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Ergasilid copepods (Poecilostomatoida) in plankton samples from Hokkaido, Japan, with reconsideration of the taxonomic status of *Limnoncaea* Kokubo, 1914

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Three species of ergasilid copepods are described from plankton samples collected in Hokkaido of northern Japan: *Ergasilus bani* n. sp., *E. hypomesi* Yamaguti, 1936 and *E. genuinus* (Kokubo, 1914) n. comb. The last was originally assigned to an enigmatic genus *Limnoncaea* Kokubo, 1914. In this paper *Limnoncaea* is relegated to a junior synonym of *Ergasilus* Nordmann, 1832, while the type species, *L. genuina* Kokubo, 1914 is transferred accordingly to *Ergasilus*. Transformation in adult female of ergasilids from the planktonic to the infesting stages is also discussed. Comparison of ovigerous females from host fish and plankton samples suggests that ergasilids may lead dual life cycles in freshwater.

KEYWORDS: Copepoda, Ergasilidae, Oncaeidae, *Ergasilus*, *Limnoncaea*, Hokkaido, Japan, life cycle.

Introduction

The Ergasilidae is a highly diverse family of copepods infesting mainly fish hosts of freshwater as well as brackish and coastal waters. They are considered as the most successful colonizers of the freshwater regime in the order Poecilostomatoida (Ho, 1991; Lin and Ho, 1998). According to the documented information, the nauplii, copepodids and early adults of the ergasilids are planktonic, the males die soon after copulation, and only adult females continue to lead their life as parasites infesting the body surface, gills and branchial and nasal cavities of fish (cf. Wilson, 1911; Yin, 1956; Kabata, 1979; Montú, 1980; Ben Hassine, 1983; Urawa *et al.*, 1991). However, ovigerous females of *Ergasilus* Nordmann, 1832, *Acusicola* Cressey, 1970 and *Gauchergasilus* Montú and Boxshall, 2002 have been frequently found in

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plankton from various parts of the world (cf. Sars, 1909; Wilson, 1911; Kokubo, 1914; Kuang and Li, 1984; Kuang and Qian, 1991; Araujo and Boxshall, 2001b; Montú and Boxshall, 2002; present study).

Kokubo (1914) established the genus *Limnoncaea* to accommodate four species of ergasilid-like copepods, namely *L. genuina*, *L. diuncata*, *L. divergens* and an unidentified species. All of them were found in plankton samples collected from fresh and brackish waters chiefly in Hokkaido, Japan. Kokubo (1914) modified the diagnosis of the Oncaeidae to include this genus, but in 1932, he moved the genus to the Ergasilidae without any comments or discussion. This silent act of Kokubo (1932) must have confused some planktologists, for Mizuno (1991) erroneously listed the genus as *Limnoncaea* Kokubo, 1932 in the family Oncaeidae. Curiously, many Japanese researchers collected *Limnoncaea* from various regions in Japan (e.g. Takayasu and Kondo, 1934; Kokubo and Kawamura, 1949; Mashiko and Inoue, 1952; Mashiko, 1955; Kadota, 1962; Okano, 1974; Tanaka, 1992), but these species have never been redescribed in spite of their poor original descriptions. Similarly, some species of *Ergasilus* were also discovered from plankton samples, but these records were not accompanied by any morphological description (Kitahara, 1895; Watanabe *et al.*, 1973). Nevertheless, Takayasu and Kondo (1934) reported that *L. genuina* was one of the most important food items of Japanese smelts (*Hypomesus nipponensis* McAllister) in Lake Yuto-numa of Hokkaido in northern Japan. Since Kokubo's (1914) original description of *Limnoncaea* was written in Japanese without an English abstract, the genus was practically unknown to Western researchers for a long time.

Recently, Huys and Böttger-Schnack (1997) concluded that *Limnoncaea* is assignable to the Ergasilidae, and commented that the genus is either 'a junior synonym of *Ergasilus* or represents an amalgamate of ergasilid genera'. In this paper we shall report the results of our studies on ergasilids found in plankton samples from Hokkaido, where Kokubo (1914) obtained his type materials.

Materials and methods

Copepods were collected with plankton nets (mesh size 0.1 mm) from the following two lakes in Hokkaido located in northern Japan during 1986–1998: Lake Ohnuma (42°00′N, 142°42′E); and Lake Nemuro-chobushi (43°36′N, 145°33′E). Plankton samples were fixed with 3–4% formalin, and then transferred to and stored in 70% ethanol or isopropyl alcohol. Copepods were cleared and dissected in 80% lactic acid. All drawings were made with the aid of a *camera lucida* attached to a compound microscope (Olympus BH). A full description is given of the female, while for the male only those features showing sexual dimorphism are presented.

Body length was measured from the anterior margin of the cephalosome to the posterior rim of the caudal rami excluding setae. Type specimens of the new species are deposited in the Natural History Museum and Institute, Chiba, Japan (CBM-ZC) and the Smithsonian Institution, National Museum of Natural History, Washington, DC, USA (USNM).

Morphological terminology follows Huys and Boxshall (1991).

Taxonomic status of *Limnoncaea* Kokubo, 1914

Kokubo (1914) amended the diagnosis of the family Oncaeidae to accommodate his newly erected *Limnoncaea*, which at the time contained four species, namely, *L. genuina*, *L. diuncata*, *L. divergens* and *Limnoncaea* sp. While both sexes of the first two species were known, only the male of the last two species was known. However, 18 years later, in his book entitled *Huyuseibutsu bunruigaku* (*Taxonomy of Plankton*), Kokubo (1932) listed *Limnoncaea* under the family Ergrasilidae without comment or note. We suspect Kokubo (1932) must have realized the mistake that he made in 1914 in overlooking the absence of the maxilliped in the female of the Ergasilidae. However, Kokubo's (1914) paper is confusing since he stated that specimens of *L. genuina* collected from Sapporo, Hokkaido (northern Japan) possessed maxillipeds, but those from Lake Kasumiga-ura in Honshu (central Japan) did not. Nevertheless, examination of the female maxilliped illustrated by Kokubo (1914: plate 7, figure 10) for the specimens from Sapporo revealed that it resembles those found in the male ergasilids (cf. Gurney, 1913; Yin, 1956; Urawa *et al.*, 1980; Araujo and Boxshall, 2001a). Thus, we concluded that Kokubo (1914) had erroneously identified the male of a co-occurring species as the female of *L. genuina*. Kokubo's (1914) observational error regarding the presence/absence of the maxillipeds in *L. genuina* was elucidated when we had the opportunity to examine specimens of this species from Lake Ohnuma in Hokkaido. Since the general anatomy and the structure of all appendages of *Limnoncaea* fit the diagnosis of the Ergasilidae (cf. Kabata, 1979, 1992b), we concur with Kokubo's (1932) transfer of the genus.

Kokubo (1914) did not designate a type species when he established *Limnoncaea*, but according to ICZN Article 69A, *L. genuina* is to be considered as the type species. Thus, based on Article 23, *Limnoncaea* Kokubo, 1914 is herein proposed as a junior subjective synonym of *Ergasilus* Nordmann, 1832. Examination of the newly collected specimens from Hokkaido indicated that while *L. genuina* should be reassigned to *Ergasilus*, *L. diuncata* is to be transferred to a different ergasilid genus. This reassignment will be discussed in detail in a forthcoming paper. As far as reassignment of *L. divergens* and *Limnoncaea* sp. is concerned, we must wait until the result of re-examination of specimens is available, because both species were established on the basis of the male only.

Description of newly collected ergasilids

Ergasilus genuinus (Kokubo, 1914) n. comb.
(figures 1–4, 5A–E)

Syn: *Limnoncaea genuina* Kokubo, 1914

Material examined. Collected from Lake Ohnuma in Hokkaido, Japan in 1986: one ♀ and three ♂♂ on 23 August, three ♀♀ and four ♂♂ on 18 September, ten ♀♀ on 25 September, one ♀ and 68 ♂♂ on 13 November, and one CV ♀ (female copepodid V) and 1 CV ♂ on 25 September.

Female. Body (figure 1A) cyclopiform, 0.78 (0.72–0.84) mm long. Prosome 2.9 times longer than urosome (figure 1B). Cephalosome (figure 1A) clearly separated from first pediger. Cephalosome (figure 1A) not so expanded postero-laterally (compare to *Ergasilus hypomesi*; figure 13A); rostrum (figure 1D) with semicircular posterior margin; posterodorsal surface with circular integumental window (figures 1A). Second pediger with paired circular integumental windows (figure 4A) laterally. Each sternite of pedigers 1–3 (figure 1E–G) with transverse row of spinules behind randomly distributed larger spinules. Urosome (figure 1B, C) comprising five segments; genital double-somite 1.1 times longer than wide, 0.9 times as long as abdomen and

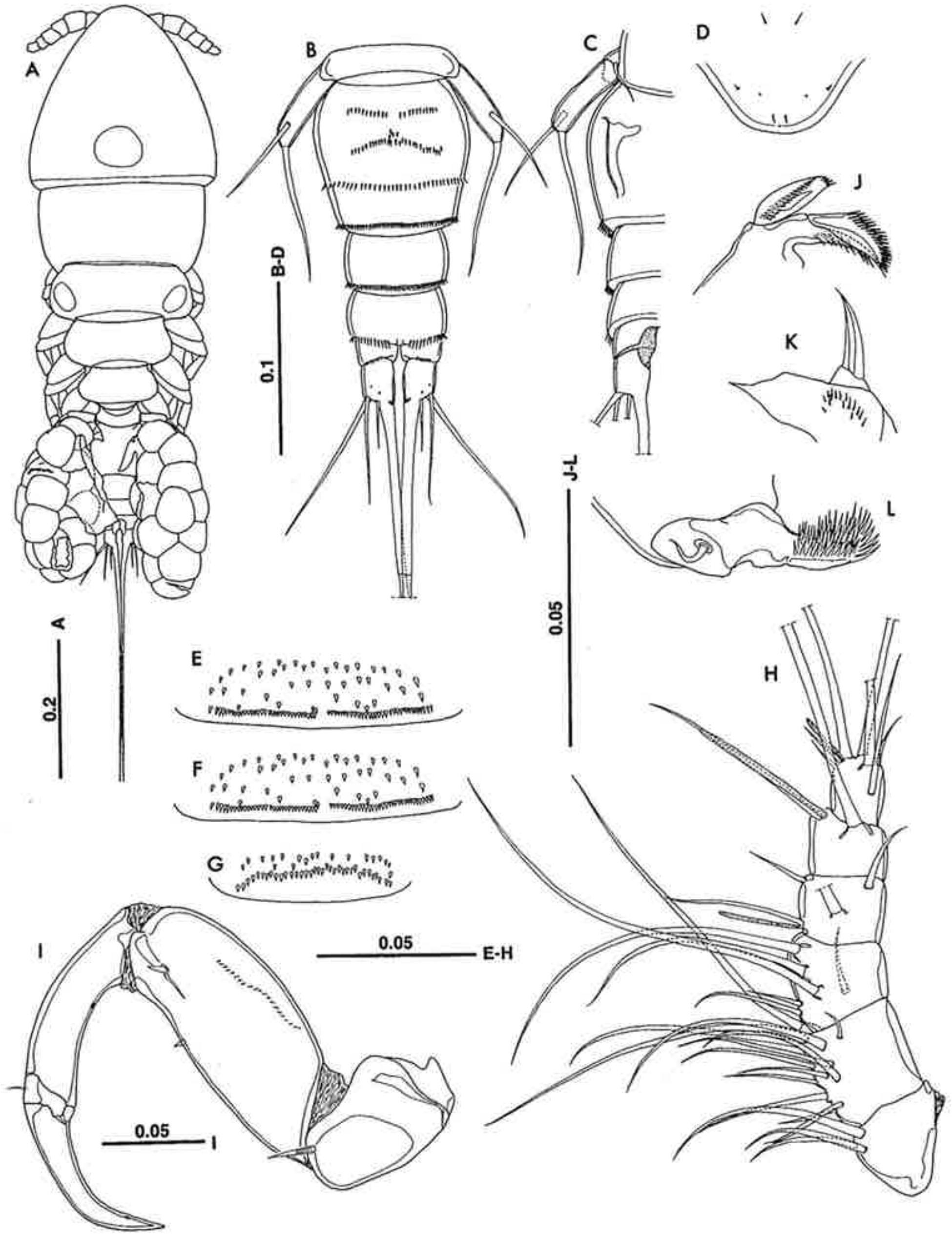

FIG. 1. *Ergasilus genuinus* (Kokubo, 1914). Female. (A) Habitus, dorsal view; (B) urosome, ventral view; (C) urosome, left half, dorsal view; (D) rostrum; (E) sternite 1; (F) sternite 2; (G) sternite 3; (H) antennule; (I) antenna; (J) mandible; (K) maxillule; (L) maxillary basis. Scales in mm.

caudal ramus combined, and furnished with four transverse rows of spinules ventrally; first abdominal somite as long as second, both fringed with row of spinules along posterior margin; anal somite with row of minute spinules ventrally on both

sides. Caudal ramus 1.3 times longer than wide, armed with three short and one long setae, but innermost long one fused to ramus. Egg-sac containing six to 19 eggs (figure 1A).

Antennule (figure 1H) six-segmented, with armature formula: 3; 14; 6; 4+ae; 2+ae; 7+ae. Antenna (figure 1I) four-segmented; coxobasis with stout distal seta; first endopodal segment (=second segment) largest, nearly straight, about 2.2 times longer than wide, armed with two spiniform setae in mediodistal region and row of spinules near outer margin; second endopodal segment smoothly curved inward and unarmed; third endopodal segment smallest, almost indistinguishable from terminal claw and bearing one outer seta; claw with minute basal setule and subterminal pore. Mandible (figure 1J), maxillule (figure 1K) and maxilla (figure 1L) as in usual ergasilid.

Legs 1–4 (figure 2A–D) biramous, with three-segmented rami, except for two-segmented exopod of leg 4. Formula of spines (in Roman numerals) and setae (in Arabic numerals) as follows:

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

Outer margin of first exopod segment sparsely fringed with spinules in all legs except leg 4 where it is smooth. Outer margin of second exopod segment with dense row of spinules on leg 1 but smooth on legs 2 and 3. Outer margin of endopod segments with coarse denticles on legs 1 and 2, and fine denticles on legs 3 and 4. Basis of leg 4 with sparsely distributed spinules on anterior surface; basal seta heavier and longer than those on other legs. Leg 5 (figure 1B, C) with single seta on pediger; free segment elongate, about one-half length of genital double-somite, and bearing one terminal and one subterminal seta.

Male. Body (figure 3A) 0.69 (0.58–0.77) mm long. Prosome about 2.5 times longer than urosome (figure 3B). Second pediger with lateral integumental windows as in female (figure 4B, indicated by large arrowhead). Sternites of pedigers 1–3 (figure 3C–E) with larger and more densely distributed spinules than in female. Urosome (figure 3B) comprising six segments. Genital somite about 0.9 times as long as abdominal segments and caudal ramus combined, with patch of sparsely distributed spinules in central part of ventral surface; first three abdominal somites bearing row of spinules along posterior margin on ventral side. Anal somite with row of minute spinules ventrally on both sides; caudal ramus about 1.4 times longer than wide, with few spinules at base of innermost, largest seta.

Antenna (figure 3F) more slender than that in female; coxobasis with stout distal seta; first endopodal segment longer than second and third segments and claw combined, about 4.8 times longer than wide and armed with a small medial seta; second endopodal segment slightly curved inward, ornamented with patch of minute spinules proximally and one middle and one subterminal short inner seta; third endopodal segment small, incompletely fused to terminal claw, which bears basal seta and subterminal pore. Maxilliped (figure 3G) three-segmented plus long terminal claw; proximal segment unarmed; second segment (=basis) with single row of

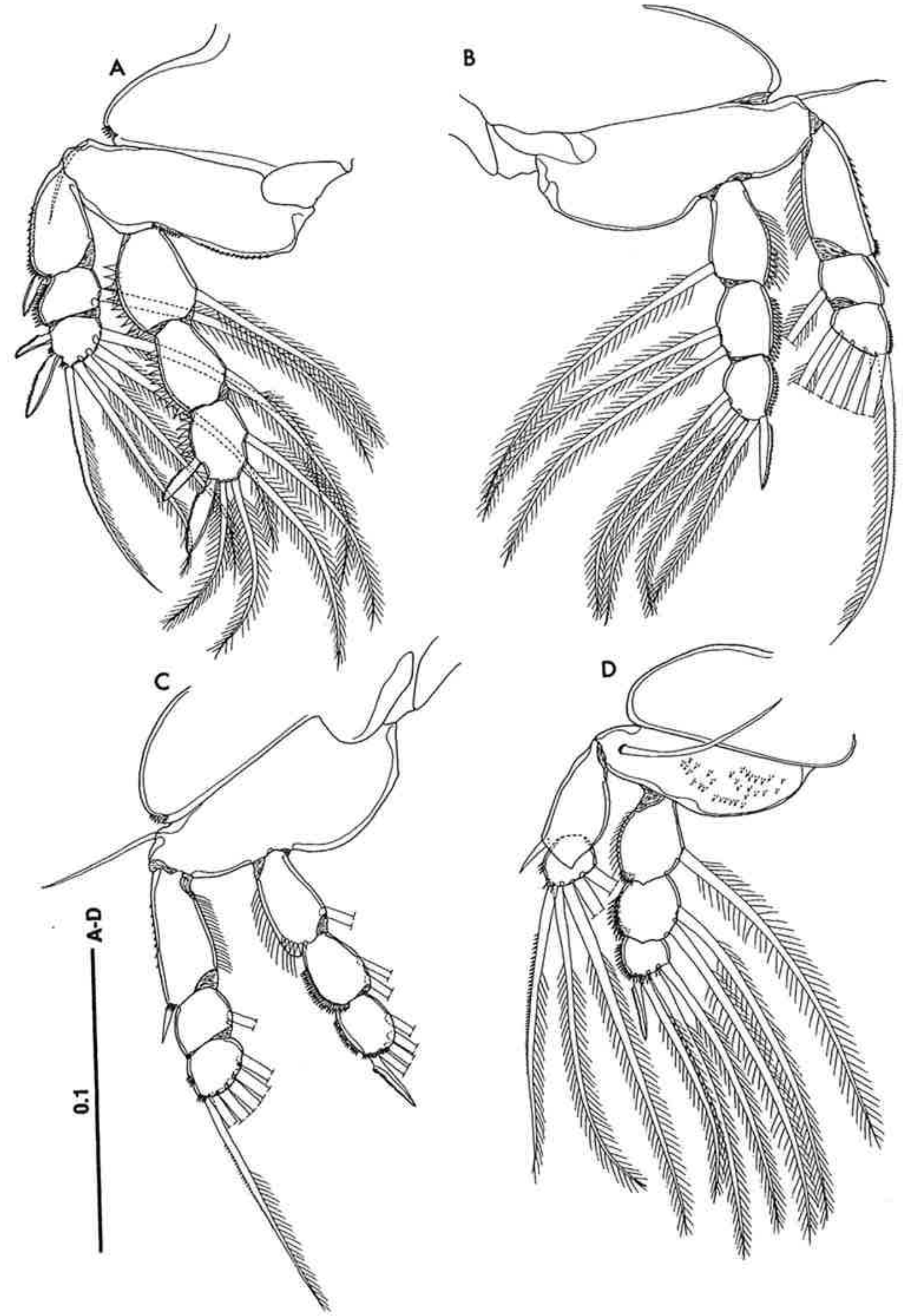

FIG. 2. *Ergasilus genuinus* (Kokubo, 1914). Female. (A) Leg 1; (B) leg 2; (C) leg 3; (D) leg 4. Scale in mm.

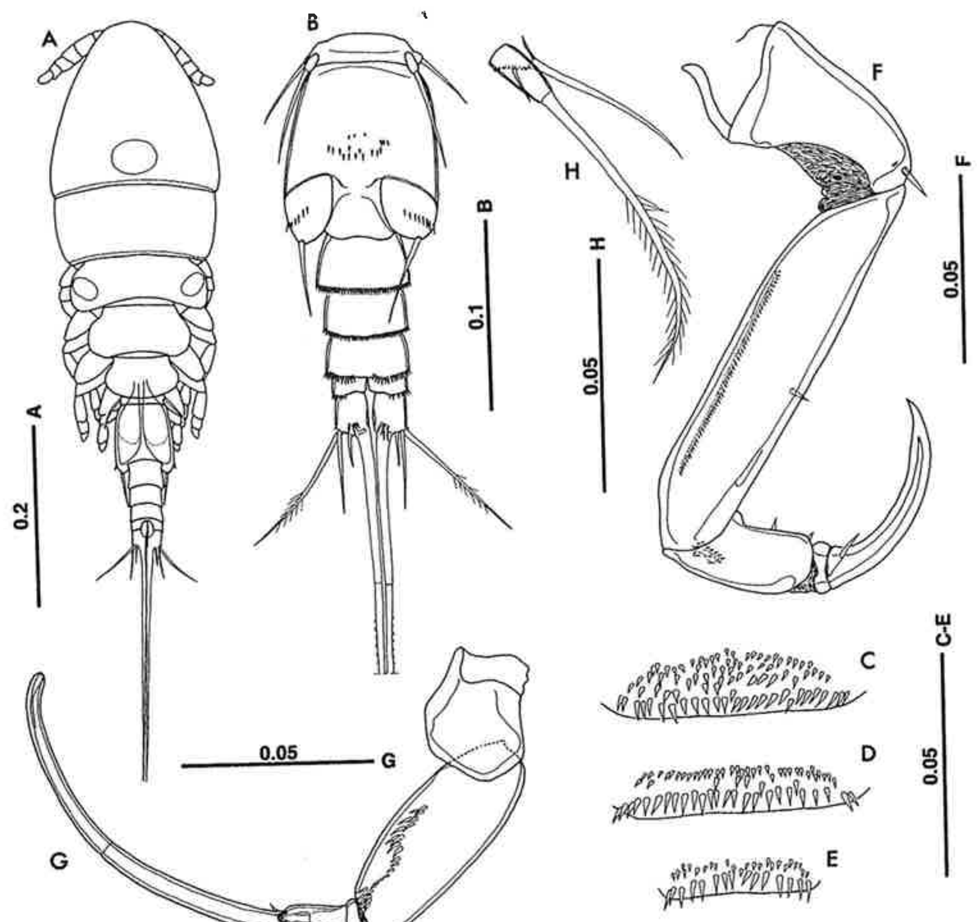

FIG. 3. *Ergasilus genuinus* (Kokubo, 1914). Male. (A) Habitus, dorsal view; (B) urosome, ventral view; (C) sternite 1; (D) sternite 2; (E) sternite 3; (F) antenna; (G) maxilliped; (H) leg 6. Scales in mm.

spinules along distal half of inner margin; third segment (=first endopodal segment) with short, thick seta; claw slender, with fine proximal setule and middle constriction.

Leg 5 (figure 3H) with large seta on pediger; free segment short, bearing one distally pinnate, long, terminal seta and another small, medial. Leg 6 (figure 3B) represented by genital operculum armed with long, terminal seta and ventral row of spinules.

Female copepodid V. Body 0.71 mm long. Urosome (figure 5A) four-segmented, comprising fifth pediger, genital double-somite and two free abdominal somites. Innermost seta on caudal ramus bifurcate.

Antennule five-segmented; with setal formula: 3; 19 (13 + 6); 4 + ae; 2 + ae; 7 + ae. Antenna (figure 5C) relatively short; first endopodal segment (=second segment) with one medial seta; second endopodal segment with two medial, marginal setae. Legs 1–4 biramous, with two-segmented rami, except for one-segmented exopod of leg 4. Formula of spines and setae as follows:

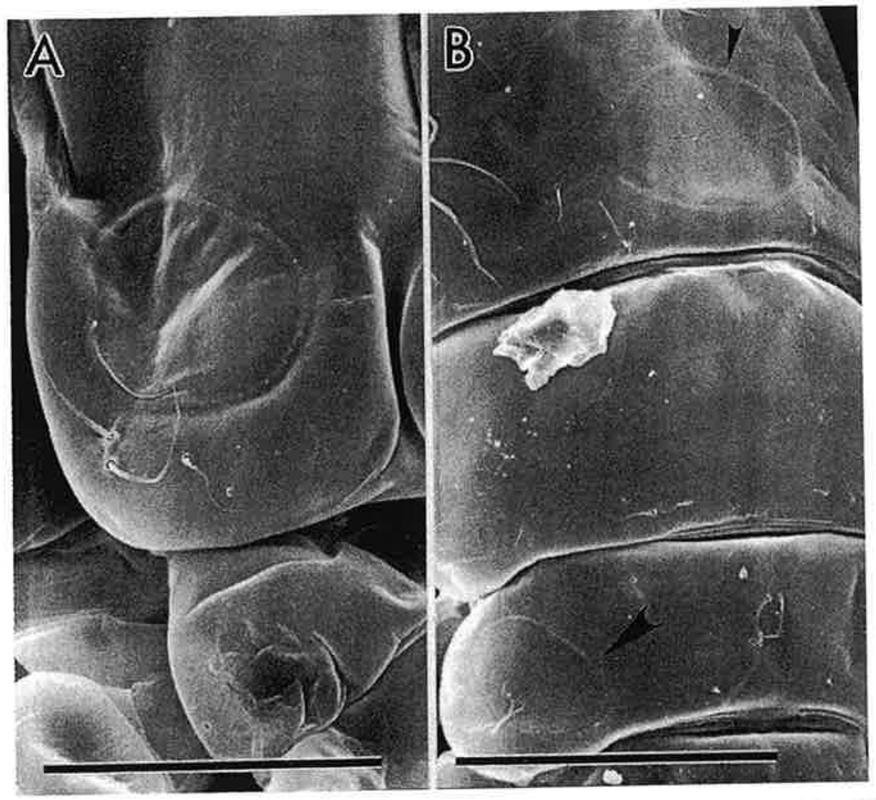

FIG. 4. SEM micrographs of second thoracic somite of *Ergasilus genuinus* (Kokubo, 1914). Female (A); male (B). (A) Lateral integumental window on second pedigerous somite; (B) integumental windows on cephalosome (small arrowhead) and second pedigerous somite (large arrowhead). Scales = 0.05 mm (A); 0.1 mm (B).

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	I-0; II, 6	0-1; II, 5
Leg 2	0-0	1-0	I-0; 7	0-1; I, 6
Leg 3	0-0	1-0	I-0; 7	0-1; I, 6
Leg 4	0-0	1-0	I, 5	0-1; I, 5

Leg 5 (figure 5A) generally as in adult except shorter free segment and terminal setae.

Male copepodid V. Body 0.62 mm long. Urosome (figure 5B) five-segmented comprising fifth pediger, genital somite and three free abdominal somites.

Antennule five-segmented (setal formula not examined). Antenna (figure 5D) as in female copepodid V, but more slender and weaker. Maxilliped (figure 5E) distinctly four-segmented; distal segment armed with a medial seta and tipped with bulbous swelling containing base of developing adult claw.

Leg 5 (figure 5B) as in adult male. Leg 6 (figure 5B) represented by terminal seta on posterolateral corner of genital somite.

Remarks. Our specimens from Lake Ohnuma, Hokkaido are identified as *Ergasilus genuinus* (Kokubo, 1914) from Sapporo, Hokkaido (type locality), on

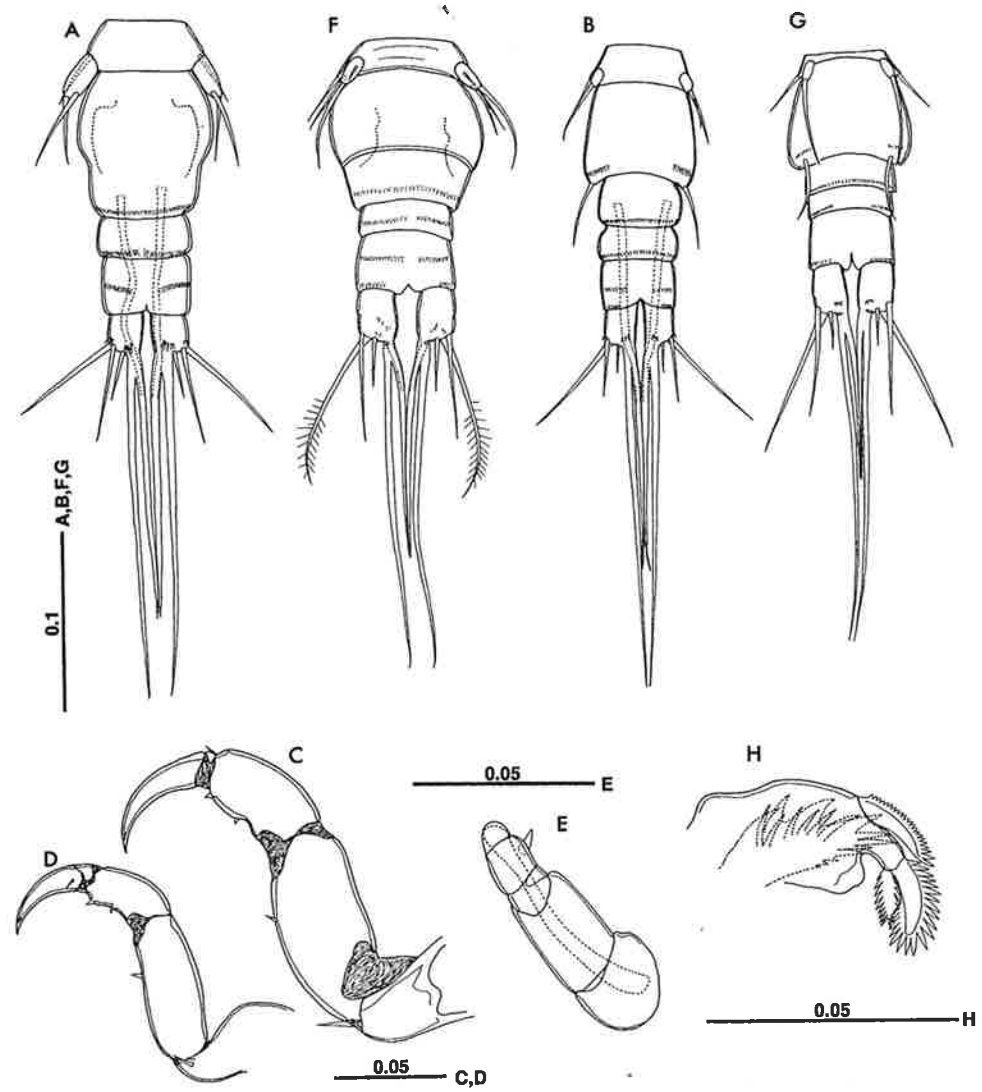

FIG. 5. Fifth copepodid stage of *Ergasilus genuinus* (Kokubo, 1914) (A–E) and *E. hypomesi* Yamaguti, 1936 (F–H). (A) Female urosome, ventral view; (B) male urosome, ventral view; (C) female antenna; (D) male antenna; (E) male maxilliped; (F) female urosome, ventral view; (G) male urosome, ventral view; (H) mandible (middle blade of adult female dotted). Note that the innermost seta of adults originates from the inner side of bifurcate seta (see A, B and F). Scales in mm.

the basis of the following features: (1) presence of ovigerous females in plankton; (2) similar shape and proportion of urosomal somites and caudal rami in both sexes; (3) same number of segments on antennules in both sexes; (4) similar shape and proportion of endopodal segments of the antennae in both sexes; (5) identical segmentation and armature formulae on legs 1–4; and (6) shape of female leg 5.

However, our specimens differ from those of Kokubo's (1914) in: (1) the absence of an outer spine on the third exopodal segment of leg 2, (2) the lack of a medial seta on the free segment of male leg 5, and (3) presence of spinules along the posterior margin of the anal somite in both sexes. Nevertheless, we believe that their overall similarity and the proximity of sampling localities are sufficient to assume conspecificity.

In addition to the present species, several other ergasilids found in plankton have been reported to possess a pair of relatively small egg-sacs (with each sac containing at most 20 eggs): *E. chautaquaensis* Fellows, 1887 (cf. Wilson, 1911); *E. longicaudatus* Kuang and Li, 1984 (Kuang and Li, 1984); *Acusicola minuta* Araujo and Boxshall, 2001 (Araujo and Boxshall, 2001a); and *Gauchergasilus euripedesi* (Montú, 1980) (Montú, 1980; Montú and Boxshall, 2002). In contrast to these species, all other ovigerous ergasilids were reported from their hosts and not from the plankton (cf. Wilson, 1911; Yin, 1956; Yamaguti, 1963; Kuang and Qian, 1991). The parasitic females generally carry relatively larger egg-sacs, each containing up to 200 eggs (Yin, 1956). The possession of a cyclopiform cephalosome as well as smaller egg-sacs in the former group of ergasilids seems to be associated with their planktonic mode of life (see Discussion).

The female of *E. genuinus* resembles most closely that of *E. glyptothoracis* Kuang, 1983 parasitic on *Glyptothorax* spp. in China (Kuang and Qian, 1991). The resemblance is found in having short caudal ramus and antenna, no spine on the terminal exopodal segments of legs 2–4, and well-developed, free, one-segmented leg 5 bearing two setae. However, *E. glyptothoracis* differs in having its cephalosome and first pediger fused and antennary claw bearing an inner proximal knob.

Kokubo's (1914) *Limnoncaea* sp. was reported carrying a bifurcate postero-medial seta on the caudal ramus just like the above-mentioned copepodid V. We suspect it is an ergasilid in its fourth or fifth copepodid stage, because it has a four-segmented antennule, two-segmented rami on legs 1–4, except for the one-segmented exopod of leg 4, in addition to a bifurcate seta on the caudal ramus. Gurney (1913), Urawa *et al.* (1980), Ben Hassine (1983), Adelhalim *et al.* (1991) and Alston *et al.* (1996) studied development in the Ergasilidae. According to their findings, copepodid I carries five or six setae on each caudal ramus; but in the following four stages, from copepodid II to V, the two medial setae fuse at the base to form a large bifurcate seta. In the next (adult) stage, the inner branch of the birfucate seta develops into the large, innermost seta, whereas the outer branch disappears. The outer and inner branches of this large seta can be considered as the original caudal setae V and VI, respectively (cf. Huys and Boxshall, 1991; Conroy-Dalton, personal communication). Such fusion and reduction of caudal setae through the copepodid stages are found also in pelagic harpacticoids of the family Miraciidae (Huys and Böttger-Schnack, 1994). In the first copepodid stage of a miraciid harpacticoid, *Macrosetella gracilis* (Dana, 1847), the branched setal complex can be regarded as fused setae V (outer) and VI (inner), which separate at the next moult. In the next stage, the caudal seta V is formed within the outer side of the branch, whereas seta VI is reduced and replaced by a small, newly formed seta at the inner distal corner of the caudal ramus (Huys and Böttger-Schnack, 1994: figure 36). In the Ergasilidae, the fate of the branching setal complex differs from that of *M. gracilis*. At the final moult the inner branch of the bifurcate seta is changed into seta VI, while the outer branch is totally reduced. Although the function of the branching setae is unknown, it may be related to the change in mode of life (see Discussion).

***Ergasilus bani* n. sp.**
(figures 6–12)

Material examined. Ten ♀♀ and 16 ♂♂ collected from Lake Nemuro-chobushi, Hokkaido on 25 July 1994. Holotype female (CBN-ZC 6465) and 19 paratypes (one ♀ and two ♂♂ dissected, received CBN-ZC 6466, seven ♀♀ and nine ♂♂ intact, CBN-ZC 00000) have been deposited in the Chiba Prefectural Museum, and remaining paratypes (three ♀♀ and three ♂♂) in the Museum of Natural History, Smithsonian Institution (NMNH 1005207).

Female. Body (figure 6A; see figure 11A) compact, cyclopiform, 0.57 (0.55–0.61) mm long. Prosome (figures 6A, B, 11A) about 3.2 times as long as urosome (figures 6C, 10A). Cephalosome nearly as long as wide, clearly separate from first pediger and with circular integumental window on posterodorsal surface. Pedigers decreasing in width antero-posteriorly; sternites of first to third pedigers bearing row of spinules along posterior margin (figure 6D–F); second pediger with lateral paired integumental windows (figures 6A, 11A, B). Urosome (figure 6C) consisting of extremely short fifth pediger, genital double-somite and indistinctly three-segmented abdomen (see figure 10A). Genital double-somite (figure 6C; also figures 10A, B, 11A) inflated, 1.2 times wider than long, about 1.4 times as long as abdominal segments and caudal ramus combined, with pair of longitudinal gonopores dorsolaterally, and rows of spinules ventrally. Leg 6 absent, but outer margin of gonopore bearing one or more peg-like integumental organs anteriorly (see figure 10B). All three abdominal somites with transverse row of minute spinules along postero-ventral margin, but incomplete on second free abdominal somite. Caudal ramus 1.2 times wider than long, tipped with one long and three short setae; longest medial seta swollen at base in holotype. Egg-sacs not seen.

Antennule (figures 6G, 9B) distinctly six-segmented, with armature formula: 3, 13, 6, 4+ae, 2+ae, 7+ae. Antenna (figures 6H, 9A, C) heavily sclerotized; coxobasis with pore and minute spine distally; first endopodal segment slightly shorter than second and third endopodal segments and claw combined, slightly curved inwards, about 2.4 times longer than wide, and bearing medial, marginal spine at mid-point; remaining part of endopod covered with minute holes; second endopodal segment armed with tiny medial spine in proximal region and small, subterminal knob along inner margin; third endopodal segment indistinctly incorporated into claw; claw strongly curved inwards, furnished with large protuberance on medial margin in basal region. Mandible (figures 6I, 9D) with uniserrated anterior and posterior blades, middle falciform blade with larger teeth. Maxillule (figures 6J, 9D) unsegmented, tipped with three setae and scattered with minute spinules anteriorly. Maxilla (figures 6K, 9A, D) two-segmented, syncoxa bearing a seta distally and basis covered distally with dense array of acute processes.

Legs 1–4 (figure 7A–E) biramous, with three-segmented rami, except for two-segmented exopod of leg 4; formula of seta and spine as in *E. genuinus*. Coxae of legs 1–4 unarmed; basis ornamented with row of spinules in legs 1 and 4 and two rows in legs 2 and 3 along inner distal margin on anterior surface. All endopodal segments of legs 1–4, terminal exopodal segments of legs 2–4 and middle exopodal segment of leg 1 with row of spinules on outer margin. Free segment of leg 5 (figure 9C) tipped with long seta.

Male. Body (figure 8A; also figure 11C) 0.61 (0.55–0.65) mm long, more slender than female. Cephalosome separate from first pediger, 1.2 times wider than long;

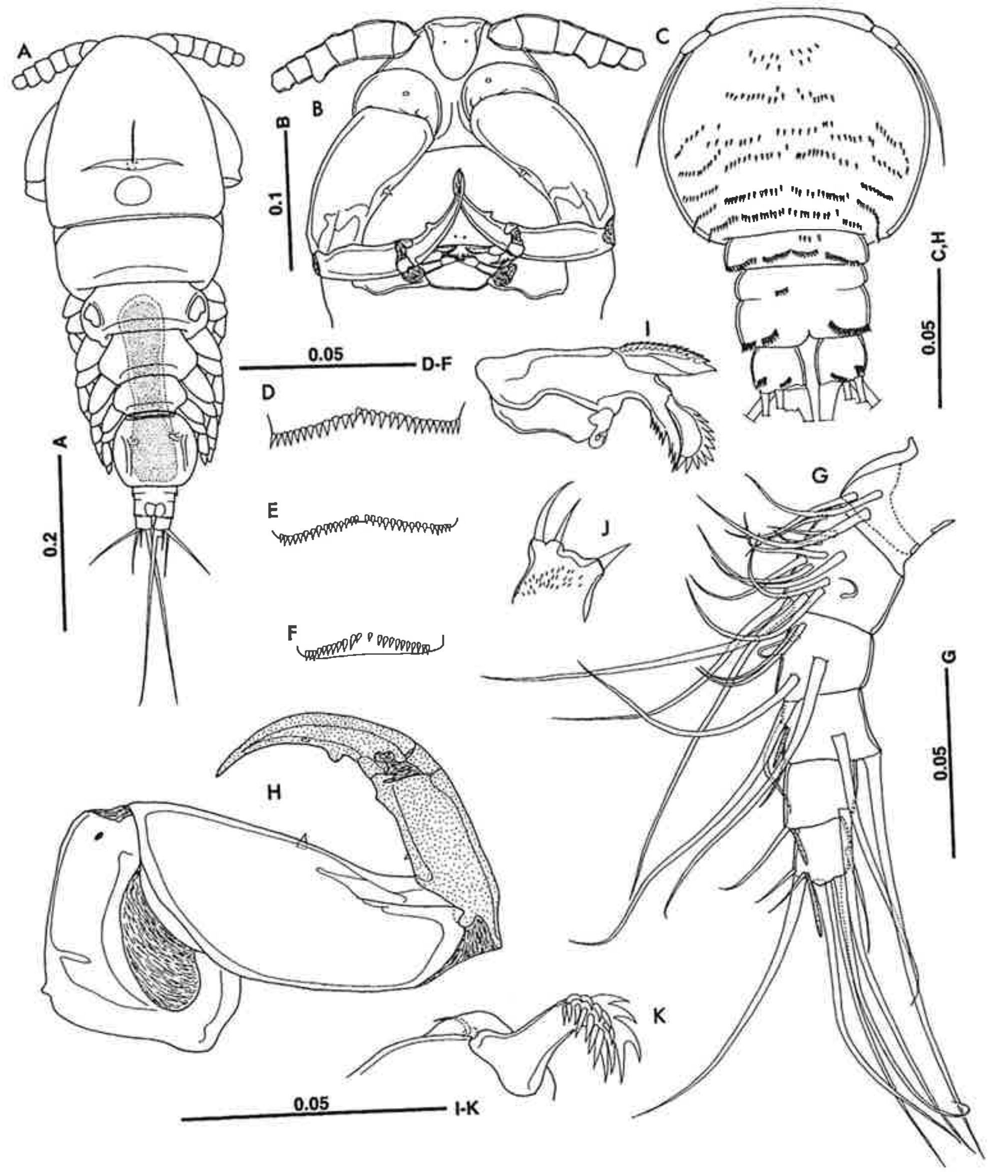

FIG. 6. *Ergasilus bani* n. sp., Female. (A) Habitus, dorsal view; (B) cephalosome, ventral view; (C) urosome, ventral view; (D) sternite 1; (E) sternite 2; (F) sternite 3; (G) antennule; (H) antenna; (I) mandible; (J) maxillule; (K) maxillary basis. Scales in mm.

second pediger with paired lateral integumental windows as in female (figures 8A, 11C, D); sternites of pedigers 1–3 ornamented with row of fine spinules along posterior margin (figure 8C–E). Urosome comprising small fifth pediger, elongate genital somite, and four-segmented abdomen plus caudal rami. Genital somite slightly longer than four abdominal segments combined, bearing patches and rows of minute spinules as shown in figure 8B. Abdominal somites with two short transverse row of spinules near posteroventral margin. Caudal ramus 1.3 times wider than long.

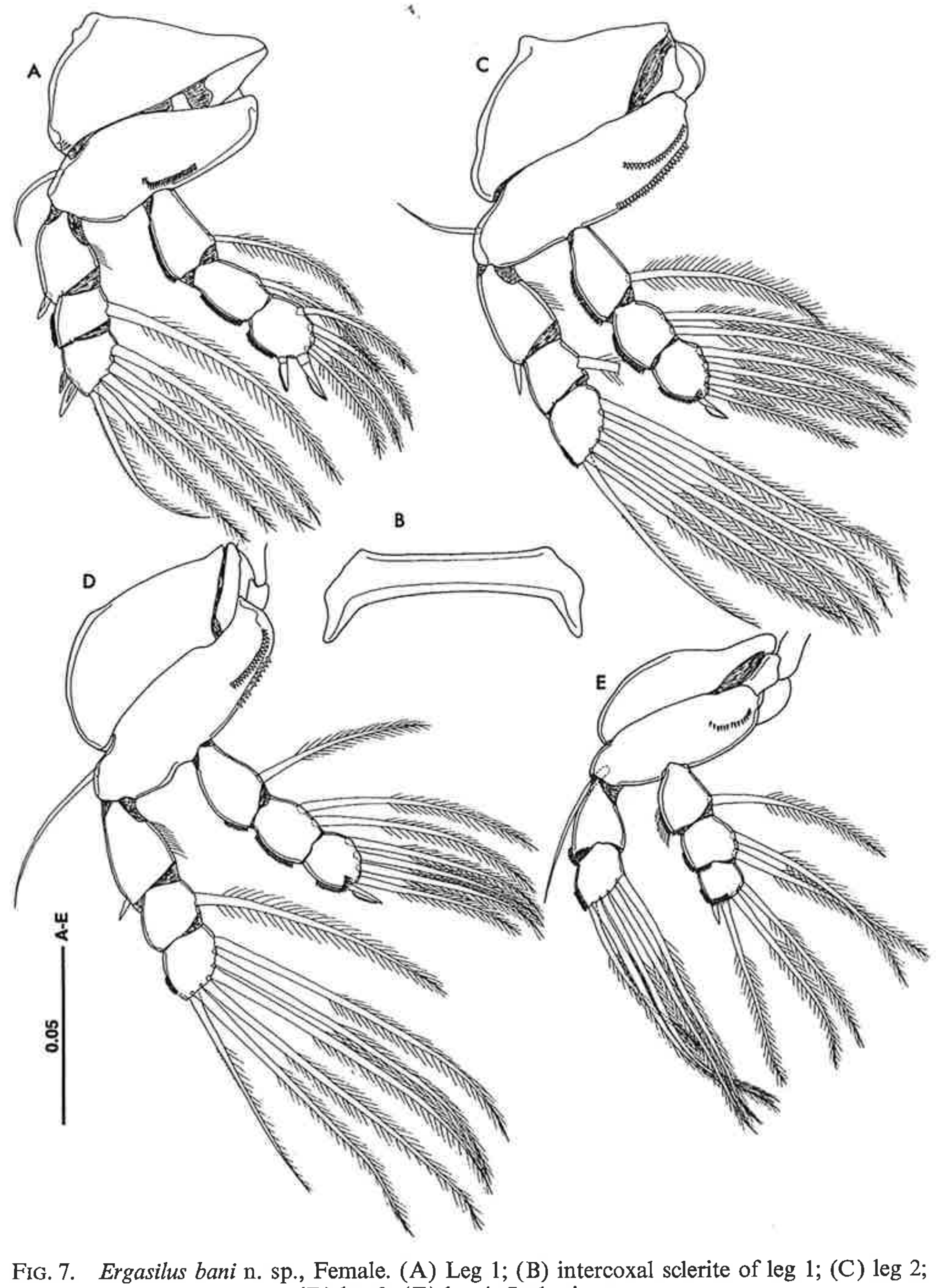

FIG. 7. *Ergasilus bani* n. sp., Female. (A) Leg 1; (B) intercoxal sclerite of leg 1; (C) leg 2; (D) leg 3; (E) leg 4. Scales in mm.

Antenna (figures 8F, 12A) four-segmented; coxobasis stout, bearing minute distal seta (not shown in figure); endopod indistinctly three-segmented; first endopodal segment longest, about 2.8 times as long as wide, with central and subterminal setae on inner margin and irregular row of minute spinules along outer margin; second segment bearing two short inner setae and patch of minute spinules; third segment

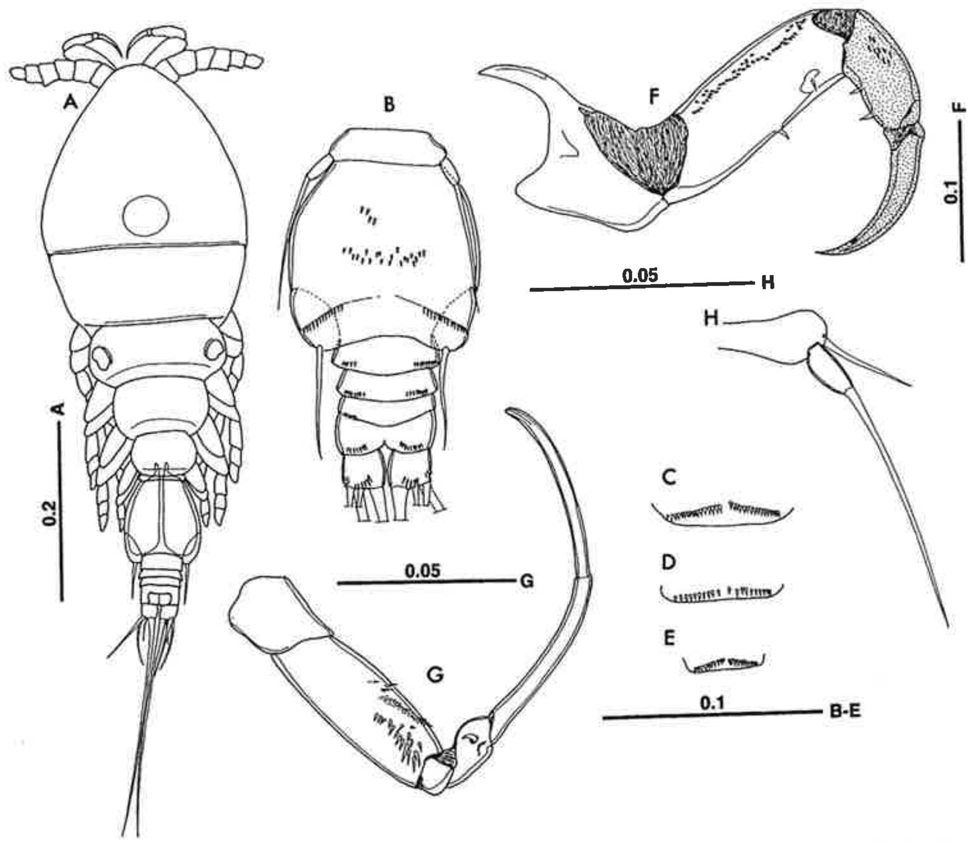

FIG. 8. *Ergasilus bani* n. sp., Male. (A) Habitus, dorsal view; (B) urosome, ventral view; (C) sternite 1; (D) sternite 2; (E) sternite 3; (F) antenna; (G) maxilliped; (H) leg 5. Scales in mm.

short, incompletely incorporated into terminal claw; claw smoothly curved inwards, with subterminal pore. Maxilliped (figures 8G, 12C, D): basis about twice as long as unarmed coxa, with two irregular rows of spinules in distal half; endopod incompletely two-segmented, first segmented unarmed, second segment with stout seta; claw smoothly curved inward, constricted at mid-point, with spatulate apex.

Leg 5 (figure 8H) generally as in female, with relatively longer terminal seta. Leg 6 (figures 8B, 10C, D) represented by single seta at tip of genital operculum.

Remarks. The new species is distinguishable from its congeners by a combination of the following features in the female: (1) the cephalosome separate from the first pediger; (2) lateral integumental windows on the second pediger (also in the male); (3) the relatively short urosome with a bulbous genital double-somite and extremely short fifth pediger; (4) a caudal ramus shorter than wide; (5) antennule six-segmented; (6) short antenna with a minute distal seta on the coxobasis and a large proximal knob on the claw along the inner margin; (7) all rami of legs three-segmented, except for two-segmented exopod of leg 4; (8) absence of outer spine on the terminal exopodal segments of legs 2–4; and (9) leg 5 with unisetose protopod and unisegmented endopod bearing a single terminal seta. The most remarkable feature of these is the presence of a lateral integumental window on the second pediger, the function of which is still unknown. This peculiar structure is found in

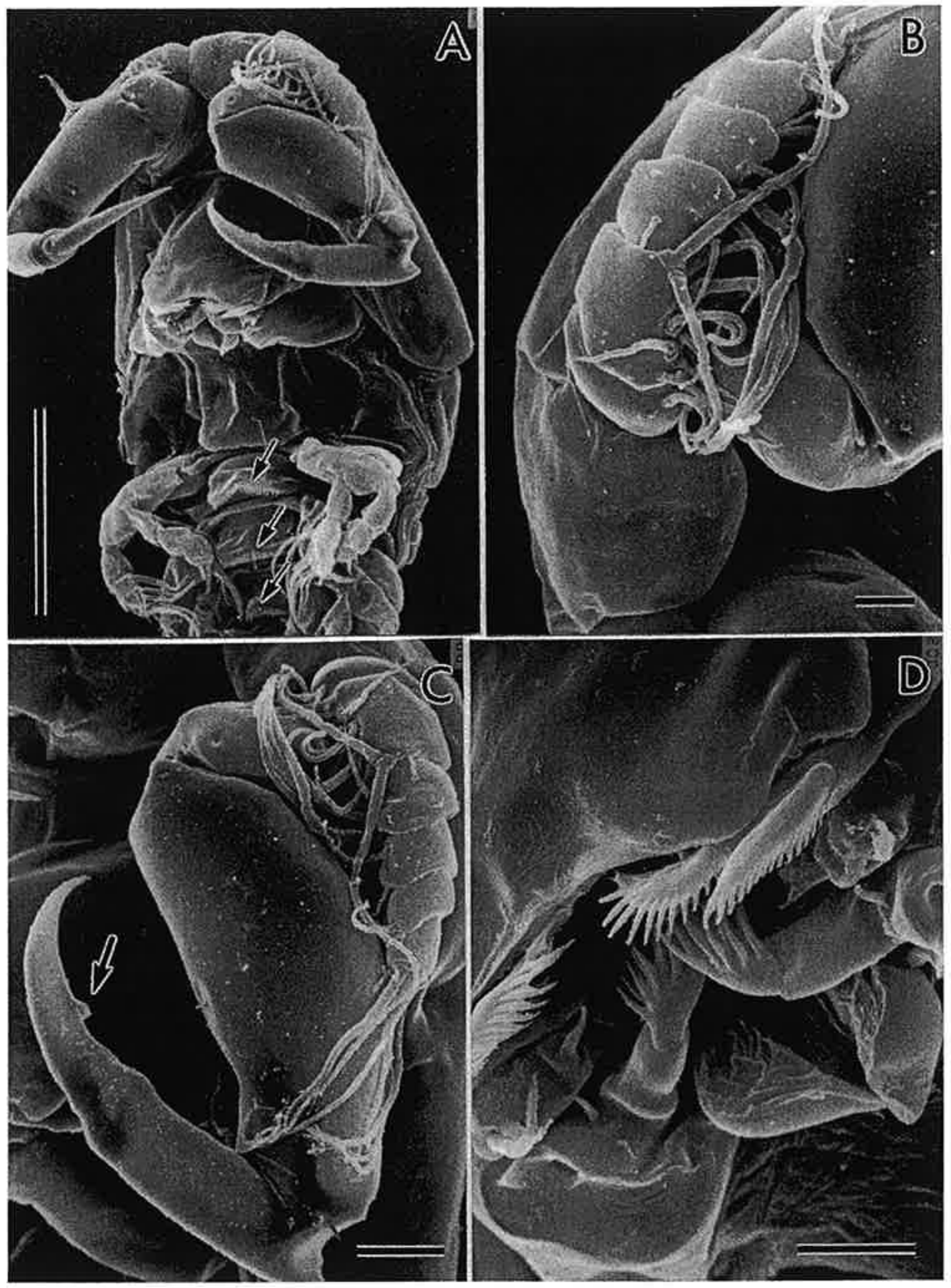

FIG. 9. SEM micrographs of *Ergasilus bani* n. sp. Female. (A) Cephalosome and pedigers, ventral view, spinular rows on sternites arrowed; (B) rostrum and antennule; (C) antennule and antenna, knob on claw arrowed; (D) labrum and mouthparts. Scales = 0.1 mm (A); 0.01 mm (B, D); 0.02 mm (C).

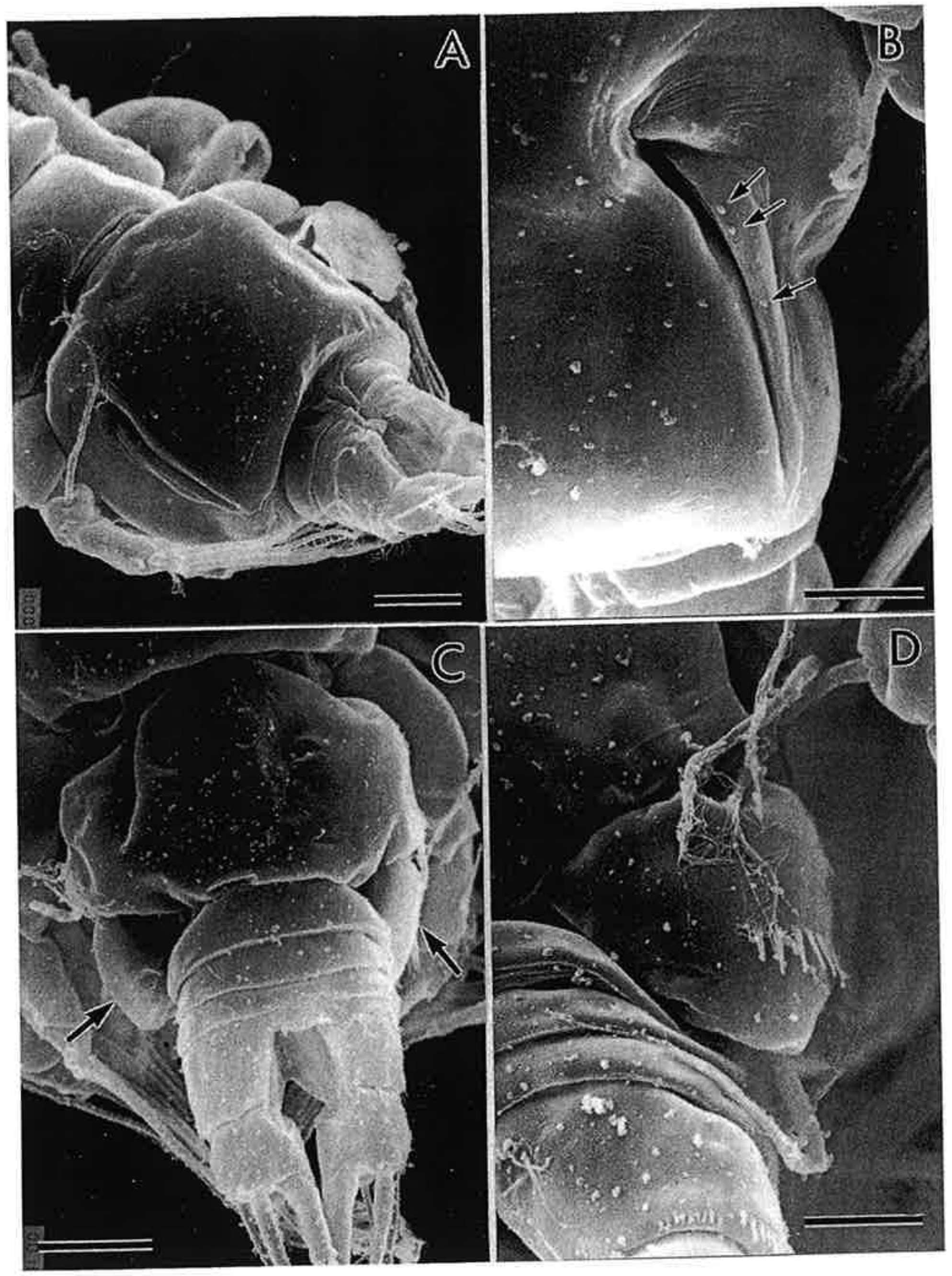

FIG. 10. SEM micrographs of *Ergasilus bani* n. sp. Female (A, B); male (C, D). (A) Urosome, dorsal view; (B) gonopore, minute integumental organs arrowed; (C) urosome, dorsal view, genital operculum arrowed; (D) genital operculum. Scales = 0.02 mm (A, C); 0.01 mm (B, D).

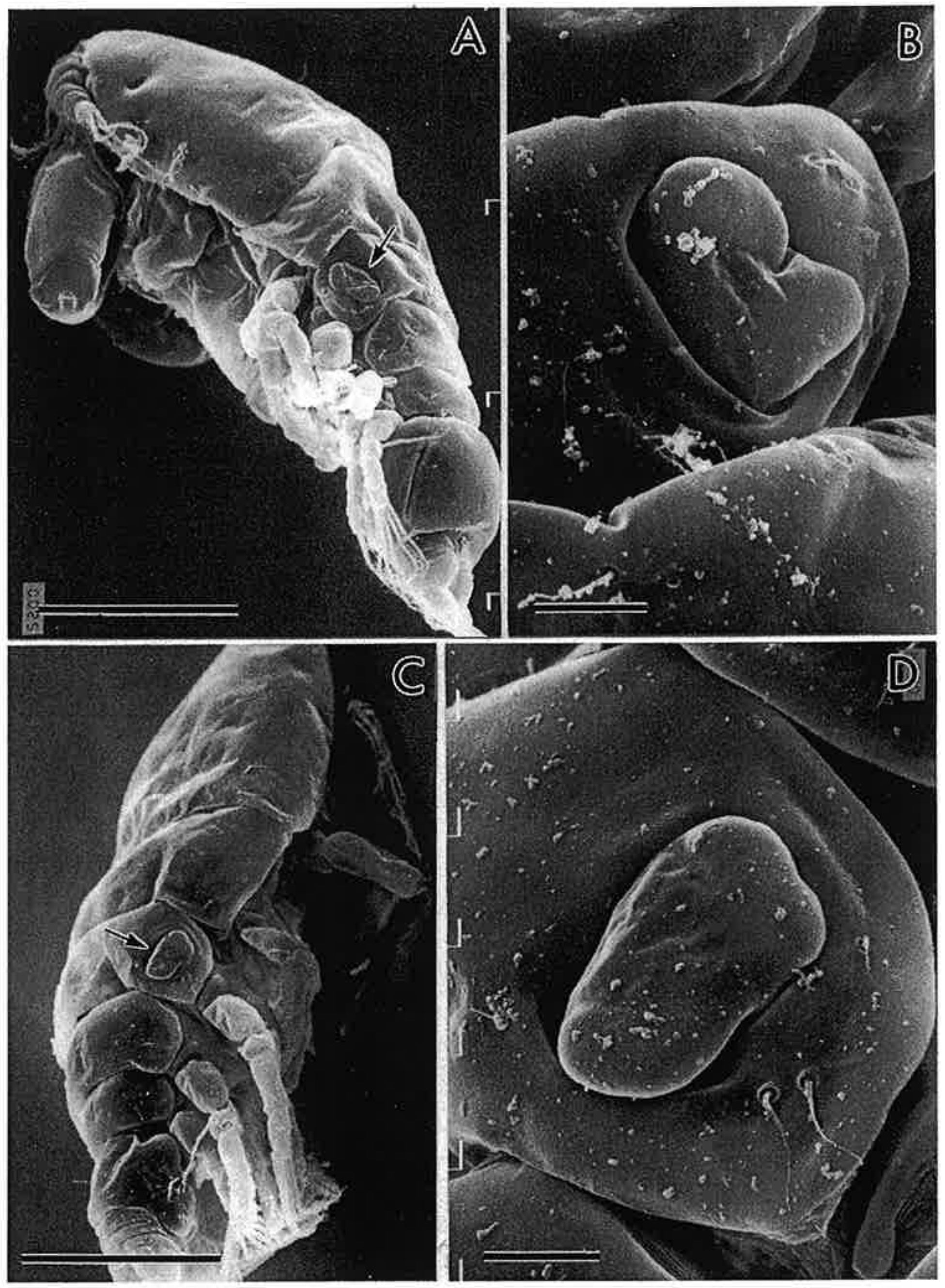

FIG. 11. SEM micrographs of *Ergasilus bani* n. sp. Female (A, B); male (C, D). (A, C) Habitus, ventrolateral view, pediger 2 indicated by arrow; (B, D) integumental window on pediger 2. Scales = 0.1 mm (A, C); 0.01 mm (B, D).

only six other species of *Ergasilus*, namely in addition to *E. genuinus*, *E. holobryconis* Malta and Varella, 1986 (South America, freshwater: Malta and Varella, 1986), *E. longicaudatus* Kuang and Li, 1984 (East Asia, freshwater: Kuang and Li, 1984),

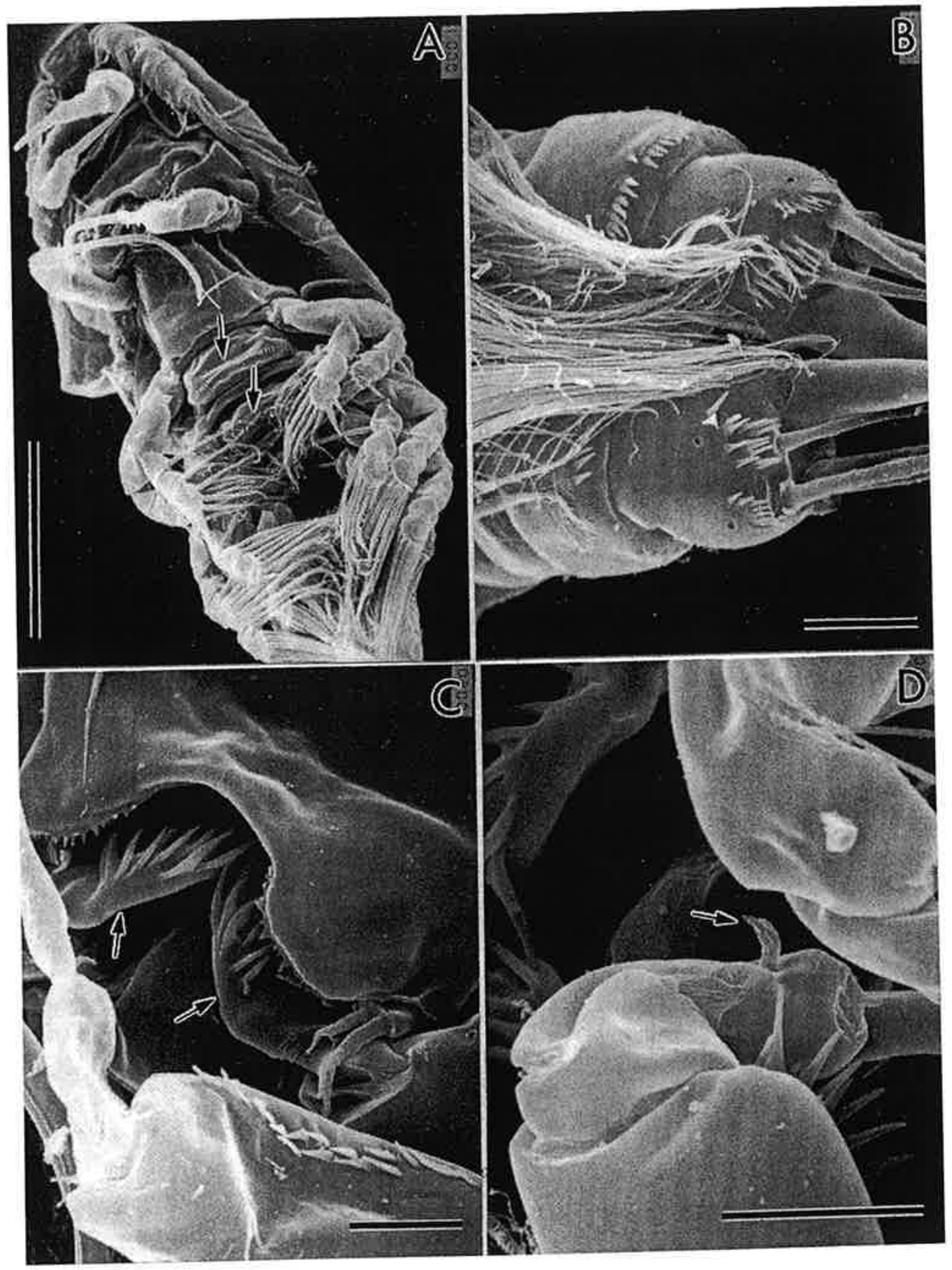

FIG. 12. SEM micrographs of *Ergasilus bani* n. sp. Male. (A) Habitus, ventral view, spinular row on sternite arrowed; (B) caudal rami, ventral view; (C) labrum, maxillule and maxilla (arrowed); (D) maxillipedal endopod, seta on second endopodal segment indicated by arrow. Scales = 0.1 mm (A); 0.01 mm (B–D).

E. yumaricus Malta and Varella, 1996 (South America, freshwater: Malta and Varella, 1996), *E. ogawai* Kabata, 1992 (Oceania, coastal: Kabata, 1992a) and *E. urupanensis* Malta, 1993 (South America, freshwater: Malta, 1993). Another characteristic feature is the presence of a large proximal knob on the concave side of the antennary claw. This feature is also found in *E. auritus* Markevich, 1940 (North America, coastal: Roberts, 1970), *E. funduli* Kroyer, 1863 (North America, freshwater: Roberts, 1970), *E. glyptothoracis* Kuang, 1983 (East Asia, freshwater: Kuang and Qian, 1983), *E. labracis* Krøyer, 1863 (North America, coastal: Roberts, 1970), *E. lucioperccarum* Henderson, 1926 (North America, freshwater: Roberts, 1970), *E. manicatus* Wilson, 1911 (North America, coastal), *E. megacheir* (Sars, 1909) (Africa, freshwater), *E. myctarothes* Wilson, 1913 (West Indies, coastal), *E. nerkae* Roberts, 1963 (North America, freshwater), *E. plecoglossi* Yamaguti, 1939 (East Asia, freshwater) and *E. turgidus* Fraser, 1920 (North America, coastal: Roberts, 1970).

In consideration of the morphology and biogeography, the new species seems to be most closely related to *E. plecoglossi* from Japan and to *E. glyptothoracis* from China. However, it differs from *E. plecoglossi* in the segmentation and armature formula of legs 2–4, and from *E. glyptothoracis* in the shape of antenna, the absence of an outer spine on the first exopodal segment of leg 4 and in carrying only one seta on the unisegmented endopod of leg 5.

No ovigerous female of *E. bani* was observed from the plankton samples. Its host is also unknown.

Etymology. The species is named in honour of Dr Shuhei Ban who kindly provided us with ergasilid material from Hokkaido, Japan.

Ergasilus hypomesi Yamaguti, 1936
(figures 5F–H, 13–15)

Material examined. Collected in 1986 from Lake Ohnuma located in Hokkaido, Japan: ten ♂♂ on 23 August, two ♀♀ and three ♂♂ on 18 September, eight ♂♂ on 25 September, one ♀ and one ♂ on 13 November, and one CV ♀ and one CV ♂ on 25 September.

Female. Body (figure 13A) 0.72 (0.64–0.80) mm long; general appearance similar to *E. genuinus*. Prosome about three times longer than urosome (figure 13B). Cephalosome with posterior third expanded laterally in dorsal view; rostrum as in *Ergasilus genuinus*; dorsomedian integumental window present posteriorly (figures 13A, 15A, B), as in *E. genuinus*; second pedigers with lateral paired integumental windows as in *E. bani* (figures 13A, 15C). Sternites of pedigers 1–3 (figure 13C–E) as in *E. bani*. Urosome (figure 13B) with prominent fifth pediger; genital double-somite as long as abdominal somites and caudal ramus combined. Caudal ramus approximately 1.4 times longer than wide, ornamented with patch of minute spinules distally on posterior surface.

Antennule (figure 13F) with same segmentation and setal formula as in *E. bani*. Antenna (figure 13G, H) with coxobasis bearing minute distal seta; first endopodal segment smoothly curved inward, relatively elongate, about four times longer than wide; second endopodal segment with rounded distal knob and minute mediomarginal seta; third endopodal segment nearly completely fused to terminal claw; claw with striation in middle region. Middle blade of mandible (figures 13I, 5H) with heavy teeth on outer margin. Maxillule (figure 13J) as in *E. bani*, but outer distal seta about twice as long as inner one. Maxilla (figure 13K) with long and pinnate basal seta.

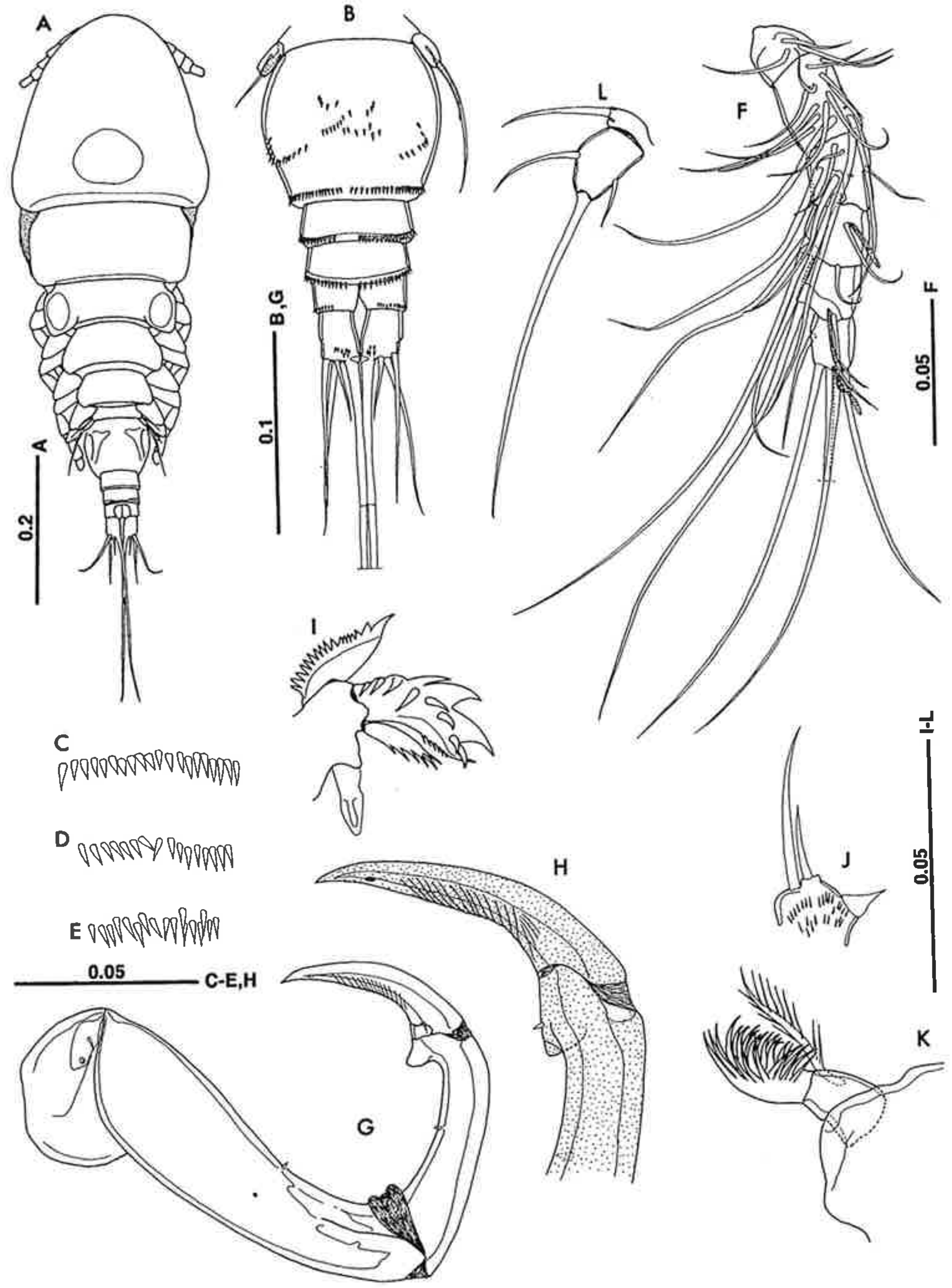

FIG. 13. *Ergasilus hypomesi* Yamaguti, 1936. Female. (A) Habitus, dorsal view; (B) urosome, ventral view, terminal seta on left endopod of leg 5 omitted; (C) spinular row of sternite 1; (D) spinular row of sternite 2; (E) spinular row of sternite 3; (F) antennule; (G) antenna; (H) terminal part of antenna; (I) mandible; (J) maxillule; (K) maxillary basis; (L) leg 5. Scales in mm.

Legs 1–4 biramous, with three-segmented rami, except for two-segmented exopod of leg 4. Formula of spines (in Roman numerals) and setae (in Arabic numerals) as follows:

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

Leg 1 as in previous two species, but legs 2, 3 and 4 different in having outer spine on terminal segment of exopod. Leg 5 (figure 13L) with unisetose protopod and one-segmented exopod bearing two marginal and one long terminal seta.

Male. Body (figures 14A) 0.82 (0.72–0.88) mm long; shaped as in *E. bani*; prosome 2.6 times as long as urosome (figure 14B). Cephalosome triangular in dorsal view; armature of sternites of pedigers 1–3 (figure 14C–E) different from those of female; rostrum (figure 14F) and lateral integumental window on second pediger (figure 15D) as in female. Fifth pediger (figure 14A, B) prominent; genital somite more expanded laterally than in *E. bani*, 0.9 times as long as abdominal somites and caudal ramus combined; genital operculum ornamented with oblique row of minute spinules; each abdominal somite fringed with minute spinules along postero-ventral margin. Caudal ramus 1.5 times longer than wide, with minute patch and row of fine spinules terminally.

Antennule (figure 14F) five-segmented; armature formula 16, 6, 4+ae, 2+ae, 7+ae. Antenna (figure 14G) with well-developed distal seta on coxobasis; first endopodal segment 3.2 times longer than wide, but shorter than second and third segments and claw combined, seta midway on medial margin; second endopodal segment bearing two inner setae and outer patch of minute spinules; third endopodal segment rudimentary; claw with short basal seta and subterminal pore. Teeth on mandibular middle blade (figure 14H) not as heavy as in female. Maxillule and maxilla (figure 14H) as in female. Maxilliped (figure 14I) with two rows of spinules in distal half; second endopodal segment with stout subterminal seta; claw long, with spatulate apex (figure 14J).

Leg 5 (figure 14B) with one seta on basis and one medial and one terminal seta on one-segmented exopod. Leg 6 represented by one long seta on genital operculum.

Female copepodid V. Body 0.72 mm long. Prosome as in adult female. Urosome (figure 5F) different from that of *E. genuinus*, comprising fifth pediger, genital somite and three abdominal somites. Caudal ramus tipped with four setae, outer three short and innermost one long and bifurcate.

Antennule four-segmented; armature formula 22, 4+ae, 2+ae, 7+ae. Antenna lacking large knob on inner distal corner. Mandible (figure 5H) as in male adult with fine teeth on middle blade (heavy adult teeth being formed within).

Legs 1–4 biramous, with two-segmented rami, except for one-segmented exopod of leg 4; seta and spine formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	I-0; II, 6	0-1; II, 5
Leg 2	0-0	1-0	I-0; 7	0-1; I, 6
Leg 3	0-0	1-0	I-0; I, 7	0-1; I, 6
Leg 4	0-0	1-0	II, 5	0-1; I, 5

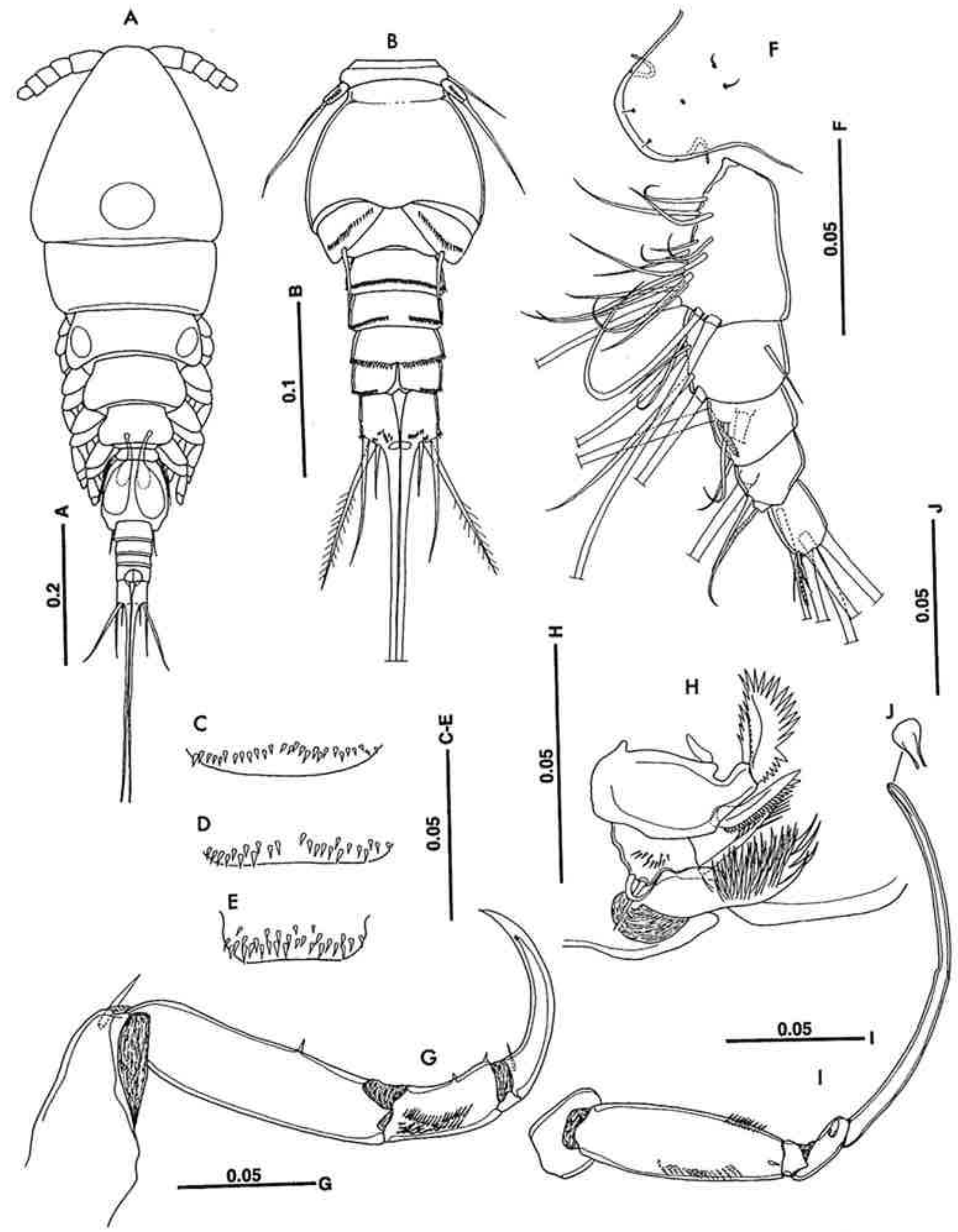

FIG. 14. *Ergasilus hypomesi* Yamaguti, 1936. Male. (A) Habitus, dorsal view; (B) urosome, ventral view; (C) sternite 1; (D) sternite 2; (E) sternite 3; (F) rostrum and antennule; (G) antenna; (H) mandible, maxillule, maxillary basis and labium; (I) maxilliped; (J) tip of maxilliped. Scales in mm.

Leg 5 as in adult.

Male copepodid V. Body 0.62 mm long. Prosome as in adult. Urosome (figure 5G) comprising short fifth pediger, elongate genital somite and three free abdominal somites; caudal setae as in female copepodid V.

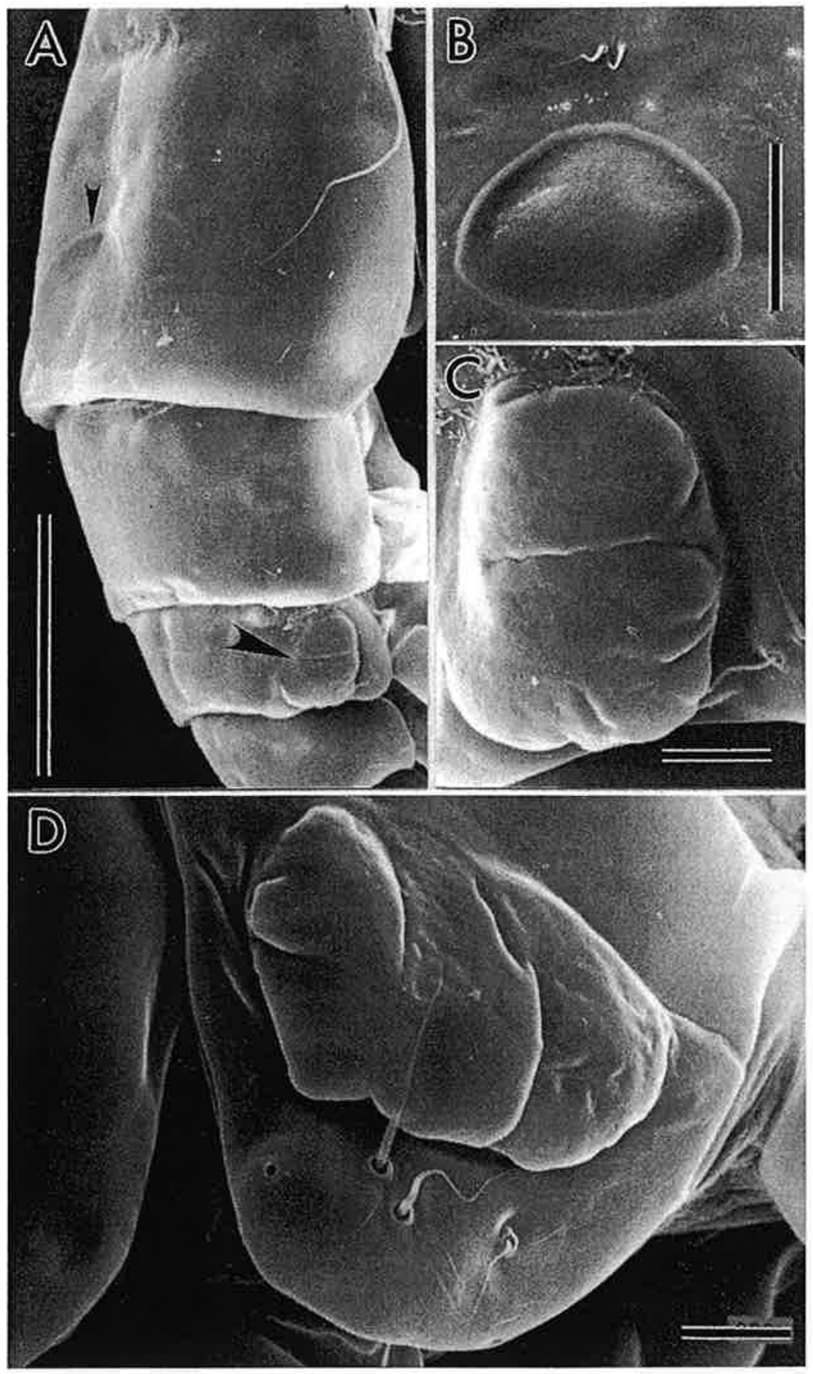

FIG. 15. SEM micrographs of *Ergasilus hypomesi* Yamaguti, 1936. Female (A–C); male (D). (A) Integumental windows on cephalosome (small arrowhead) and second pedigerous somite (large arrowhead); (B) dorsomedian integumental window on cephalosome; (C, D) lateral integumental windows on second pedigerous somite. Scales = 0.1 mm (A); 0.05 mm (B); 0.01 mm (C, D).

Antennule, mandible, maxillule and maxilla as in female copepodid V. Antenna constructed as in adult, but first endopodal segment relatively short. Maxilliped as in *E. genuinus*, comprising coxa, basis and indistinctly two-segmented endopod; second endopodal segment with short seta; claw short, bulbous.

Legs 1–4 as in female copepodid V. Legs 5 and 6 as in male copepodid V of *E. genuinus*.

Remarks. *Ergasilus hypomesi* is so far known from the gills, body surface and fins of fish such as *Chaenogobius laevis* (Steindachner), *C. urotaenia* (Hilgendorf), *Hypomesus nipponensis* and *Tribolodon hakonensis* (Günther) from Japan (Yamaguti, 1936; Nagasawa, 1994), and *Hemibarbus maculatus* Bleeker, 1871, *Hyporhomphus* sp., *Carassius auratus auratus* (Linnaeus, 1758), *Neosalanc* sp., *Luciobrama macrocephalus* (Lacepède, 1803) (as *L. typus*) and *Elopichthys bambusa* (Richardson, 1845) from China (Yin, 1956; Chen *et al.*, 1973; Kuang and Qian, 1991). An adult male of *E. hypomesi* has also been reported as plankton from a lake in Hokkaido, northern Japan (Nagasawa *et al.*, 1989). Although our planktonic specimens from Lake Ohnuma do not have a swollen cephalothorax as in typical *E. hypomesi*, the female antenna, mandible and structures of legs 1–4 are all very much like those found in that species. The segmentation and swelling of the cephalothorax are assumed to be modifications acquired after the settlement of the postmated female on the fish. The females from Lake Ohnuma have a minute seta on the ventral side of the exopod of leg 5. Due to its small size and being easily overlooked, this seta was not mentioned in previous reports on *E. hypomesi*.

This is the first description of the male of this species. It exhibits sexual dimorphism in the mandible and maxilliped. The middle mandibular blade of the male is not as strongly serrated as in the female. The fifth copepodid in our samples shows that the mandibles of both sexes are similar to each other at this stage, and the characteristic feature of the adult female (with large teeth on the middle blade) does not appear until the final moult.

The fifth copepodid stages of both sexes of *E. hypomesi* differ from those of *E. genuinus* described above. In the female of *E. hypomesi* the genital double-somite of the adult female appears after the final moult, whereas it is already formed at the fifth copepodid stage in *E. genuinus*. In the Ergasilidae it is so far known that the genital double-somite is formed at the fifth copepodid stage (Izawa, 1991). Thus, the formation of the genital double-somite one moult later in this example is interpreted as a result of heterochrony. Formation of genital complex in the female takes place at the final moult in the most primitive poecilostomatoid genus *Hemicyclops* Boeck, 1873 (Clausidiidae) (Kim and Ho, 1992; Itoh and Nishida, 1995). Hence the earlier formation observed in ergasilids except for *E. hypomesi* may be regarded as pre-displacement.

Discussion

Life cycle and morphology of the Ergasilidae

Ben Hassine (1983) clearly described the life cycle of *Ergasilus lizae* Krøyer, 1863, which can be generalized for those of other ergasilids. It is, however, likely on the basis of the present and previous studies that in the Ergasilidae there are two basic patterns of feeding/reproduction in adult females. The first type seems to be adopted by most ergasilids. After settlement of the female on the host, it does not leave the host, and continues to produce eggs on the host until its death. This type is characterized by all or some of the following remarkable transformations to adapt itself to the parasitic life, i.e. reproduction and attachment on the host. The cephalosome and pedigerous somite(s) become increasingly expanded or elongated with maturity (cf. Yin, 1956; Roberts, 1970; Kabata, 1979; Ben Hassine, 1983; Urawa *et al.*, 1991). This phenomenon is found in such genera as *Nipergasilus* Yin, 1949, *Pseudergasilus* Yamaguti, 1939, *Sinergasilus* Yin, 1949, *Thersitina*, and some species of *Ergasilus* and *Neoergasilus* Yin, 1956 (cf. Yin, 1956; Kabata, 1979; Boxshall and Montú, 1997). Antennary transformations are most likely to enhance grasping efficiency: (1) formation of an inflated membrane between the coxobasis and the first endopodal segment of the antenna in the genus *Ergasilus* (cf. Roberts, 1970; Kabata, 1979; El-Rashidy and Boxshall, 2002); (2) formation of a loose, cuticular membrane completely or incompletely covering the antenna in *Dermoergasilus* Ho and Do, 1982 and *Ergasilus extensus* El-Rashidy and Boxshall, 2002 (cf. Roberts, 1970; Kabata, 1979; Ho and Do, 1982; El-Rashidy and Boxshall, 2001a, 2001b, 2002); and (3) interlocking of the claws and endopodal segments of the right and left antennae in *Dermoergasilus* and *Acusicola* Cressey, 1970 (cf. Kabata, 1979, 1992a). In highly modified ergasilid genera such as *Mugilicola* Tripathi, 1960, *Paeonodes* Wilson, 1944 and *Therodamas* Krøyer, 1863, an extremely elongated neck (elongation of postcephalic somites or of a part of the cephalosome) penetrates deeply into host tissues, which functions as a powerful anchor to the host (Hewitt, 1969; Banning, 1974; Boxshall, 1986; Amado and Rocha, 1996; El-Rashidy and Boxshall, 2001b). Since free-living (=premetamorphic) adult females of *Therodamas* are typically ergasiliform (Araujo and Boxshall, 2001b), the neck formation evidently occurs after settlement on the host. The female that adopts the first type of life-style tends to produce larger egg-sacs containing more numerous eggs (up to 200 eggs: Yin, 1956) than in the second type mentioned below. This seems to be due to continuous nutrition absorption by the parasite from the host.

The second type is as yet incompletely proven by either field observations or laboratory experiments, but there are several indirect lines of evidence to support the possibility of the life cycle. Females belonging to this type feed and reproduce without permanent attachment on their host. Such a life-style is similar to that of copepodids and adult male stages of the Ergasilidae. Females do not undergo significant transformation in the body and appendages, and carry relatively small egg-sacs (at most 20 eggs: Yin, 1956; Montú and Boxshall, 2002; present study). For example, ovigerous females of *Ergasilus longicaudatus* have never been found from host fish, and possess only four to eight eggs in each egg-sac (Kuang and Qian, 1991). In Brazilian freshwater bodies the occurrence of ovigerous female ergasilids in the plankton is common (Montú and Boxshall, 2002).

Acknowledgements

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