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**Two new species in Leptocheliidae (Crustacea: Peracarida: Tanaidacea) from Japan,
with notes on their phylogenetic position and aspects of morphology**

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ABSTRACT

We describe two new species of leptocheliid tanaidaceans, *Chondrochelia sublitoralis* sp. nov. and *Neoleptochelia japonica* sp. nov., from Japan. *Chondrochelia* individuals were collected from 113–185 m depth in the Kumano Sea. *Chondrochelia sublitoralis* sp. nov. resembles *C. africana*, *C. corsica*, *C. taitungensis*, and *C. tanykeraia* in having females with slender chelipeds but differs from them in the length ratio of antennular articles and the setal pattern on maxillipeds, cheliped, pereopods 4–6, and pleopods. Males differ from *C. durbanensis*, for which information on females is lacking, in having a wide chelipedal fixed finger and a uniarticulate uropodal exopod. *Chondrochelia sublitoralis* sp. nov. varies intraspecifically in the number of female antennular articles, five in larger and four in smaller females. *Neoleptochelia japonica* sp. nov., collected from the coast of Okinawa Island, differ from *N. javaensis* (previously the sole species in *Neoleptochelia*) in the setal pattern on antennae, maxillipeds, cheliped, and pleopods in females; and that on the cheliped in males. Male pereopods 1–3 show a unique subchelate condition that we speculate may function for clasping during copulation. Several females in both species had the second thoracomere demarcated on the carapace, whereas others did not. Cytochrome *c* oxidase subunit I (COI) gene sequences determined for *C. sublitoralis* sp. nov. and *N. japonica* sp. nov. showed intraspecific K2P distances of 0–0.4% and 0–0.5%, respectively. We inferred the phylogenetic positions of the two species in Leptocheliidae based on COI data.

Keywords: DNA barcode, integrative taxonomy, Paratanaoidea, phylogeny, sexual dimorphism, subchelate

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1. Introduction

Most species in the family Leptocheliidae (superfamily Paratanaoidea) have been reported from coastal regions, occasionally at high densities (e.g., 32,159 individuals/m² for *Hargeria rapax* [Harger, 1879]; Sheridan, 1997). The approximately 130 leptocheliid species currently known are classified in 33 genera representing three subfamilies (Konariinae, Leptocheliinae, and Metaleptocheliinae; Anderson, 2023). Five species have been reported from Japanese waters: *Chondrochelia savignyi* (Krøyer, 1842), *Makassaritanais itoi* (Ishimaru, 1985), *Makassaritanais modestus* (Kussakin & Tzareva, 1972), *Mesotanais biridi* Larsen & Shimomura, 2007, and *Parakonarus kajii* Kakui, Uyeno & Naruse, 2019 (Kakui, 2016b; Kakui et al., 2019), although Bamber (2010), which provided a detail redescription of *C. savignyi*, concluded that Japanese individuals identified as *C. savignyi* should be regarded as species indeterminate.

Leptocheliid species generally show large sexual dimorphism, with conspecific male–female pairs recognized by similarity in the setation pattern on chelipeds and pereopods and the pigmentation pattern. Some male–female pairs identified as conspecific on the basis of morphology later proved not to be conspecific (Bamber, 2013), indicating that molecular confirmation of conspecificity is advisable.

Our study involved two undescribed leptocheliid species from Japan. One belongs in *Chondrochelia* Guțu, 2016, the most speciose leptocheliid genus with 30 members (Jarquín-González and Carrera-Parra, 2022; Guțu, 2023a, b), and is the host species for the nicothoid copepod *Rhizorhina ohtsukai* Kakui, 2016 (Kakui, 2016a). The other belongs in *Neoleptochelia* Guțu, 2011, which currently contains only one species, *Neoleptochelia javaensis* Guțu, 2011, reported from Indonesia (Guțu, 2011). For both species, we determined partial sequences of the cytochrome *c* oxidase subunit I (COI) gene to verify conspecific male–female pairs and to infer their phylogenetic position in Leptocheliidae. Here we describe these species and discuss intraspecific variation in female antennules in the *Chondrochelia* species and in the female carapace of both species. We also discuss the possible function of subchelate pereopods 1–3 seen in males of our *Neoleptochelia* species.

2. Material and methods

Chondrochelia specimens were collected by biological dredge from the Kumano Sea off Mie, Japan, during research cruises in 2014, 2017, and 2019 (Table 1). All specimens were fixed and preserved in 70% or 99% ethanol; one female and one male were photographed alive before fixation. *Neoleptocheilia* specimens were collected from intertidal algae and coral rubble at Bise (26°42'40.2"N 127°52'43.2"E), Okinawa, Japan (Table 2). All specimens were fixed and preserved in 70% or 99% ethanol; one male was photographed alive before fixation. The methods used for dissection, preparation of slides, light microscopy, and drawing were as described by Kakui and Angsupanich (2012). Specimens studied were deposited in the Invertebrate Collection of the Hokkaido University Museum (ICHUM), Sapporo.

Orientation and terminology here follow Larsen (2003), except that the term "plumose sensory seta" (PSS; Bird, 2011) is used instead of "broom seta," and "protopod" is used instead of "basal article" for pleopods and uropods; the terms "step-tipped plumose seta" (Kakui et al., 2010) and "vestigial proximal article" (Bird, 2012) were also used. The new term "setulate puff" was used for a swelling covered with tiny setules, located on the ventro-subdistal margin of the propodi of pereopods 1–3 in our male *Neoleptocheilia* specimen. Body length (BL) was measured from the base of the antennules to the tip of the pleotelson, and body width at the widest portion of the cephalothorax (CW, cephalothorax width). Measurements were made axially from digital images by using ImageJ (Rasband, 2023): dorsally on pleopods and uropods; laterally on the body, antennules, antennae, chelipeds, and pereopods. Lengths and widths of congeners were measured from original illustrations if measurements were not provided in descriptions. Here postmancae with genital cones were treated as males and other postmancae as females.

Total DNA was extracted from the cheliped or a pereopod by using the NucleoSpin Tissue XS Kit (Macherey-Nagel, Germany). Primers for PCR and cycle sequencing were LCO1490/HCO2198 for *Neoleptocheilia* (Folmer et al., 1994) and Chond_LCO/Chond_HCO for *Chondrochelia* (newly designed, see below). To determine sequences for the *Chondrochelia* species, we first used primer pair LCO1490 and HCO2198, but this resulted in multiple sequence signals. To circumvent this problem, a new primer (L_HCO: AAAGTACTTATAAAATTAATTGCTCCTGC) was designed from an alignment of four leptocheiliid and one teleotanaid sequences (accession numbers LC472886, MH087501, LC473040, HM016215, and KP254788) with the aid of Primer3Plus (Untergasser et al., 2007). This primer used in conjunction with LCO1490 amplified a single sequence (accession number LC655992) that contained a

stop codon in the 5' half, suggesting it represents a pseudogene. We then designed another two new primers, Chond_LCO (CGGAGTTTATAAAGGAGTTCTAGG) and Chond_HCO (GGGGTATAAAAATTTTCGATCTGT) by reference to transcriptome data (accession number GJCT00000000.1) and with the aid of Primer3Plus, which were used successfully.

Conditions for PCR amplification of COI from *Chondrochelia* with KOD One PCR Master Mix (Toyobo, Japan) were 45 cycles of 98°C for 10 s, 55°C for 5 s, and 68°C for 1 s; those for *Neoleptocheilia* with TaKaRa Ex Taq DNA polymerase (Takara Bio, Japan) were 94°C for 1 min; 35 cycles of 98°C for 10 s, 50°C for 30 s, and 72°C for 50 s; and 72°C for 2 min. All nucleotide sequences were determined with the BigDye Terminator Kit ver. 3.1 and a 3730 DNA Analyzer (Life Technologies, USA). The sequences we determined were deposited in the International Nucleotide Sequence Database (INSD) through the DNA Data Bank of Japan (DDBJ).

The COI dataset for a phylogenetic analysis included eight sequences we determined, and 64 other leptocheiliid sequences and an outgroup sequence (*Hamatipeda kohtsukai* Kakui & Hiruta, 2021, Hamatipedidae; LC632703) taken from the INSD or the Barcode of Life Data System (BOLD) (see Supplementary Material 1). These sequences were aligned by using MUSCLE (Edgar, 2004) and trimmed to the shortest length among the sequences; 33 identical sequences were removed in MEGA7 (Kumar et al., 2016). The aligned dataset contained 40 sequences and 405 positions (Supplementary Material 2). The optimal substitution models determined under the corrected AIC (Akaike information criterion) in ModelFinder (Kalyaanamoorthy et al., 2017) were TIM2+F+I+G4, TN+F+I+G4, and TPM2+F+G4 for the first, second, and third codon positions, respectively. A partitioned maximum likelihood (ML) analysis was conducted in IQ-TREE ver. 2.1.2 (Minh et al., 2020); nodal support values were obtained from the Shimodaira–Hasegawa-like approximate likelihood-ratio test (SH-aLRT) with 1000 replicates (Guindon et al., 2010) and an ultrafast bootstrap (UFBoot) analysis of 1000 pseudoreplicates under the “bnni” option (Minh et al., 2013; Hoang et al., 2018). The ML tree was drawn with FigTree v1.4.4 (Rambaut, 2023). Kimura (1980) 2-parameter (K2P) distances among leptocheiliid species were calculated with MEGA7.

3. Results

3.1. Taxonomy

Family Leptocheliidae Lang, 1973

Genus *Chondrochelia* Guţu, 2016

***Chondrochelia sublitoralis* sp. nov.**

[New Japanese name: Tsutsusode-tanaisu]

(Figs 1–7)

Leptochelia sp.: Kakui 2016a, fig. 1.

Chondrochelia sp.: Kakui et al. 2021.

Type material. See Table 1.

Etymology. This specific name *sublitoralis* (Latin: sublittoral) is an adjective referring to collection of this species from the sublittoral zone.

Diagnosis. Female: in antennules, combined length of articles 3 and succeeding article(s) at least 1.5 times as long as article 2 (1.56–1.82 times in type series); maxillipedal palp articles 2 and 4 each with outer seta; cheliped slender, having carpus with parallel dorsal and ventral margins and length at least two times width (2.54–3.27 times in type series), with merus bearing inner simple seta and carpus bearing two dorsal simple setae; carpus of pereopods 4–6 with three ventral spiniform setae; protopod of pleopods 1–5 with inner plumose setae. Male: propodus of pereopod 1 without ventrodistal spiniform setae; uropodal exopod uniarticulate.

Description of female, based on holotype. Body (Figs 1A, B, 2A, B) slightly dorsoventrally flattened, 7.95 times as long as CW, translucent, slightly yellowish when alive (Fig. 1A, B). Cephalothorax ovate, 0.19 times as long as BL, 1.55 times as long as wide, with two pairs of lateral simple setae posterior to eye and pair of mid-lateral simple setae; anterodorsal region orangish in living animal (Fig. 1A); second thoracomere demarcated dorsally on carapace (Fig. 7C); eyes well developed, pigmented, dark brown in living animal (Fig. 1B). Pereon 0.19 times as long as BL. Pereonites 1–6 with length ratio 1.00 : 1.55 : 1.52 : 1.75 : 1.61 : 1.40; pereonite 1 with pair of lateral setae in anterior region and another pair in posterior region;

pereonites 2, 4–6 with pair of lateral setae; pereonite 3 without setae. Pleon 0.19 times as long as BL.

Pleonites as wide as pereonite 6; all wider than long, similar in shape; pleonites 1–4 with pair of lateral setae, pleonite 5 with two pairs of lateral setae. Pleotelson (Fig. 2C) 0.52 times as long as wide, narrower than pleonite 5, trapezoid in dorsal view (Fig. 2C), with pair of lateral setae and two pairs of posterior setae.

Antennule (Fig. 3A) with five articles (article 5 cap-like), slender, 7.12 times as long as wide, 1.08 times as long as cephalothorax; articles 1–5 with length ratio 1.00 : 0.23 : 0.22 : 0.20 : 0.04. Article 1 with one mid-outer, one mid-ventral, one outer distal, and one inner distal simple setae; two proximal, four mid-outer, and four distal PSS; and several inner-proximal setae. Article 2 with one outer distal and one inner distal simple setae, and one inner PSS. Article 3 naked. Article 4 with one simple seta and one PSS in distal region. Article 5 with three distal simple setae and one distal PSS.

Antenna (Fig. 4A) 0.70 times as long as antennule, with six articles; articles 1–6 with length ratio 1.00 : 1.30 : 0.87 : 2.96 : 1.63 : 0.20. Article 1 with one ventrodiscal seta. Article 2 with one dorsodistal and one ventrodiscal spiniform setae and one dorso-subdistal simple seta. Article 3 with dorsodistal spiniform seta. Article 4 with one mid-inner and three distal simple setae (shorter than article-4 length) and several PSS. Article 5 with two distal simple setae and one PSS. Article 6 with five distal simple setae.

Labrum (Fig. 4B) not projecting anteriorly, setulate. Mandibles (Fig. 4C, D) with molar well developed; masticatory region broad. Incisor of left mandible (Fig. 4C) with six small teeth; lacinia mobilis with four small and one large teeth; incisor process with six small teeth. Incisor of right mandible (Fig. 4D) bifurcate distally, with anterior subdistal crenulation. Labium (Fig. 4E) bilobed; inner and outer lobes setulate. Maxillule (Fig. 4F, G) with setulate endite bearing 11 distal spines; palp ending in two long simple setae. Maxilla lost during dissection. Maxillipeds (Fig. 4H) with bases not fused medially, both bearing four simple setae at insertion of palp. Endites (Fig. 4J) not fused medially, reaching distal margin of palp article 1, each with outer distal long simple seta, three distal flat spiniform setae (two longer and one shorter, relatively rounded), two inner distal coupling hooks, and two outer distal setulations. Palp (Fig. 4I) article 1 naked; article 2 with one outer short and four inner long distal setae; article 3 with eight inner simple setae; article 4 with one outer and ten distal simple setae. Epignath (Fig. 4K) elongate, slender, setulate.

Cheliped (Fig. 4L) chelate, with triangular articulation with cephalothorax via sclerite; sclerite with simple seta. Basis 1.69 times as long as wide, with free posterior portion and outer simple seta. Merus with

three ventral and one inner simple setae. Carpus 2.54 times as long as wide, longer than basis, with two dorsal and three ventro-subdistal simple setae; outer ventrodistal margin not extending as cuff over proximal region of propodus. Propodal palm with simple seta at insertion of dactylus and inner comb-row of six setae (Fig. 4M, N). Fixed finger with three dorsal and four ventral simple setae, and cone shaped claw. Dactylus and unguis fused to claw, as long as fixed finger; dactylus with inner proximal simple setae.

Pereopods 1–6 cylindrical, with length ratio 1.00 : 0.55 : 0.50 : 0.56 : 0.55 : 0.58. Pereopod 1 (Fig. 5A) 0.31 times as long as BL, with length ratio of articles from basis to dactylus-unguis 1.00 : 0.05 : 0.33 : 0.34 : 0.64 : 0.95. Coxa with simple seta. Basis slightly arched, 5.09 times as long as wide, with dorsoproximal simple seta. Ischium wider than long, with ventral simple seta. Merus 1.76 times as long as wide, with ventrodistal short simple seta. Carpus 1.81 times as long as wide, with five distal simple setae. Propodus 4.80 times as long as wide, with three dorso-subdistal and one ventro-subdistal simple setae. Dactylus with proximal simple seta. Unguis 0.73 times as long as dactylus, naked. Pereopod 2 (Fig. 5B) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.07 : 0.36 : 0.37 : 0.52 : 0.17. Coxa with simple seta. Basis cylindrical, 3.95 times as long as wide, with dorsoproximal simple seta and two PSS. Ischium wider than long, with one ventral simple seta. Merus 1.76 times as long as wide, with ventrodistal simple seta and ventrodistal spiniform seta. Carpus 2.07 times as long as wide, with one dorsodistal and one ventrodistal simple setae and two ventrodistal spiniform setae. Propodus 3.91 times as long as wide, with four dorso-subdistal simple setae and ventrodistal spiniform seta. Dactylus with simple proximal seta. Unguis 0.40 times as long as dactylus, naked. Pereopod 3 (Fig. 5C) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.07 : 0.31 : 0.35 : 0.58 : 0.14; similar to pereopod 2, except basis with one proximodorsal PSS and propodus with three dorso-subdistal setae. Pereopod 4 (Fig. 5D) lacking coxa, with length ratio of articles from basis to dactylus-unguis 1.00 : 0.06 : 0.36 : 0.35 : 0.44 : 0.33. Basis thick, 2.59 times as long as wide, with three dorsal and one ventral PSS. Ischium wider than long, with two ventral simple setae. Merus 2.11 times as long as wide, with two ventrodistal spiniform setae. Carpus 1.95 times as long as wide, with two dorsodistal simple setae and three ventrodistal spiniform setae. Propodus 3.69 times as long as wide, with five dorsodistal simple setae, dorsodistal serrated spiniform seta, and two ventro-subdistal spiniform setae. Dactylus naked. Unguis 0.33 times as long as dactylus, naked. Pereopod 5 (Fig. 5E) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.09 : 0.43 : 0.44 : 0.36 : 0.27; similar to

pereopod 4, except basis with ventral simple seta and two ventral PSS. Pereopod 6 (Fig. 5F) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.04 : 0.36 : 0.37 : 0.37 : 0.30; similar to pereopod 4, except basis with one dorsal PSS and ventral simple setae, carpus with distal simple seta, and propodus with seven serrated spiniform setae and four simple setae.

Pleopods five pairs, all similar. Pleopod 1 (Fig. 5G, H) protopod with inner plumose seta. Exopod with vestigial proximal article bearing ventral plumose seta; remaining portion with 25 outer plumose setae. Endopod with one inner-subdistal, 13 outer plumose setae, and outer distal step-tipped plumose seta. Setal numbers/conditions in pleopods 2–5 summarized in Supplementary Material 3.

Uropod (Fig. 5I) with naked protopod. Endopod with five articles; article 1 with simple seta; article 2 with two distal simple setae and distal PSS; article 3 with distal simple seta; article 4 with one distal simple seta; article 5 with one middle and three distal simple setae. Exopod uniarticulate, shorter than endopodal article 1, with one middle and two distal simple setae.

Description of male, based on allotype. Body (Figs 1C, D, 2D, E) slightly dorsoventrally flattened, 6.19 times as long as CW, translucent, slightly yellowish in living animal (Fig. 1C, D). Cephalothorax ovate in outline, 0.20 times as long as BL, 1.25 times as long as wide, with pair of mid-lateral simple setae; anterodorsal region orangish in living animal (Fig. 1C); second thoracomere not demarcated dorsally on carapace; eyes well developed, pigmented, dark brown in living animal. Pereon 0.52 times as long as BL. Pereonites 1–6, with length ratio 1.00 : 1.31 : 1.64 : 2.20 : 1.92 : 1.64; all wider than long; pereonites 1–3 with pair of lateral setae in anterior region and another pair in posterior region; pereonites 4–6 with two pairs of lateral setae. Pleon 0.28 times as long as BL. Pleonites as wide as pereonite 6; all wider than long, similar in shape; all with pair of lateral setae. Pleotelson (Fig. 2F) 0.43 times as long as wide, narrower than pleonite 5, pentangular in dorsal view, with two pairs of posterior setae.

Antennule (Fig. 3C) with 12 articles, 1.67 times as long as cephalothorax; articles 1–12 with length ratio 1.00 : 0.39 : 0.14 : 0.12 : 0.12 : 0.13 : 0.11 : 0.12 : 0.10 : 0.09 : 0.02 : 0.01. Article 1 with one outer distal and one inner distal setae, and three outer distal PSS. Article 2 with one mid-inner and one distal simple setae, and four distal PSS. Article 3 with one distal simple seta and one PSS. Article 4 with two ventral rows of aesthetascs. Articles 5–10 each with ventral row of aesthetascs. Article 11 with one distal simple seta and two aesthetascs. Article 12 with two distal simple setae.

Antenna (Fig. 6A) 0.46 times as long as antennule, with six articles; articles 1–6 with length ratio 1.00 : 1.16 : 0.79 : 3.11 : 2.58 : 0.32. Article 1 naked. Articles 2–6 similar to those of female; spiniform setae on article 2 thinner than females; simple setae on article 4 longer than article-4 length.

Maxillule with two distal setae (Fig. 6B). Maxillipedal endite lacking, palp lacking. Cheliped (Fig. 6C, D) chelate, with triangular articulation with cephalothorax via sclerite; sclerite with simple seta. Basis 1.19 times as long as wide, with one outer seta. Merus with three ventral and one inner simple setae. Carpus slender, 4.74 times as long as wide, longer than basis, with three dorsal and three ventrodiscal simple setae; outer ventrodiscal margin extending as cuff over proximal region of propodus. Propodus also slender, as long as carpus. Propodal palm with outer simple seta at insertion of dactylus, and inner comb-row of 21 setae; comb-row almost parallel with dorsal margin of propodal palm. Fixed finger robust, width of region between two apophyses 0.83 times width of base of fixed finger, with two dorsal apophyses and three ventral and three dorsal simple setae (one of three ventral setae broken). Dactylus and unguis fused to claw, nearly as long as fixed finger, with inner proximal simple seta and eight ventral spiniform setae.

Pereopods 1–6 cylindrical, with length ratio 1.00 : 0.59 : 0 : 52 : 0.67 : 0.64 : 0.61. Pereopod 1 (Fig. 6E) 0.46 times as long as BL, with length ratio of basis, ischium, merus, carpus, propodus, and dactylus-unguis 1.00 : 0.06 : 0.35 : 0.36 : 0.69 : 0.71. Setation on coxa, ischium, carpus, propodus, and dactylus-unguis similar to that in female. Basis cylindrical, narrow, 5.76 times as long as wide, with dorsoproximal simple seta and PSS. Ischium wider than long. Merus 2.97 times as long as wide, with dorsodistal and inner distal simple setae. Carpus 3.11 times as long as wide. Propodus 8.22 times as long as wide. Unguis 0.69 times as long as dactylus. Pereopod 2 (Fig. 6F) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.08 : 0.34 : 0.33 : 0.57 : 0.32. Setation of articles from coxa to dactylus-unguis similar to that in female. Basis cylindrical, 5.58 times as long as wide. Ischium wider than long. Merus 2.40 times as long as wide. Carpus 2.19 times as long as wide. Propodus 5.45 times as long as wide. Unguis 0.79 times as long as dactylus. Pereopod 3 (Fig. 6G) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.06 : 0.32 : 0.34 : 0.58 : 0.37; similar to pereopod 2, except basis with one PSS and propodus with three dorso-subdistal simple setae. Pereopod 4 (Fig. 6H) without coxa, with length ratio of articles from basis to dactylus-unguis 1.00 : 0.04 : 0.32 : 0.35 : 0.50 : 0.39. Setation on ischium, merus, and dactylus-unguis similar to that in

female. Basis cylindrical, 3.17 times as long as wide, with two proximodorsal and midventral PSS. Ischium wider than long. Merus 2.28 times as long as wide. Carpus 2.56 times as long as wide, serrate ventrally, with two dorsodistal simple setae and one long and three short distal spiniform setae. Propodus 5.91 times as long as wide, with four longer and two dorsodistal serrated spiniform setae (tip broken), and two ventro-subdistal spiniform setae. Dactylus and unguis fused to claw. Pereopod 5 (Fig. 6I) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.08 : 0.40 : 0.49 : 0.61 : 0.50; similar to pereopod 4, except basis with dorsal PSS but lacking ventral PSS and propodus with six dorsodistal simple setae (one tip broken). Pereopod 6 (Fig. 6J) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.06 : 0.38 : 0.48 : 0.51 : 0.34; similar to pereopod 4, except basis with dorso-subdistal simple seta and propodus with four simple setae and four serrated spiniform setae in dorsodistal region.

Pleopods five pairs, all similar. Pleopod 1 (Fig. 6K, L) protopod with inner plumose seta. Exopod with vestigial proximal article bearing ventral plumose seta; remaining portion with 23 outer plumose setae. Endopod with one inner-subdistal and 13 outer plumose setae, and outer distal step-tipped plumose seta. Setal numbers/conditions in pleopods 2–5 summarized in Supplementary Material 3.

Uropod (Fig. 6M) with protopod bearing six inner distal simple setae. Endopod with six articles; article 1 with two distal simple setae and distal PSS; article 2 with three distal simple setae and distal PSS; article 3 with simple seta; article 4 with two distal simple setae and two distal PSS; articles 5 and 6 each with distal simple seta. Exopod uniarticulate, shorter than endopodal article 1, with one middle and two distal simple setae.

Variation. In addition to holotype and allotype, four female (ICHUM6345, ICHUM6346, ICHUM6348, ICHUM6349) and one male (ICHUM6347) paratypes of *Chondrochelia sublitoralis* sp. nov. were dissected, and selected characters were observed for the carapace, antennule, antenna, maxillipeds, cheliped, pereopods 1–6, pleopods 1–5, and uropods (see Supplementary Material 3). The following character states were shared with all specimens (selected characters only are presented): antennular article 1 with mid-inner and mid-outer setae (females) or without middle setae (males); antenna with article 2 bearing one dorsodistal and one ventrodistal spiniform setae, article 3 bearing dorsodistal spiniform seta; maxillipedal palp with article 2 bearing outer seta (female) and article 4 bearing outer seta (female); cheliped slender (female), i.e., carpus with parallel dorsal and ventral margins and at least two times longer than wide;

chelipedal merus with one inner seta (female); chelipedal carpus with two (female) or three (male) dorsal setae; fixed finger robust (male), width of region between two apophyses more than 0.75 times width of base of fixed finger; carpus of pereopods 2 and 3 with one dorsal and one ventral simple setae and two ventrodiscal spiniform setae; carpus of pereopods 4–6 with three distal spiniform setae (female); protopod of pleopods 1–5 with inner plumose seta; uropodal exopod uniarticulate.

The following characters varied among specimens (selected characters only are presented; states are in parentheses): length/width of female cephalothorax (1.31–1.57); dorsal demarcation of second thoracomere on carapace (present, slight, lacking) (Fig. 7C, D); number of antennular articles in females (4–5) (Fig. 3A, B); combined length of articles 3 and succeeding article(s) relative to article 2 length in female antennules (1.56–1.82); number of distal simple setae on maxillipedal basis in females (2–4); number of inner simple setae on palp article 4 of maxilliped in females (8–10); length/width of chelipedal carpus in females (2.54–3.27); width of region of fixed finger between two apophyses (0.83 or 0.86 times width of base of fixed finger); number of ventral simple setae on fixed finger of cheliped (3–4); number of distal simple setae on carpus of pereopod 1 (3–5); number of ventrodiscal simple setae on merus of pereopods 2 and 3 (0 or 1); number of simple setae on ischium of pereopods 4–6 (1–2); and number of articles of uropodal endopod in females (3–5).

Genetic information. A partial COI sequence was determined from the allotype and three paratype specimens (Table 1). Among four sequences (541 bp, encoding 180 amino acids; LC655988–LC655991), there were 0–2 synonymous nucleotide substitutions, i.e., K2P distances among them were 0–0.4%. Interspecific variation between this species and eight congeneric species was 23.1–33.7% K2P distance (Supplementary Material 4).

Distribution. So far known only from the Kumano Sea, northwestern Pacific, 113–185 m depth.

Genus *Neoleptochelia* Guțu, 2011

Neoleptochelia japonica sp. nov.

[New Japanese name: Kagishippo-tanaisu]

(Figs 8–12)

Type material. See Table 2.

Etymology. The specific name is an adjective referring to Japan, the country wherein lies the type locality.

Diagnosis. Female: antenna with article 1 bearing ventrodistal simple seta and article 2 bearing outer simple seta; maxilliped-palp article 4 with outer seta; chelipedal carpus with seven dorsal simple setae; pleopodal protopods with inner plumose seta. Male: chelipedal carpus with seven dorsal simple setae and ventral simple setae; fixed finger with five ventral simple setae.

Description of female, based on holotype. Body (Fig. 9A, B) slightly dorsoventrally compressed, 6.91 times as long as CW. Cephalothorax ovate, length 0.18 times BL, 1.24 times as long as wide, with pair of lateral simple setae posterior to eye and pair of mid-lateral simple setae; second thoracomere not demarcated dorsally on carapace; eyes well developed, pigmented. Pereonites 1–6 with length ratio 1.00 : 1.13 : 1.33 : 1.64 : 1.60 : 1.28; all wider than long, rectangular; pereonite 1 with pair of proximodorsal setae and three pairs of lateral setae in anterior region, and pair of lateral setae in posterior region; pereonites 2 and 3 with pair of proximodorsal setae and pair of lateral setae in anterior region, and pair of lateral setae in posterior region; pereonites 4–6 with pair of anterior dorsolateral setae (except pereonite 5) and pair of lateral setae. Pleon length 0.24 times BL. Pleonites as wide as pereonite 6; all wider than long, similar in shape, each with two pairs of lateral setae; pleonites 3–5 with pair of anterodorsal setae. Pleotelson 0.50 times as long as wide, narrower than pleonite 5, pentangular in dorsal view, with pair of anterodorsal setae, pair of anterior dorsolateral setae, and two pairs of posterior setae.

Antennule (Fig. 10A) with four articles (article 4 cap-like), stout, 4.98 times as long as wide, 0.79 times as long as cephalothorax; articles 1–4 with length ratio 1.00 : 0.25 : 0.28 : 0.04. Article 1 with two mid-outer, one mid-ventral, one mid-inner, one outer distal, and one inner distal simple setae; two proximal, one mid-outer and two distal PSS; and several inner-proximal setae. Article 2 with one outer distal and one inner distal simple setae, and inner distal PSS. Article 3 with two simple setae, one PSS, and aesthetasc in distal region. Article 4 with four distal simple setae (three broken) and one distal PSS.

Antenna (Fig. 10B) with six articles, 0.92 times as long as antennule; articles 1–6 with length ratio 1.00 : 1.56 : 1.04 : 2.34 : 0.96 : 0.22. Article 1 with ventrodistal seta. Article 2 with dorsodistal and ventrodistal spiniform setae and one outer distal simple seta. Article 3 with dorsodistal spiniform seta

(shorter than any on previous article). Article 4 with one mid-outer, one mid-inner, and three distal simple setae and several PSS. Article 5 with two distal simple setae. Article 6 with six distal simple setae.

Labrum (Fig. 10C) not projecting anteriorly, setulate. Mandibles (Fig. 10D, E) with molar well developed; masticatory region broad. Incisor of left mandible (Fig. 10D) with slightly bifurcate tip; lacinia mobilis with four small and one large teeth; incisor process with two small and one large teeth. Incisor of right mandible (Fig. 10E) bifurcate distally, with anterior subdistal crenulation. Labium (Fig. 10F) bilobed; inner and outer lobes setulate. Maxillule (Fig. 10G, H) with setulate endite bearing 11 distal spines; palp ending in two long simple setae. Maxilla lost during dissection. Maxillipeds (Fig. 10I) with bases not fused medially, both bearing four long setae and one short seta at insertion of palp. Endites (Fig. 10K) not fused medially, reaching distal margin of palp article 1, each with outer distal long setulate seta, three distal flat spiniform setae (two longer and one short, relatively rounded; all with distal serration), three inner distal coupling hooks, and outer distal setulations. Palp (Fig. 10J) article 1 naked; article 2 with one outer short and four inner long distal setae; article 3 with one (left) or two (right) outer and eight inner simple setae; article 4 with one outer and nine distal simple setae. Epignath (Fig. 10L) elongate, slender, setulate distally.

Cheliped (Fig. 10M) chelate, with triangular articulation with cephalothorax via sclerite; sclerite with simple seta. Basis 1.60 times as long as wide, with free posterior portion and outer simple seta. Merus with three ventral and two inner simple setae. Carpus 1.91 times as long as wide, longer than basis, with seven dorsal and three ventrodistal simple setae; outer ventrodistal margin not extending as cuff over proximal region of propodus. Propodal palm with simple seta at insertion of dactylus and inner comb-row of five setae (Fig. 10N, O). Fixed finger with three dorsal and two ventral simple setae, and cone shaped claw. Dactylus and unguis fused to claw, as long as fixed finger, with several broad teeth; dactylus with inner proximal simple seta.

Pereopods 1–6 cylindrical, with length ratio 1.00 : 0.54 : 0.55 : 0.68 : 0.65 : 0.56. Pereopod 1 (Fig. 11A) length 0.27 times BL, with length ratio of articles from basis to dactylus-unguis 1.00 : 0.09 : 0.42 : 0.37 : 0.66 : 0.64. Coxa with simple seta. Basis arched, 3.57 times as long as wide, with dorsoproximal simple seta and PSS. Ischium wider than long, with ventral simple seta. Merus 1.88 times as long as wide, with one dorsal and one ventrodistal simple setae. Carpus 1.67 times as long as wide, with five distal simple setae. Propodus 3.23 times as long as wide, with three dorso-subdistal and one ventro-subdistal simple setae.

Dactylus with proximal simple seta. Unguis 1.34 times as long as dactylus, naked. Pereopod 2 (Fig. 11B) with length ratio of articles from basis to propodus 1.00 : 0.08 : 0.39 : 0.35 : 0.58. Coxa with simple seta. Basis cylindrical, 2.18 times as long as wide, with dorsoproximal simple seta and two PSS. Ischium wider than long, with one ventral simple seta. Merus 1.26 times as long as wide, with one spiniform seta. Carpus 1.13 times as long as wide, with dorsal and ventrodiscal simple setae, one very long ventrodiscal simple seta (longer than propodus and dactylus combined) and two ventrodiscal spiniform setae. Propodus 2.39 times as long as wide, with two simple setae and ventrodiscal spiniform seta. Dactylus with one simple seta. Unguis 0.40 times as long as dactylus, naked. Pereopod 3 (Fig. 11C) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.10 : 0.43 : 0.33 : 0.54 : 0.31; similar to pereopod 2, except carpus lacking ventrodiscal simple seta and propodus with one dorsodiscal simple seta. Pereopod 4 (Fig. 11D) without coxa, length ratio of articles from basis to dactylus-unguis 1.00 : 0.11 : 0.37 : 0.27 : 0.33 : 0.26. Basis thick, 2.38 times as long as wide, with ventral simple seta and three dorsal PSS. Ischium wider than long, with two ventral simple setae. Merus 1.98 times as long as wide. Carpus 1.13 times as long as wide, with one simple seta and three serrated spiniform setae. Propodus 2.59 times as long as wide, with two dorsodiscal serrate setae, dorsodiscal serrated spiniform seta, and two short ventro-subdiscal spiniform setae. Dactylus and unguis fused to claw; claw carved, serrated. Pereopod 5 (Fig. 11E) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.10 : 0.39 : 0.32 : 0.31 : 0.21; similar to pereopod 4, except basis with ventral PSS but lacking three dorsal PSS. Pereopod 6 (Fig. 11F) with length ratio of articles from basis to propodus 1.00 : 0.11 : 0.47 : 0.38 : 0.39; similar to pereopod 4, except basis with one dorsal PSS and propodus with six dorsodiscal serrated setae.

Pleopods five pairs, all similar. Pleopod 1 (Fig. 11G, H) protopod with inner plumose seta. Exopod with vestigial proximal article bearing ventral plumose seta; remaining portion with 20 outer plumose setae. Endopod with one inner-subdiscal and 10 outer plumose setae, and outer distal step-tipped plumose seta. Setal numbers/conditions in pleopods 2–5 summarized in Supplementary Material 5.

Uropod (Fig. 11I) with protopod bearing simple seta. Endopod with three articles; article 1 with two simple setae; article 2 with four distal simple setae; article 3 with three middle and two distal simple setae and two PSS. Exopod uniarticulate, longer than endopodal article 1, with one middle and two distal simple setae.

Description of male, based on allotype. Body (Figs 8A, B, 9E, E) slightly dorsoventrally compressed, 5.18 times as long as CW, slightly reddish in the living animal (Fig. 8A, B). Cephalothorax pear-shaped in dorsal view, length 0.22 times BL, 1.13 times as long as wide, with pair of lateral simple setae posterior to eye and pair of mid-lateral simple setae; second thoracomere not demarcated dorsally on carapace; eyes well developed, pigmented. Pereonites 1–6 with length ratio 1.00 : 1.27 : 1.33 : 1.98 : 1.23 : 1.52; all wider than long; pereonite 1 with three pairs of lateral setae in anterior region and pair of lateral setae in posterior region; pereonites 2 and 3 with pair of anterodorsal setae and pair of lateral setae in anterior region, and pair of anterior dorsolateral setae; pereonites 4–6 with pair of anterodorsal setae and three pair of lateral setae (Fig. 12I, J); pereonite 4 with pair of anterior dorsolateral setae. Pleon length 0.27 times BL. Pleonites slightly wider than pereonite 6; all wider than long, similar in shape, each with two pairs of lateral setae; pleonites 2–5 with pair of anterodorsal setae. Pleotelson (Fig. 9F) length 0.38 times width, narrower than pleonite 5, pentangular in dorsal view, with pair of anterodorsal setae and pair of anterior dorsolateral setae, and two pairs of posterior setae.

Antennule (Fig. 12A) with 12 articles, 2.66 times as long as cephalothorax; articles 1–12 with length ratio 1.00 : 0.52 : 0.12 : 0.03 : 0.08 : 0.10 : 0.10 : 0.08 : 0.05 : 0.07 : 0.09 : 0.01. Article 1 with one mid-outer, one outer distal, and one inner distal setae; three ventro-subproximal and four outer distal PSS; and several inner-proximal setae. Article 2 with two distal simple setae and four distal PSS. Article 3 with two distal simple setae and one PSS. Articles 4–10 each with ventral row of aesthetascs. Article 11 with two simple setae and aesthetasc. Article 12 with four simple setae and one PSS.

Antenna (Fig. 12B) with seven articles, 0.43 times as long as antennule; articles 1–7 with length ratio 1.00 : 1.38 : 1.30 : 2.03 : 2.08 : 1.73 : 0.16. Article 1 with ventrodistal seta. Article 2 with dorsodistal and ventrodistal spiniform setae and one outer distal simple seta. Article 3 with spiniform seta (broken). Article 4 with one outer and one inner distal simple setae, and one inner PSS. Article 5 with three distal simple setae and several PSS. Article 6 with two distal simple setae. Article 7 with five distal simple setae.

Maxillipedal endite lacking, palp lacking (Fig. 12C).

Cheliped (Fig. 12D, E) chelate, with triangular articulation with cephalothorax via sclerite; sclerite with simple seta. Basis 1.54 times as long as wide, with one outer seta. Merus with three ventral and two inner simple setae. Carpus slender, 8.87 times as long as wide, longer than basis, with seven dorsal (four

broken) and three ventrodistal simple setae; outer ventrodistal margin not extending as cuff over proximal region of propodus. Propodus also slender, nearly as long as carpus. Propodal palm with outer simple seta at insertion of dactylus and inner comb-row of 13 setae; comb-row nearly parallel to dorsal margin of propodal palm. Fixed finger curved distally, with three dorsal and five ventral simple setae. Dactylus and unguis fused to claw, curved distally, slightly longer than fixed finger; dactylus with ventral apophysis, inner proximal simple seta, and 13 ventral spiniform setae.

Pereopods 1–6 cylindrical, with length ratio 1.00 : 0.82 : 0.69 : 0.78 : 0.74 : 0.69. Pereopod 1 (Fig. 12F) 0.47 times as long as BL, with length ratio of articles from basis to dactylus-unguis 1.00 : 0.09 : 0.51 : 0.40 : 0.66 : 0.48. Setation of coxa, ischium, merus, carpus, and unguis similar to those of female. Coxa with simple seta. Basis slightly arched, 5.33 times as long as wide, with dorsoproximal simple seta. Ischium wider than long. Merus 3.38 times as long as wide. Carpus 2.56 times as long as wide. Propodus 5.00 times as long as wide, with three dorso-subdistal simple setae, ventro-subdistal spiniform seta, and ventro-subdistal setulate puff. Dactylus strongly bent ventrally at subproximal point (cf. Fig. 8E), serrated. Unguis 0.48 times as long as dactylus. Pereopod 2 (Fig. 12G) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.06 : 0.33 : 0.37 : 0.61 : 0.36. Setation of coxa, merus, and unguis similar to those of female. Basis cylindrical, 4.74 times as long as wide, with dorsoproximal simple seta and PSS. Ischium wider than long, with two ventral simple setae. Merus 2.13 times as long as wide. Carpus 2.45 times as long as wide, with three distal simple setae and two ventrodistal spiniform setae. Propodus 4.14 times as long as wide, with two dorso-subdistal simple setae, ventrodistal spiniform seta, and ventro-subdistal setulate puff (Fig. 8C, D). Dactylus strongly bent ventrally at subproximal point, with one simple seta; serrated. Unguis 0.77 times as long as dactylus. Pereopod 3 (Fig. 12H) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.05 : 0.32 : 0.37 : 0.51 : 0.38; similar to pereopod 2, except propodus with one dorsal simple seta. Pereopod 4 (Fig. 12I) without coxa, length ratio of articles from basis to dactylus-unguis 1.00 : 0.07 : 0.27 : 0.43 : 0.65 : 0.36. Setation on basis and ischium similar to that in female. Basis proportionally narrower than in female, 3.21 times as long as wide. Ischium wider than long. Merus 2.00 times as long as wide, with two ventral spiniform setae and serration. Carpus 2.97 times as long as wide, with one simple seta and four spiniform setae. Propodus 6.89 times as long as wide, with three dorsodistal simple setae and two ventro-subdistal spiniform setae. Dactylus and unguis fused to claw; claw nearly straight, serrated. Pereopod 5 (Fig.

12J) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.12 : 0.30 : 0.50 : 0.73 : 0.38; similar to pereopod 4. Pereopod 6 (Fig. 12K) with length ratio of articles from basis to dactylus-unguis 1.00 : 0.06 : 0.34 : 0.42 : 0.61 : 0.34; similar to pereopod 4, except basis lacking PSS and propodus having five dorsodistal serrated spiniform setae.

Pleopods five pairs, all similar. Pleopod 2 (Fig. 12L, M) protopod with inner plumose seta. Exopod with vestigial proximal article bearing ventral plumose seta; remaining portion with 21 outer plumose setae. Endopod with one inner-subdistal, 13 outer plumose setae, and outer distal step-tipped plumose seta. Setal numbers/conditions in pleopods 1, 3–5 summarized in Supplementary Material 5.

Uropod (Fig. 12N) with protopod bearing six simple setae. Endopod with five articles; article 1 with five simple setae and PSS; article 2 with five distal simple setae and PSS; article 3 with four simple setae; article 4 with one simple seta; article 5 with four simple setae. Exopod uniarticulate, longer than endopodal article 1, with one middle and two distal simple setae.

Variation. In addition to holotype and allotype, two female (ICHUM8470, ICHUM8471) paratypes of *Neoleptocheilia japonica* sp. nov. were dissected, and selected characters were observed for the carapace, antennule, antenna, maxillipeds, cheliped, pereopods 1–6, pleopods 1–5, and uropods (see Supplementary Material 5). The following character states were shared with all specimens (selected characters only are presented; states are in parentheses): antennule with four articles (female); antennular article 1 with two mid-outer simple setae (female); antenna with article 1 bearing one ventral simple seta and article 2 bearing one outer simple seta; maxillipedal palp with article 2 bearing one outer simple seta (female) and article 4 bearing one outer simple seta (female); cheliped with merus bearing three ventral simple setae and carpus bearing seven dorsal setae; fixed finger with two (female) or five (male) ventral simple setae; pereopod 1 with merus bearing one dorsal and one ventral distal setae and propodus bearing three dorsodistal setae; carpus of pereopods 4–6 with three (female) or four (male) spiniform setae; protopod of pleopods 1–5 with inner plumose seta; uropodal exopod uniarticulate.

The following characters varied among females (selected characters only are presented; states are in parentheses): dorsal demarcation of second thoracomere on carapace (present, absent); number and length of distal simple setae on maxillipedal basis (1 short and 4 long; 1 medium and 3 long; 1 short, 1 medium, and 5 long); number of inner simple setae on chelipedal merus (1, 2); number of simple setae on pereopod 2

ischium (1, 2); number of ventrodistal simple setae on pereopod-3 carpus (1, 2); number of simple setae on pereopod-4 ischium (0, 2); number of articles on uropodal endopod (3, 4).

Genetic information. A partial COI sequence was determined from the holotype, allotype, and two paratype specimens (Table 2). Among the four sequences (658 bp, encoding 219 amino acids; LC745706–LC745709), there were 0–3 synonymous nucleotide substitutions; K2P distances among them were 0–0.5%. Our sequences were the first from any *Neoleptochelia* species deposited in public databases.

Distribution. Presently known only from the intertidal zone at the type locality, Bise, Okinawa Island, Okinawa, Japan.

3.2. COI-based phylogeny within Leptocheliidae

Most phylogenetic relationships in our COI tree (Fig. 13) show faint support, but six moderately or strongly supported clades are evident: Clade A contains the other five clades; Clade A1; Clade A2 contains Clade A2 α ; and Clade A3 contains Clade A3 α . Clade A, comprising all leptocheliid species except *C. sublitoralis* sp. nov., is moderately well supported (SH-aLRT = 98.2%; UFBoot = 88%). Clade A1 is highly supported (SH-aLRT = 99.9%; UFBoot = 99%). Clade A2 (SH-aLRT = 99.1%; UFBoot = 100%) contains two *Chondrochelia* species from Middle America and a *Hargeria* clade (Clade A2 α). Clade A3 is moderately well supported (SH-aLRT = 95.7%; UFBoot = 86%) and includes three leptocheliine species—*Neoleptochelia japonica* from Japan, *Leptochelia forresti* (Stebbing, 1896) from Florida, USA (type locality, Antigua and Barbuda in the Caribbean; Stebbing, 1896), and “*Leptochelia longichelipes*” from Belize (this species name is not available; see Jarquín-González et al., 2015)—along with a Konariinae clade (Clade A3 α). Leptocheliinae and *Chondrochelia* were not monophyletic in our tree.

4. Discussion

4.1. Molecular confirmation of conspecific male–female pairs

Since most leptocheliids, including *Chondrochelia* and *Neoleptochelia* species, show large sexual dimorphism, morphology-based recognition of conspecific male and female pairs should be confirmed with molecular data. There are to date few examples of molecularly confirmed (by similarity of COI sequences)

conspecific male–female pairs in Leptocheliidae: *Chondrochelia africana* (Larsen & Froufe, 2013), *Chondrochelia mexicana* (Jarquín-González, García-Madrigal & Carrera-Parra, 2015), *Chondrochelia ortizi* (Jarquín-González, 2016), *Hargeria chtumalensis* Jarquín-González & Carrera-Parra, 2019, *Leptochelia forresti*, and *Parakonarus kajii* (Larsen and Froufe, 2013; Leray and Knowlton, 2015; Kakui et al., 2019; Jarquín-González and Carrera-Parra, 2019, 2022). In these six species, the maximum intraspecific K2P distance observed was 4.1% in *C. africana* (Supplementary Material 4).

We determined 541 bp COI sequences from four *Chondrochelia* individuals (two males and one female with five-articulate antennule, and one female with four-articulate antennule). The K2P distances among them were 0–0.4%. Our 658-bp COI sequences from four *Neoleptochelia* individuals (one male and three females) showed 0–0.5% K2P distance. These values are lower than or similar to intraspecific variation previously observed in leptocheliid COI sequences (up to 4.1%; see above) and in *Hexapleomera* Dudich, 1931 (Tanaididae; up to 1.1% p-distance; Wi et al., 2018), *Zeuxo* Templeton, 1840 (Tanaididae; up to 1.5% K2P distance; Okamoto et al., 2020), *Sinelobus* Sieg, 1980 (Tanaididae; up to 1.5% K2P distance; Hirano and Kakui, 2022), *Mesokalliapseudes* Lang, 1956 (Kalliapseudidae; up to 3% p-distance; Drumm and Kreiser, 2012), and *Carpoapseudes* Lang, 1968 (Apseudidae; up to 0.8% p-distance; Kakui et al., 2020). We thus concluded that our specimens comprise one *Chondrochelia* and one *Neoleptochelia* species.

Although it was observed only in living animals, the cephalothorax having an anterodorsal orangish area may help to match females and males of *C. sublitoralis* sp. nov. The short uropods comprised thick endopodal articles, one of diagnostic character states of *Neoleptochelia* (Guțu, 2011), may be used to find females and males of *N. japonica* sp. nov. among the leptocheliid specimens collected from the type locality; but, as we cannot rule out the possibility that there are multiple sympatric *Neoleptochelia* species, it should be used with caution.

4.2. Intraspecific variation in the number of female antennular articles in *C. sublitoralis* sp. nov.

The number of female antennular articles was four or five in *C. sublitoralis* sp. nov. In comparing the proportion of each article in the two types of antennules in *C. sublitoralis* sp. nov., article 3 in the four-articulate antennule seems to correspond to articles 3 and 4 in the five-articulate one (cf. Fig. 3A, B; Fig. 7A, B). Among eight females (BL 2.12–4.63 mm), the four-articulate condition was found in five smaller

females (BL 2.12–4.08 mm) and the five-articulate condition in three larger females (BL 4.27–4.63 mm) (cf. Table 1). These observations suggest that article number increases ontogenetically from four to five in this species, with article 3 in four-articulate antennules dividing to become articles 3 and 4 in five-articulate antennules. Intraspecific variation in the number of female antennular articles has been reported in several other leptocheiliid species, including *Chondrochelia bispinosa* (Guțu, 2011), *Chondrochelia savignyi* (Krøyer, 1842), and *Ektraleptocheilia oculifurcillata* (Guțu, 2016) (Bamber, 2010; Guțu, 2011, 2016). Bamber (2010) regarded *C. savignyi* individuals with five-articulate antennules as “pre-adult males” but presented no information on the presence or absence of genital cones in these individuals. Our individuals with five-articulate antennules lacked genital cones, i.e., they were females. This suggests that the five-segmented antennules previously reported may represent a developmental stage in females.

4.3. Morphological comparison between *C. sublitoralis* sp. nov. and congeners

Females of *Chondrochelia sublitoralis* sp. nov. resemble those of *C. africana*, *C. corsica* (Dollfus, 1898), *C. taitungensis* (Tzeng & Hsueh, 2015), and *C. tanykeraia* (Bamber, 2009 in Bamber et al. [2009]) in having a slender cheliped in which the carpus has parallel dorsal and ventral margins and is two or more times as long as wide. *Chondrochelia sublitoralis* sp. nov. differs from these four species in the combination of seven character states (Table 3): the combined length of article 3 and succeeding article(s) is at least 1.5 times as long as article 2, maxillipedal palp articles 2 and 4 each have one outer seta, the chelipedal merus bears one inner simple seta and the carpus two dorsal simple setae, the carpus of pereopods 4–6 has three distal spiniform setae, and the pleopodal protopod has one inner plumose seta.

Males of *Chondrochelia sublitoralis* sp. nov. differ from those of *C. durbanensis* (Brown, 1957), for which information on females is lacking, in having the following character states (character state of *C. durbanensis* in parentheses): pereopod-1 propodus lacks ventrodistal spiniform setae (one spiniform seta) and the uropodal exopod has one article (two articles).

4.4. Morphological comparison between *N. japonica* sp. nov. and *N. javaensis*

Females of *Neoleptocheilia japonica* sp. nov. differ from those of *N. javaensis* in having the following character states (character state of *N. javaensis* in parentheses): antennal article 1 with a

ventrodistal simple seta (without setae); antennal article 2 with outer simple seta (without seta); maxilliped-palp article 4 with outer seta (without seta); chelipedal carpus with seven dorsal simple setae (with eight); pleopodal protopod with inner plumose seta (without setae). Although details for most appendages were not available for *N. javaensis*, *N. japonica* sp. nov. males differ from those of *N. javaensis* in having the chelipedal carpus with seven dorsal and three ventral simple setae (with five or six dorsal and two ventral setae) and the fixed finger with five ventral simple setae (three ventral setae).

Our male individual of *N. japonica* sp. nov. has a seven-articulate antenna, whereas females have a six-articulate one. In Leptocheliidae, the seven-articulate condition has been reported in males in two species of *Metaleptochelia* (*Metaleptocheliinae*; Guțu, 2016), and in *Alloleptochelia longimana* (Shiino, 1963) and *Alloleptochelia evansi* (Edgar, 2012) (*Leptocheliinae*; Shiino, 1963, fig. 24F; Edgar, 2012, fig. 6-A2). In non-leptocheliid paratanaoideans, this condition is known only in males and females in Heterotanoididae (Bird, 2012). Observation of more males is needed to check whether the seven-articulate antenna is a stable male trait in *Neoleptochelia*, as Guțu (2011) did not indicate the number of male antennal articles in the type species *N. javaensis*, and we observed only one male for *N. japonica* sp. nov.

4.5. Possible function of subchelate pereopods 1–3 bearing a “setulate puff” in male *N. japonica* sp. nov.

Pereopods 1–3 of male *N. japonica* sp. nov. show some uncommon features: their propodi bear a “setulate puff” on the ventro-subdistal margin; and the dactyli bend strongly ventrally subproximally, forming a subchelate condition along with a ventro-subdistal spiniform seta (Fig. 8C–E). To our knowledge, these features have not previously been reported in Leptocheliidae. Since information on the male pereopods is lacking for *N. javaensis*, it is unclear whether these features are stable in the genus. We observed duct-like structures and a pore in the dactylus-unguis of pereopods 1–3 under light microscopy, suggesting these pereopods in male *N. japonica* sp. nov. may function to spin silk for nest building, as in other leptocheliids (cf. Kakui, 2021).

Subchelate pereopods 1–3 in *N. japonica* sp. nov. were observed only in our male specimen, not in females, suggesting that this uncommon feature may be related to reproductive or courtship behaviors. This condition is reminiscent of the male claspers used to hold females in various crustaceans, such as

spinicaudatan clam shrimps and pontellid copepods (e.g., Blades and Youngbluth, 1979; Sigvardt et al., 2017). The behavioral sequence of copulation in Tanaidacea has been observed only in two tube-dwelling tanaidacean species to date, namely the leptocheliid *Heterotanais oerstedii* (Krøyer, 1842) and the tanaidid *Tanais dulongii* (Audouin, 1826). In both species, a male and a female face each other ventrally in a tube during copulation (Bückle Ramírez, 1965; Johnson and Attramadal, 1982); in *T. dulongii*, Johnson and Attramadal (1982) observed that a male occasionally gripped the female chela with its chela. The male chelipeds in *N. japonica* sp. nov. appear to be too long for this purpose in a narrow nest; instead, the subchelate pereopods might be used to hold the female during copulation, and the setulate puff might be a physical sensor for detecting a successful hold on the female. *Neoleptocheilia* females have a long ventrodistal seta on the carpus of pereopods 2 and 3 (Fig. 11B, C), a trait unique to Leptocheiliidae. The male subchelate pereopods might function to grasp these setae.

4.6. Taxonomic importance of dorsal demarcation of the second thoracomere on the carapace in Leptocheiliidae

In the two leptocheliine species we studied, the second thoracomere was demarcated dorsally on the carapace in some females but not in others; the condition was not related to body size (see Table 1; Fig. 7C, D). The presence or absence of the demarcation has been used to distinguish Leptocheiliinae (absent) from the other two subfamilies (present) (Guțu, 2016). Our literature survey revealed, however, that (as in our two species) females with the demarcation have been reported in the leptocheliine *Paraleptocheilia magnispina* Guțu, 2016 (Guțu, 2016, fig. 51a). This suggests that this character may not be valid for distinguishing among subfamilies.

4.7. COI-based phylogeny and taxonomic framework in Leptocheiliidae

In our COI based ML tree, *C. sublitoralis* sp. nov. appeared as sister to Clade A comprising the other leptocheliids. In our dataset, *C. sublitoralis* sp. nov. was the only leptocheliid species collected from 100 m or deeper bottoms; the other leptocheliids were from shallower waters, up to 40 m depth (*P. kajii*; Kakui et al., 2019). This suggests the possibility that there are deep-water clade and shallow-water clade in

Leptocheliidae. To test this hypothesis, sequences from other deep-sea members, such as species in *Mesotanais* Dollfus, 1897, are needed.

The monophyly of *Chondrochelia* was not supported. At least, *C. sublitoralis* sp. nov. would not be congeneric to the other *Chondrochelia* species used in our analysis. We need the data from topotypic specimens of the type species of *Chondrochelia*, i.e., *Chondrochelia distincta* Guțu, 2016 specimens from the Celebes Sea, to conclude which clade corresponds to *Chondrochelia* sensu stricto. That two sequences from specimens identified as *C. dubia* (one from California and another from Florida) did not form a clade indicates the existence of cryptic species in *Chondrochelia* and suggests the importance of use of topotypic specimens in leptocheliid systematics.

Interestingly, we recovered a strongly supported clade, Clade A2, containing *C. mexicana*, *C. ortizi*, and *Hargeria* clade (Clade A2 α). The taxonomic status of *Hargeria* have been discussed for long years; it currently is regarded as a valid genus (Jarquín-González and Carrera-Parra, 2019). Our result may reboot the debates on the validity/definition/species-composition of *Hargeria*.

Guțu (2016) recently provided a comprehensive taxonomic revision of Leptocheliidae. Our tree suggests, however, that it needs further revision with an integrative morphological and molecular approach; Clade A3, comprising leptocheliine and konariine sequences, requires the modification of even the subfamily-level taxonomic framework. The molecular data currently available are limited; our aligned COI data set contains only 405 positions and six of 33 leptocheliid genera. Further studies with broader taxon sampling and additional molecular markers are badly needed. Bamber (2010) emphasized the importance of species distinction based on females in Leptocheliidae; on the other hand, diverse male cheliped shapes bring us a lot of hints to construct leptocheliid taxonomic framework. Given the situation, we should also accelerate to accumulate sequences from conspecific male–female pairs.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could appear to have influenced the work reported in this paper.

Data availability

Regarding data availability, the sampling locality, sampling date, condition of each specimen, museum where the specimens were deposited, and deposition numbers are included in the “Material and methods” and “Type material” sections in the manuscript.

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Appendix A. Supplementary Materials

Supplementary data of this article can be found online at <https://doi.org/10.1016/xxxxxxxxxxxxxxxxxxxxx>.

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Figure legends

Fig. 1 *Chondrochelia sublitoralis* sp. nov., living paratype female (ICHUM6351) (**A, B**) and allotype male (**C, D**) in dorsal (**A, C**) and lateral (**B, D**) views. Scale bar: 1 mm

Fig. 2 *Chondrochelia sublitoralis* sp. nov., holotype female (**A–C**) and allotype male (**D–F**); **A, D** body, dorsal view; **B, E** body, lateral view; **C, F** posterior region of body, dorsal view. Scale bars: 1 mm

Fig. 3 Right antennules of *Chondrochelia sublitoralis* sp. nov.; **A** holotype female, five-articulate state; **B** paratype female (ICHUM6345), four-articulate state; **C** allotype male. Scale bars: 0.1 mm

Fig. 4 *Chondrochelia sublitoralis* sp. nov., holotype female; **A** right antenna; **B** labrum; **C, D** left and right mandibles; **E** labium; **F, G** left and right maxillules; **H** maxilliped (setae on palp articles 3 and 4 omitted); **I** same, left palp articles 3 and 4 (inner setae on palp article 2 omitted); **J** same, endite; **K** right epignath; **L** right cheliped, outer view; **M, N** same, distal portion of chela, outer (**M**) and inner (**N**) views. Scale bars: 0.1 mm

Fig. 5 *Chondrochelia sublitoralis* sp. nov., holotype female; **A–F** right pereopods 1–6; **G** right pleopod 1 (most setal ornamentation and most outer plumose setae on endopod omitted); **H** same, endopod (most setal ornamentation omitted); **I** right uropod. Scale bars: 0.1 mm

Fig. 6 *Chondrochelia sublitoralis* sp. nov., allotype male; **A** right antenna; **B** mouthparts; **C** right cheliped, outer view; **D** same (basis not illustrated), inner view; **E–J** right pereopods 1–6; **K** right pleopod 1 (most setal ornamentation and outer plumose setae on endopod omitted); **L** same, endopod (most setal ornamentation omitted); **M** right uropod. Scale bars: 0.1 mm

Fig. 7 Antennules (**A, B**) and carapaces (**C, D**) of *Chondrochelia sublitoralis* sp. nov., females; **A** five-articulate state; **B** four-articulate state; **C, D** carapaces with (**C**) and without (**D**) dorsal demarcation. Scale bars: 0.5 mm

Fig. 8 *Neoleptocheilia japonica* sp. nov., allotype male; **A, B** living individual in dorsal (**A**) and lateral (**B**) views; **C, D** distal portion of right pereopod 2; **E** distal portion of right pereopod 3; arrowheads, setulate puff; arrow, point where dactylus is strongly bent ventrally. Scale bars: 1 mm (**A, B**), 0.1 mm (**C, E**), and 0.05 mm (**D**)

Fig. 9 *Neoleptocheilia japonica* sp. nov.; holotype female (**A–C**) and allotype male (**D–F**); **A, D** body, dorsal view; **B, E** body, lateral view; **C, F** posterior region of body, dorsal view. *p*3, 4, pereonites 3 and 4. Scale bars: 1 mm (**A, B, D, E**) and 0.5 mm (**C, F**)

Fig. 10 *Neoleptocheilia japonica* sp. nov., holotype female; **A** right antennule; **B** right antenna; **C** labrum, **D, E** left and right mandibles; **F** labium; **G, H** left and right maxillules; **I** maxilliped, dorsal view (setae on palp and basis omitted); **J** same, palp and distal portion of bases, ventral view; **K** same, endite, dorsal view; **L** epignath; **M** right cheliped, outer view; **N, O** same, distal portion of chela, outer (**N**) and inner (**O**) views. Scale bars: 0.1 mm

Fig. 11 *Neoleptocheilia japonica* sp. nov., holotype female; **A** left pereopod 1; **B–F** right pereopods 2–6; **G** right pleopod 1 (most setal ornamentation and most outer plumose setae on endopod omitted); **H** same, endopod (most setal ornamentation omitted); **I** right uropod. Scale bars: 0.1 mm

Fig. 12 *Neoleptocheilia japonica* sp. nov., allotype male; **A** right antennule (most aesthetascs omitted); **B** right antenna; **C** maxillipeds; **D** right cheliped, outer view; **E** same, chela, inner view; **F–H, J, K** right pereopods 1–3, 5, 6; **I** left pereopod 4; **L**, right pleopod 2 (most setal ornamentation and most outer plumose setae on endopod omitted); **M** same, endopod (most setal ornamentation omitted); **N** right uropod. Scale bars: 0.5 mm (**A, D, E**) and 0.1 mm (all others)

Fig. 13 ML tree for leptocheliid tanaidaceans based on COI (405 positions); numbers near nodes are SH-aLRT (left of slash) and ultrafast bootstrap (UFBoot; right of slash) values in percent; only values of SH-aLRT $\geq 70\%$ and UFBoot $\geq 80\%$ are shown; *, unavailable name (see Jarquín-González et al., 2015). Scale at bottom indicates branch length in substitutions per site

Captions for Supplementary Materials

Supplementary Material 1. List of species included in the molecular phylogenetic analysis, including their INSD or BOLD accession numbers

Supplementary Material 2. Aligned COI sequences used for the maximum-likelihood analysis, trimmed in MEGA7 to the shortest length among the sequences

Supplementary Material 3. Variation in characters among dissected specimens of *Chondrochelia sublitoralis* sp. nov.

Supplementary Material 4. K2P distances (in percent) among COI sequences from leptocheliid species (405 positions).

Supplementary Material 5. Variation in characters among dissected specimens of *Neoleptochelia japonica* sp. nov.

Table 1 Collection information for type material of *Chondrochelia sublitoralis* sp. nov.; *, fully developed marsupium observed; females with five-articulate antennules are in bold font.

ICHUM	INSD	Sex, status, BL/CW (mm)	Station (Geographical coordinates; depth; date)
6343	-	Female *, holotype, 4.45/0.56	Stn 7 (34:10.13, 136:44.56; 130.9–132 m; 9 Nov. 2017)
6344	LC655988	Male, allotype, 3.91/0.63	Stn d-4 (34:09.228, 136:49.751; 148–151 m; 30 Oct. 2014)
6345	LC655989	Female, paratype, 3.43/0.42	Stn d-4
6346	LC655990	Female *, paratype, 4.27/0.55	Stn 5 (34:10, 136:44; 131 m; 26 Nov. 2019)
6347	LC655991	Male, paratype, 4.23/0.73	Stn d-4
6348	-	Female, paratype, 2.98/0.43	Stn d-6 (34:09.30, 136:50.37; 179–185 m; 30 Oct. 2014)
6349	-	Female, paratype, 3.00/0.42	Stn d-6
6350	-	Female, paratype, 2.10/0.30	Stn 8 (34:11.232, 136:43.145; 113 m; 9 Nov. 2017)
6351	-	Female, paratype, 4.08/0.64	Stn d-4
6352	-	Female , paratype, 4.63/0.59	Stn d-4

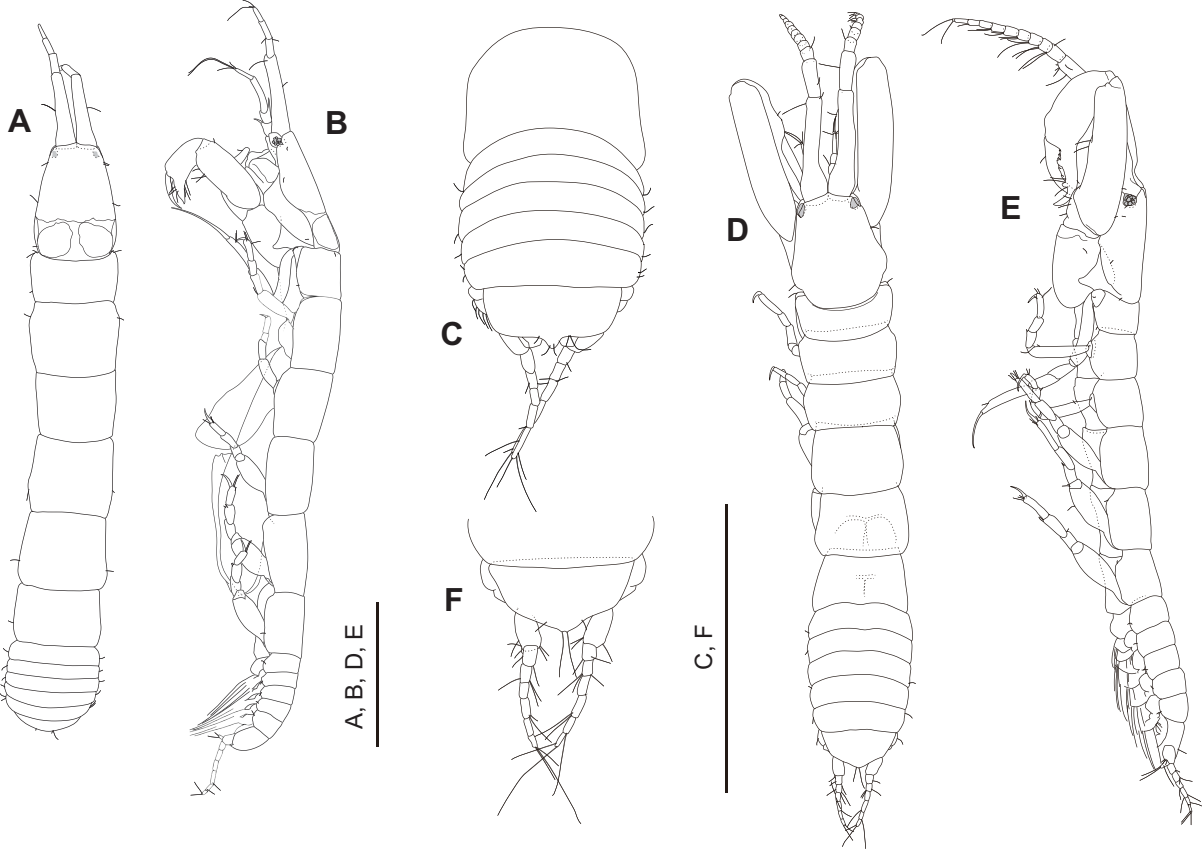
Table 2. Collection information for type material of *Neoleptochelia japonica* sp. nov.; *, fully developed marsupium observed.

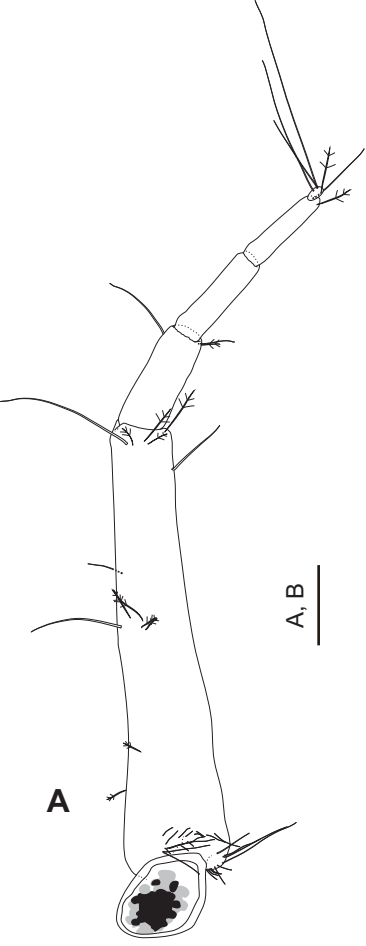
ICHUM	INSD	Sex, status, BL/CW (mm)	Date; collector
8468	LC745706	Female, holotype, 3.60/0.52	2 Aug. 2008; Keiichi Kakui
8469	LC745707	Male, allotype, 2.88/0.56	2 Apr. 2021; Aoi Tsuyuki
8470	LC745708	Female, paratype, 3.66/0.58	1 Apr. 2021; Aoi Tsuyuki
8471	LC745709	Female, paratype, 3.28/0.45	2 Aug. 2008; Keiichi Kakui
8472	-	Female, paratype (intact), 3.14/0.53	1 Apr. 2021; Aoi Tsuyuki
8473	-	Female*, paratype (intact), 3.55/0.54	2 Aug. 2008; Keiichi Kakui

Table 3. Comparison of selected female characters for five *Chondrochelia* species having a slender cheliped (carpus with parallel dorsal and ventral margins, and length/width greater than 2.0); *, only when antennules have five articles.

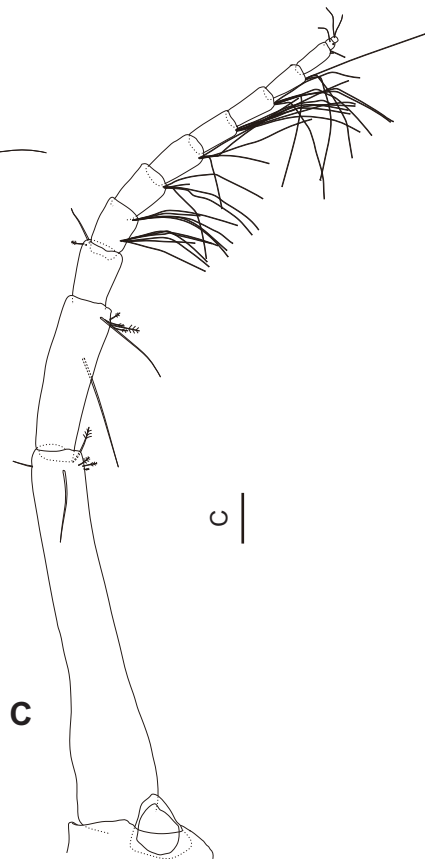
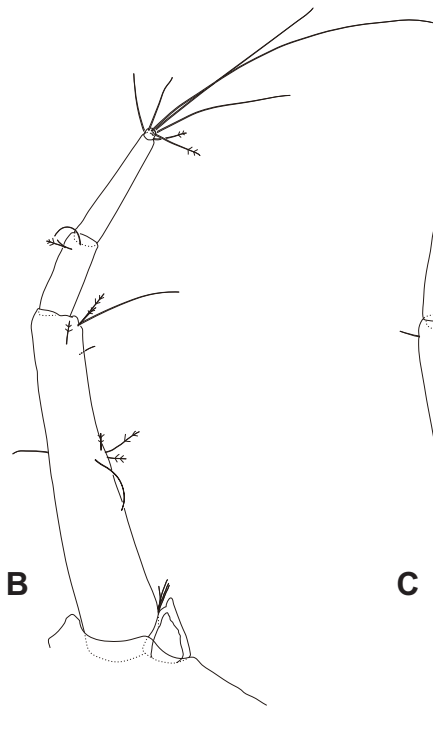
	<i>C. sublitoralis</i> sp. nov.	<i>C. africana</i>	<i>C. corsica</i>	<i>C. taitungensis</i>	<i>C. tanykeraia</i>
Antennule					
Relative length of articles 3+4(+5*) to article 2	1.56–1.82	1.08	1.1	0.83	1.31
Maxillipedal palp					
Outer simple seta on article 2	1	1	1	0	1
Outer simple seta on article 4	1	1	1	0	1
Cheliped					
Inner simple setae on merus	1	0	0	0	0
Dorsal simple setae on carpus	2	2	2	3	3
Pereopods 4–6					
Distal spiniform setae on carpus	3	3	2	3	3
Pleopodal protopod					
Inner plumose setae	1	0	0	1	1
Reference	This study	Larsen and Froufe (2013)	Guğu (2011)	Tzeng and Hsueh (2015)	Lubinevsky et al. (2022)

A**B****C****D**

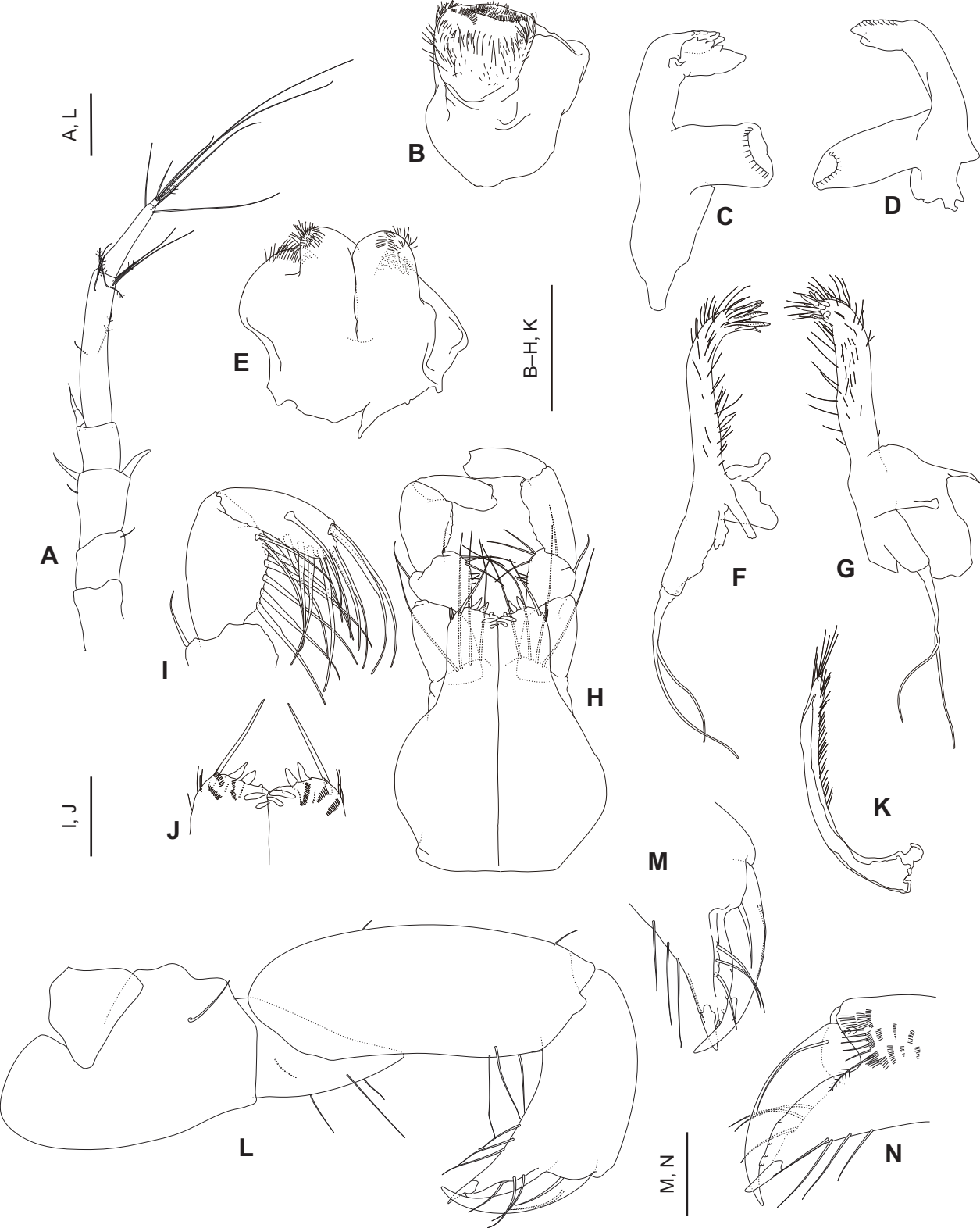


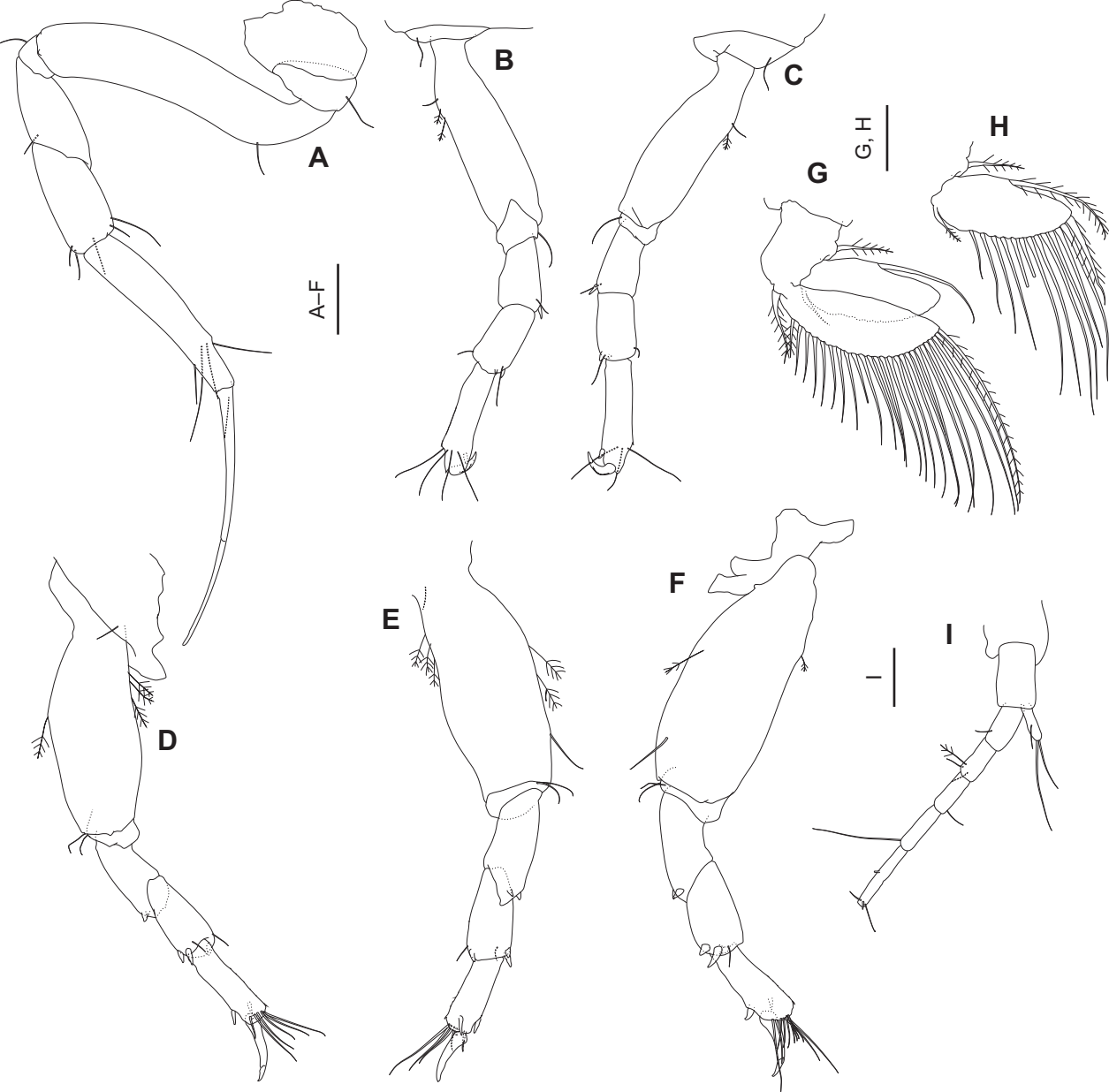


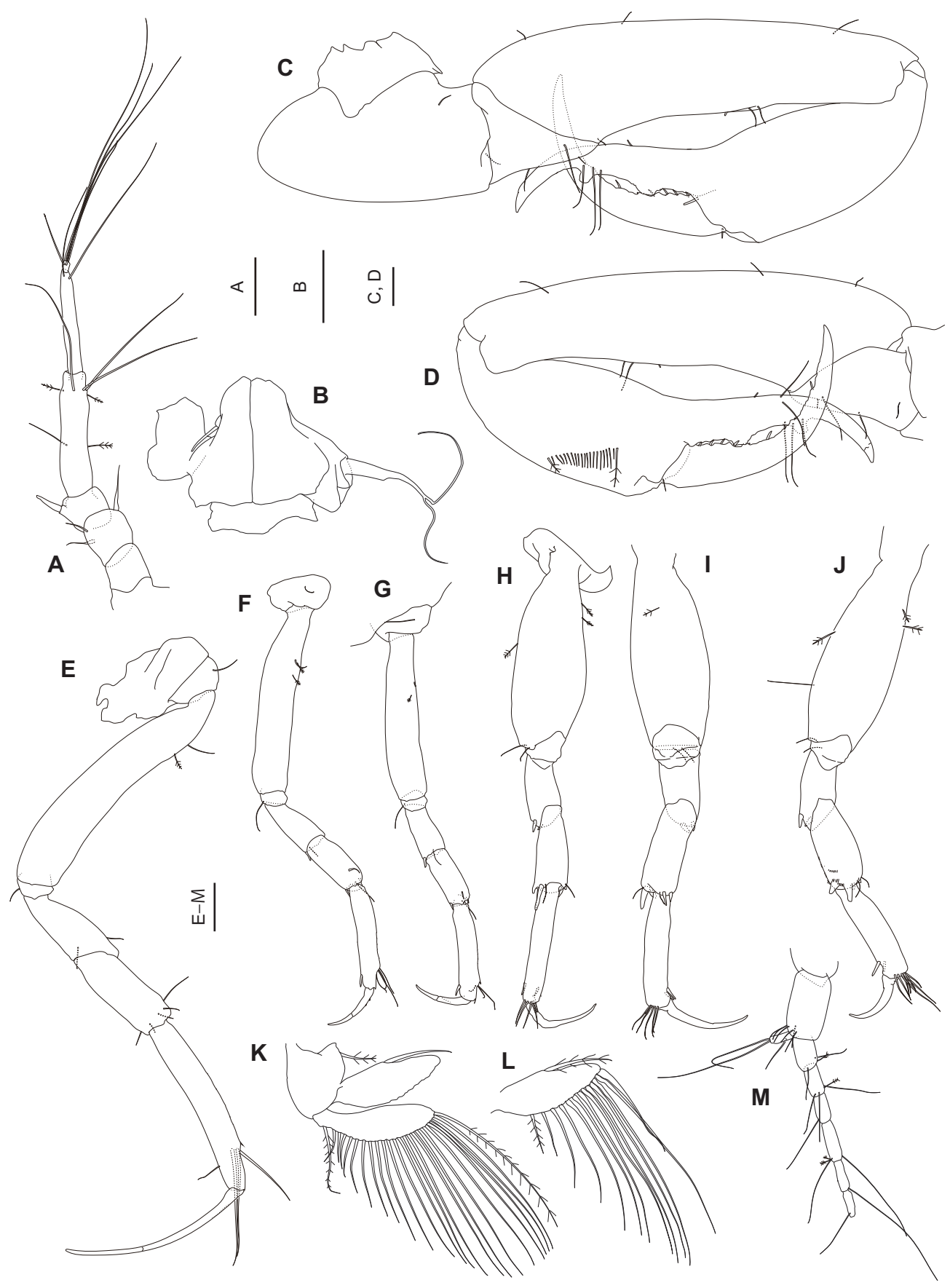
A, B

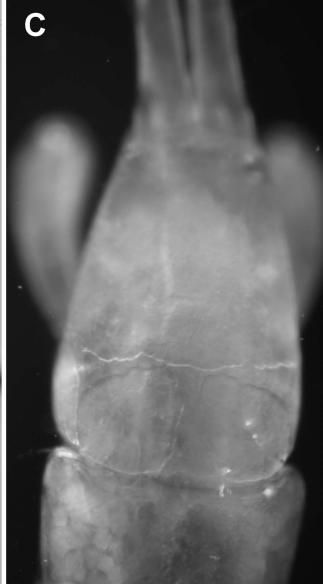


C



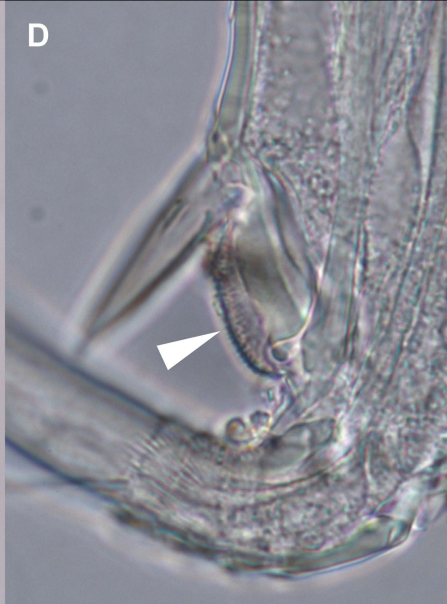






A**B**

A, B

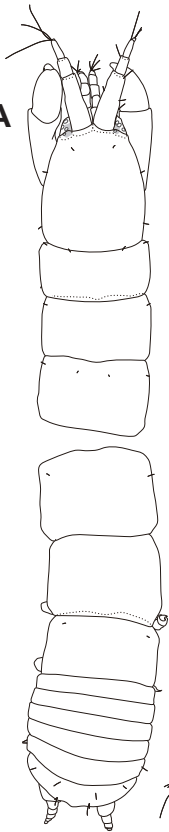
**C****D****E**

C-E

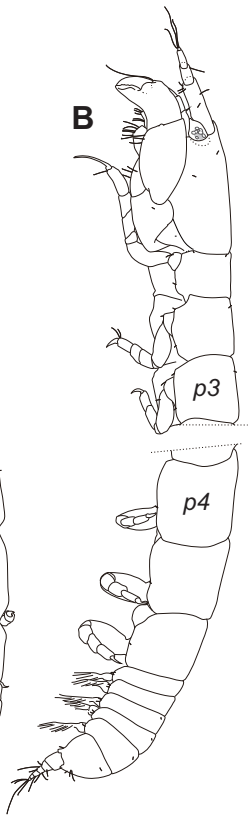


A, B, D, E

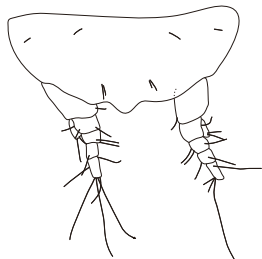
A



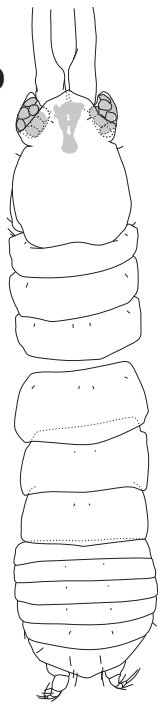
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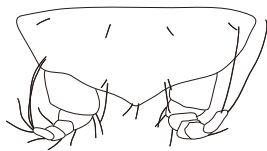
C



D



F



C, F

E





