsally; second urosomite constricted proximally; anal somite slightly shorter than preceding somite, with paired pores dorsally; caudal rami symmetrical, bearing 2 short outer setae and long, inner seta fused to ramus at base.

Antennule (Figures 9A,C, 10B) 2-segmented; setal formula 2, 9 + aesthetasc; aesthetasc large, reaching beyond mid-length of cephalothorax (Figure 9A). Antenna (Figures 9C, 10B,C) short, 3-segmented; first and second segments each with fine outer seta; third segment with 3 unequal elements terminally. Oral cone (Figures 9A,C, 10D) as in adult, but terminal sucker surrounded by fewer setules. Mandible (Figures 9C, 10D) and maxillule (Figure 11A) as in adult male. Maxilla (Figures 9C, 10A,B, 11B) stout, 3-segmented; syncoxa swollen, with conspicuous serrations along middle section of inner margin; basis unarmed; endopod represented by tapering claw. Maxilliped (Figures 9A,C, 10A, 11C) 4-segmented; syncoxa elongate, with longitudinal rows of prominences along posterior margin; basis unarmed; endopod 2-segmented, first segment as long as basis, with inner subterminal spine, second segment claw-like. Legs 1 and 2 (Figures 9A,D-G, 10A, 11D) each with 1-segmented protopod and 1-segmented rami; intercoxal sclerites concealed beneath postmaxillipedal pouch; protopod bears patch of minute prominences at inner proximal corner (Figure 11D); seta and spine formula of exopods of both legs III, 1, 3; endopods of legs 1

and 2 with formula I, 2, 4 and I, 2, 3, respectively. Leg 3 represented by 2 unequal setae at distal corner of somite.

Egg-sac. Ovigerous females carried 2 to > 28 egg-sacs (N = 23) (Figure 12A). Number of eggs per egg-sac 9–71 (N = 4). Diameter of egg-sac 0.29–0.42 mm (mean 0.36 mm, N = 15), whereas that of mysid eggs was 0.35–0.53 mm (mean 0.44 mm, N = 50). Copepodid just before hatching sometimes visible within egg membrane (Figure 12B).

Discussion

The life-cycle of *Neomysidion rahotsu* n. g., n. sp. is incompletely understood. Generally nicothoids hatch from eggs as the first copepodid stage (Hansen, 1897; Bradford, 1975; Heron & Damkaer, 1986). In the Nicothoidae there are three basic types of postlarval development (Hansen, 1897; Heron & Damkaer, 1986): (1) direct metamorphosis from copepodids to adults in both sexes; (2) indirect metamorphosis from copepodids via an intermediate pupal stage(s) to both sexes of adults; and (3) direct in one sex, but indirect in the other. Females of the mysid-infesting genera *Hansenulus* and *Mysidion* appear to pass through two and three pupal stages, respectively (Hansen, 1897; Heron & Damkaer, 1986). On the other hand males of *Hansenulus* lack an intermediate stage (Heron & Damkaer, 1986). Although our samples were not large enough to elucidate all of the developmental stages of *N. rahotsu*, no pupal stage has been found so far. Our comparisons between the free-swimming and attached copepodids suggest that expansion of cephalothorax in *N. rahotsu* seems to commence after attachment to the host. Such remarkable metamorphoses without a moult are widely known in adult females of a wide variety of parasitic copepods, and have been inferred as enhancing attachment and/or egg production (Kabata, 1979; Smith & Whitfield, 1988; Ohtsuka et al., 2004b). In female *N. rahotsu* the trunk is distinctly modified at maturity (see Figure 2). We interpret these differences in trunk morphology as developmental stages of the same individual, rather than as different pupal stages, because of the absence of attachment filaments and the lack of change in the appendages. The two or three

pupal stages of *Mysidion* and *Hansenulus* are characterised by the presence of filaments and by changes in the appendages (Hansen, 1897; Heron & Damkaer, 1986). In *N. rahotsu* the trunk expansion appears to be related to the development of the female genital system after consumption of host eggs and embryos. Oviposition appears to commence after full expansion of the trunk. Modification (constriction and narrowing) of the trunk at later stages may provide space for the numerous egg-sacs (more than 28) deposited within the host marsupium.

Bowman & Kornicker (1967) suggested that in host marsupium-living members of the Nicothoidae, egg mimicry is essential not only to avoid ejection from the host but also to reduce vulnerability to predators. In *N. rahotsu*, the diameter of the egg-sac is approximately 0.36 mm, which is nearly equal to that of the host's eggs (c.0.44 mm). In addition, fully-mature females of this ectoparasite just fit into the space within the host marsupium, which may deceive the host into sensing the presence of eggs/embryos within the marsupium. We observed a parasitised mysid moving the brooding plates rhythmically, a behaviour pattern which seems to be involved in ventilation of the host eggs/embryos. Since mysids can not only groom themselves but also adopt eggs/embryos that have been lost from or escaped from the marsupium (Wittmann, 1978; Mauchline, 1980; Acosta & Poirrier, 1992; Sato & Murano, 1994), egg mimicry seems to be important in preventing parasite removal from the marsupium by grooming activities of the host.

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