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Description of a New Species of *Sternomoera* (Crustacea: Amphipoda: Pontogeneiidae) from Japan, with an Analysis of the Phylogenetic Relationships Among the Japanese Species Based on the 28S rRNA Gene

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A new species of amphipod, *Sternomoera morinoi* Tomikawa and Ishimaru, is described from subterranean aquatic habitats in Shiga Prefecture, Japan. In addition, *Relictomoera tsushimana* (Uéno, 1971) from a well on the island of Tsushima in Japan is transferred to *Sternomoera* and redescribed based on the holotype. *Sternomoera morinoi* sp. nov. is most similar to *S. tsushimana* (Uéno, 1971) comb. nov., but is distinguished by having many fine setae on the body, a shorter antenna 1, fewer C-setae on mandibular palp article 3, a shorter mandibular palp article 3, sparsely setose anterior margins of coxae 1–4, a different armature of the palmar margins of gnathopods 1 and 2, and no long setae on the posterior margin of the basis in gnathopod 2 and pereopods 3 and 4. The phylogenetic relationships among the Japanese species of *Sternomoera* are also estimated, based on partial DNA sequences of the nuclear 28S rRNA gene.

Key words: *Sternomoera*, Amphipoda, Japan, new species, new combination, taxonomy, phylogeny

INTRODUCTION

The genus *Sternomoera* (Amphipoda: Pontogeneiidae) is known as an inhabitant of epigean freshwater, confined to Japan and a nearby Russian island (Tattersall, 1922; Uéno, 1933; Stephensen, 1944; Kuribayashi et al., 1994, 1996; Labay, 1997; Sidorov, 2010; Ishimaru, 2011; Tomikawa and Sidorov, 2014). *Sternomoera* is similar to the cosmopolitan genus *Paramoera*, most species of which live in marine habitats although some are freshwater inhabitants. *Sternomoera* was erected by subdivision of *Paramoera* to include species with a unique character, that is, cuticular branchial processes (= sternal gills) on the pereonal sternum (Barnard and Karaman, 1982). Five species of *Sternomoera* have been described: *S. japonica* (Tattersall, 1922) from Honshu, Japan, *S. yezoensis* (Uéno, 1933) from Hokkaidô, *S. hayamensis* (Stephensen, 1944) from Honshu, *S. rhyaca* Kuribayashi, Mawatari and Ishimaru, 1996 from Honshu and Hokkaidô, and *S. moneronensis* Labay, 1997 from Moneron Island, Russia, in the northern Sea of Japan. Since *S. hayamensis* was synonymized with *S. japonica* by Kuribayashi et al. (1996), there are four valid species in *Sternomoera* at the present time.

During field surveys of the subterranean aquatic fauna of Shiga Prefecture, Japan, one of the authors (MJG) and his colleagues collected some specimens of *Sternomoera* from interstitial waters and wells. This species is the first subterranean member of *Sternomoera*, described here as a new species.

Interestingly, the general appearance of the new species is similar to *Relictomoera tsushimana* (Uéno, 1971), which was first described as *Paramoera tsushimana* based on a single male specimen from a well on the island of Tsushima, Japan. Subsequently, this species was transferred by Barnard and Karaman (1982) to their new genus *Relictomoera* together with its type species *Paramoera relicta* Uéno, 1971. To date, only the above two species have been assigned to *Relictomoera*. *Relictomoera* and *Paramoera* have similar morphologies, with no sternal gills, but the former was supposedly characterized by its unique head shape with an unusual sinusoidal anterolateral margin. Hirayama (1990) examined the type specimens of *R. relicta* and *R. tsushimana* and pointed out observational errors in the original descriptions (Uéno, 1971a, b). The head shape,

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a purportedly diagnostic character for *Relictomoera*, was in fact an ordinary one found in many species of *Paramoera* and its relatives. He therefore suggested that *Relictomoera* is invalid, and that both *Relictomoera* species should belong to *Paramoera*, but he did not formally adopt this new classification.

For comparison with the new species, we examined the type specimen of *R. tsushimana*. We re-confirmed Hirayama's (1990) observation on the head shape, and also confirmed the presence of sternal gills as in *Sternomoera*. *Relictomoera tsushimana* is here transferred and redescribed as *Sternomoera tsushimana* comb. nov. based on the holotype from Tsushima, which is deposited in the Tsukuba Collection Center of the National Museum of Nature and Science, Tokyo (NSMT).

Recently, DNA nucleotide sequence data have been used successfully to analyze phylogenetic relationships among species of Amphipoda (Hou et al., 2007; Tomikawa et al., 2007a, b, 2010, 2012). Therefore, we also investigated the molecular phylogeny of the species of *Sternomoera* in Japan using partial sequences of the nuclear 28S rRNA gene.

The taxonomic description was prepared by and is to be attributed to the first and fourth authors (KT and SI). The second and third authors (NK and MK) conducted the molecular analysis, and the fifth author (MJG) provided the material of the new species and assisted in manuscript preparation.

MATERIALS AND METHODS

Samples for morphological observation and molecular phylogenetic study

Specimens of four species of *Sternomoera* were collected from 28 localities in Hokkaidô and Honshu, Japan (Fig. 1). Specimens other than *S. morinoi* sp. nov. were collected by scooping various surface fresh-waters with a fine-mesh hand-net and fixing the material in 80% or 99% ethanol at the site. A few specimens of *S. morinoi* from Shiga Prefecture were also taken and preserved this way, but most, also those used for morphological observations, were pumped up from temporary wells about 70 cm deep bored in poorly sorted, muddy and sandy gravel bars in river beds, or from deeper permanent wells elsewhere. Permanent wells were sampled by lowering a plankton net on a rope. Most of the specimens of *S. morinoi* were fixed in 70% ethanol. Since *Paramoera* is regarded as the most closely related genus to *Sternomoera*, three species of *Paramoera*, *P. erimoensis* Kuribayashi and Kyono, 1995, *P. koysama* Kuribayashi and Kyono, 1995, and *Paramoera* sp., were used as outgroup taxa (Table 1). *Paramoera erimoensis* and *Paramoera* sp. were collected at a river mouth, and *P. koysama* from the intertidal zone.

Morphological observation

All appendages of the examined specimens of *Sternomoera morinoi* were dissected in 99% ethanol and mounted in gum-chloral medium on glass slides under a stereomicroscope (Olympus SZX7). Specimens were examined using a light microscope (Olympus BH2) and illustrated with the aid of a camera lucida. The body length from the tip of the rostrum to the base of the telson was measured along the dorsal curvature to the nearest 0.1 mm. The nomenclature of the setal patterns on the mandibular palp follows Stock (1974). Type specimens are deposited in the Lake Biwa Museum (LBM), in Kusatsu, Shiga Prefecture, Japan.

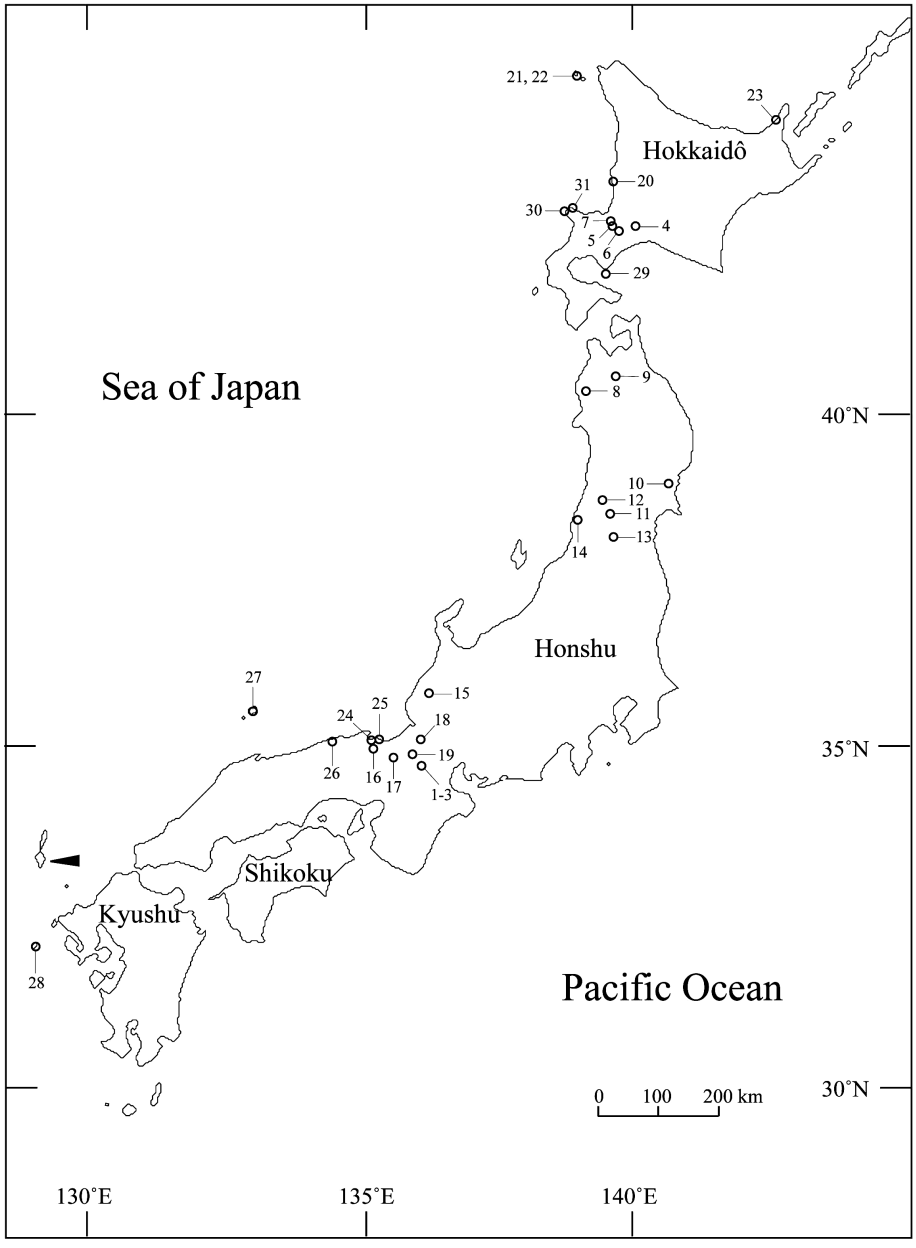

Fig. 1. Sampling localities for morphological observations and molecular phylogenetic study. Localities are numbered as in Table 1. The arrowhead indicates the island of Tsushima, the type locality of *Sternomoera tsushimana* comb. nov.

DNA extraction, PCR amplification, and DNA sequencing

Total genomic DNA was extracted from pereopod musculature of each sequenced amphipod, one to four individuals per species (Table 1), by means of the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany); the final volume of the DNA solution following extraction was 200 μl. Part of the 28S rRNA gene was amplified by polymerase chain reaction (PCR) using the following primer pair: 28SF [5'-AGG TCG TAA ACT CGA TCT AAG-3'] and 28SR [5'-CAC ACA TGC TAT ACT CCT TGG-3'] (Tomikawa et al., 2012). PCR reactions containing 0.5 μl template solution, 2 mM $MgCl_2$, 2.5 mM dNTP, 10 pmol of each primer, and 5 U/μl Taq polymerase (TaKaRa Ex Taq®) in 1X buffer provided by the manufacturer were performed in 10-μl volumes in an PC-320 thermal cycler (ASTEC). Amplification conditions were as follows: initial denaturation for 7 min at 94°C; 35 cycles of denaturation for 45 s at 94°C, annealing for 1 min at 30–42°C depending on sample, and extension for 1 min at 72°C; and final extension for 7 min at 72°C. Amplification products were purified by the silica method (Boom et al., 1990). All sequencing reactions were performed according to the manufacturer's instructions using the BigDye Terminator v3.1 Cycle Sequencing Reaction Kit (Applied Biosystems, Foster City, CA). Cycle sequencing conditions were 25 cycles of 10 s at 96°C, 5 s at 50°C, and 4 min at 60°C. Sequencing reaction products were purified by ethanol precipitation. Labeled fragments were analyzed using an ABI 3130x Genetic Analyzer (Applied Biosystem). Sequences were obtained from both strands of the gene segments for verification using the same primers. The nucleotide sequences have been submitted to the DNA Databank of Japan (DDBJ) nucleotide-sequence database (linked to the EMBL and GenBank databases) under accession numbers AB778479–AB778502.

Molecular phylogenetic analyses

The nucleotide sequences were aligned using the multiple alignment algorithm in Clustal W (Thompson et al., 1994) with default setting (i.e., gap opening penalty = 15, gap extension penalty = 6.66, transition weight = 0.5). Phylogenetic relationships were reconstructed by the Neighbor-joining method (NJ; Saitou and Nei, 1987), the equally weighted maximum parsimony method (MP), and the maximum likelihood method (ML) with MEGA 5.05 software (Tamura et al., 2011). Indels were treated as missing data in all analyses. In the NJ analysis, the Kimura 2-parameter (K2P) model (Kimura, 1980) of nucleotide substitution was used to estimate genetic distances. In the MP analysis, a tree was obtained using the Close-Neighbor-Interchange algorithm, in which the initial trees were obtained with the random addition of sequences (10 replicates). The ML analysis used the K2P + G model; this was selected as the best-fit model using the Bayesian information criterion (BIC) in MEGA 5.05. To estimate statistical support for branching patterns, 1000 bootstrap replications each (Felsenstein, 1985) were performed for the NJ, MP, and ML analyses.

RESULTS

Molecular phylogenetic analysis

Alignment gaps were observed at several nucleotide sites; these sites were excluded and the remaining 542 sites

Table 1. Species, sampling localities, and number of specimens used for molecular phylogenetic study.

Species	Locality	Haplotype (N)	DDBJ Acc. No
Sternomoera morinoi sp. nov.	1. Gokashô-Kondô, Higashiômi, Shiga	SM (2)	AB778479
	2. Inukami River, Kawanai, Taga, Shiga	SM (1)	AB778479
	3. Ogawara, Kôra, Shiga	SM (1)	AB778479
Sternomoera yezoensis	4. Eniwa, Hokkaidô	SY1 (2)	AB778480
	5. Kitanosawa, Sapporo, Hokkaidô	SY2 (1)	AB778481
	6. Bankei, Sapporo, Hokkaidô	SY2 (1)	AB778481
	7. Kotonihassamu River, Sapporo, Hokkaidô	SY2 (1)	AB778481
Sternomoera japonica	8. Wakitsubo Pond, Iwasaki, Aomori	SJ1 (1)	AB778482
	9. Lake Towada, Kosaka, Aomori	SJ2 (2)	AB778483
	10. Rikuzentakata, Iwate	SJ3 (1)	AB778484
	11. Funagata, Yamagata	SJ4 (2)	AB778485
	12. Mamurogawa, Yamagata	SJ5 (1), SJ6 (2)	AB778486, AB778487
	13. Hazukashi River, Yamagata, Yamagata	SJ5 (2)	AB778486
	14. Atsumi, Yamagata	SJ7 (1)	AB778488
	15. Takinami, Fukui	SJ8 (2)	AB778489
	16. Kanabiki Falls, Miyazu, Kyôto	SJ9 (1)	AB778490
	17. Miyama, Kyôto	SJ10 (1)	AB778491
	18. Nishiazai, Nagahama, Shiga	SJ11 (1)	AB778492
	19. Kitakomatsu, Ôtsu, Shiga	SJ12 (2)	AB778493
Sternomoera rhyaca	20. Gokibiru, Ishikari, Hokkaidô	SR1 (2)	AB778494
	21. Tonnai River, Rebun, Hokkaidô	SR1 (2)	AB778494
	22. Besshu River, Rebun, Hokkaidô	SR1 (4)	AB778494
	23. Oshokomanai River, Shari, Hokkaidô	SR1 (1)	AB778494
	24. Shishizaki, Miyazu, Kyôto	SR2 (1)	AB778495
	25. Maizuru, Kyôto	SR3(1)	AB778496
	26. Iwami, Tottori	SR3 (2)	AB778496
	27. Dankyô Falls, Okinoshima, Shimane	SR4 (2)	AB778497
	28. Dondonbuchi Falls, Gotô, Nagasaki	SR5 (2)	AB778498
Paramoera koysama	29. Muroran, Hokkaidô	PK (2)	AB778499
Paramoera erimoensis	30. Yobetsu River, Shakotan, Hokkaidô	PE1 (1), PE2 (1)	AB778500, AB778501
Paramoera sp.	31. Horonaifu River, Shakotan, Hokkaidô	PS (2)	AB778502

were used for further analyses (of which 280 sites were variable and 188 were parsimony-informative). One haplotype of *Sternomoera morinoi* (SM), two of *S. yezoensis* (SY1–2), 12 of *S. japonica* (SJ1–12), five of *S. rhyaca* (SR1–5), two of *P. erimoensis* (PE1–2), one of *P. koysama* (PK), and one of *Paramoera* sp. (PS) were detected. Nucleotide frequencies among all samples were biased with 46.2% A + T (mean: A = 24.2%, C = 24.4%, G = 29.4%, T = 22.0%). The average value of transitions (Ti)/transversions (Tv) was 0.88. Maximum parsimony analysis recovered 62 most-parsimonious trees with a tree length of 373 steps (consistency index [CI] = 0.692, retention index [RI] = 0.796).

Figure 2 shows the phylogenetic tree of the 28S rRNA sequences constructed using the NJ method. Although the topologies of the phylogenetic trees constructed using the other two methods differed from the NJ tree in some points, the following nodes were supported by bootstrap values of > 60% in all methods: 1) *Sternomoera* formed a monophyletic group, 2) *S. morinoi* was the first diverged species in the genus, and 3) *S. japonica* from Aomori, Iwate, and Yamagata Prefectures (haplotypes SJ1–7) formed a monophyletic group.

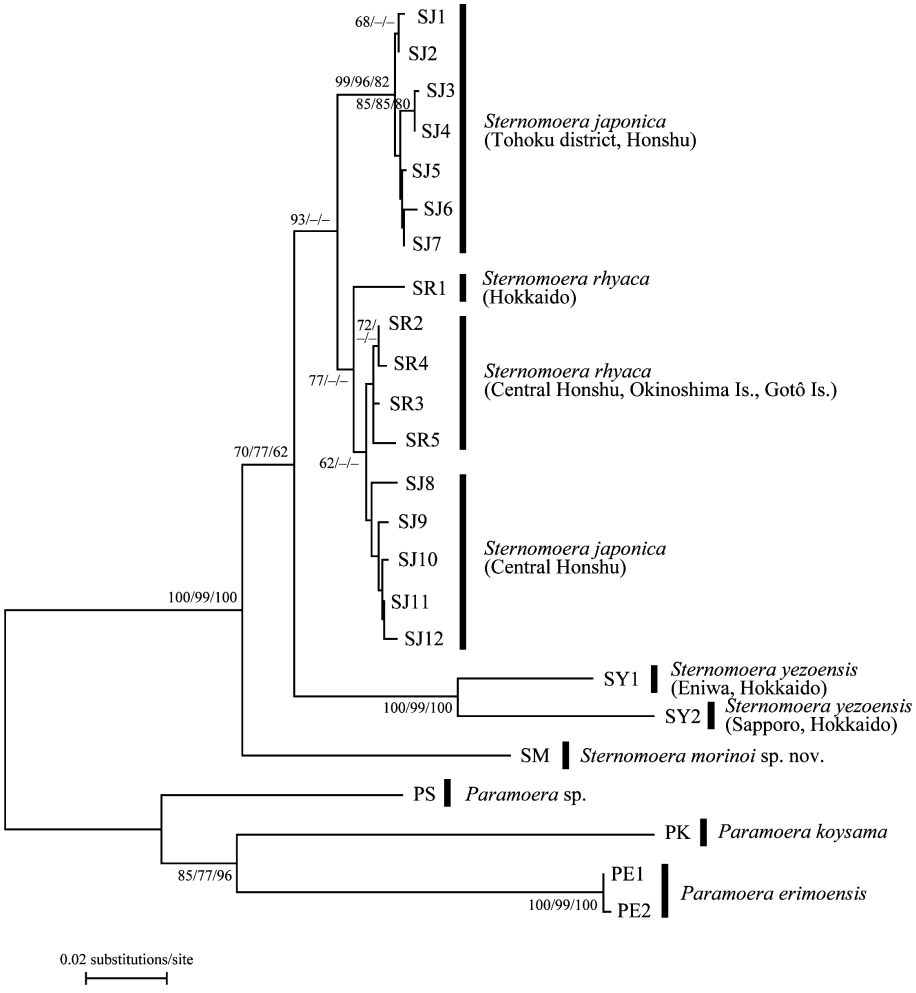

Fig. 2. Neighbor-joining tree based on genetic distances estimated from partial sequences of the 28S rRNA gene of *Sternomoera*. Distances were calculated from Kimura's (1980) two parameter model using a 542-bp data set. Numbers beside internal branches indicate bootstrap probabilities of NJ, MP, and ML trees, respectively, based on 1000 replicates.

SYSTEMATICS

Sternomoera Barnard and Karaman, 1982

Sternomoera Barnard and Karaman, 1982: 169; Barnard and Karaman, 1991: 341; Kuribayashi, Mawatari and Ishimaru, 1996: 1224.

Type species. *Paramoera yezoensis* Uéno, 1933.

Diagnosis (amended). Body smooth, with or without fine setae. Rostrum short; antennal sinus rounded or sharply incised. Antenna 1 longer than 2, both antennae with calceoli only in male; accessory flagellum uniarticulate, scale-like. Upper lip with fine setae on rounded ventral margin. Mandible: incisors 6- or 7-dentate; left lacinia mobilis 4- or 5-dentate, right one bifid or trifid; molar triturative; palp 3-articulate, article 2 with or without setae. Maxilla 1: inner plate with medial plumose setae; outer plate with 10 or 11 serrate robust setae apically; palp biarticulate. Maxilla 2: inner plate with oblique setal row. Maxilliped: outer plate not exceeding palp article 2; palp 4-articulate.

Coxa 4 expanded with shallow posterior concavity, coxae 5 and 6 bilobed. Gnathopods 1 and 2 subchelate, not of eusirid form; palm oblique, with simple robust setae; posterior margin of dactylus serrate or smooth. Pereopods 3–7: bases of pereopods 3 and 4 not anteriorly lobate; bases of pereopods 5–7 lobate posteriorly; dactyli of pereopods smooth or weakly cusped, with 2 setae near distal part.

Coxal gills present on gnathopod 2 and pereopods 3–7; accessory lobe absent. Pereonites 2–7 each with sternal gills.

Pleopods 1–3: peduncles with retinacula on inner distal part; rami developed, longer than peduncles; inner basal margins of inner rami with bifid plumose setae; outer ramus of male pleopod 2 modified or not.

Uropod 1: peduncle longer than rami, with lateral and medial robust setae, lacking basofacial robust setae; outer ramus subequal to or shorter than inner ramus. Uropod 2: peduncle subequal to or slightly longer than inner ramus, with lateral and medial robust setae. Uropod 3: peduncle shorter than rami; both rami uniarticulate, almost equal in length, lateral and medial margins of inner ramus and medial margin of outer ramus with plumose setae. Telson cleft for more than 70% of length.

Included species. *Sternomoera* includes six species: *S. japonica*, *S.*

moneronensis, *S. morinoi* sp. nov., *S. rhyaca*, *S. tsushimana*, and *S. yezoensis*.

Sternomoera morinoi Tomikawa and Ishimaru sp. nov.
(Japanese name: Morino-yokoebi, new)
(Figs. 3–8)

Material examined. Holotype: LBM 1430005402, male (5.3 mm), well at gateway to Ômishônin Yashiki Tonomura Uhe-e House (35°09′17.1″N, 136°10′48.5″E), Gokashô-Kondô, Higashiômi, Shiga Prefecture, Japan, collected by M. J. Grygier and J. T. Høeg on 27 June 2011. Paratypes: LBM 1430005403, non-ovigerous female (7.7 mm), data same as for holotype; LBM 1430005404, male (4.1 mm), garden well at Ômishônin Yashiki Tonomura Shigeru House (35°09′16.7″N, 136°10′47.4″E), Gokashô-Kondô, Higashiômi, Shiga Prefecture, collected by M. J. Grygier on 27 June 2011; LBM 1430005405, male (6.6 mm), house well (35°13′10″N, 136°15′ 44″E), Ogawara, Kôra, Shiga Prefecture, collected by J.–L. Cho on 7 March 2012; LBM 1430005406, non-ovigerous female (5.6 mm), river bar, north branch of Inukami River (35°12′34″N, 136°20′10″E), Same, Taga, Shiga Prefecture, collected by K. Tanida and party on 26 May 2011; LBM 1430005407, male (5.2 mm), river bar, Seri River (35°15′02″N, 136°19′55″E), Byôbu, Taga, Shiga Prefecture, collected by M. J. Grygier and party on 16 November 2011; LBM 1430005408, 2 juveniles (2.6 and 2.9 mm), river bar, north branch of Inukami River (35°12′34″N, 136°20′10″E), Same, Taga, Shiga Prefecture, collected by M. J. Grygier and party on 20 November 2011; LBM 1430005409, non-ovigerous female (6.3 mm), river bar, Yasu River (34°57′47″N, 136°09′37″E), Kitanaiki, Minakuchi (currently Minakuchichô-Kitanaiki, Kôka), Shiga Prefecture, collected by M. J. Grygier on 1 September 2008; LBM 1430005542, 4 non-ovigerous females (3.6–4.5 mm), river bar, north bank of Yasu River about 280 m downstream from Minakuchi Weir (34°57′36″N, 136°11′39″E), Minakuchichô-Shinjô, Kôka, Shiga Prefecture, collected by T. Karanovic on 11 November 2012.

Additional material sacrificed for 28S rRNA gene sequencing: one specimen, river bar, Seri River (35°14′22″N, 136°18′38″E), Kurusu, Taga, Shiga Prefecture, collected by K. Tanida and party on 25 May 2011 (DNA sequencing failed); one specimen, river bar, north branch of Inukami River (35°11′25″N, 136°19′06″E), Kawanai, Taga, Shiga Prefecture, collected by M. J. Grygier and party on 20 November 2011 (see Table 1).

Description of male (holotype, LBM 1430005402). Body (Fig. 3) with numerous fine setae. Head (Fig. 3) as long as pereonites 1 and 2 combined, rostrum short, antennal sinus rounded, eye absent. Epimeral plates 1–3 (Fig. 7G–I) with seven, four, and one setae on respective ventral margins, and three, three, and one setae on respective posterior margins; posterodistal corner of plate 2 weakly acute, that of plate 3 subquadrate.

Antenna 1 (Figs. 3, 4A): length 1.6 × antenna 2; pedun-

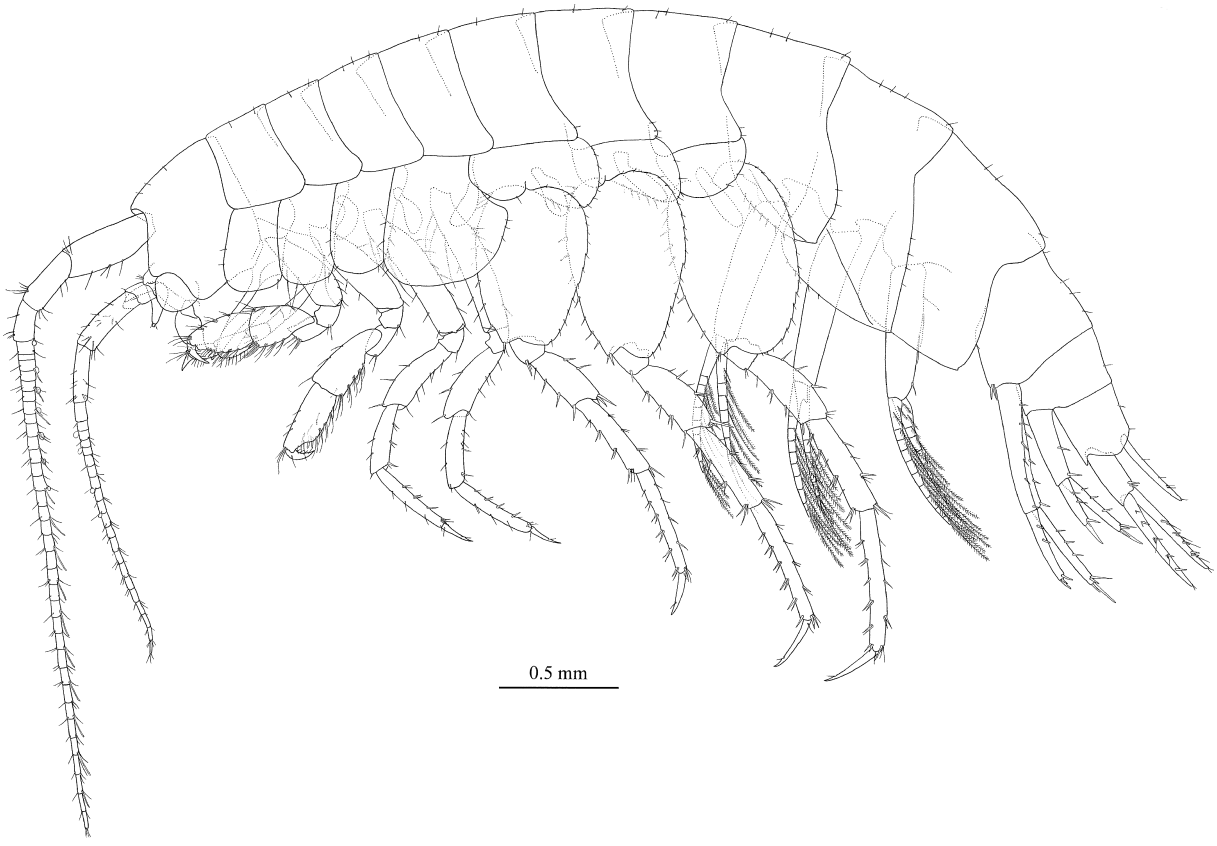

Fig. 3. *Sternomoera morinoi* sp. nov., holotype, male (5.3 mm), LBM 1430005402, well at Gokashô-Kondô, Higashiômi, Shiga Prefecture, Japan. Habitus, lateral view.

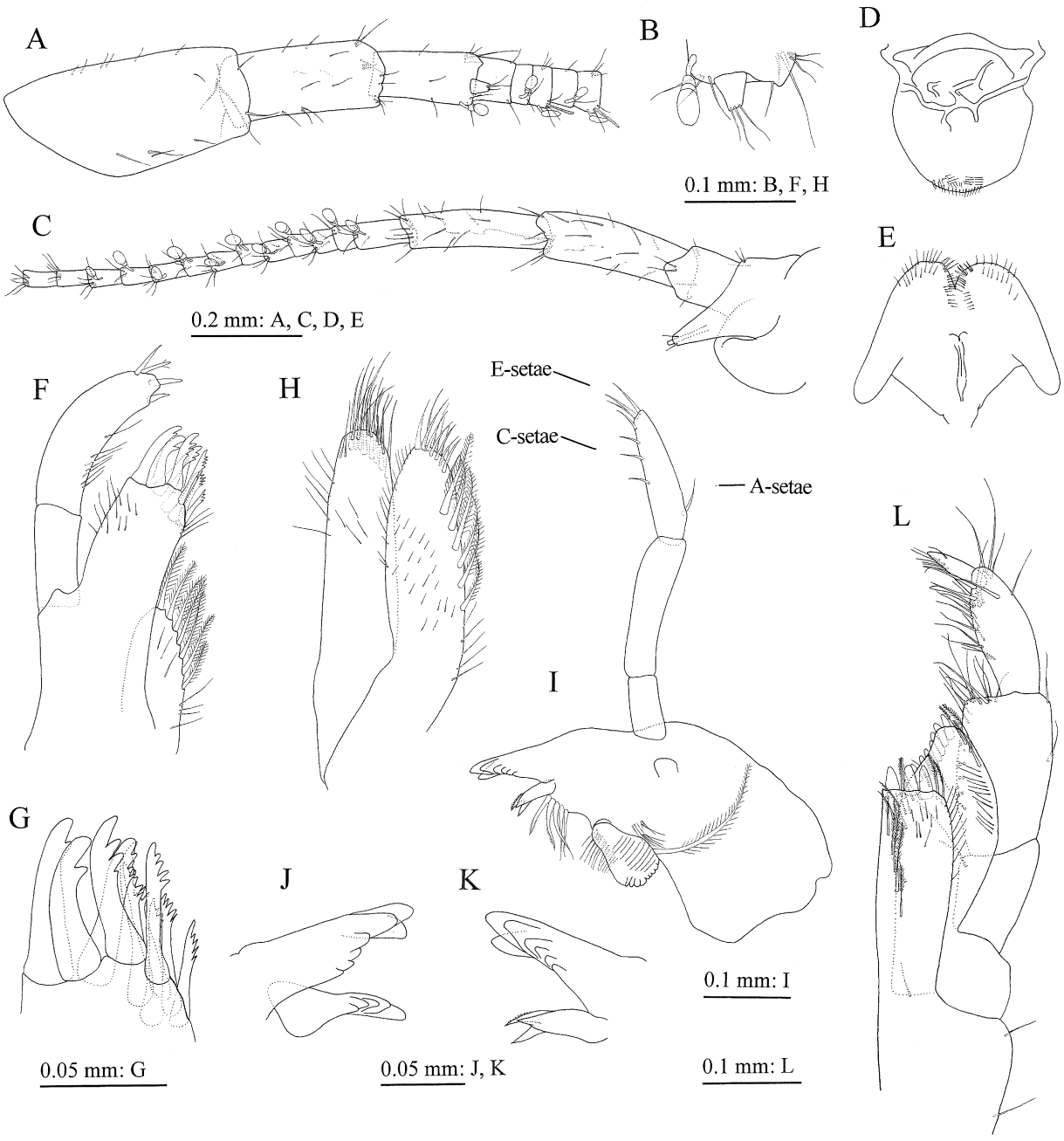

Fig. 4. *Sternomoera morinoi* sp. nov., holotype, male (5.3 mm), LBM 1430005402, well at Gokashô-Kondô, Higashiômi, Shiga Prefecture, Japan. **(A)** Peduncular articles 1–3, primary flagellar articles 1–5, and accessory flagellum of antenna 1, medial view. **(B)** Peduncular article 3 and accessory flagellum of antenna 1, medial view. **(C)** Peduncular articles 1–5 and flagellum articles 1–13 of antenna 2, medial view. **(D)** Upper lip, anterior view. **(E)** Lower lip, ventral view. **(F)** Maxilla 1, dorsal view. **(G)** Apical part of outer plate of maxilla 1, dorsal view. **(H)** Maxilla 2, dorsal view. **(I)** Right mandible, medial view. **(J)** and **(K)** Incisors and laciniae mobili of left and right mandibles, respectively, medial views. **(L)** Maxilliped, dorsal view.

cular articles 1–3 with length ratio of 1.0 : 0.7 : 0.5; peduncular article 1 with two single setae and one pair of setae on posterior margin and six setae on anterior margin, peduncular article 2 with single seta and pair of setae on posterior margin and two setae on anterior margin, peduncular article 3 with one seta each on posterior and anterior margins and calceolus on posterodistal corner; accessory flagellum (Fig. 4B) uniarticulate, triangular, with three apical setae; primary flagellum more than 33-articulate, calceoli on proximal one-third.

Antenna 2 (Fig. 4C): gland cone of peduncular article 2 prolonged, with two apical setae; peduncular article 4 slightly longer than article 5; flagellum 21-articulate, calceoli on proximal half.

Mouthparts. Upper lip (Fig. 4D) with fine setae on rounded ventral margin. Lower lip (Fig. 4E) with broad outer lobes, inner lobes absent. Mandibles (Fig. 4I–K) with both left and right incisors 7-dentate; left lacinia mobilis 5-den-

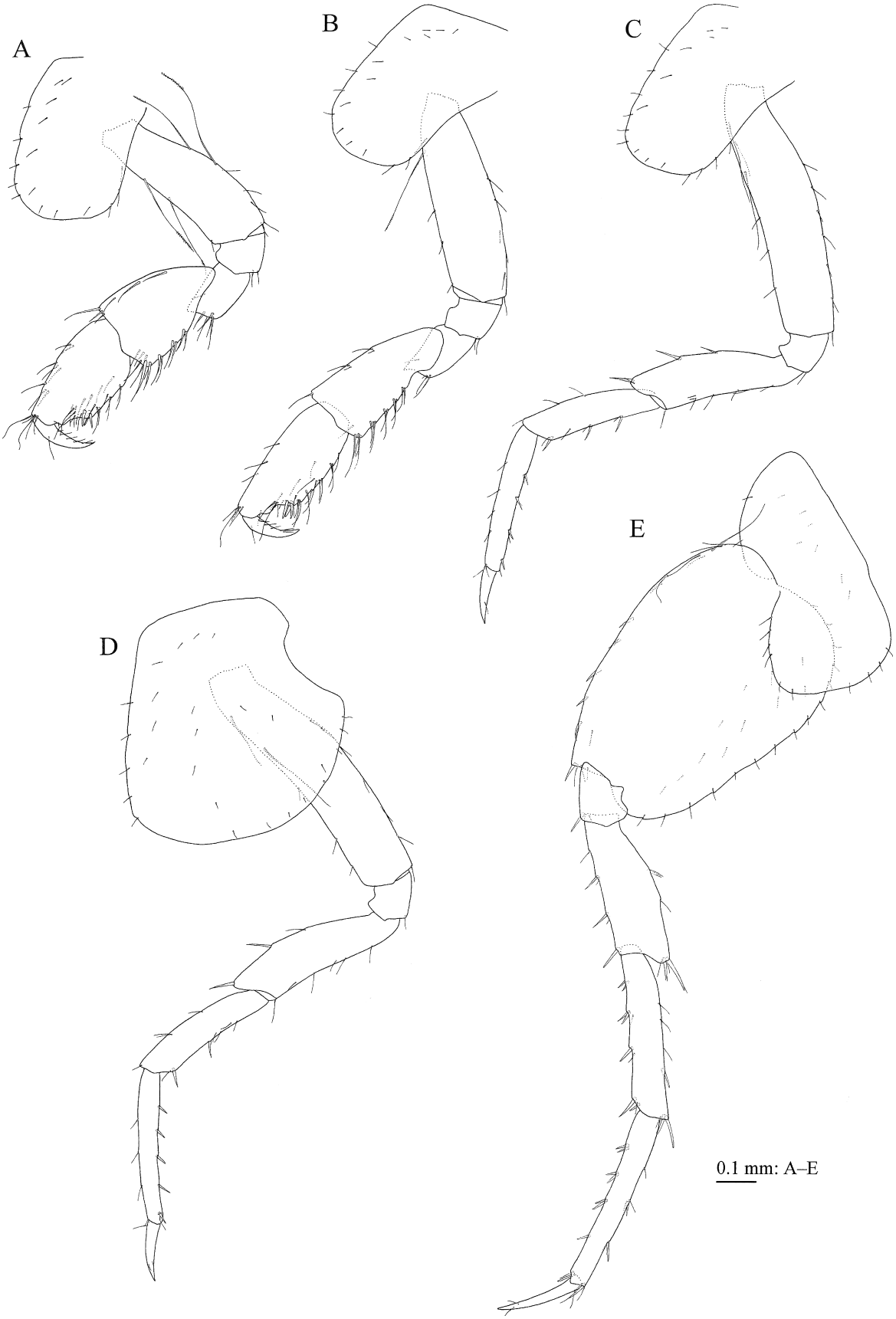

Fig. 5. *Sternomoera morinoi* sp. nov., holotype, male (5.3 mm), LBM 1430005402, well at Gokashô-Kondô, Higashiômi, Shiga Prefecture, Japan. **(A)** and **(B)** Gnathopods 1 and 2, lateral views. **(C)** and **(D)** Pereopods 3 and 4, lateral views. **(E)** Pereopod 5, medial view.

tate, right one trifid, bearing small grains; accessory setal row consisting of weakly pectinate setae; molar triturative, with one long pappose seta; palp 3-articulate with length ratio of 1.0 : 2.2 : 2.2, article 1 twice as long as wide, articles 1 and 2 lacking setae, article 3 with one A-seta, three C-setae, and four E-setae. Maxilla 1 (Fig. 4F, G) with seven plumose setae on medial margin of inner plate, inner surface of plate setulose; outer plate subrectangular, with 10 serrate robust setae apically; palp 2-articulate, slender, exceeding tip of outer plate, article 1 lacking setae, article 2 with four robust setae apically, lacking subapical setal row, medial margin with setae. Maxilla 2 (Fig. 4H) with row of setae on apical margin of inner plate, fine setae on medial margin, and oblique setal row consisting of six plumose setae. Maxilliped (Fig. 4L) with inner plate long, exceeding palp article 1, bearing three nodular robust setae apically; outer plate with apical plumose setae, medial robust setae, and medial slender setae; palp 4-articulate, articles 2 and 3 slender, article 2 with inner marginal and submarginal rows of setae, articles 3 and 4 straight, article 4 half of article 3, with medial setae.

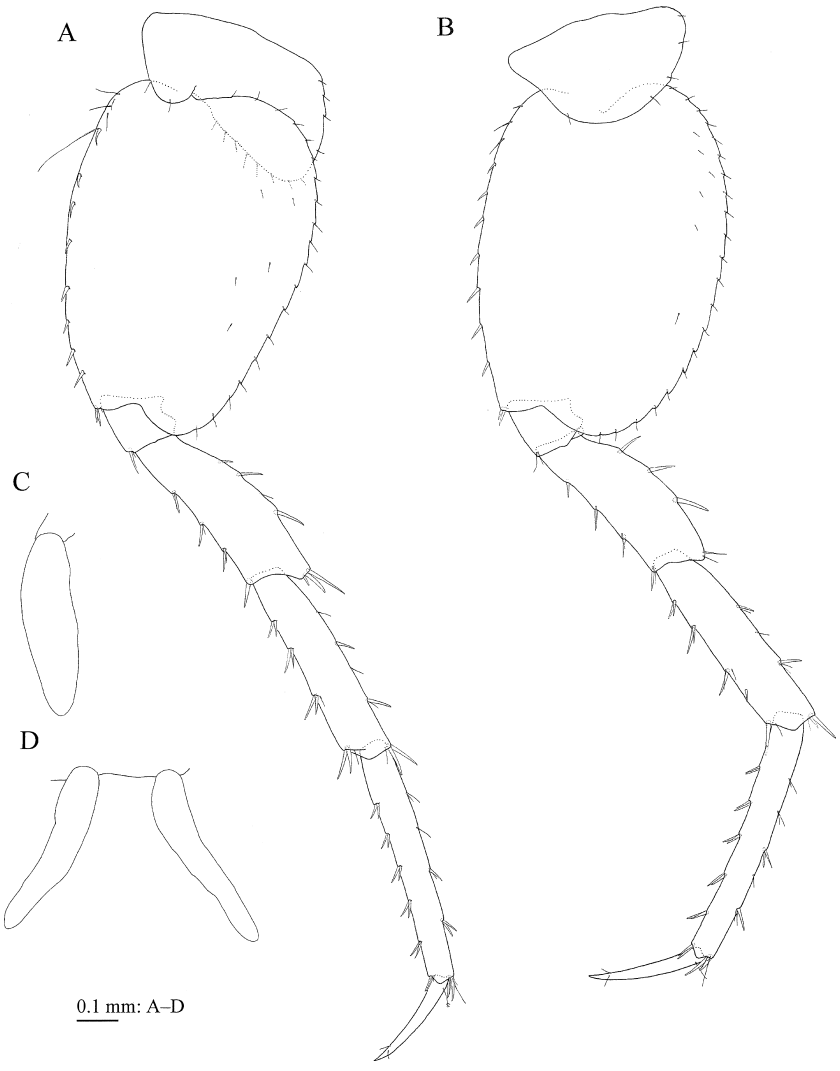

Fig. 6. *Sternomoera morinoi* sp. nov. **(A)** and **(B)**, holotype, male (5.3 mm), LBM 1430005402, well at Gokashô-Kondô, Higashiômi, Shiga Prefecture, Japan. **(C)** and **(D)**, paratype, male (6.6 mm), LBM 1430005405, house well, Ogawara, Kôra, Shiga Prefecture, Japan. **(A)** and **(B)** Pereopods 6 and 7, lateral views. **(C)** Coxal gill 5, lateral view. **(D)** Sternal gills of pereonite 5, anterior view.

Gnathopod 1 (Figs. 5A, 7A): coxa subrectangular, anterior margin with five setae, posterodistal corner with three setae; anterior and posterior margins of basis with two long setae each; carpus length 1.6 × width, wider than propodus, with weak posterodistal lobe, posterodistal corner with serrate setae, anterior margin with three setae, anterodistal corner with three setae; propodus not powerful, length 1.9 × width, as long as carpus, weakly tapering distally, anterior margin with three clusters of setae, palmar margin weakly sinuous, lacking marginal setules, palmar corner with one lateral and two medial robust setae; dactylus curved inward, posterior margin smooth, with five long marginal setae.

Gnathopod 2 (Figs. 5B, 7B) more elongate and slender than gnathopod 1: coxa subrectangular, slightly longer than coxa 1, anterior margin with four setae, posterodistal corner with three setae; basis with long seta on anterior margin, posterior margin lacking long setae; carpus elongate, length 2.1 × width, narrower than that of gnathopod 1, anterior margin with two pairs of setae, anterodistal corner with seta; propodus not powerful, length 2.4 × width, as long as carpus, anterior margin with three setae, palmar margin weakly sinuous, lacking marginal setules, palmar corner with one lateral and two medial robust setae; dactylus curved inward, posterior margin smooth, with four long marginal setae.

Pereopod 3 (Fig. 5C): coxa similar to coxa 2, anterior margin with six setae, posterodistal corner with 4 setae; basis long, length 5.2 × width, anterior margin with three long setae, posterior margin lacking long setae; merus, carpus, propodus, and dactylus in length ratio of 1.0 : 0.9 : 1.0 : 0.4, merus with two robust setae on anterior margin; carpus with two robust setae on posterior margin; propodus with four robust setae on posterior margin and one seta on posterodistal corner; dactylus lacking protuberance on posterior margin.

Pereopod 4 (Fig. 5D): coxa expanded with shallow posterior concavity, anterior margin with five setae; basis length 5.3 × width, anterior margin with two long setae, posterior margin lacking long setae; merus, carpus, propodus, and dactylus in length ratio of 1.0 : 0.9 : 1.0 : 0.4, merus with one robust seta on anterior margin; carpus with one robust seta on posterior margin; propodus with four robust setae on posterior margin, and one robust seta and one seta on posterodistal corner; dactylus lacking protuberance on posterior margin.

Pereopod 5 (Fig. 5E): coxa bilobed, anterior margin of anterior lobe with setae, ventral and posterior margins of

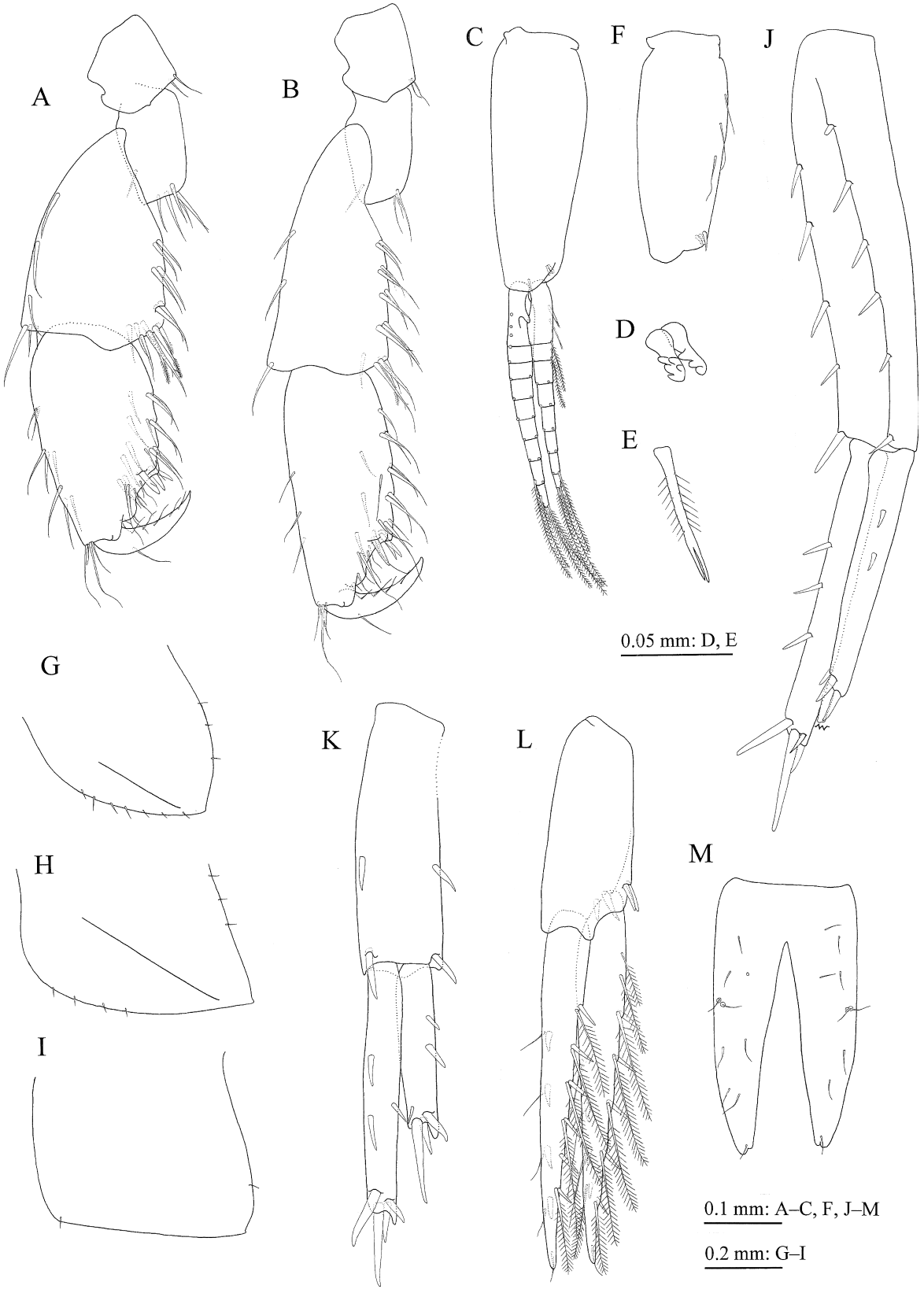

Fig. 7. *Sternomoera morinoi* sp. nov., holotype, male (5.3 mm), LBM 1430005402, well at Gokashô-Kondô, Higashiômi, Shiga Prefecture, Japan. **(A)** Ischium to dactylus of gnathopod 1, lateral view. **(B)** Ischium to dactylus of gnathopod 2, lateral view. **(C)** Pleopod 2, lateral view. **(D)** Retinacula on peduncle of pleopod 2, medial view. **(E)** Bifid plumose seta on inner basal margin of inner ramus of pleopod 2, medial view. **(F)** Peduncle of pleopod 3, lateral view. **(G)–(I)** Epimeral plates 1–3, respectively, lateral views. **(J)** Uropod 1, lateral view. **(K)** Uropod 2, dorsal view. **(L)** Uropod 3, ventral view. **(M)** Telson, dorsal view.

posterior lobe each with five setae; anterior margin of limb from basis to propodus and posterior margin from merus to propodus with robust setae; merus, carpus, propodus, and dactylus in length ratio of 1.0 : 1.3 : 1.5 : 0.6; dactylus lacking protuberance on anterior margin. Pereopod 6 (Fig. 6A): coxa bilobed, anterior lobe small with setae, ventral and posterior margins of posterior lobe with setae; articles longer than those of pereopod 5, with merus, carpus, propodus, and dactylus in length ratio of 1.0 : 1.0 : 1.2 : 0.5; dactylus lacking protuberance on anterior margin. Pereopod 7 (Fig. 6B): coxa semicircular; articles longer than those of pereopod 6, with merus, carpus, propodus, and dactylus in length ratio of 1.0 : 1.2 : 1.4 : 0.6; dactylus lacking protuberance on anterior margin.

Coxal gills (Figs. 3, 6C) small, present on gnathopod 2 and pereopods 3–7; accessory lobe absent. Pereonites 2–7 each with two slender sternal gills (Fig. 6D).

Pleopods 1–3 (Fig. 7C–F) unmo-dified; peduncles with two retinacula (Fig. 7D), inner basal margins of inner rami with bifid plumose setae (clothespin setae) (Fig. 7E), article 1 of each outer ramus with small process; medial margins of peduncles of pleopods 1 and 2 without setae, margin of pleopod 3 (Fig. 7F) with long setae.

Uropods. Uropod 1 (Fig. 7J): peduncle with five lateral and four medial robust setae marginally, basofacial seta absent; outer ramus length 0.6 × peduncle, lateral margin with two robust setae; inner ramus length 1.2 × outer ramus, medial margin with three robust setae, both rami with four terminal robust setae. Uropod 2 (Fig. 7K): peduncle with one lateral and one medial robust seta marginally; outer ramus length 0.6 × peduncle, lateral margin with two robust setae; inner ramus length 1.5 × outer ramus, lateral and medial margins with one and two robust setae, respectively, both rami with four terminal robust setae. Uropod 3 (Fig. 7L) long: peduncle length 0.9 × peduncle of uropod 2, with robust setae distally; both rami uniarticulate; inner ramus length 1.7 × peduncle and slightly longer than outer ramus, both margins with robust setae and plumose setae; on outer ramus, lateral margin with both robust setae and simple setae, medial margin with both robust setae and plumose setae.

Telson (Fig. 7M) long, 1.9 × width, margins almost parallel, cleft for 78% of length in V-shape; each lobe slender, with several facial setae; apex subacute, with minute subterminal seta, setal length 0.07 times that of telson.

Description of non-ovigerous female (paratype, LBM 1430005403). Very similar to male, sexual dimorphism subtle. Antennae 1 and 2 (Fig. 8A, B) lacking calceoli. Mandibular palp article 3 with two A-setae. Maxilla 1: inner plate with eight plumose setae on medial margin. Maxilla 2 with oblique setal row consisting of seven plumose setae. Gnathopod 1 (Fig. 8C): carpus length 1.5 × width; propodus length 1.8 × width, palmar margin with two lateral and two medial robust setae, concavity shallower than in male. Gnathopod 2 (Fig. 8D): carpus length 2.2 × width; propodus length 2.4 × width, palmar margin with two lateral and two medial robust setae, concavity shallower than in male.

Etymology. The new species is named in honor of Dr. Hiroshi Morino, who has contributed greatly to the taxonomy of the Japanese Amphipoda.

Distribution. Only known from Shiga Prefecture.

Habitat. Wells and interstitial water of riverbeds.

Remarks. *Sternomoera morinoi* sp. nov. is most similar to *S. tsushimana* comb. nov. in having the following features not shared with other congeners: eyes absent, gland cone of peduncular article 2 of antenna 2 long, palp of mandible

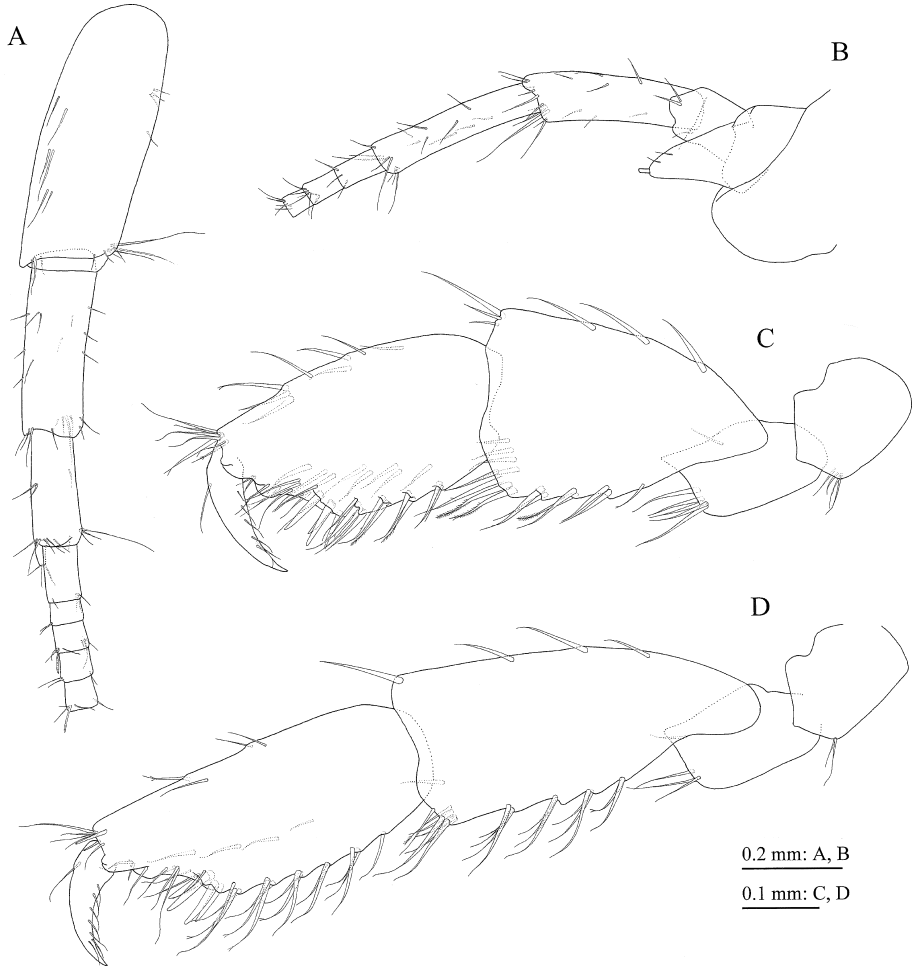

Fig. 8. *Sternomoera morinoi* sp. nov., paratype, female (7.7 mm), LBM 1430005403, well at Gokashô-Kondô, Higashiômi, Shiga Prefecture, Japan. **(A)** Peduncular articles 1–3, primary flagellar articles 1–5, and accessory flagellum of antenna 1, ventral view. **(B)** Peduncular articles 1–5 and flagellum articles 1–3 of antenna 2, medial view. **(C)** Ischium to dactylus of gnathopod 1, lateral view. **(D)** Ischium to dactylus of gnathopod 2, lateral view.

slender, palp article 2 of mandible lacking setae, coxae 2–4 with setal row on outer surface along anterior margin, palmar margins of gnathopods 1 and 2 lacking marginal setae, posterior margins of dactyli of gnathopods 1 and 2 smooth with long marginal setae, and dactyli of pereopods 3–7 lacking protuberance. However, *S. morinoi* differs from *S. tsushimana* as follows (features of *S. tsushimana* in parentheses): body with many (a few) fine setae, antenna 1 about 1.6 times (twice) as long as antenna 2, mandibular palp article 3 with three C-setae (9), mandibular palp article 3 as long as (longer than) article 2, anterior margins of coxae 1–4 with setae (absent except on anterodistal corner), palmar corners of gnathopods 1 and 2 each with fewer robust setae, posterior margins of bases of gnathopod 2 and pereopods 3 and 4 without (with) long setae, and telson cleft in V-shape (narrowly cleft). The length of the terminal seta of the telson differs between the holotypes of *S. morinoi* and *S. tsushimana*, but this feature is variable in the former species: a minute seta in the holotype of *S. morinoi*, a longer seta (0.15 times as long as the telson) in two paratypes (a male of 6.6 mm and a female of 4.1 mm). Therefore, this feature cannot be used to distinguish these two species.

Sternomoera tsushimana (Uéno, 1971) comb. nov.
(Japanese name: Tsushima-dôkutsu-yokoebi)
(Figs. 9–12)

Paramoera tsushimana Uéno, 1971b: 196, fig. 1.

Relictomoera tsushimana: Barnard and Karaman, 1982: 168; Hirayama, 1990: 958; Tomikawa and Morino, 2012: 42.

Material examined. Holotype: NSMT-Cr 4136, male (6.9 mm), driven well at Tendôshige, Izuhara (currently the city of Tsushima), Tsushima Island, Nagasaki Prefecture, Japan, collected by S. Uéno and Y. Morimoto on 18 October 1969.

Description of male (Holotype, NSMT-Cr 4136). Specimen partly damaged: lower lip, maxillae 1 and 2, maxillipeds, and some articles of pereopods missing, some coxal gills and sternal gills possibly also missing.

Body (Fig. 9) with few fine setae. Head (Fig. 9) shorter than pereonites 1 and 2 combined, rostrum short, antennal sinus rounded, eye absent. Epimeral plates 1–3 (Fig. 12F–H) without setae on ventral margins, posterior margins of plates 1 and 2 each with 1 seta; posterodistal corner of plate 2 quadrate, that of plate 3 rounded.

Antenna 1 (Figs. 9, 10A): length 2.0 × antenna 2; peduncular articles 1–3 with length ratio of 1.0 : 0.6 : 0.4; peduncular articles 1–3 with three, two, and no setae on respective posterior margins, posterodistal corner of article 3 with calceolus; accessory flagellum (Fig. 10B) 1-articulate, rounded, with two long setae and two short plumose setae apically; primary flagellum 36-articulate, calceoli on proximal one-fourth.

Antenna 2 (Fig. 10C): gland cone of peduncular article 2 prolonged, with five marginal setae; peduncular article 4 length 1.3 × article 5; flagellum 22-articulate, calceoli on proximal half.

Mouthparts. Upper lip (Fig. 10D) with fine setae on rounded ventral margin. Mandibles (Fig. 10E, F) with both left and right incisors 6-dentate; left lacinia mobilis 4-dentate, right one bifid, bearing small grains; accessory setal row consisting of weakly pectinate setae; molar triturative, with two pappose setae; palp 3-articulate with length ratio of 1.0 : 1.7 : 2.6, article 1 length 2 × width, articles 1 and 2 bare, article 3 with two A-setae, nine C-setae, and four E-setae.

Gnathopod 1 (Fig. 10G, H): coxa subcircular, anterior margin bare, anterodistal corner with one seta, posterodistally bearing four setae; anterior

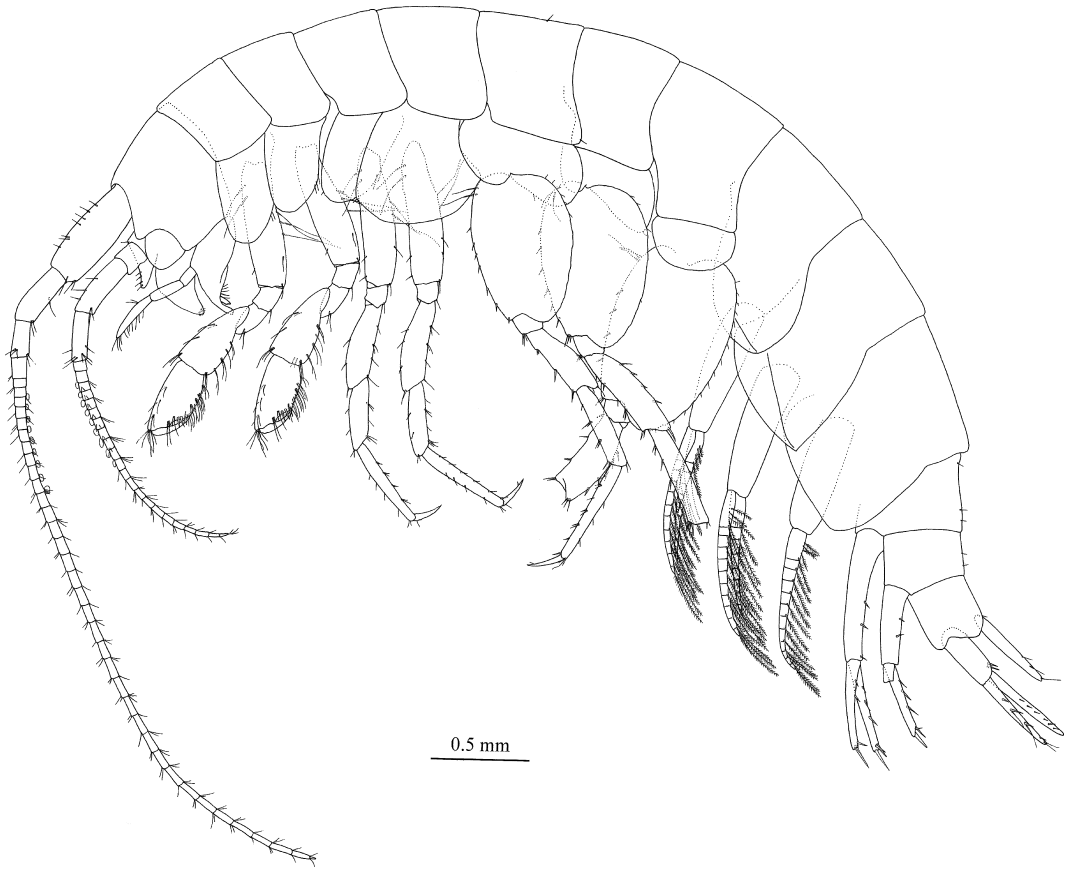

Fig. 9. *Sternomoera tsushimana* comb. nov., holotype, male (6.9 mm), NSMT-Cr 4136, driven well at the former town of Izuhara (now the city of Tsushima), Tsushima Island, Nagasaki Prefecture, Japan. Habitus, lateral view.

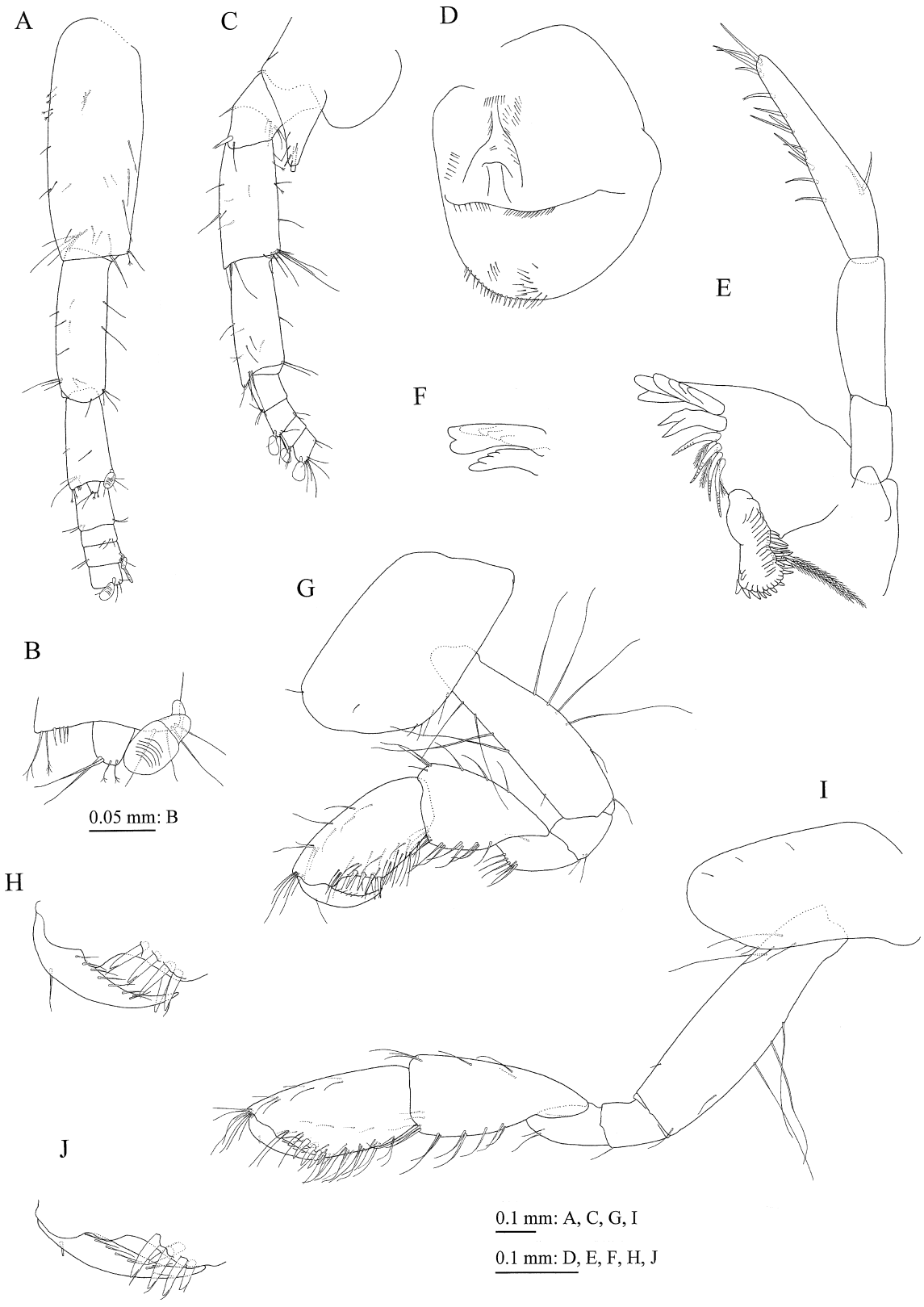

Fig. 10. *Sternomoera tsushimana* comb. nov., holotype, male (6.9 mm), NSMT-Cr 4136, driven well at the former town of Izuhara (now the city of Tsushima), Tsushima Island, Nagasaki Prefecture, Japan. **(A)** Peduncular articles 1–3, flagellar articles 1–4, and accessory flagellum of antenna 1, medial view. **(B)** Distal part of peduncular article 3 of antenna 1, medial view. **(C)** Peduncular articles 1–5 and flagellar articles 1–4 of antenna 2, medial view. **(D)** Upper lip, anterior view. **(E)** Right mandible, medial view. **(F)** Incisor and lacinia mobilis of left mandible, lateral view. **(G)** Gnathopod 1, lateral view. **(H)** Palmar margin of propodus and dactylus of gnathopod 1, lateral view. **(I)** Gnathopod 2, lateral view. **(J)** Palmar margin of propodus and dactylus of gnathopod 2, lateral view.

and posterior margins of basis with four long setae each; carpus length 1.8 × width, anterior margin with three setae; propodus not powerful, length 2.1 × width, anterior and posterior margins almost parallel, palmar margin weakly sinuous, lacking marginal setules, with 4 lateral and 1 medial robust setae; dactylus curved inward, posterior margin smooth, with 8 long marginal setae.

Gnathopod 2 (Fig. 10I, J) more elongate and slender

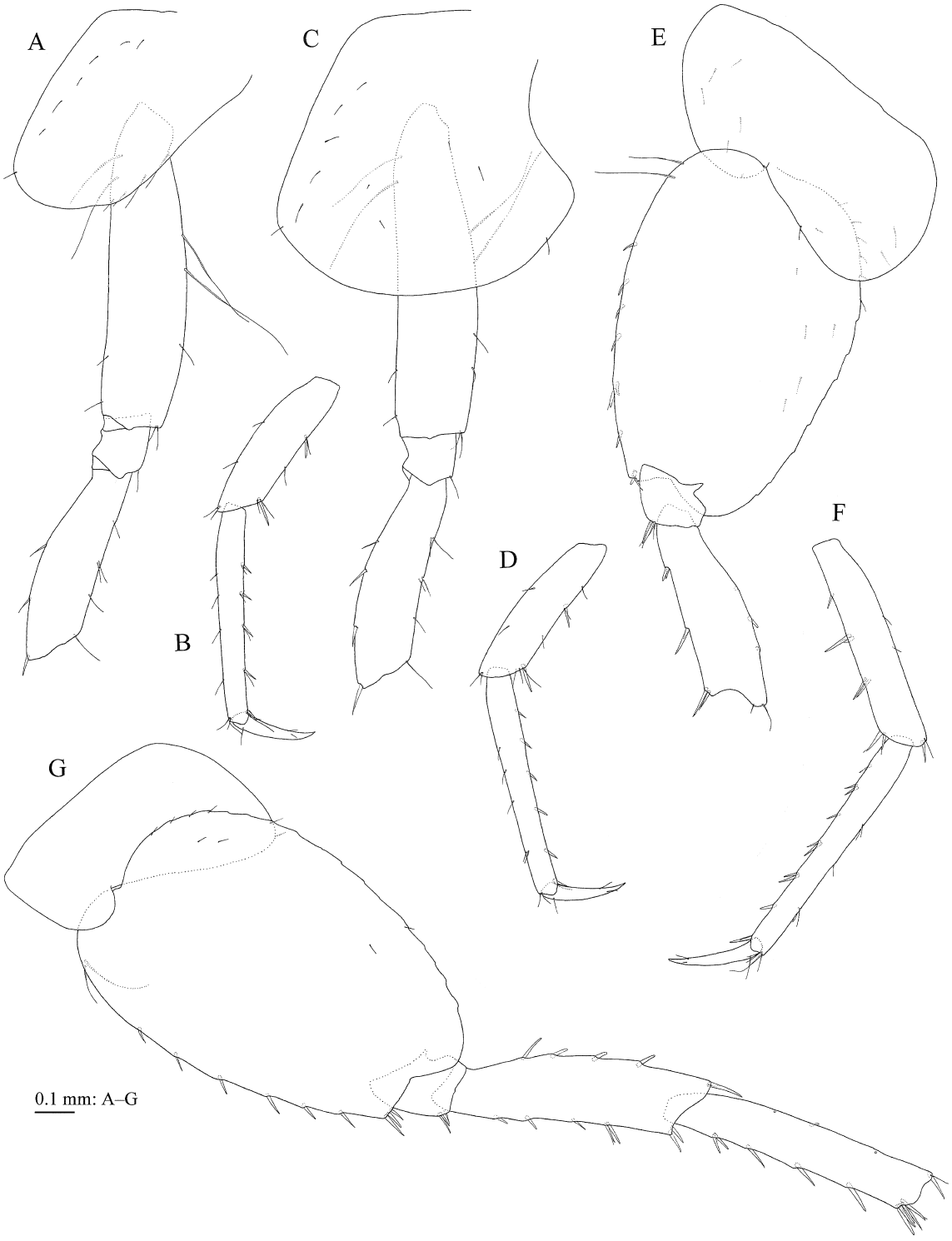

Fig. 11. *Sternomoera tsushimana* comb. nov., holotype, male (6.9 mm), NSMT-Cr 4136, driven well at the former town of Izuhara (now the city of Tsushima), Tsushima Island, Nagasaki Prefecture, Japan. **(A)** Coxa to merus of pereopod 3, lateral view. **(B)** Carpus to dactylus of pereopod 3, lateral view. **(C)** Coxa to merus of pereopod 4, lateral view. **(D)** Carpus to dactylus of pereopod 4, lateral view. **(E)** Coxa to merus of pereopod 5, medial view. **(F)** Carpus to dactylus of pereopod 5, medial view. **(G)** Coxa to carpus of pereopod 6, lateral view.

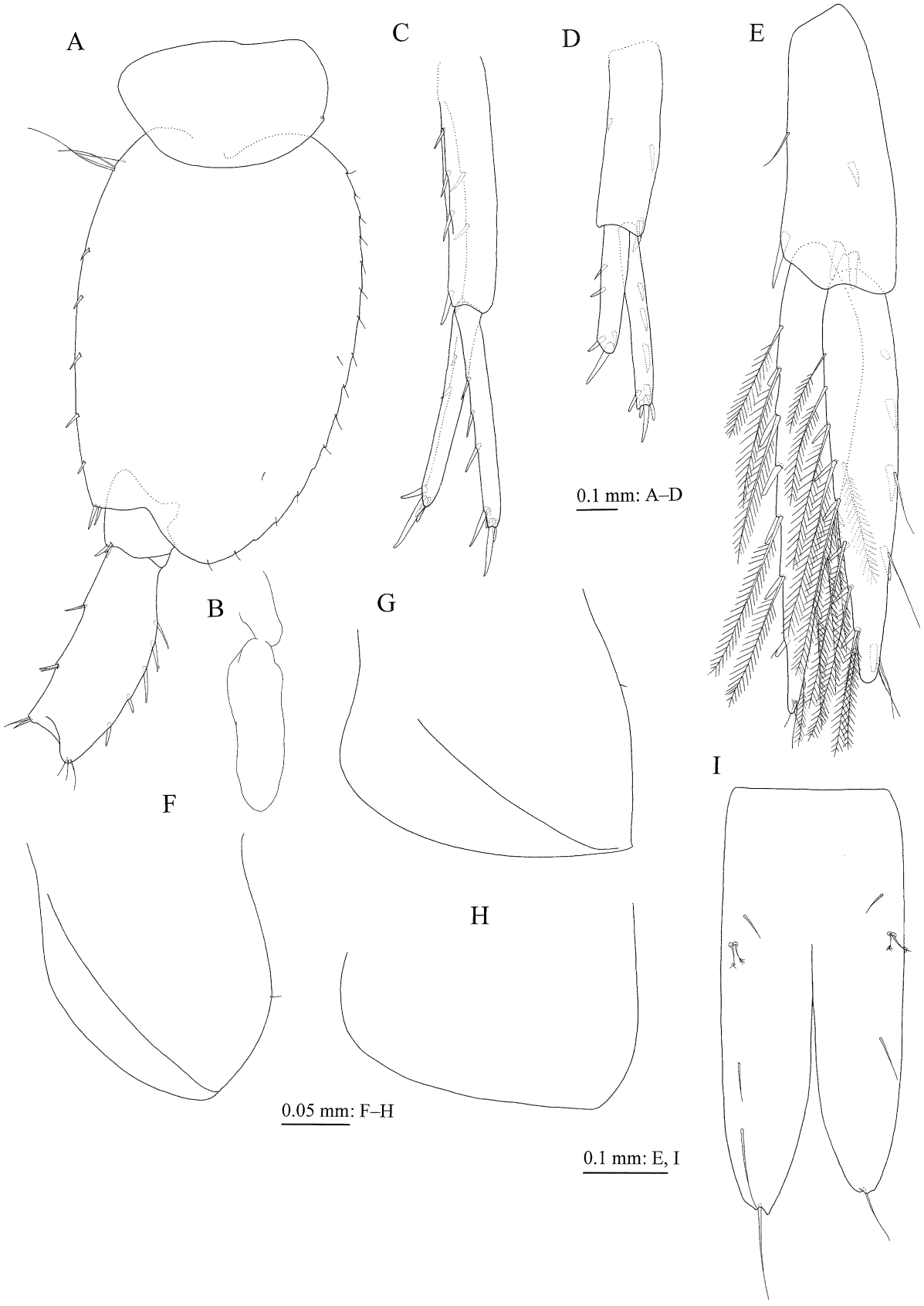

Fig. 12. *Sternomoera tsushimana* comb. nov., holotype, male (6.9 mm), NSMT-Cr 4136, driven well at the former town of Izuhara (now the city of Tsushima), Tsushima Island, Nagasaki Prefecture, Japan. **(A)** Coxa to merus of pereopod 7, lateral view. **(B)** Coxal gill 7, lateral view. **(C)** Uropod 1, medial view. **(D)** and **(E)** Uropods 2 and 3, ventral views. **(F)–(H)** Epimeral plates 1–3, lateral views. **(I)** Telson, dorsal view.

than gnathopod 1; coxa slightly longer than coxa 1; basis with two and three long setae on anteroproximal and posterior margins, respectively; carpus elongate, length 2.2 × width; propodus not powerful, length 2.1 × width, shorter than carpus, palmar margin weakly sinuous, lacking marginal setules, with three lateral and twomedial robust setae; dactylus curved inward, posterior margin smooth, with seven long marginal setae.

Pereopod 3 (Fig. 11A, B): coxa with one seta on anterodistal corner, four setae posterodistally; basis long, length 4.1 × width, anterior and posterior margins each with two long setae; merus, carpus, propodus, and dactylus in length ratio of 1.0 : 0.8 : 1.1 : 0.4, merus with two robust setae on anterior margin; carpus with one robust seta on posterior margin; propodus with four robust setae on posterior margin; dactylus lacking protuberance on posterior margin.

Pereopod 4 (Fig. 11C, D): coxa expanded with shallow posterior concavity, anterodistal corner with one seta; basis length 4.2 × width, anterior and posterior margins each with two long setae; merus, carpus, propodus, and dactylus in length ratio of 1.0 : 0.8 : 1.1 : 0.4, merus with two robust setae on anterior margin; carpus with one robust seta on posterior margin; propodus with five robust setae on posterior margin; dactylus lacking protuberance on posterior margin.

Pereopod 5 (Fig. 11E, F): coxa bilobed, ventral margin of posterior lobe with a seta; anterior margin of limb from basis to propodus and posterior margin of merus with robust setae; merus, carpus, propodus, and dactylus in length ratio of 1.0 : 1.0 : 1.2 : 0.4; dactylus lacking protuberance on anterior margin. Pereopod 6 (Fig. 11G): coxa bilobed, anterior lobe small, posterior margin of posterior lobe with setae; articles longer than those of pereopod 5, merus almost as long as carpus. Pereopod 7 (Fig. 12A): coxa semicircular; anterior and posterior margins of merus with robust setae.

Coxal gills (Fig. 12B) small, present on pereopods 5–7; accessory lobe absent. Pereonites 4–5 each with two slender sternal gills. Some coxal and sternal gills possibly missing.

Pleopods 1–3 unmodified.

Uropods. Uropod 1 (Fig. 12C): peduncle with two lateral and three medial robust setae marginally, basofacial seta absent; outer ramus length 0.8 × peduncle, lateral margin with 2 robust setae; inner ramus length 1.1 × outer ramus, medial margin with three robust setae; both rami with four terminal robust setae. Uropod 2 (Fig. 12D): peduncle with one lateral and one medial robust setae marginally; outer ramus length 0.7 × peduncle, lateral margin with two robust setae; inner ramus length 1.4 × outer ramus, medial margin with three robust setae; both rami with four terminal robust setae (one robust seta on outer ramus broken). Uropod 3 (Fig. 12E) long; peduncle length 0.8 × peduncle of uropod 2, with robust setae and slender seta; both rami uniarticulate; outer ramus length 1.6 × peduncle and 0.9 × inner ramus, lateral margin with both robust setae and simple setae, medial margin with both robust setae and plumose setae; both margins of inner ramus with robust setae and plumose setae.

Telson (Fig. 12I) long, 2.4 × width, margins parallel, narrowly cleft for 63% of length; each lobe slender, with several facial setae; apex subacute, with 1 long terminal seta.

Distribution. Only known from Tsushima Island (Uéno, 1971b).

Habitat. Groundwater accessed via a well.

Remarks. *Sternomoera tsushimana* comb. nov. may be a very rare species. Only the holotype male specimen is known to date. We found, as was noted by Hirayama (1990), that the head of *S. tsushimana* has a normal-shaped antennal sinus and does not exhibit a sinusoidal anterolateral margin as Uéno (1971b) described. Here we have illustrated for the first time the true form of the head (Fig. 9). We have additionally confirmed the presence of sternal gills on pereonites 4–5, which were overlooked in the previous papers (Uéno, 1971b; Hirayama, 1990). In the family Pontogeneiidae, only members of *Sternomoera* are known to have sternal gills. Based on the normal shape of antennal sinus and the presence of sternal gills, we reassign this species from *Relictomoera* to *Sternomoera*.

DISCUSSION

The present study raises the number of Japanese species of *Sternomoera* from three to five. With respect to their previously uninvestigated phylogenetic relationships, our analysis of all the Japanese *Sternomoera* species, except *S. tsushimana*, based on the nuclear 28S rRNA gene, has shown that they form a monophyletic group, a result that supports inferences based on morphological observations. *Sternomoera morinoi* appears to have diverged first from the common ancestor of *Sternomoera*. *Sternomoera morinoi* and *S. tsushimana* inhabit hyporheic or other subterranean interstitial waters. All species other than these occur in fresh surface waters (Kuribayashi et al., 1994, 1996; Labay, 1997). Possibly the ancestor of *Sternomoera* invaded the freshwater environment from the sea through interstitial waters. To clarify the evolution of the life habits of *Sternomoera*, more detailed molecular studies of many samples, including species of related genera (e.g., *Paramoera* and *Relictomoera*), are needed.

The monophylies of *Sternomoera yezoensis* and the Tohoku populations of *S. japonica* (locality numbers 8–14 in Fig. 1 and Table 1) are strongly supported by high bootstrap values, but the phylogenetic relationships among *S. yezoensis*, *S. japonica*, and *S. rhyaca* were not clearly resolved in our study. Especially, low bootstrap support makes it unclear whether *S. japonica* and *S. rhyaca* even represent monophyletic units.

Sternomoera yezoensis included two haplotypes, SY1 and SY2, with relatively high genetic divergence (*p*-distance: 7.9%). SY1 was found in Eniwa, and SY2 in Sapporo, both in Hokkaidô. Kuribayashi et al. (1994) pointed out morphological differences between the populations of Chitose (near Eniwa) and Sapporo, the former having two bundles of setae on the ventral margin of peduncular article 2 of the antenna 1 (vs. only one bundle in Sapporo specimens) and the telson short and semi-rounded (vs. long and semi-rectangular in Sapporo specimens). Our specimens from Eniwa shared the same morphological features as the Chitose specimens reported by Kuribayashi et al. (1994). These genetic and morphological differences are assumed to reflect long disjunction without gene flow between the Eniwa and the Sapporo populations. It is possible that the populations of Eniwa (Chitose) and Sapporo might be part

of a complex of cryptic species. To clarify this point, future detailed research covering the whole area of distribution of *S. yezoensis* is required.

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