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A new genus and two new species of monstrilloid copepods (Copepoda: Monstrillidae): integrating morphological, molecular phylogenetic, and ecological evidence

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ABSTRACT

Caromiobenella **gen. nov.**, represented by males of two new species of monstrilloid copepods (Copepoda: Monstrillidae), *Caromiobenella castorea* **sp. nov.** (type species) and *C. polluxea* **sp. nov.**, is established based on morphological, molecular, and ecological evidence. The genus is characterized by the following new combination of morphological characters: 1) relatively short cephalothorax, 2) inconspicuous oral papilla located anteriorly, 3) last antennular segment modified into serrate ridges on the inner distal margin with a general absence of branched setae, 4) modified spinous element $2d_2$ (elongated, biplumose or both), and 5) two pairs of prominent, crater-like, concave depressions on the anterior dorsum of the cephalothorax. These characters are also shared by several other nominal species hitherto assigned to *Monstrilla* Dana, 1849. Molecular analyses of mitochondrial cytochrome *c* oxidase subunit I (mtCOI) genes and nuclear 28S ribosomal RNA (28S rRNA) genes indicate both that these species are distinct from each other and that, as a group, they are isolated from other known monstrilloid genera. Furthermore, previous studies have shown that one of these species differs from other species of *Monstrilla* in utilizing a different group of invertebrate hosts, namely gastropods. Based on this integrated data, the new genus comprises six additional species: *C. helgolandica* (Claus, 1863) comb. nov., *C. sericornis* (Sars, 1921) comb. nov., *C. arctica* (Davis & Green, 1974) comb. nov., *C. hamatapex* (Grygier & Ohtsuka, 1995) comb. nov., *C. pygmaea* (Suárez-Morales, 2000) comb. nov., and *C. patagonica* (Suárez-Morales, Ramírez & Derisio, 2008) comb. nov.

Key Words: Korea, Mollusca, parasitism, plankton, Polychaeta, taxonomy

INTRODUCTION

The order Monstrilloida Sars, 1901 is distinguished from other copepod groups by the life cycle of its members and a set of intriguing morphological characters. Monstrilloids have a protelean life history that includes an endoparasitic juvenile phase and a planktonic adult phase. The infective nauplii hatching from eggs are free-living, but soon infect hosts including polychaetes, prosobranch molluscs, mussels, and sponges (Caullery & Mesnil, 1914; Pelseneer, 1914; Huys & Boxshall, 1991; Huys *et al.*, 2007; Suárez-Morales *et al.*, 2010; Suárez-Morales *et al.*, 2014). Following infection, an encapsulated endoparasitic stage ensues. Details of molt stages are unclear, but the larva appears to at least pass through several copepodite instars (Malaquin, 1901; Raibaut, 1985; Suárez-Morales *et al.*, 2014). The male and female pre-adults, presumably at the last copepodite stage, emerge from the hosts, undergo the final molt to the adult stage, and adopt a planktonic mode of life. The adults have antennules and swimming legs but lack antennae and all feeding appendages (Malaquin, 1901; Raibaut, 1985; Huys & Boxshall, 1991).

The order currently comprises more than 130 nominal species worldwide in five valid genera: *Monstrilla* Dana, 1849, *Cymbasoma* Thompson, 1888, *Monstrillopsis* Sars, 1921, *Maemonstrilla* Grygier & Ohtsuka, 2008, and *Australomonstrillopsis* Suárez-Morales & McKinnon, 2014 (Razouls *et al.*, 2005–2017; Suárez-Morales, 2011, 2015). Six species of monstrilloids have been reported from Korea: *Monstrilla grandis* Giesbrecht, 1891, *M. hamatapex* Grygier & Ohtsuka, 1995, *M. ilhoii* Lee & Chang, 2016, *Cymbasoma striifrons* Chang, 2012, *Monstrillopsis longilobata* Lee, Kim & Chang, 2016, and *M. coreensis* Lee, Kim & Chang, 2016. These reports from

Korea were mainly based on morphological and distributional data (Chang, 2012, 2014; Lee & Chang, 2016; Lee *et al.*, 2016).

We describe two new species of monstrilloids from Korea that are distinguished from most other members of the order by a defined set of morphological and molecular features. We consider this combination of characters, which is also shared by several species hitherto assigned to *Monstrilla*, to be diagnostic at the generic level. Because of this morphological similarity, significant genetic divergence from other monstrilloids, and a particular host specificity involving gastropods, we propose the establishment of a new genus for the two new species and the transfer of several previously known species of *Monstrilla* to the new genus.

MATERIAL AND METHODS

Sample collection and treatment for morphological analysis

The materials were collected using a hand-made light trap: a 400 mm long PVC pipe with a mouth diameter of 100 mm, a cone-shaped entry funnel, and the other end completely closed with a cap. A light-emitting diode (LED) flashlight of 110 lumens was used as the light source (KBL-T1301, KOVEA, Inchon, Korea). The trap was deployed on rocky bottoms or floated less than 50 cm above muddy bottoms.

The trap was emptied through a sieve of 63 μm mesh after each deployment. The material on the sieve, including copepods, was immediately washed several times with 99.5% ethanol. Samples were fixed in 99.5% ethanol after washing and the fixative was changed to freshly prepared 99.5% ethanol upon arrival at the laboratory. All samples were stored in a 4 °C refrigerator. Monstrilloids were sorted out under a SMZ645 stereomicroscope (Nikon, Tokyo, Japan).

The monstrilloid specimens were examined as whole mounts on depression slides. Because some of the specimens had become distorted as a result of the ethanol fixation, 0.25–0.5% sodium phosphate tribasic dodecahydrate ($Na_3PO_4{\cdot}12H_2O$) solution was used as a mounting medium to restore the original shape (Van Cleave & Ross, 1947). Drawings were made using an Eclipse 80i compound microscope (Nikon) with differential interference contrast optics and a drawing tube. After the observation of habitus, the specimens were dissected and each part was mounted on a slide glass with lactophenol for further microscopic observation. All measurements were done using AxioVision LE64 software (AxioVs40x64v 4.9.1.0; Carl Zeiss, Oberkochen, Germany).

For scanning electron microscopy (SEM), adult specimens were dehydrated with absolute ethanol for 15 min. The usual procedure of using a graded ethanol series was skipped because the specimens were initially stored in 99.5% ethanol. For sample drying, hexamethyldisilazane, HMDS, $(CH_3)_3SiNHSi(CH_3)_3$, was used (Braet *et al.*, 1997; Shively & Miller, 2009). Specimens dehydrated using ethanol were immersed in 1–2 ml HMDS in a 24-well plate, and the plate placed in a fume hood until the HMDS had totally evaporated. Dried specimens were mounted on aluminum SEM stubs. Observations were carried out with an S-3000N scanning electron microscope (Hitachi, Tokyo, Japan) operating at an accelerating voltage of 20.0 kV.

Description of morphological characters

Total body length was measured from the anteriormost part of the cephalothorax to the posterior margin of the anal somite, thus excluding the caudal rami. The length of the caudal ramus was measured along the line connecting the inner proximal articulation of the ramus to the most distal tip of the ramus between caudal setae III and IV; the width was measured perpendicular to the length at the level of the insertion of caudal seta I.

The terms proposed by Grygier & Ohtsuka (1995) were mainly used to describe the body segments and the antennular setation patterns. Because the terminology of the antennules they used was proposed exclusively on the basis of female monstrilloids, a modification of the method originally devised for the antennules of males (Huys *et al.*, 2007) was used as well. The concepts of "A–E" for dichotomously branched setae ("highly branched b-setae" *sensu* Grygier & Ohtsuka, 1995) was expanded to include the unbranched setae as well but also restricted to "well-developed setae" that are relatively thick and long. The unmodified spinous setal elements 1, 2, and 5 ("$6_{1, 2}$ and 5" *sensu* Grygier & Ohtsuka, 1995) are here termed "spines" owing to their rigidity, and progressively marked as "$6_{1–3}$" from distal to proximal. Unmodified and flexible setal elements 3 and 4 ("simple b-setae" *sensu* Grygier & Ohtsuka, 1995) are labelled using lower-case letters from distal to proximal. Setal element 6 ("Vv" *sensu* Grygier & Ohtsuka, 1995) is referred to as "Vv" because it has proven to be a relatively stable feature among various species of monstrilloids. The proximalmost minute spine on the inner margin of the fifth antennular segment is labelled "7" as in Huys *et al.* (2007), and the distalmost minute spine on the fourth antennular segment is marked as "$4d_a$". A new term, "pseudoral cone" is introduced for a cone-shaped protuberance that is located anterior to the oral papilla.

Preparations for molecular analysis

Chelex® 100 chelating resin (molecular biology grade, 200–400 mesh, sodium form; Bio-Rad, Hercules, CA, USA) was used to extract genomic DNA. The general procedures of the extraction were as previously described (Estoup *et al.*, 1996; Casquet *et al.*, 2012) with some modification of the total volume mainly due to the small size of the specimens.

Two genes, mtCOI and 28S rRNA, were amplified using the AccuPower® HotStart PCR PreMix kit (Bioneer, Daejeon, Korea), and thermal cycling was performed using Matercycler® (Eppendorf, Hamburg, Germany). For mtCOI gene amplification, LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') primers (Folmer *et al.*, 1994) were used. 20 μl of total reaction volume per tube was achieved by adding 16 μl of distilled water, 2 μl of DNA template, and 1 μl each of the forward and reverse primers. The thermocycling profile was 5 min at 94 °C for initial denaturation, 1 min at 94 °C for denaturation, 1 min at 46°C for annealing, 1 min at 72 °C for extension, and 7 min at 72 °C for final extension. The thermal cycle from denaturation to extension was repeated 35 times. For 28S rRNA gene amplification, 28S-F1a (5'-GCGGAGGAAAAGAAACTAAC-3') and 28S-R1a (5'-GCATAGTTTCACCATCTTTCGGG-3') primers (Ortman, 2008) were used. 20 μl of total reaction volume per tube was achieved by adding 17 μl of distilled water, 1 μl of DNA template, and 1 μl each of the forward and reverse primers. The thermocycling profile was 5 min at 94 °C for initial denaturation, 1 min at 94 °C for denaturation, 1 min at 50 °C for annealing, 1 min at 72 °C for extension, and 7 min at 72 °C for final extension. The thermal cycle from denaturation to extension was repeated 30 times. PCR products were run on a 1% Tris acetate-EDTA agarose gel for 20 min at a voltage of 100 V with 100 bp DNA ladder (Bioneer). The PCR products with positive results were sent to Macrogen (Seoul, Korea) for purification and DNA sequencing. Sequencing reactions were performed in a DNA Engine Tetrad 2 Peltier Thermal Cycler (Bio-Rad) using the ABI BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) following the protocols supplied by the manufacturer. Single-pass sequencing was performed on each template using the corresponding primer. The fluorescent-labeled fragments were purified by the method recommended by the manufacturer in order to remove the unincorporated terminators and dNTPs. For electrophoresis, the samples were injected into an ABI 3730xl DNA Analyzer (Applied Biosystems). The sequencing chromatograms were read using FinchTV ver 1.4.0 software.

Inspected sequences were taken to MEGA7 (ver 7.0.21) and then both the forward and reverse primer sites were excluded. The forward and reverse strands were aligned by ClustalW embedded in MEGA7.

Forty-one specimens of Korean monstrilloids comprising five genera and nine species, including two species of the new genus (see Supplementary material Table S1), were used to determine mtCOI and 28S rRNA sequences. Additional sequences of mtCOI genes from five monstrilloids (two *Monstrilla hamatapex* Grygier & Ohtsuka, 1995 [= *Caromiobenella hamatapex* comb. nov.], two *Cymbasoma reticulatum* (Giesbrecht, 1893), and one *Cymbasoma* sp.), and three outgroup taxa (*Calanus sinicus* Brodsky, 1965 (Calanoida), *Tigriopus japonicus* Mori, 1938 (Harpacticoida), and *Lepeophtheirus salmonis* (Krøyer, 1837) (Siphonostomatoida)) were retrieved from GenBank; additional sequences of 28S rRNA from the same three monstrilloid species and the same three outgroup taxa were also retrieved from GenBank (accession numbers in Table 1).

Phylogenetic analyses using Maximum Likelihood (ML) and Bayesian Inference (BI) were carried out. The best-fit model for ML analysis was sought using jModelTest 2.1.10 v20160303 (Darriba *et al.*, 2012). ML analyses for both mtCOI and 28S rRNA data sets were conducted using MEGA7 ver. 7.0.21 (Kumar *et al.*, 2016) under the General Time Reversible model with a proportion of invariable sites and a gamma-shaped distribution of rates (GTR+I+Γ) based on the results of best-fit model selection. One thousand bootstrapping replicates were generated for the reconstructions of the phylogenetic tree. A BI tree for each gene data set was constructed with MrBayes v3.2.6 x64 (Ronquist *et al.*, 2012) under the same model condition as the ML analyses with following likelihood parameters: nst = 6, rates = invgamma, and ngammacat = 4. Markov Chain Monte Carlo (MCMC) was run with following parameters: ngen = 5,000,000, nchain = 4, samplefreq = 100, printfreq = 500, and diagnfreq = 1000. The BI trees were constructed with the "sumt" command with burninFrac = 0.25, thus the first 25% generations were discarded. The ML and BI trees were visualized using FigTree v1.4.3.

SYSTEMATICS

Order Monstrilloida Sars, 1901
Family Monstrillidae Dana, 1849
Genus *Caromiobenella* gen. nov.

Diagnosis (male): Cephalothorax relatively short, not exceeding half of total body length. Anterior margin generally round, lacking 2 usual short sensilla. Body segmented, consisting of 9 parts: cephalothorax with incorporated first pedigerous somite, free pedigers 1–3, first urosomal somite, genital somite, postgenital somite, penultimate somite, anal somite. Antennules with 5 segments and modified fifth segment: inner distal margin formed into several comb-like rows of spinules. Oral papilla on anterior ventral surface of cephalothorax, low, somewhat inconspicuous. Genital apparatus consisting of robust genital shaft plus 2 short, subtriangular genital lappets diverging from distal posterior end of shaft. Branched setae of distal antennular segment replaced by unbranched, well-developed simple setae in most species (branched setae reportedly in *Caromiobenella arctica* comb. nov.). Spine $2d_2$ on second segment of antennules elongated, biserially plumose, or both depending on species. Distal end of genital shaft with deep notch or medial protrusion, and 5 or 6 caudal setae on each caudal ramus, depending on species. Two pairs of prominent crater-like depressions on anterior dorsum of cephalothorax. Posterior dorsum of cephalothorax (i.e. incorporated first pedigerous somite) with 2 longitudinal rows of 4 pores each, arranged in pairs across midline.

Species included: *Caromiobenella castorea* **sp. nov.** (type species), *C. polluxea* **sp. nov.**, *C. helgolandica* (Claus, 1863) comb. nov., *C. serricornis* (Sars, 1921) comb. nov., *C. arctica* (Davis & Green, 1974) comb. nov., *C. hamatapex* (Grygier & Ohtsuka, 1995) comb. nov., *C. pygmaea* (Suárez-Morales, 2000) comb. nov., *C. patagonica* (Suárez-Morales, Ramírez & Derisio, 2008) comb. nov., and *Caromiobenella* sp. [= *Monstrilla* sp. in Huys & Boxshall (1991)].

Etymology: Generic name derived from Italian song *Caro mio ben* by the addition of the feminine diminutive suffix *ella*.

Nomenclatural statement: A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:0C81F82A-DF17-462D-A876-3E82BFD89FCE.

Caromiobenella castorea sp. nov.
(Figs. 1–5)

Type material: Male holotype (NIBRIV0000324922): dissected on six slides and used for drawings. Seven paratypes undissected: four of each vial contain a single specimen (NIBRIV0000324923–0000324926), a vial contains three specimens (NIBRIV0000808113); the type series were deposited in the National Institute of Biological Resources (NIBR), Incheon, Korea. Three additional paratypes were used for SEM and deposited in Chonnam National University, Yeosu, Korea. Three non-type specimens were sacrificed for molecular analysis.

Type locality: Baegya-ri (34°36′45.4″N, 127°39′10.4″E), Hwajeong-myeon, Yeosu-si, Jeollanam-do, Korea. English equivalents of political divisions in Korea: ri = village; myeon = township; si = city; do = province.

Material examined: Specimens were collected by using a light trap on 10 November 2014, from 17:40 to 21:00 h alongside a seawall

Table 1. Eight additional gene sequence data of three monstrilloids and three outgroup copepod taxa from GenBank with accession numbers.

Order	Species	GenBank Accession Number	
		mtCOI	28S rRNA
Monstrilloida	*Caromiobenella hamatapex* comb. nov.*	KR048992	-
	Caromiobenella hamatapex comb. nov.*	KR048994	KR048920
	Cymbasoma reticulatum	KR048990	KR048917
	Cymbasoma reticulatum	KR048991	-
	Cymbasoma sp.	KR048989	KR048918
Siphonostomatoida	*Lepeophtheirus salmonis*	KR049052	KR048867
Harpacticoida	*Tigriopus japonicus*	KR049010	EU054307
Calanoida	*Calanus sinicus*	KR048947	KR048902

**Monstrilla hamatapex* in Grygier & Ohtsuka, 1995

at the type locality. The depth at the collecting site was less than 2 m and the water temperature was 14.0 °C.

Diagnosis (male): Total body length 0.91–1.14 mm (mean = 0.99; N = 8). Ratio of lengths of cephalothorax, metasome, urosome 36.2 (34.4–37.7):40.4 (38.0–43.6):23.4 (19.0–26.0) in lateral view. Oral papilla low, set ventrally at 27% (23.5–31.1) of distance from anterior end of cephalothorax. Length of antennules in relation to total body length 31.9% (29.7–35.5), ratio of antennular segment length from proximal to distal 18.2 (15.9–20.3):18.5 (14.8–21.6):16.5 (11.6–19.8):22.7 (19.8–28.0):24.1 (21.9–29.6). Spine 6_1 on distal antennular segment pinnate; robust, rough spines 6_2, 6_3 plumose with fine setules. Branched setae absent, replaced by unbranched simple setae. Spinous elements on first three antennular segments pinnate. Outer proximal margin of third antennular segment with protrusion plus distal groove. Outermost two setae on third exopodal segments of all legs with serrations along outer margin. Genital shaft robust, 0.06 mm (0.047–0.063), long, with 2 short, subtriangular lappets separated by deep notch; inner side of each lappet denticulate. Genital opercular openings covered by pair of pinnate, distally bifid opercular flaps at distal end of genital shaft. Each caudal ramus with 6 setae; dorsal apical seta VI conspicuously shorter than others.

Description of male holotype: Total body length 1.01 mm in dorsal view, 1.06 mm in lateral view. Body segmented, consisting of 9 parts: cephalothorax incorporating first pedigerous somite, free somites 1–3, first urosomal somite, genital somite, postgenital somite, penultimate somite, and anal somite. Length of somites as percent of total body length: 36:15:15:11:6:5:4:4:4 in dorsal view; 37:17:15:11:6:5:4:3:2 in lateral view.

Cephalothorax incorporating first pediger rather short, 0.36 mm long in dorsal view, 0.39 mm in lateral view, generally bullet-shaped in dorsal view with convex anterior margin (Fig. 1A). Length 1.5 times greater than maximal width, lateral contours slightly broadening to anterior one-third length then gradually tapering to midlength, narrowest (0.19 mm) at 52.9% of way from anterior end. Width of incorporated first pediger 0.24 mm near posterior margin (at 92.4% of way from anterior end), this being widest part of cephalothorax. Anterior dorsal part of cephalothorax with pores of variable shapes and sizes. Most pores round, but some fused with adjacent ones thus irregular in form. Pores generally located symmetrically. Two pairs of prominent concave depressions posterior to porose region (Fig. 1A, B), with anterior pair closer to central body axis than posterior pair.

Tergite of incorporated first pediger with 5 pairs of pit-setae *sensu* Grygier & Ohtsuka (1995) (Fig. 1A, B): one pair (no. 1) situated dorsally, 4 pairs laterally (nos. 2–5). Pit-seta groups of left and right sides separated by 2 longitudinal rows of at least 4 pores each, these arranged in pairs across midline (Fig. 1A) with some variation (e.g., 4 pores on right side, only 3 on left side in holotype). These pores generally larger than others, defined by prominent rims. Ventral side of cephalothorax with 3 pairs of scars (Figs. 1B, 2A): 2 prominent pairs posterior to antennular bases, relatively inconspicuous pair more laterally at one-third length of cephalothorax. Oral papilla ventral, low, situated between posterior scar pair, with apical pore (Figs. 1B, 2A). Basal part of oral papilla with at least 2 pores. Region between antennular bases slightly bulging, ornamented with fine wrinkles.

Two lateral, one ventral eyes present within anterior one-fourth of cephalothorax, moderately developed, pigmented (Fig. 1A, B). Ventral eye positioned slightly anterior to lateral eye cups. Lateral eyes round, 0.05 mm in diameter, 0.03 mm apart across midline. Ventral cup round in dorsal view, but oval-shaped, compressed vertically in lateral view. Ventral cup slightly smaller in diameter (0.04 mm) than lateral ones in dorsal view.

Antennules clearly 5-segmented, generally directed straight forward, but bent slightly upward at joint between third, fourth segments (Figs. 1A, B, 3A). Geniculation present between fourth, fifth segments, with fifth segment bent almost 180° to inner side (Fig. 2B). Length 0.38 mm, 35.5% of total body length, 95.5% of cephalothorax length. Length ratio of 5 segments 18.0:18.2:16.4:24.6:22.8. First antennular segment armed with pinnate spine 1 on inner distal part, arising slightly dorsally. Second antennular segment armed with 6 setal elements: 4 robust, densely pinnate spines ($2v_{1–3}$, $2d_1$); biserially plumose IId seta developed in typical strap-like form; elongated spine $2d_2$, biserially plumose with fine setules, reaching proximal margin of fourth antennular segment. Third antennular segment armed with 3 setal elements: pinnate spine 3 on inner distal side and 2 biserially plumose strap-like setae IIId, IIIv located more proximally; IIId short, only as long as its segment, IIIv slightly longer than IIId. Outer proximal region of third segment with groove (Figs. 2B, 3A, 4A). Proximal half of fourth antennular segment robust, distal part thinner, segment armed with 8 setal elements ($4V_{1–3}$, $4d_{1, 2}$, $4d_a$, IVv, 4aes). Five short spines $4v_{1–3}$, $4d_{1, 2}$ robust, pinnate on inner side, all subequal in length but $4v_3$ slightly longer than others; minute spine $4d_a$ naked, notably thinner than others. Fifth antennular segment armed with 12 setal elements (Figs. 2C, 3A). Typical branched setae absent. Short apical aesthetasc (6aes) arising from tip. Three robust spines (6_1, 6_2, 6_3) on distal part of segment: most distal spine 6_1 laterally on outer side; 6_2 near 6_1 but more dorsally, slightly proximal to it; most proximal spine 6_3 situated dorsally; 6_1 pinnate with short spinules, 6_2 and 6_3 with relatively long, thin setules (Fig. 3A). Medium long, biserially plumose seta Vv situated ventrally. Six unmodified setae (A–D, a, and b) arising from outer distal part, setal elements A–D relatively longer, thicker than elements a, b. Inner distal margin with 5 transverse serrate ridges consisting of numerous minute spinules (Fig. 3A).

Body somites from first free pediger ("second pedigerous somite") to fourth free pediger ("first urosomal somite") with several pore pairs in various regions (Fig. 1A, B). First free pediger with 3 pairs of pit-setae posteriorly (nos. 6–8: 2 pairs laterally, other pair dorsally), plus pair of simple pores anterior to dorsal pair of pit-setae. Second free pediger with 4 pairs of pit-setae posteriorly (nos. 9–12: 2 pairs laterally, other 2 pairs dorsally), plus pair of simple pores anterior to dorsal pair of pit-seta. Third free pediger with 2 pairs of pit-setae posteriorly (nos. 13, 14), all aligned transversally across dorsum, plus pair of simple pores anterior to them. Fourth free pediger with pair of pit-setae (no. 15) on posterior dorsal surface. Each free pediger also with 1 or 2 pairs of anterior dorsal pores, usually covered by extension of posterior margin of preceding somite.

Incorporated first pedigerous somite and 3 succeeding free pedigers each with pair of well-developed swimming legs (Figs. 2A, 3C–E). Leg 5 absent. Each protopod consisting of large, square coxa, relatively small basis. Border between coxa and basis on anterior face incompletely defined by diagonal seam on outer half, but posterior diagonal articulation clearly expressed (Fig. 4B). Basis of legs 1, 2, 4 with simple seta proximally on outer margin, reaching approximately to midlength of first exopodal segment; this seta longer and coarsely biplumose on leg 3, reaching midlength of second exopodal segment (Fig. 3D). Coxae of each leg pair joined by longitudinally elongated, rectangular intercoxal sclerite (Figs. 2A, 3C–E, 4B), its length in legs 1 to 4 respectively 1.5, 1.7, 1.6, 1.8 times proximal width (mean = 1.6). Basis with tri-articulate endopod and exopod on distal margin, with endopod always set more anteriorly than exopod. Endopod of all legs shorter than exopod, reaching or slightly exceeding distal margin of second exopodal segment. First, third exopodal segments of almost same length, second exopodal segment half as long. All endopodal segments subequal in length. Setal armament patterns alike in all legs except for leg 1 having one fewer seta on third exopodal segment. Exopodal segments 1, 3 each armed with short, robust, pinnate spine on outer distal corner, second exopodal segment lacking any setal element on outer margin. Rest of setae

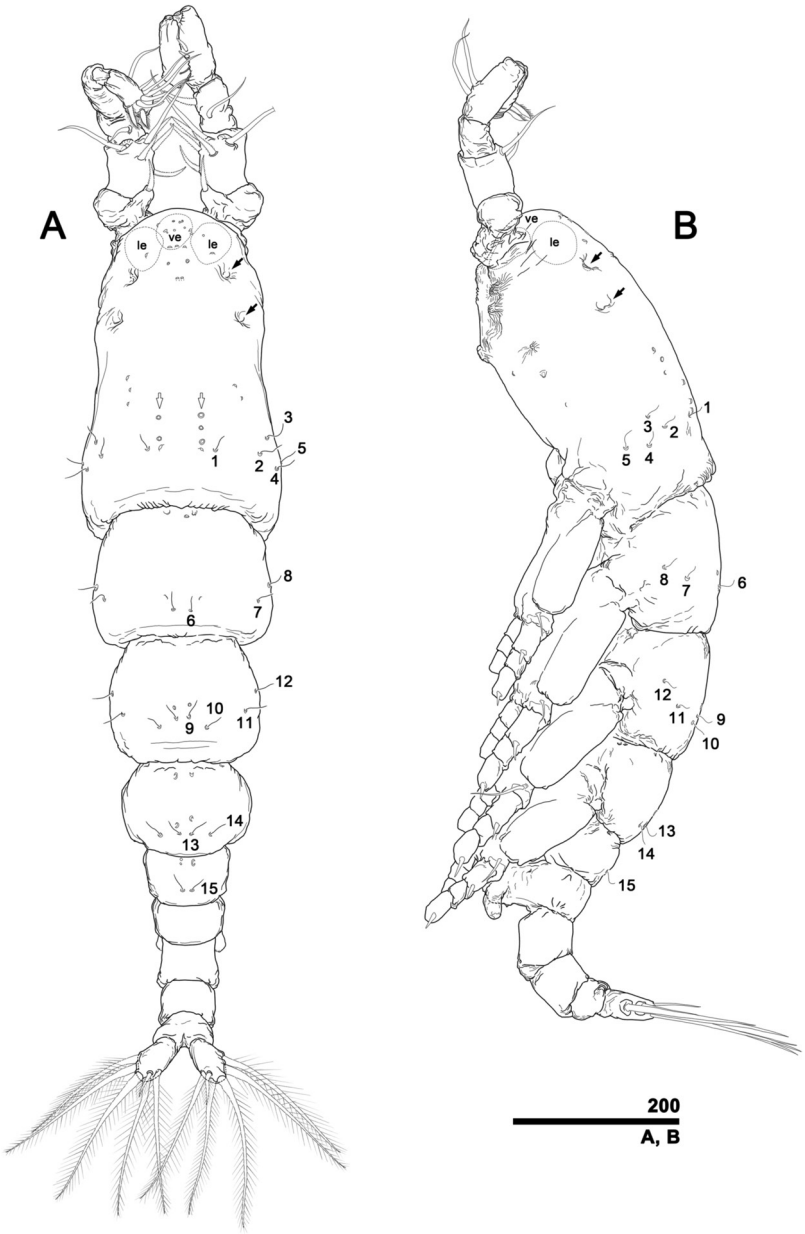

Figure 1. *Caromiobenella castorea* **sp. nov.**, male holotype. **A,** habitus showing crater-like depressions (arrows), dorsal; **B,** habitus (arrows indicate crater-like depressions); lateral. le, lateral eye; ve, ventral eye; Arabic numerals indicate pit-setae. Scale bar in μm.

on legs biserially plumose. Inner margin of exopodal, endopodal segments 1, 2 armed with single seta. Third endopodal segment with 5 setae: one on outer distal corner, 2 on distal margin, 2 on inner margin. Third exopodal segment of leg 1 with 2 distal setae, 2 setae on inner margin; those of legs 2–4 with 2 distal setae, 3 on inner margins. All setae subequal in length, inner seta on first endopodal segment shorter, thinner than others. Outer margin of endopodal segments 1, 2 of all legs fringed with fine setules. Last segment of each ramus with pore(s) on anterior face (Figs. 2A, 3C–E). 2 outermost setae of third exopodal segments of all legs serrate along outer margin while inner margin uniserially plumose (Figs. 3C–E, 4C, D).

Genital somite with genital apparatus on ventral side, composed of robust genital shaft plus 2 short, subtriangular lappets (Fig. 2D, E). Opercular flaps on distal part of genital shaft with split ends with numerous minute spinules (Figs. 2E, 5A, B). Each lappet with several rows of minute teeth on inner side (Fig. 5C).

Caudal rami close together on posterior margin of anal somite, diverging (Fig. 2D), each 0.07 mm long, 0.04 mm wide, armed with 6 setae: 2 on outer lateral side (I, II), 2 terminally (III, IV), one on inner terminal corner (V), one on posterior dorsal surface (VI). Setae I–V subequal in length. Dorsal seta VI noticeably shorter than others (Figs. 1A, 2D). All caudal setae biserially plumose. Two pores present on posterior ventral surface (Fig. 2D, arrows).

Etymology: Named after Castor (Κάστωρ), one of the representative stars of the constellation Gemini. The species name is a noun in apposition and was formed by adding the feminine suffix *ea* to the stem to avoid confusion such as mistaking the specific name for a personal name.

Remarks: The examined male specimens are most similar to *Caromiobenella patagonica* comb. nov., which was originally reported from off Argentina (Bahía Brown, Beagle Channel). Those two

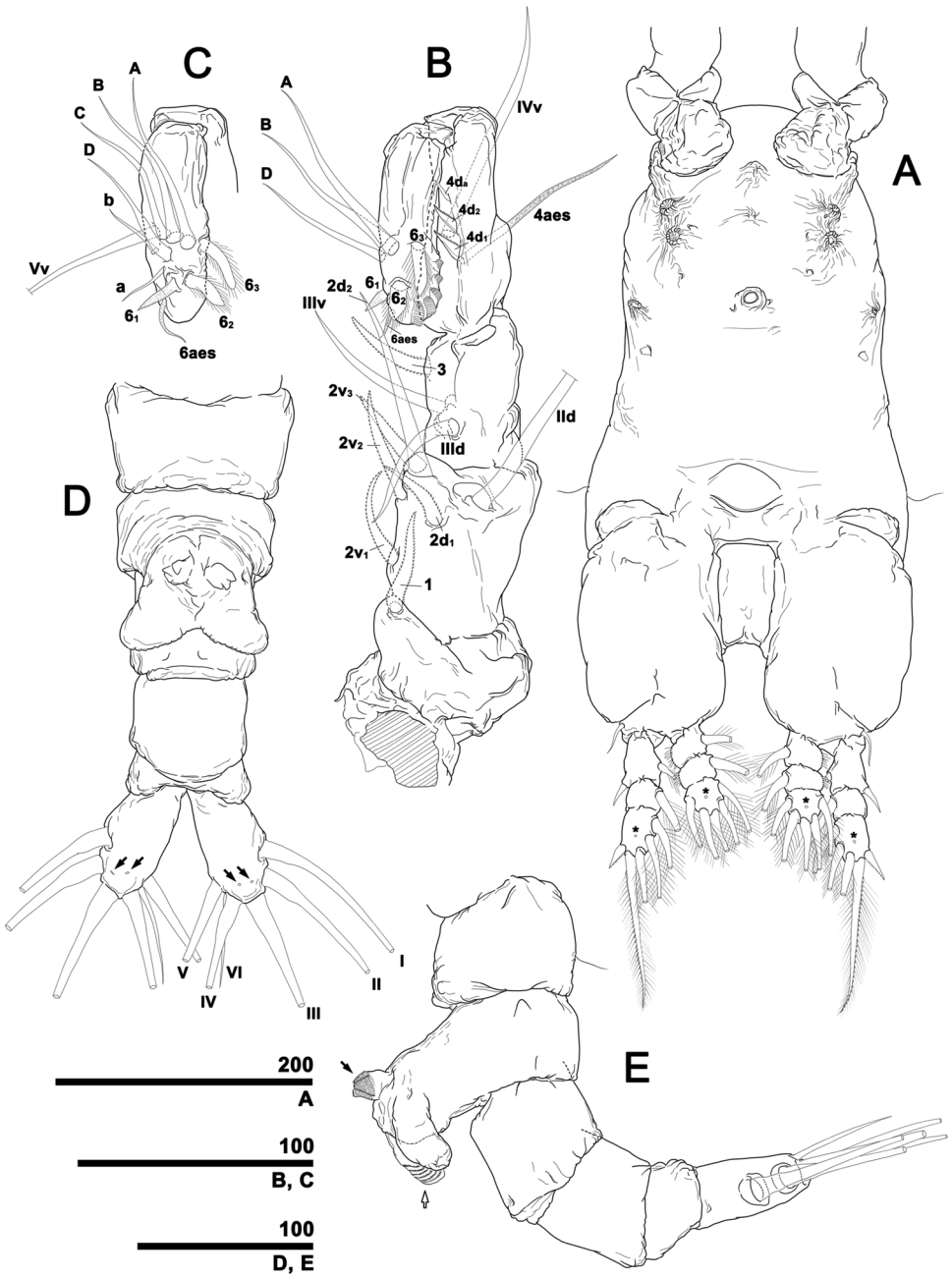

Figure 2. *Caromiobenella castorea* **sp. nov.**, male holotype. **A,** cephalothorax with leg 1 (asterisks indicate anterior pores), ventral; **B,** antennule, right, dorsal; **C,** fifth antennular segment, right, outer lateral; **D,** urosome (arrows indicate ventral pores), ventral; **E,** urosome showing genital opercular flaps (arrow) and serrate inner face of lappet (hollow arrow), lateral. Scale bars in μm.

species are distinguished from their congeners by having six caudal setae, five of them long and one noticeably shorter. *Caromiobenella patagonica* has a rounded, bulging proximal lateral margin of the fourth antennular segment, with blister-like cuticular ornamentations (Suárez-Morales *et al.*, 2008), whereas the new species has a proximal outer protrusion and a distal groove on the third antennular segment. The new species has the usual five spines and one dorsal seta IId on the second antennular segment as defined in Grygier & Ohtsuka (1995). Among these elements, spiniform $2v_{1-3}$ and $2d_1$ are pinnate, whereas spine $2d_2$ is developed into a long, biserially plumose seta that is nonetheless still clearly distinguished from strap-like setal element IId by its rigidity. The holotype and paratypes have an almost straight $2d_2$ spine that extends to the proximal part of the fourth segment without significant curvature, whereas the IId seta exhibits various shapes that attest to its flexibility. *Caromiobenella patagonica* has only four spines on the corresponding antennular segment, lacking spine $2d_2$. Among the four specimens that were examined, the distalmost dorsal spine (supposed $2d_1$ of Suárez-Morales *et al.*, 2008) was depicted as plumose and this plumosity makes it likely that this spine is actually homologous with spine $2d_2$ of other congeners. This element is much shorter in *C. patagonica*, than the corresponding element in the new species.

Caromiobenella arctica comb. nov. also appears to be closely related to *C. castorea* **sp. nov.** in having six caudal setae. *Caromiobenella arctica* nevertheless exhibits unusual morphological features such as the three dichotomously branched setae on the last antennular segment, whereas its congeners lack dichotomous setae. This species is also characterized by a mid-dorsal rostral protuberance,

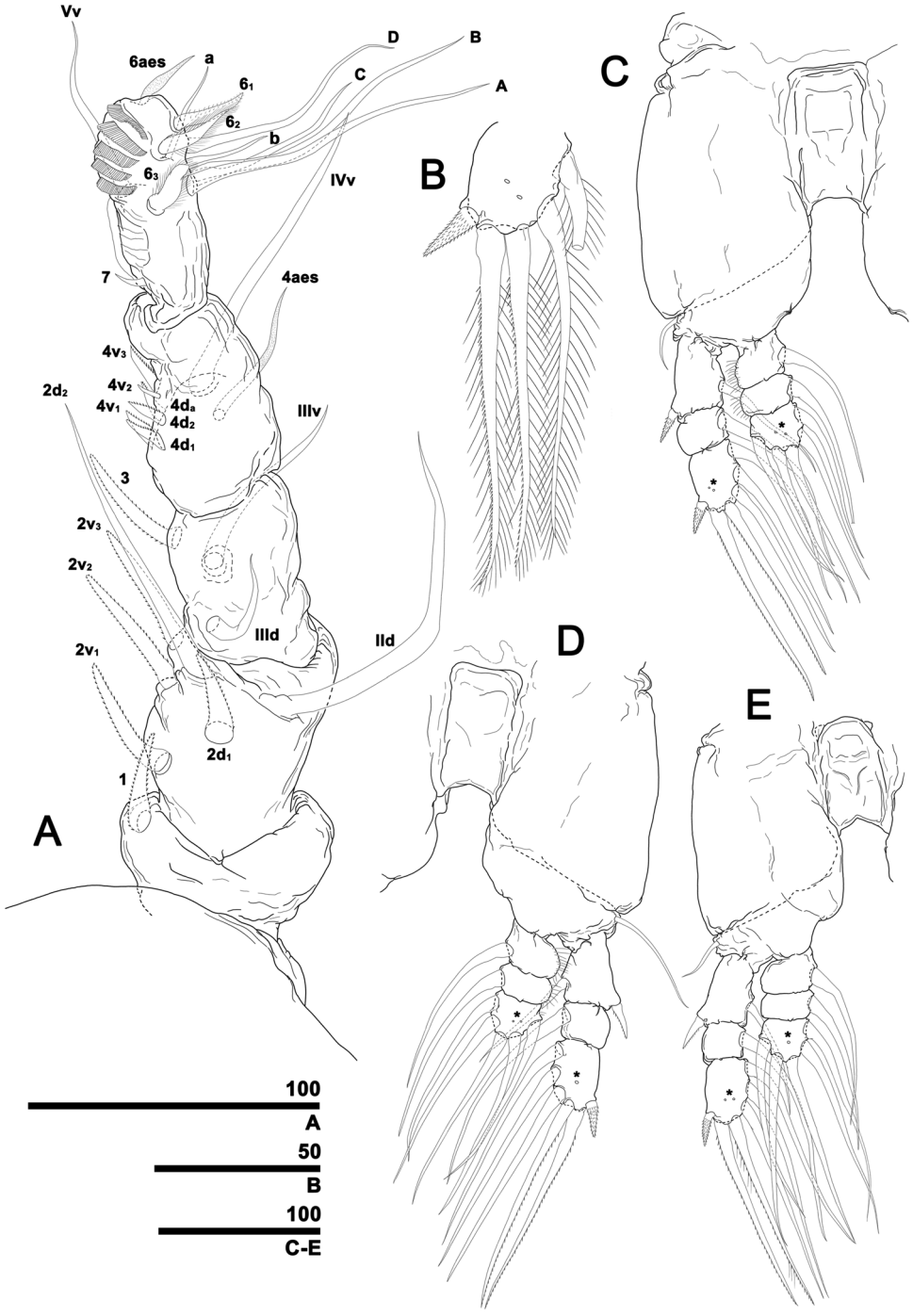

Figure 3. *Caromiobenella castorea* **sp. nov.**, male paratype. **A,** antennule, right, dorsal; male holotype. **B,** third exopodal segment of leg 1 showing two serrate outermost setae, anterior; **C,** leg 2, right, anterior; **D,** leg 3, left, anterior; **E,** leg 4, right, anterior. Asterisks indicate anterior pores. Scale bars in μm.

which is uncommon in Monstrilloida (Suárez-Morales & Vásquez-Yeomans, 1996). Two other species, *Monstrilla spinosa* Park, 1967 and *M. nasuta* Davis & Green, 1974 (Huys & Boxshall, 1991) are currently known to have such an anterior projection. Although *C. arctica* displays some unique features, it still much resembles other members of the new genus in having a relatively short cephalothorax, an inconspicuous oral papilla, an elongated $2d_2$ spine, and antennules with a similarity modified last segment.

Nomenclatural statement: A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:0C81F82A-DF17-462D-A876-3E82BFD89FCE.

Caromiobenella polluxea sp. nov.

(Figs. 6–10)

Type material: Male holotype (NIBRIV0000808114): dissected on seven slides and used for drawings. Three paratypes in a vial (NIBRIV0000808115) undissected; the type series were deposited in the National Institute of Biological Resources (NIBR), Incheon, Korea. Three additional paratypes were used for SEM and deposited in Chonnam National University, Yeosu, Korea. Three non-type specimens were sacrificed for molecular analysis.

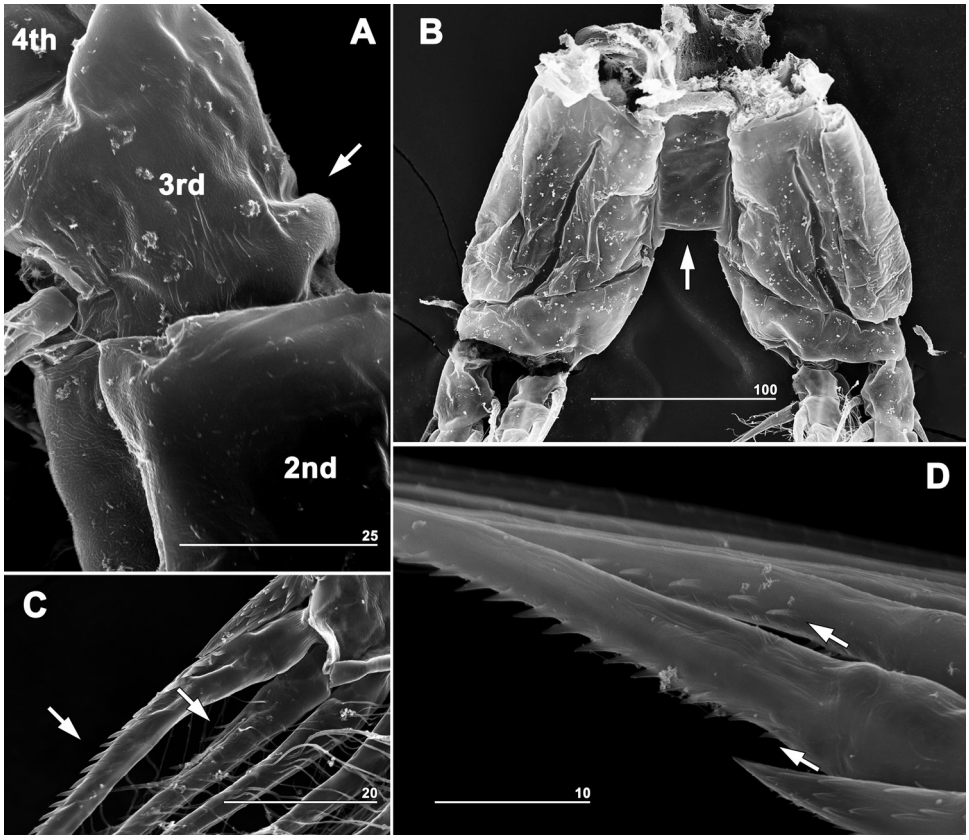

Figure 4. *Caromiobenella castorea* **sp. nov.**, male paratypes. **A,** third antennular segment showing proximal outer bump and groove (arrow), left, ventral; **B,** leg 3 joined by rectangular intercoxal sclerite showing plain distal margin (arrow), posterior; **C,** two outermost serrate setae (arrows) of third exopodal segment of leg 3, left, posterior; **D,** two outermost serrate setae (arrows) of third exopodal segment of leg 4, left, outer lateral. Scale bars in μm.

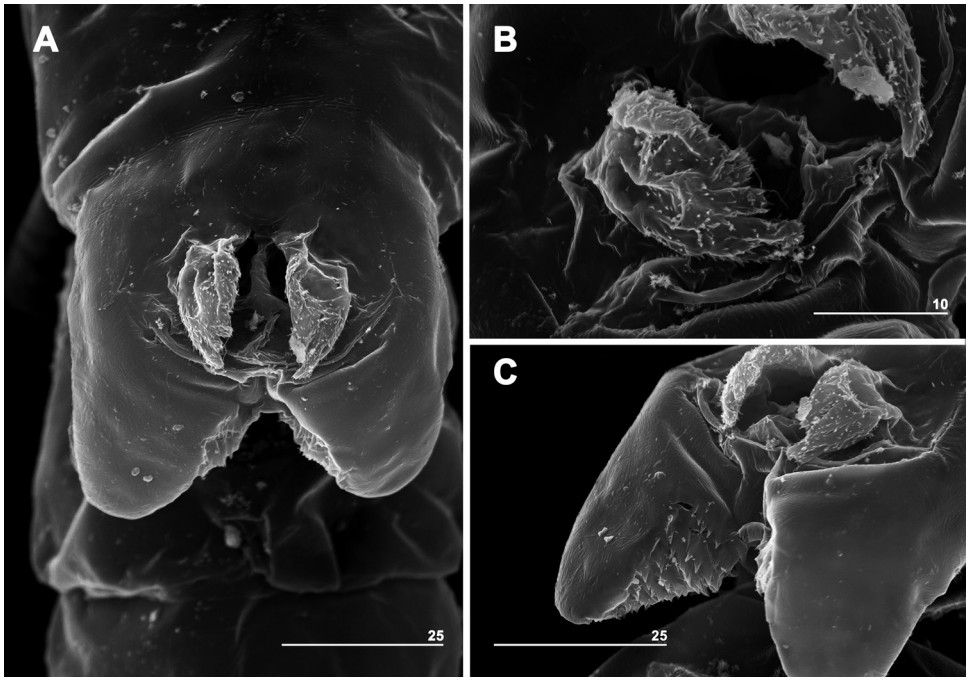

Figure 5. *Caromiobenella castorea* **sp. nov.**, male paratype. **A,** genital apparatus showing opercular flaps, ventral; **B,** opercular flaps, latero-ventral; **C,** serrate inner margin of lappet. Scale bars in μm.

Type locality: Geumgye-ri (34°26′43.3″N, 126°21′57.3″E), Gogunmyeon, Jindo-gun, Jeollanam-do, Korea. English equivalents of political divisions in Korea: ri = village; myeon = township; gun = county; do = province.

Material examined: Specimens were collected by using a light trap on 21 September 2016, from 20:00 to 23:00 h alongside a seawall (Yongho Seawall) at the type locality. The depth was about 3 m. Water temperature was not measured.

Diagnosis (male): Total body length 1.14–1.15 mm (mean = 1.14; $N = 4$). Ratio of lengths of cephalothorax, metasome, and urosome 38.6 (37.9–39.2):38.1 (35.7–39.4):23.3 (21.7–25.1) in lateral view. Pseudoral cone with no apical pore situated in anterior ventral region between antennular bases and oral papilla. Dorsal medial half of cephalothorax slightly swollen, forming small mound with 2 pairs of pores. Oral papilla low, located ventrally at 36.2% (33.0–39.2) of distance from anterior end of cephalothorax. Length of antennules in relation to total body length 28.7% (27.9–29.7), ratios of antennular segment lengths from proximal to distal 16.7 (15.8–17.3):19.7 (18.4–20.4):16.6 (15.8–17.1):22.6 (21.2–23.7):24.3 (23.5–25.4). Spine 6_1 on fifth antennular segment naked. Branched setae absent, replaced by unbranched simple setae. Spinous elements on first 3 antennular segments biserrate along outer margin. $4d_{1,2}$, $4v_3$ relatively long, slender; spines $4v_{1,2}$ rather short, robust. Inner distal corners of protopods of legs 1–4 bulging. Distal margin of intercoxal sclerites of all legs triangularly incised. Outermost seta on third exopodal segments of legs with dense serrations along outer margin. Leg 5 absent, but at least 2 specimens out of 4, including holotype, with unilateral nipple-like protuberance on posterior ventral part of first urosomal somite (fourth free pediger). Genital shaft robust, 0.06 mm (0.064–0.066) long, with genital opercular openings at distal end covered by two opercular flaps; pair of short, subtriangular distal lappets separated by posterior medial protrusion of shaft, each lappet with inner side corrugated, coarsely denticulate. Each caudal ramus with 5 plumose setae, outermost 2 (I, II) coarsely bipinnate. All caudal setae subequal in length except for noticeably shorter dorsal seta VI.

Description of male holotype: Total body length 1.15 mm in dorsal view, 1.14 mm in lateral view. Body segmented, consisting of 9 parts: cephalothorax incorporating first pedigerous somite, free somites 1–3, first urosomal somite, genital somite, postgenital somite, penultimate somite, and anal somite. Length ratios of somites as percent of total body length 38:16:12:9:5:5:6:4:4 in dorsal view; 39:14:12:10:6:5:6:4:4 in lateral view.

Cephalothorax incorporating first pediger rather short, bullet-shaped, 0.44 mm long in dorsal view, 0.45 mm in lateral view (Figs. 6A, 9A), almost twice as long as its greatest width, gradually broadening to anterior one third then slightly tapering to two-thirds length, with minimum width of 0.20 mm at 68.1% of distance from anterior end. Rounded anterior end of cephalothorax lacking usual 2 short, thin sensilla. Width of incorporated first pediger 0.23 mm near posterior margin (90.6% of distance from anterior end), this being widest part of cephalothorax although anterior broadened region of almost same width. Anterior dorsal part of cephalothorax with a number of pores, generally arranged symmetrically, mostly lying together on foremost part. Posterior to this porose region, 2 pairs of prominent concave depressions (Figs. 6A, B, 9B), with anterior pair closer to central body axis than posterior pair. Low mound situated slightly anterior to midlength of cephalothorax, with 2 pairs of pores arranged in 2 longitudinal rows (Figs. 6A, B, 9B).

Tergite of incorporated first pediger with 5 pairs of pit-setae (Fig. 6A, B): one pair situated dorsally (no. 1), 4 pairs laterally (nos. 2–5). Pit-seta groups of left and right sides separated by 4 pairs of pores arranged in 2 longitudinal rows (see Fig. 9C), these pores more prominent than other simple pores. Antero-dorsal part of incorporated pediger with another 2 pairs of simple pores. Ventral side of cephalothorax with 3 pairs of scars (Figs. 6B, C, 9D): 2 prominent pairs posterior to antennular bases, relatively small, inconspicuous pair situated more laterally, all bilaterally symmetrical. Slightly swollen area with 2 pores situated between antennular bases. Pseudoral cone (oral-papilla-like protuberance) without apical pore (Figs. 6C, 9D) situated between anterior pair of scars. Oral papilla low, situated at 39% of distance from anterior end, with apical pore. Two pairs of pores situated near oral papilla.

Two lateral, one ventral eyes within anterior fourth of cephalothorax, moderately developed, pigmented (Fig. 6A, B). Lateral eyes oval, 0.07 mm long, 0.06 mm wide, 0.05 mm apart across midline. Ventral eye round, smaller in diameter (0.05 mm) than lateral eyes.

Antennules 5-segmented, directed straight forward (Fig. 7A). Geniculation present between fourth, fifth segments. Length 0.34 mm, 29.7% of total body length, 75.8% of cephalothorax length. Length ratio of 5 segments 17:20:16:23:23. First antennular segment armed with spine 1 on inner distal part, arising slightly dorsally. Second antennular segment armed with 6 setal elements: 4 generally long, slender spines ($2v_{1-3}$, $2d_1$); elongated spine $2d_2$ reaching slightly beyond midlength of fourth antennular segment, biserially plumose with fine setules; biserially plumose seta IId arising from dorso-distal margin of segment. Third antennular segment armed with 3 setal elements: 2 medium-long, strap-like setal elements IIIv, IIId close to proximal margin and spine 3 situated on inner distal margin. Fourth antennular segment with 8 setal elements ($4v_{1-3}$, $4_{1,2}$, $4d_a$, IVv, 4aes). Short spines $4v_1$, $4v_2$ robust (Figs. 7A, 9E), but spines $4d_{1,2}$, $4v_3$ relatively longer, slender. Minute spine $4d_a$ arising from inner side of distal third of segment. Ventral proximal part armed with IVv and 4aes, latter situated close to proximal margin of segment. Fifth antennular segment with 12 setal elements (A–D, a, b, 7, 6_{1-3}, Vv, 6aes), mainly on distal part of segment except for minute spine 7 situated close to proximal margin. Most distal spine 6_1 robust, naked (Figs. 7A, 9F); 2 spines 6_2, 6_3 also robust but biserially plumose. Short subapical 6aes arising from ventral side. Outer distal half of fifth segment armed with 4 simple, medium-long setae (A–D) and 2 unmodified, short setae (a, b); branched setae absent. Setal element Vv situated ventrally. Inner distal margin with 5 transverse serrate ridges composed of numerous minute spinules (Fig. 7A).

Body somites from first free pediger to fourth free pediger with several pore pairs in various regions (Fig. 6A, B). First free pediger with 3 pairs of pit-setae posteriorly (nos. 6–8: 2 pairs laterally, other pair dorsally) plus pair of simple pores anterior to dorsal pair of pit-setae. Second free pediger with 4 pairs of pit-setae posteriorly (nos. 9–12: 2 pairs laterally, other 2 pairs dorsally) plus pair of simple pores anterior to dorsal pairs of pit-setae. Third free pediger with 2 pairs of pit-setae posteriorly (nos. 13, 14), all aligned transversally across dorsum, plus pair of simple pores anterior to them. Fourth free pediger with pair of pit-setae (no. 15) on posterior dorsal surface.

Incorporated first pedigerous somite and 3 succeeding free pedigers each with pair of well-developed swimming legs (Figs. 8A–D, 10B). Leg 5 absent. Each protopod with large, long, rectangular coxa, relatively small basis. No clear border between coxa and basis on anterior face, but posterior diagonal articulation clearly expressed, outer edge with slight notch as evidence of separation between coxa, basis (Fig. 10A, B). Each basis with short, simple seta on outer margin, reaching proximal margin of first exopodal segment except seta on leg 3 longer, biplumose, reaching distal margin of first exopodal segment (Fig. 8C). Intercoxal sclerites rectangular, distal margin triangularly incised (Figs. 8A–D, 10B); from leg 1 to leg 4 these sclerites respectively 1.9, 1.7, 1.9, 2.2 times longer than their proximal width (mean = 1.9). Basis bulging on inner distal corner, with tri-articulate endopod and exopod on distal margin, with endopod always set more anteriorly than exopod. First, third exopodal segments almost

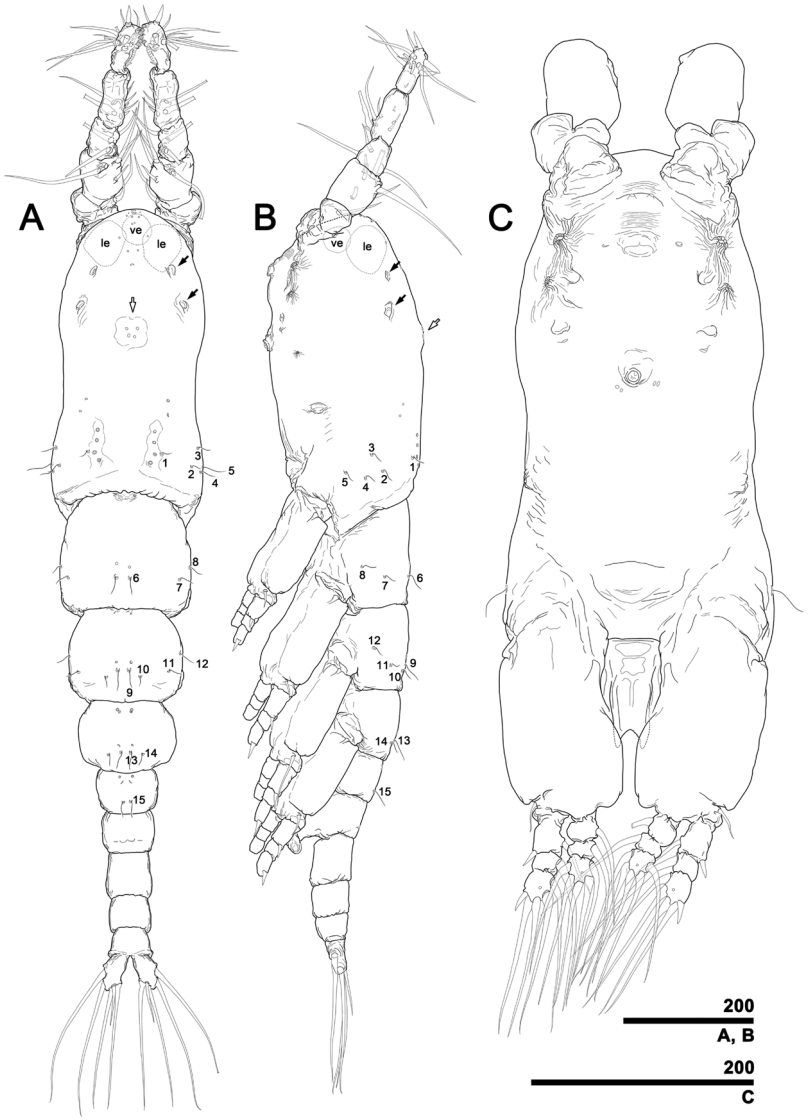

Figure 6. *Caromiobenella polluxea* **sp. nov.**, male holotype. **A,** habitus showing crater-like depressions (arrows) and dorsal mound with two pairs of pores (hollow arrow), dorsal; **B,** habitus (arrows indicate crater-like depressions), lateral; **C,** cephalothorax with leg 1, ventral. le, lateral eye; ve, ventral eye; Arabic numerals in **A** and **B** indicate pit-setae. Scale bar in μm.

same in length, second exopodal segment half as long; proportions of endopodal segments similar. Endopod of all legs shorter than exopod, reaching midlength of third exopodal segment. Setal armament patterns generally alike in all legs except leg 1 having one fewer seta on third exopodal segment. Exopodal segments 1, 3 each armed with short, robust, pinnate spine on outer distal corner, second exopodal segment lacking any setal element on outer margin. Inner margin of exopodal and endopodal segments 1, 2 armed with single seta each. Third endopodal segment armed with 5 setae: one on outer distal corner, 2 on distal margin, 2 on inner margin. Third exopodal segment of leg 1 armed with 2 distal setae, 2 inner setae; that of leg 2–4 armed with 2 distal setae, 3 on inner margin. Outermost seta of third exopodal segments of all legs densely serrate along outer margin, inner margin uniserially plumose (Fig. 8A–D). All setae subequal in length but inner seta on first exopodal segment shorter, thinner. Outer margin of endopodal segments 1, 2 of all legs fringed with fine setules. Last segment of each ramus with pore on anterior face (Fig. 8A–D).

Genital somite with genital apparatus on ventral side, composed of robust genital shaft plus 2 short, subtriangular lappets with coarsely denticulate inner distal margin (Figs. 7B, C, 10C, D). Tip of shaft developed into rounded medial protrusion, covered by opercular flaps with split ends (Figs. 7C, 10C).

Two caudal rami situated close together on posterior margin of anal somite, diverging (Fig. 7C), each 0.06 mm long, 0.03 mm wide, armed with 5 setae: 2 on outer lateral side (I, II), 2 terminally (IV, V), one on posterior dorsal surface (VI). Seta III absent. Setae I, II, IV, V subequal in length, dorsal seta VI noticeably shorter than others. All caudal setae biserially plumose, setae I, II coarsely denticulate (Fig. 7C). Single pore situated on posterior ventral surface of each ramus (Fig. 7C).

Etymology: Named after Pollux, one of the representative stars of the constellation Gemini. The species name is a noun in apposition and formed by adding the feminine suffix *ea* to the stem.

Remarks: The males examined are easily distinguished from the type species *Caromiobenella castorea* **sp. nov.** and its close congeners by having five instead of six caudal setae. Three other species of *Caromiobenella* **gen. nov.** share this feature, *C. helgolandica* comb. nov., *C. serricornis* comb. nov., and *C. pygmaea* comb. nov., but they all

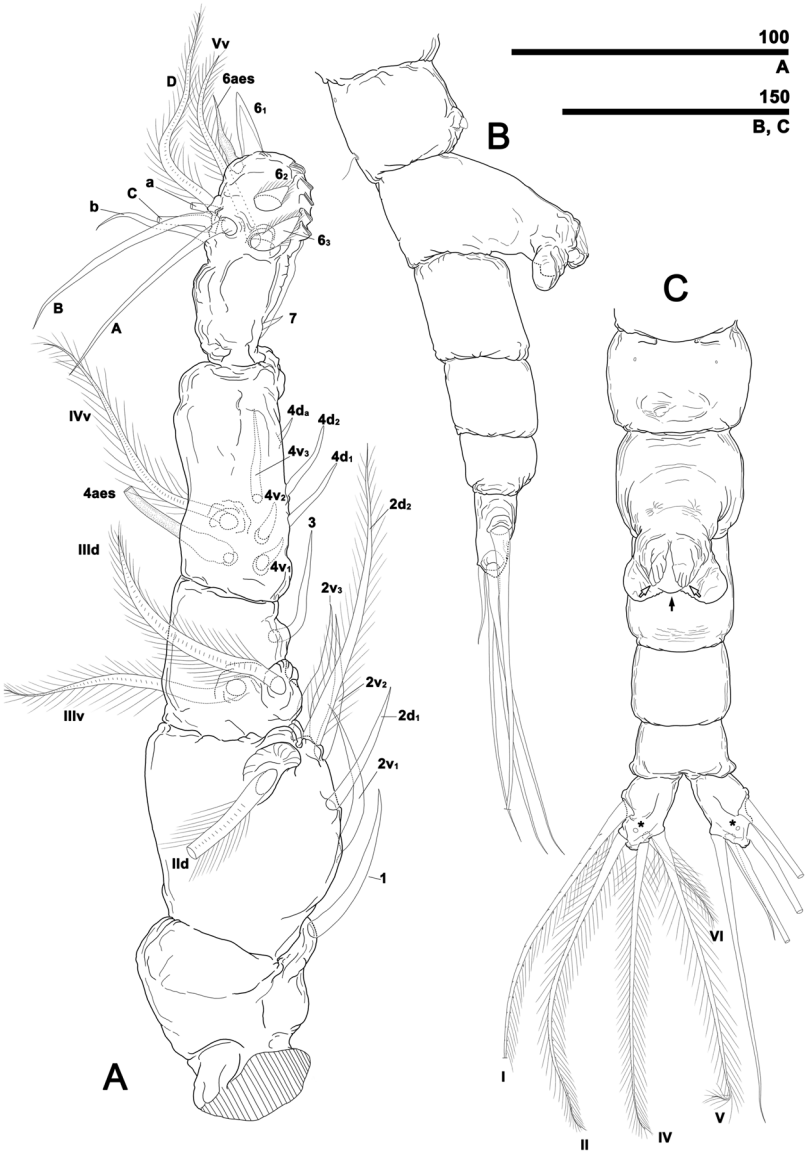

Figure 7. *Caromiobenella polluxea* **sp. nov.**, male holotype. **A,** antennule, left, dorsal; **B,** urosome, lateral; **C,** urosome showing genital opercular flaps (hollow arrows), medial protrusion (filled arrow) between lappets and asterisks on caudal rami indicate ventral pores, ventral. Scale bars in μm.

differ from each other in details of the caudal setae and in several other aspects. The caudal ramus of *C. pygmaea* is armed with three terminal, one inner distal, and one outer setae; the second innermost seta (i.e. the most inner terminal seta) is slightly longer than the others, which are subequal in length (Suárez-Morales, 2000). In contrast, the new species has two outer lateral, one terminal, and one inner distal setae in addition to a seta that clearly arises from the dorsal face and is markedly shorter than the others.

One potentially unique feature of the caudal setae of the new species, not reported in the descriptions of congeners, is the combination of pinnation and plumosity on the outermost seta (I) and the adjacent outer seta (II); the plumose elements are arranged bilaterally, whereas the pinnate elements are lined up along the dorsal and ventral sides of these setae.

The general shape of the genital apparatus is similar to that of *Caromiobenella castorea* **sp. nov.** by having a robust genital shaft and two short, diverging lappets, although the new species has a smooth medial protrusion on the distal posterior margin, whereas *C. pygmaea* has a deep notch. The type of genital structure in *C. polluxea* **sp. nov.** is characteristic of *C. serricornis* as well, but the five caudal setae of *C. serricornis* are all subequal in length. Furthermore, the length ratio of the distal four antennular segments (second to fifth segments) is 87:54:134:100 in *C. serricornis* (Suárez-Morales, 2000: table 1) but 87:70:100:100 in *C. polluxea* **sp. nov**.

Differences in body size are also evident. *Caromiobenella pygmaea*, as the name implies, is the smallest monstrilloid, with a body length of 0.43 mm (Suárez-Morales, 2000), whereas a Norwegian specimen of *C. serricornis* was 1.75 mm long (Sars, 1921). The mean body length of the new species, 1.14 mm, is intermediate. The relative length of the antennules compared to body length is 40.6% in *C. pygmaea* but 28.7% in the new species; however, the new species appears to be similar to the other congeners, *C. helgolandica* and *C. serricornis*, in this respect.

Monospecificity of *Caromiobenella helgolandica* has been questioned in several studies (Grygier & Ohtsuka, 1995; Suárez-Morales, 2010, 2011). The partial redescription of *C. helgolandica* by Huys & Boxshall (1991) provided evidence of differences from *C. polluxea* **sp. nov.** in the setal array on the distal antennular segment. In *C. polluxea* **sp. nov.** this segment is armed with 12 setal elements, but only 10 elements in *C. helgolandica*; the inner proximal minute spinous element 7 is present in both species but that

of *C. helgolandica* is split in two threads from midlength (Huys & Boxshall, 1991: fig. 2.5.6D), whereas that of *C. polluxea* **sp. nov.** is developed normally. The segmental length ratio in the urosome are 28:22:23:16:10 in *C. helgolandica* based on the illustrations of Huys & Boxshall (1991), but 24:20:24:26:16 in the new species; the latter thus appearing to have a shorter first urosomal somite and relatively long anal somite.

Nomenclatural statement: A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:0C81F82A-DF17-462D-A876-3E82BFD89FCE.

MOLECULAR ANALYSIS

Nucleotide sequences of the mtCOI and 28S rRNA genes were obtained from 41 individuals representing five genera and nine species of monstrilloids from Korea. As a result, 24 partial mtCOI sequences from eight species in all five genera, and 36 partial 28S rRNA sequences from a closely overlapping set of eight species in the same five genera, were obtained (see Supplementary material Table S1). No sequences were obtained for the mtCOI gene of *Monstrilla grandis* and the 28S rRNA gene of *Monstrilla* sp. 02.

The length of the newly obtained mtCOI sequences ranged from 655 to 670 base pairs (bp). Five additional monstrilloid mtCOI gene sequences acquired from GenBank were shorter, with a range of 582 to 588 bp. In all, 32 fragments including the corresponding sequences of three copepod outgroup taxa were aligned and trimmed at both ends to a length of 600 bp to retain only well-matched data. Among the 600 sites, 395 (65.8%) were variable and 375 (62.5%) were parsimony-informative. The average GC content was 28.8%.

Genetic mean divergences of monstrilloid mtCOI gene sequences at various taxonomic levels were calculated under the Kimura two-parameter model (K2P) with 3,000 bootstrapping replicates. The mean divergences were 0.47% (0.00–1.25) within-species, 23.24% (14.53–36.14) within-genus and 40.06% within Monstrillidae. The mean divergence of between-species across the genera was 44.37%, and between-genera divergence was 48.15%. The intra generic divergence within each genus was 19.05% in *Caromiobenella* **gen. nov.**, 14.53% in *Monstrilla*, and 36.14% in *Cymbasoma*, but not calculated for *Monstrillopsis* and *Maemonstrilla*, which were each represented in the date set by a single species. The inter-generic divergences between the species of *Caromiobenella* **gen. nov.** and those of *Monstrilla* were 42.18% on average, with the details shown in Table 2.

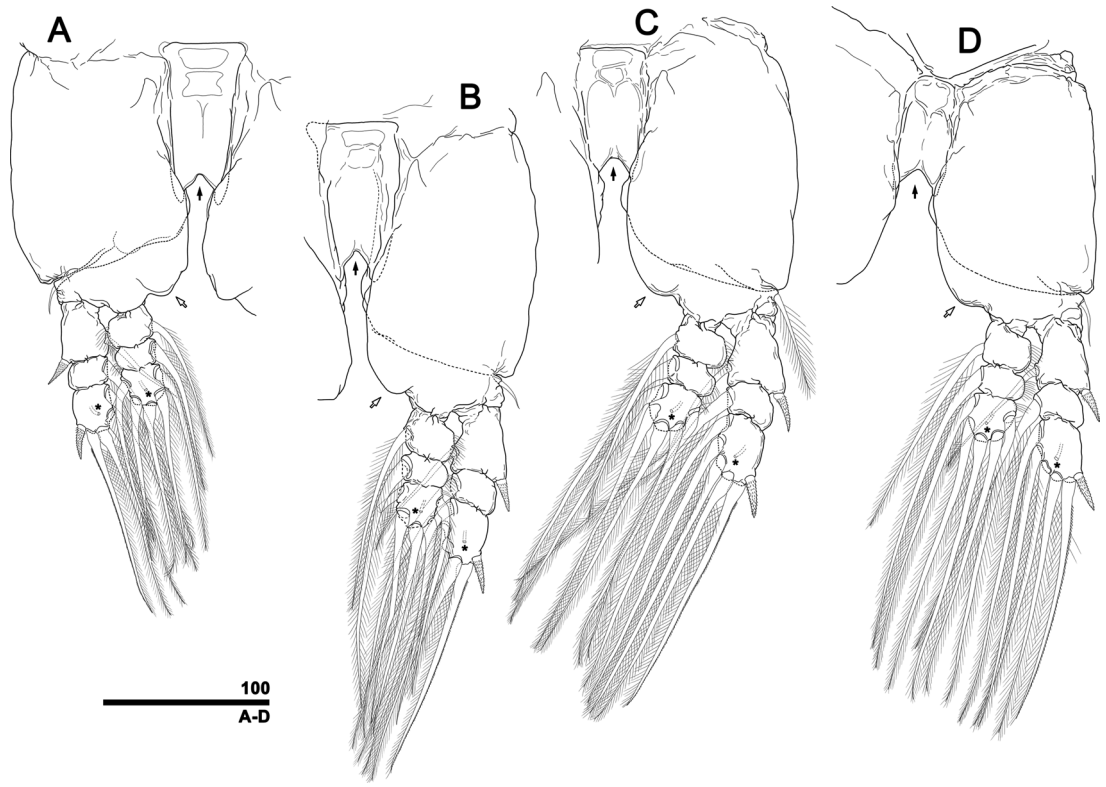

Figure 8. *Caromiobenella polluxea* **sp. nov.**, male holotype, legs 1–4 showing plunging distal margin of intercoxal sclerites (filled arrows) and inner distal bulging of bases (hollow arrows), asterisks indicate anterior pores. **A,** leg 1, right, anterior; **B,** leg 2, left, anterior; **C,** leg 3, left, anterior; **D,** leg 4, left, anterior. Scale bar in μm.

Table 2. Intergeneric divergences between the species of *Caromiobenella* **gen. nov.** and of *Monstrilla* based on mtCOI and 28S rRNA genes (mtCOI / 28S rRNA; in percentage, %; ND: no data)

	***Caromiobenella castorea* sp. nov.**	***Caromiobenella polluxea* sp. nov.**	***Caromiobenella hamatapex* comb. nov.**
Monstrilla ilhoii	42.13 / 28.08	40.30 / 24.59	46.44 / 25.86
Monstrilla sp.01	40.67 / 29.13	39.32 / 25.57	45.41 / 26.68
Monstrilla sp.02	40.98 / ND	41.11 / ND	43.23 / ND
Monstrilla grandis	ND / 27.27	ND / 26.17	ND / 26.69

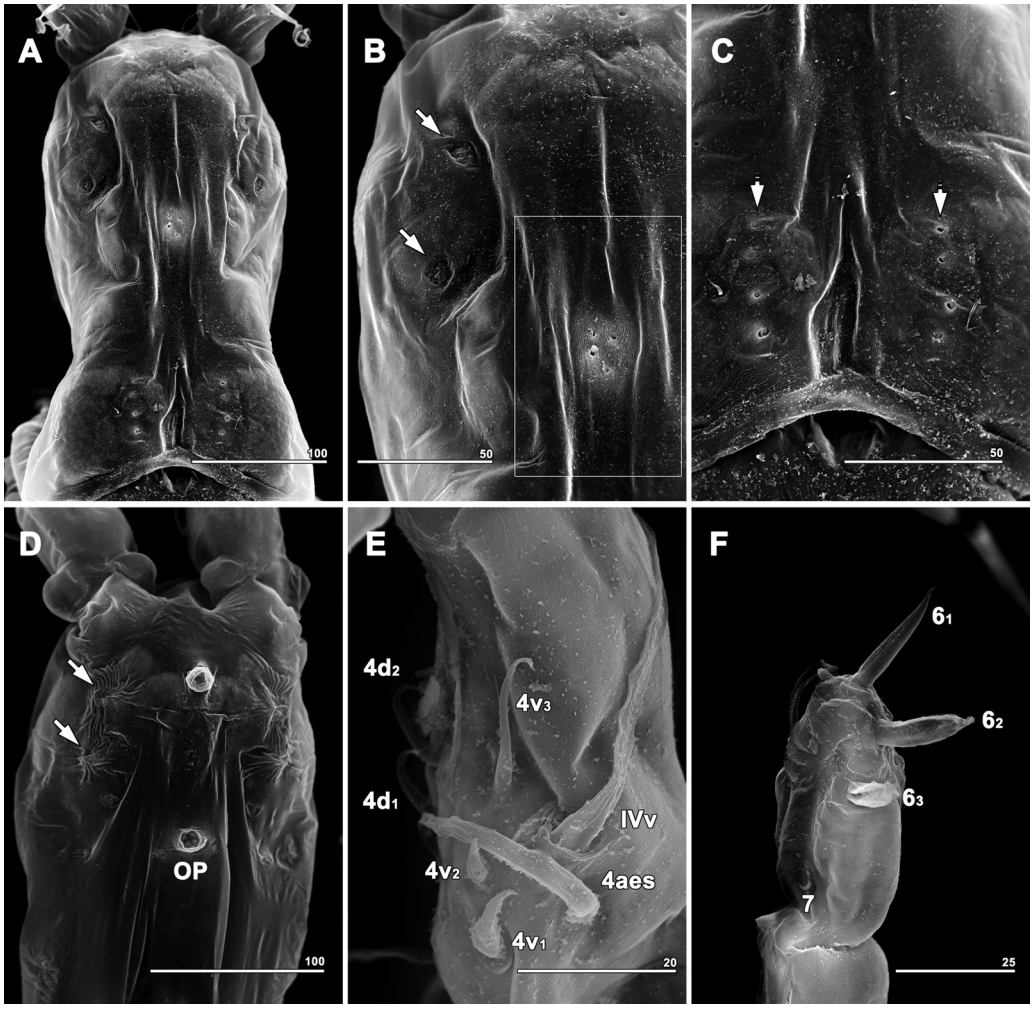

Figure 9. *Caromiobenella polluxea* **sp. nov.**, male paratypes. **A,** cephalothorax, dorsal; **B,** anterior dorsum of cephalothorax showing crater-like depressions (arrows) and low mound with two pairs of pores (in box); **C,** four pairs of longitudinally aligned pores (arrows) on dorsum of incorporated first pedigerous somite; **D,** cephalothorax showing two prominent scars (arrows) and oral papilla (OP), ventral; **E,** fourth antennular segment with setal elements, left, ventral; **F,** fifth antennular segment armed with naked distalmost spine 6_1, right, dorsal. Scale bars in μm.

The 28S rRNA sequences from 36 individuals were more various than those of mtCOI, showing a range of 755 to 816 bp. The three monstrilloid 28S rRNA sequences were added from the GenBank were longer, ranging from 908 to 921 bp. In all, 42 gene sequences including three from outgroup copepods were aligned and then trimmed to 901 bp at both ends. Among the 901 sites, 386 (42.8%) were variable and 266 (29.5%) were parsimony-informative. The average GC content was 49.6%.

Mean genetic divergences of monstrilloid 28S rRNA sequences were 11.50% (8.41–14.28) within-genus and 21.73% within Monstrillidae. There was no genetic variability at the within-species level. The mean divergence between species across the genera was 21.73% and the between-genera divergence was 22.07%. The intra-generic divergence for each genus was 11.81% in *Caromiobenella* **gen. nov.**, 8.41% in *Monstrilla*, and 14.28% in *Cymbasoma*, but the data set included only one species each for *Monstrillopsis* and *Maemonstrilla*, so this value could not be calculated. The inter-generic divergences between the species of *Caromiobenella* **gen. nov.** and those of *Monstrilla* were 26.67% on average (Table 2).

In general, the genetic divergences calculated based on both mtCOI and 28S rRNA sequences increased with higher taxonomic rank, but to a lesser extent for 28S rRNA gene.

DISCUSSION

Taxonomic considerations

The two new species of *Caromiobenella* **gen. nov.**, both known only from males, closely resemble each other in many morphological aspects, sharing a relatively short cephalothorax, antennules with five segments and a modified distal segment, a poorly developed and low oral papilla, absence of branched setae on the distal antennular segment, a setiform modified spine $2d_2$, two pairs of large pores in the form of concave craters on the anterior dorsum of the cephalothorax, eight pores arranged pairwise in two antero-posterior rows of four pores on the medial dorsum of the incorporated first pediger, and the general features of the genital apparatus, including a robust shaft and short, subtriangular lappets. Some of these features also characterize several species of *Monstrilla* that have been previously reported from various regions: *Monstrilla helgolandica*, *M. serricornis*, *M. arctica*, *M. hamatapex*, *M. pygmaea* and *M. patagonica*. Only two of these species, *M. helgolandica* and *M. patagonica*, have been known from both sexes and *M. hamatapex* is so far known only from females. The remaining four are known only from males.

The listed species, which are known from males, are all characterized by a modified distal antennular segment, one of the four kinds of distal antennular segment of male monstrilloids that have

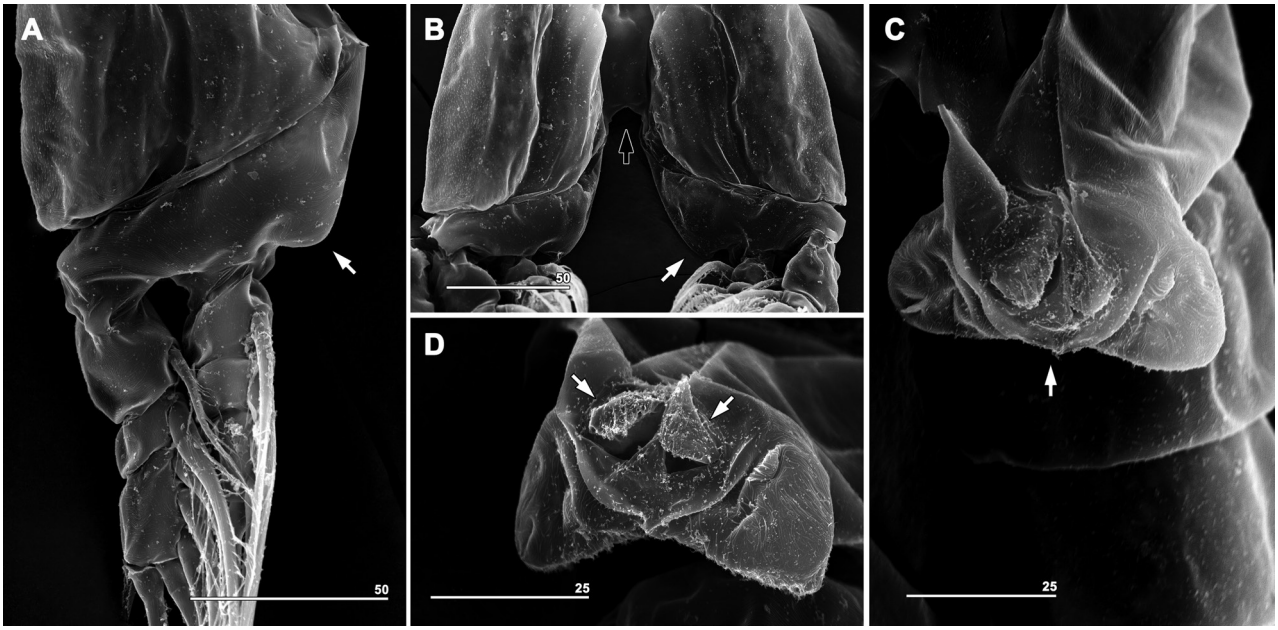

Figure 10. *Caromiobenella polluxea* **sp. nov.**, male paratypes. **A,** leg 1 showing bulging inner distal corner of basis (arrow), left, posterior; **B,** leg 3 joined by intercoxal sclerite (filled arrow) and showing bulging inner distal corner of basis (hollow arrow), posterior; **C,** genital apparatus showing posterior protrusion (arrow), ventral; **D,** opercular flaps (arrows) on distal margin of genital shaft, ventral. Scale bars in μm.

been defined (Huys & Boxshall, 1991; Suárez-Morales, 2011). The first three kinds have a distal segment showing no specific modification (Type 1), a distal segment with a hyaline bump on the inner proximal margin and a gradually tapered curved tip (Type 2), and a distal segment with transverse serrate ridges on the inner distal margin (Type 3). The fourth type is similar to the third, but much less well developed (Huys & Boxshall, 1991: fig. 2.5.7C). Antennular type 1 is present in many species of *Monstrilla* and *Cymbasoma*. Type 2 is specific for males of *Monstrillopsis*, and has often been regarded as a diagnostic feature of this genus (Huys & Boxshall, 1991; Suárez-Morales *et al.*, 2006). Type 3 is specific to the males of *Caromiobenella* **gen. nov.**, which had previously been recognized as a small group within *Monstrilla* (Sars, 1921; Huys & Boxshall, 1991; Suárez-Morales *et al.*, 2008). Despite the worldwide distribution of the species of *Caromiobenella* **gen. nov.**, which have been recorded from Norway, England, northern France, the Mediterranean, Canada, United States, Argentina, Indonesia, Singapore, Japan, and Korea (Grygier & Ohtsuka, 1995; Suárez-Morales *et al.*, 2008), this antennular modification is very similar among all species. Such morphological uniqueness and stability suggest that a type-3 antennular structure should be regarded as a diagnostic feature of males of *Caromiobenella* **gen. nov.** and type-2 for males of *Monstrillopsis*. Sars (1921) emphasized the modifications on the distal antennular segment of *Monstrilla sericornis* in questioning whether that species truly belonged to *Monstrilla*, but the morphological uniqueness and the importance of this feature were undervalued as additional related species were described.

Besides having a common antennular morphology, the males of all species of the new genus share a low, rather poorly developed and somewhat inconspicuous oral papilla that is mainly found on the anterior ventral surface of the cephalothorax (Sars, 1921; Davis & Green, 1974; McAlice, 1985; Suárez-Morales, 2000; Suárez-Morales *et al.*, 2008). In contrast, females of *C. hamatapex* from Korea and Japan have a relatively prominent oral papilla (Grygier & Ohtsuka, 1995; Chang, 2014). Other females such as *C. helgolandica* and *C. patagonica* also have a prominent oral papilla, which is located in the middle or close to the mid-ventral surface of the cephalothorax (Claus, 1863; Scott, 1909; Sars, 1921; Gallien, 1934; Sewell, 1949; Park, 1967; Ramírez, 1971; McAlice, 1985; Suárez-Morales *et al.*, 2008). The general morphological features of the oral papilla in *Caromiobenella* **gen. nov.** thus appear to be sexually dimorphic.

Grygier & Ohtsuka (1995) proposed four kinds of setae for the basic setal armature of the antennules of female monstrilloids, (see also Suárez-Morales, 2011). The second antennular segment typically bears five spines ($2v_{1-3}$ and $2d_{1, 2}$) and a long, setulose, strap-like dorsal seta (IId). The second antennular segment of the males of both new species of *Caromiobenella* **gen. nov.** also bear the same elements, but spine $2d_2$ is typically distinguished from the other spinous elements $2v_{1-3}$ and $2d_1$ in some characters: it may be biserially plumose, elongated, or both. An elongated and plumose spine $2d_2$ has been observed in *C. helgolandica* (females in Park, 1967) and *C. pygmaea* (Suárez-Morales, 2000) as well as the two new species. It has been shown as elongated in males of three species, *C. helgolandica* (McAlice, 1985), *C. sericornis* (McAlice, 1985), and *C. arctica* (Davis & Green, 1974), but without sufficient descriptions or illustrations of plumosity. Two other species, females of *C. hamatapex* (Grygier & Ohtsuka, 1995; Chang, 2014) and males of *C. patagonica* (Suárez-Morales *et al.*, 2008), have a plumose but not elongated spine $2d_2$, which is of almost the same length as the other spinous elements on the second segment. The female of *C. patagonica* from Argentina (Ramírez, 1971; Suárez-Morales *et al.*, 2008) has an elongated spine of unclear identity. The extent to which such variation constitutes sexual dimorphism or species differences is unclear. By including a modified spine $2d_2$ as one of the generic characters of *Caromiobenella* **gen. nov.**, however, the elongated spine of female *C. patagonica* may be interpreted as $2d_2$ and not $2d_1$ as originally proposed.

The modified setal element $2d_2$ has also been reported in some males of *Cymbasoma* Thompson, 1888 (Suárez-Morales & McKinnon, 2016): *C. longispinosum* (Bourne, 1890) (Giesbrecht, 1893; Martin Thompson, 1973; Huys & Boxshall, 1991), *C. tropicum* (Wolfenden, 1905) (Sewell, 1949), *C. chelemense* Suárez-Morales & Escamilla, 1997, *C. rochai* Suárez-Morales & Dias, 2001, *C. bullatum* (Scott, 1909) (Suárez-Morales, 2007), and *C. bitumidum* Suárez-Morales & McKinnon, 2016, which generally, but not always, bear an elongated spine 1 on the first antennular segment, which is only moderately developed in *Caromiobenella* **gen. nov**.

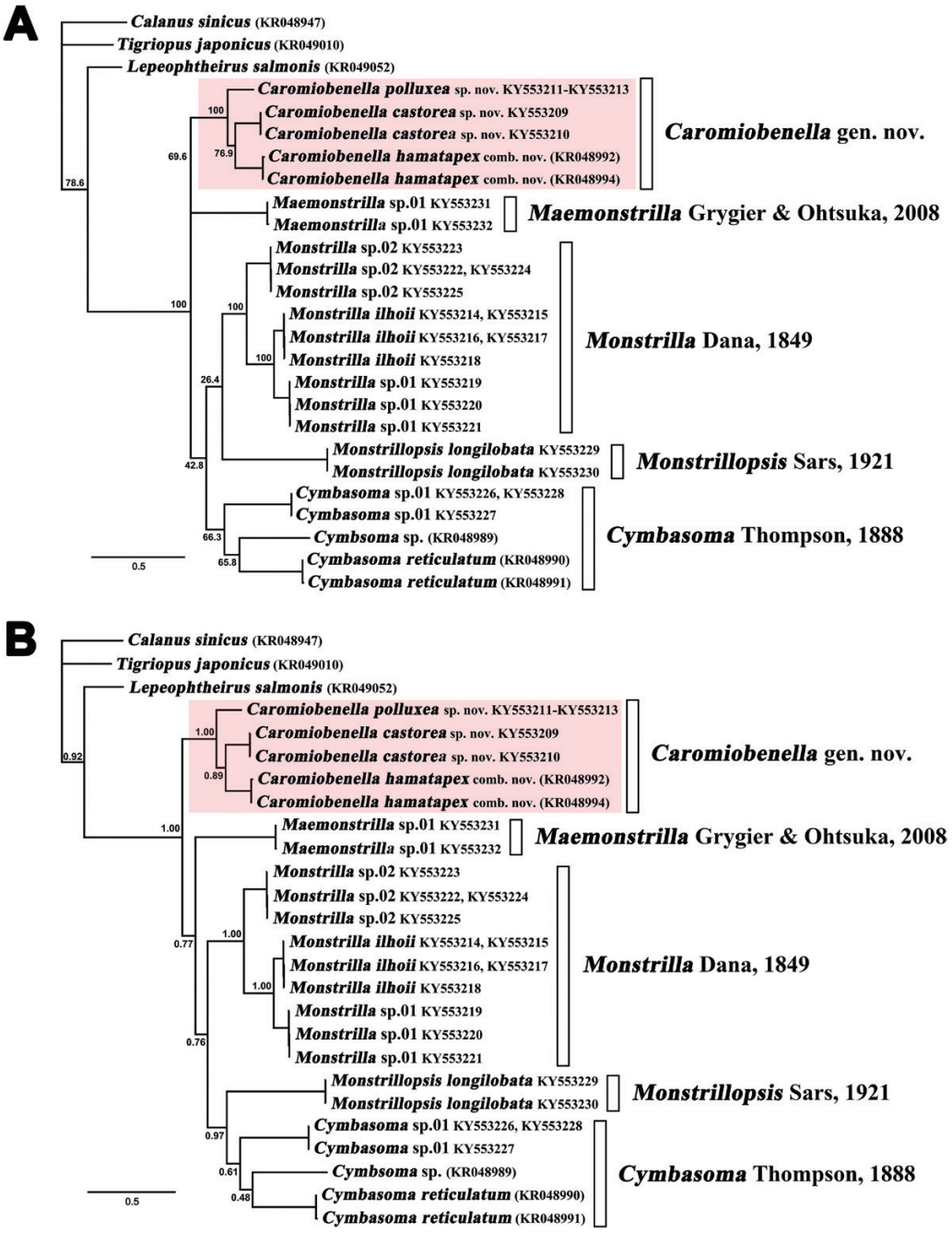

Figure 11. Phylogenetic trees reconstructed based on the sequences of mtCOI derived from five genera and 11 species of monstrilloids including three outgroup taxa, *Calanus sinicus* (Calanoida), *Tigriopus japonicus* (Harpacticoida) and *Lepeophtheirus salmonis* (Siphonostomatoida). **A,** Maximum likelihood (ML) tree topology; **B,** Bayesian inference (BI) tree topology. Numbers above or below branches indicate bootstrapping value (BP, in percentage, %) and Bayesian posterior probabilities (BPP, in probability, *p*) of ML and BI trees, respectively. Each species name followed by the GenBank accession number(s); the numbers in brackets indicate the data from the other sources while the number for the sequences without brackets were prepared by the current authors.

A modified spine $2d_2$ is rare in *Monstrilla*. Females of two species, *M. inserta* Scott, 1909 and *M. brasiliensis* Suárez-Morales & Dias, 2000, have an elongated setal element on the second antennular segment, but this has been recognized as spine $2v_3$, not $2d_2$, on account of its position among the other spines (Scott, 1909; Suárez-Morales & Dias, 2000; Suárez-Morales, 2001).

Two types of male genitalia have been recognized in the new genus, those with a deep triangular notch on the posterior distal margin of the genital shaft and those with a smooth medial protrusion instead. *Caromiobenella castorea* **sp. nov.**, *C. helgolandica*, *C. pygmaea*, and *C. patagonica* show the first type, and *C. polluxea* **sp. nov.** and *C. serricornis* the second. The male genitalia of *C. arctica* were not described or illustrated in sufficient detail, and that of *C. hamatapex* remain unknown. Davis & Green (1974: 59) described "a pair of small spine-like processes" arising from distal end of the genital shaft in *C. arctica* and compared them with those of *Monstrilla canadensis* (= *C. helgolandica*). McMurrich (1917: 48) also noted "the notch leading to the genital orifice being guarded on either side by about three short spines." The spinous structures mentioned in both studies could be opercular flaps. The distal ends of the opercular flaps of the two new species often protrude in lateral view and split into several fine strands near the tip. The

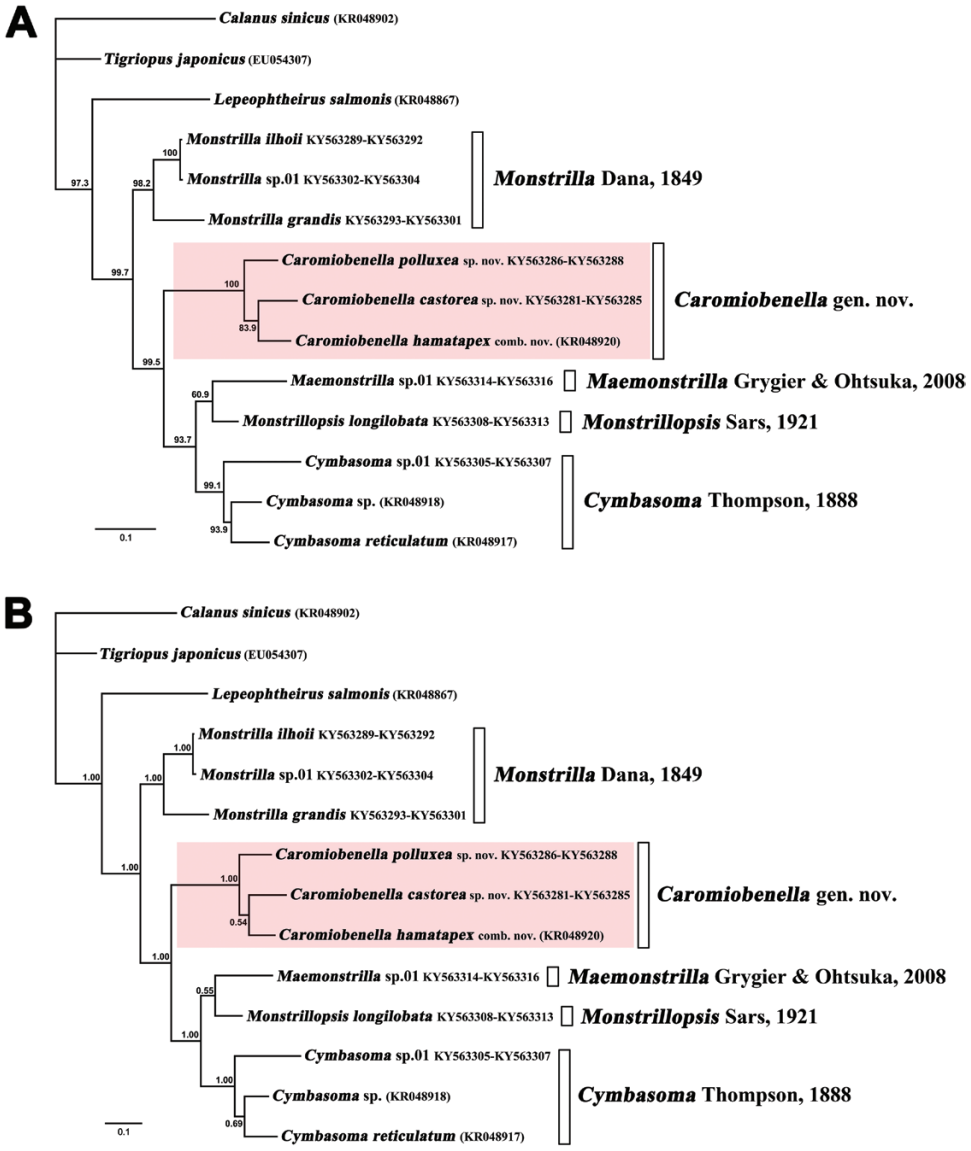

Figure 12. Phylogenetic trees reconstructed based on the sequences of 28S rRNA derived from five genera and 11 species of monstrilloids including three outgroup taxa, *Calanus sinicus* (Calanoida), *Tigriopus japonicus* (Harpacticoida) and *Lepeophtheirus salmonis* (Siphonostomatoida). **A,** Maximum likelihood (ML) tree topology; **B,** Bayesian inference (BI) tree topology. Numbers above or below branches indicate bootstrapping value (BP, in percentage, %) and Bayesian posterior probabilities (BPP, in probability, *p*) of ML and BI trees, respectively. Each species name followed by the GenBank accession number(s); the numbers in brackets indicate the data from the other sources while the number for the sequences without brackets were prepared by the current authors.

split tips are covered with numerous fine setules in *C. castorea* **sp. nov**. The general resemblance among species of the genitalia, with a robust shaft, short lappets, and often protuberant opercular flaps, could be regarded as another diagnostic feature of *Caromiobenella* **gen. nov**.

In terms of number of caudal setae, *Caromiobenella* **gen. nov.** can be divided into two subgroups: *C. castorea* **sp. nov.**, *C. arctica*, *C. hamatapex*, and *C. patagonica* having six setae on each caudal ramus, and *C. polluxea* **sp. nov.**, *C. helgolandica*, *C. serricornis*, and *C. pygmaea* having five. The caudal armament varies in terms of setal length and ornamentation within each group. The two species groups based on the number of caudal setae are inconsistent with those based on male genitalia, so no formal division of the genus into subgenera can be done at the present time.

At least some species of *Caromiobenella* **gen. nov.** have two pairs of large, crater-like pores on the anterior dorsal surface of the cephalothorax. Although not previously regarded as significant, this pore structure and pattern occur consistently in males of the two new species, as well as in males of our other unpublished *Caromiobenella* **gen. nov.** species. Females of *C. hamatapex* from Tanabe and Ago bays, Japan (Sekiguchi, 1982; Grygier & Ohtsuka, 1995), also have pores of this sort on the corresponding sites of the cephalothorax, and these are expressed even more clearly in Korean specimens of *C. hamatapex* (see Chang, 2014). Two longitudinal rows of four pores each, arranged in pairs across midline, are also regularly present on the posterior dorsal surface of the cephalothorax in female *C. hamatapex*.

The new genus displays a unique set of characters, but some ambiguity is present in the generic assignment of all species of *Caromiobenella* **gen. nov.** mentioned, including the two new species. For example, the numbers of urosomal somites and caudal setae match those of *Monstrilla*, whereas the modifications of setal element $2d_2$ involving elongation and plumosity, are more like those in some species of *Cymbasoma*. Molecular analysis provides an alternative means of compensating for uncertainties and defects caused by insufficient morphological information, and it

has been regarded as useful both for distinguishing species and the proper matching of males and females of the same species (Suárez-Morales, 2011). The molecular evidence presented herein strongly supports the separation of *Caromiobenella* **gen. nov.** from *Monstrilla*, with an about two-fold difference between the within-genus and between-genera divergences: 23.24% within-genus, 48.15% between-genera for mtCOI and 11.50% within-genus, 22.07% between-genera for 28S rRNA. The mean genetic divergences between the two genera were 42.18% and 26.67%, respectively, for mtCOI and 28S rRNA. The intra-generic divergences of *Caromiobenella* **gen. nov.** (19.05%, 11.81%) and *Monstrilla* (14.53%, 8.41%) were low compared to any between-genera comparisons (Table 2), which indicates that the species of the two genera can hardly be classified together as a single lineage. The ML and BI trees (Figs. 11, 12) also show clear separations of the two genera with high branch supporting values, although the topologies of the phylogenetic trees, especially those based on mtCOI data (Fig. 11), seem somehow blurry with low branch confidence values. Machida & Tsuda (2010) pointed out potential limits on using mtCOI genes as barcodes for species identification by considering the existence of nuclear mitochondrial pseudogenes, the occurrence of mitochondrial introgression, and the pattern of descent, via maternal inheritance. Such unpredictable factors may also be responsible for some uncertainties in the phylogenetic trees. In contrast, the phylogenetic trees based on 28S rRNA (Fig. 12) showed rather rigid generic-level clustering with high supporting values. Although the 28S rRNA trees do not present exactly the same topologies as those based on mtCOI, this discrepancy is not important for the limited question of the relationship between *Caromiobenella* **gen. nov.** and *Monstrilla*. It is, however, still worth noting that molecular analyses with other genes such as mitochondrial cytochrome *b*, 12S ribosomal RNA, and nuclear 18S ribosomal RNA, as well as combined data analyses of such multi-gene sequences, would help lead us toward a better understanding of the true molecular phylogenetic relationships among the genera.

The mean within-species genetic divergence of mtCOI sequences was 0.47%. The value was even lower, at 0.18%, for *Caromiobenella castorea* **sp. nov.** and 1.07% for *C. hamatapex*; the three sequenced specimens of *C. polluxea* **sp. nov.** were identical in this respect. Previous molecular studies based on more than eight animal phyla indicate that a genetic divergence threshold of about 10% is typical between congeneric species (Hebert *et al.*, 2003), with Crustacea showing 15.4% mean genetic divergence among congeneric species (Hebert *et al.*, 2003: table 1), and with the majority of such species exhibiting 16% to 32% divergence. Three species of *Caromiobenella* **gen. nov.** showed 19.05% within-genus mean divergence, and 23.24% between-species mean divergence. The within-genus and between-species values are much higher than the threshold of 10% generally used for distinguishing species. These results are generally consistent with another molecular study of Korean monstrilloids (Baek *et al.*, 2016). The ML and BI trees show clear separations between *C. castorea* **sp. nov.**, *C. polluxea* **sp. nov.**, and *C. hamatapex* as well (Figs. 11, 12). The molecular results based on 28S rRNA show no genetic differences within nominal species, 11.50% within-genus mean divergence for each monstrilloid genus, and particularly 11.81% divergence in the new genus. These results also tend to support the establishment of *Caromiobenella* **gen. nov.**, for *C. castorea* **sp. nov.** and *C. polluxea* **sp. nov**.

Remarks on Haemocera

Haemocera Malaquin, 1896, one of the doubtfully valid monstrilloid genera according to Grygier & Ohtsuka (2008) and Suárez-Morales (2011), is usually considered to contain at least four nominal species, *Haemocera danae* (Claparède, 1863) (type species), *H. roscovita* Malaquin, 1901, *H. filogranarum* (Malaquin, 1896), and *H. ostroumowii* (Karavayev, 1895) (Malaquin, 1896, 1897, 1901), although several other species have at one time or another been assigned to this genus. In order to propose the present new genus, we must be sure that its type species, *C. castorea* **sp. nov.**, is not a congener of the type species of *Haemocera*.

Suárez-Morales *et al.* (2006) tentatively assigned *Haemocera filogranarum* to *Monstrillopsis* because the original figure (Malaquin, 1901: fig. 3) showed four caudal setae, two postgenital somites, and an unarmed, reduced inner lobe on the fifth leg. The status of *H. danae* and *H. roscovita* remained uncertain. The illustrations of urosomes by Malaquin (1901: figs. 2, 5) also showed some of the generic characters of *Monstrillopsis* but they also show three caudal setae. The two new species of *Caromiobenella* **gen. nov.** have different numbers of caudal setae, six in *C. castorea* **sp. nov.** and five in *C. polluxea* **sp. nov**. Our molecular results, however, demonstrate that caudal seta number is not crucial for distinguishing the new genus since both species were placed into a single lineage (Figs. 11, 12). Some variability in the number of caudal setae, either three or four, occurs in *Cymbasoma* as well, including between two sexes of *C. rigidum* Thompson, 1888, *C. longispinosum*, *C. tumorifrons* (Isaac, 1975), *C. quintanarooense* (Suárez-Morales, 1994), and *C. chelemense* Suárez-Morales & Escamilla, 1997. The number of caudal setae thus cannot be used to strictly distinguish genera.

The illustrations of adult *Haemocera danae* provided by Malaquin (1901: pl. 2) show more details. Despite having three caudal setae, the female shows several *Monstrillopsis*-like features in its prosomal part, such as the prominent eye and anteriorly located oral papilla. The male also appears as a typical *Monstrillopsis* with four caudal setae and a type-2 distal antennular segment (*sensu* Huys & Boxshall, 1991) with a hyaline bump on the inner proximal margin and a slightly curved, sabre-like apical spine. Because the female and male specimens of Malaquin (1901) were obtained from the same polychaete host, *Salmacina dysteri* (Huxley, 1855), both sexes seem to be conspecific. The two other *Haemocera* species in Malaquin (1901), *H. danae* and *H. roscovita*, which are known only from females, also seem to be assignable to *Monstrillopsis* even though they have three rather than the usual four caudal setae. If all of Malaquin's species of *Haemocera*, in particular its type species *H. danae*, are referable to *Monstrillopsis*, then none is congeneric with *C. castorea* **sp. nov.** and we are free to erect the present new genus. A nomenclatural problem arises because *Haemocera* has priority over *Monstrillopsis*, resolution of this latter problem is, however, beyond the scope of the present study.

Differentiation of monstrilloid genera by their hosts

Monstrilloid juveniles have been reported as endoparasites of several kinds of marine invertebrates (Boxshall & Halsey, 2004; Huys *et al.*, 2007). At least 10 species of polychaetes are known as hosts (Table 3).

These polychaete hosts can be broadly divided into two groups on the basis of their habitat and lifestyle: a benthic group living in or on the sediment (families Syllidae, Capitellidae, and Spionidae) and a group of sedentary forms inhabiting calcareous tubes (Serpulidae). Several species of *Monstrilla* and *Cymbasoma* with type-1 male antennules have been reported from the first group, whereas *Monstrillopsis* with type-2 male antennules have been reported from the second. Although information is limited, host specificity so far appears to be consistent with antennular modification.

Concerning host specificity the species of *Haemocera* infecting polychaetes, Nelson-Smith & Gee (1966) emphasized the occurrence of different monstrilloids in different polychaete hosts (*Cymbasoma rigidum* (= *H. danae*) in *Salmacina* and *C. filogranarum* (= *H. filogranarum*) in *Filograna implexa* Berkeley, 1835) to reinforce the contention that these two polychaete species are distinct. Kupriyanova *et al.* (2001) confirmed that the polychaete host of Malaquin (1901) infected by "*H. danae*" was indeed a species of *Salmacina*. The copepods behind the record of monstrilloid

Table 3. Polychaete hosts of monstrilloid copepods.

Polychaete	Family	Habitats	Associated monstrilloid	Currently accepted name (or possible genus)
Syllis gracilis Grube, 1840	Syllidae	Common on hard substrata, also inhabiting marine sediments, especially coarse sand. Most having an interstitial lifestyle (San Martín & Worsfold, 2015)	*Thaumaleus malaquini*	*Cymbasoma malaquini* (Caullery & Mesnil, 1914)
Exogene sp.			unidentified monstrilloid	-
Haplosyllis sp.			*Monstrilla* sp.	*Monstrilla* sp.
Capitella capitata oculata Hartman, 1961	Capitellidae	Found in many sediment types from intertidal to deep sea. Most living in mucous-lined tubes or burrows (Dean, 2001)	*Monstrilla capitellicola*	*Monstrilla capitellicola* Hartman, 1961
Dipolydora giardi (Mesnil, 1893)	Spionidae	Most living on soft bottoms, moving freely in sediment near the surface or dwelling in more or less temporary or permanent tubes (Radashevsky, 2012)	*Thaumaleus germanicus*?	*Cymbasoma* sp.*
Polydora ciliata (Johnston, 1838)			*Thaumaleus germanicus*	*Cymbasoma germanicum* (Timm, 1893)
Salmacina dysteri	Serpulidae	Sedentary polychaetes inhabiting calcareous tubes (Ten Hove & Kupriyanova, 2009)	*Haemocera danae*	*Monstrillopsis danae***
Salmacina setosa Langerhans, 1884			*Haemocera roscovita*	*Monstrillopsis roscovita***
Filograna implexa			*Haemocera filogranarum*	*Monstrillopsis filogranarum***
Serpula vermicularis Linnaeus, 1767			unidentified monstrilloid	*Monstrillopsis* sp.****

* Caullery & Mesnil (1914) tentatively identified the endoparasitic monstrilloid juveniles from *Dipolydora giardi* as *Thaumaleus germanicus*.
** The present study proposed possible synonymy of *Haemocera* and *Monstrillopsis*.
*** The species identified based on the illustrations of Huys & Boxshall (1991: fig 2.5.3A–C).

juveniles in *F. implexa* from near Plymouth, U.K (Faulkner, 1930), and records from Okinawa (Nishi, 1991) of juvenile monstrilloids infecting both *S. dysteri* and *F. implexa* (see Nishi in Grygier, 1995 for the latter) remain unidentified. This subject is complicated by the fact that several authors have identified *H. danae* of Malaquin, a parasite of the serpulid polychaete *Salmacina dysteri*, with *Thaumaleus rigidus* Thompson, 1888 (currently *Cymbasoma rigidum*), whereas several others have disagreed (reviewed by Grygier, 1995). Suárez-Morales (2006) considered *C. rigidum* a species complex in needed of revision, but did not discuss its possible synonymy with Malaquin's *H. danae*.

We tentatively recognize Malaquin's species of *Haemocera* as belonging to *Monstrillopsis* based on the figures of Malaquin (1901) and the current generic diagnosis of *Monstrillopsis*, although a possible nomenclatural problem between *Haemocera* and *Monstrillopsis* then arises. It may further be that *H. danae* of Malaquin and part of the so-called *C. rigidum* belong to a single species of *Monstrillopsis* (or *Haemocera*). In any case, all of the monstrilloid species so far discussed and possibly assignable to *Monstrillopsis* (or *Haemocera*, depending on nomenclature) were from serpulid tubeworms.

It is worth noting that the endoparasitic stages of *Caromiobenella helgolandica* have been reported from the pyrimidellid gastropod *Brachystomia scalaris* (MacGillivray, 1843) (as *Odostomia rissoides* Hanley, 1844; see Pelseneer, 1914; Gallien, 1934). Gallien (1934) found both sexes of *C. helgolandica* in the same host and the males he depicted show the type-3 antennular modification. Perhaps the other species of *Caromiobenella* **gen. nov.** infect gastropods as well.

Unknown females of the new species

The diagnosis for *Caromiobenella* **gen. nov.** is exclusively based on males of the two new Korean species. *Caromiobenella hamatapex* is currently known only from females, and females of some other congeners are known, but the generic diagnosis was not based on these females. We did not find female monstrilloids in the same samples where the males of *C. castorea* **sp. nov.** and *C. polluxea* **sp. nov.** were found, and the generic diagnosis will remain incomplete until information on the females of these species becomes available. Previous studies provide some relevant information of the morphological characters of females that might be diagnostic, but such information must be used with caution. Pelseneer (1914) mentioned a bent, unarticulated fifth leg for the adult female of *Monstrilla helgolandica* (= *C. helgolandica*), and this feature is shared by the specimens of Claus (1863) and Timm (1896) as well as other material of female *M. helgolandica* (Scott, 1909; Sars, 1921; Gallien, 1934; Sewell, 1949; Park, 1967; McAlice, 1985). Not all of these

records are likely to pertain to the same species, but may represent a species complex (Suárez-Morales, 2011). Suárez-Morales *et al.* (2008) also suggested that the Argentine specimens recorded as female *M. helgolandica* (*sensu* Ramírez, 1971) could be conspecific with the male *M. patagonica* (= *C. patagonica*). These females also share a similar leg 5 structure with the *M. helgolandica* species complex. Females of *M. hamatapex* (= *C. hamatapex*) also have the same type of uniramous fifth legs (Grygier & Ohtsuka, 1995; Chang, 2014). In contrast, females of most species of *Monstrilla* have biramous fifth legs, albeit with quite variable setation patterns (Suárez-Morales, 2011), so a uniramous leg 5 is potentially a characteristic feature, if not an exclusive one, of female *Caromiobenella* **gen. nov**.

Two studies of female *Caromiobenella hamatapex* (as *Monstrilla hamatapex*) with unusually detailed illustrations of integumental structures (Grygier & Ohtsuka, 1995; Chang, 2014) provide some morphological congruence with the males of the two new species. These common features might eventually prove suitable for the generic diagnoses of both sexes. These mainly concern pore patterns, including the two pairs of prominent, crater-like pores on the anterior dorsum of the cephalothorax and the two longitudinal rows of four pores each, arranged in pairs across midline, on the dorsum of the incorporated first thoracic segment. A modified antennular setal element (spine $2d_2$) is also consistently present in both males and females, as far as is known.

Another morphological feature that might be diagnostic for the new genus is the absence of two short, thin sensilla on the forehead. The actual status of this feature in female *Caromiobenella hamatapex*, which has not been illustrated or explicitly described, remains uncertain.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

Table S1. Specimens analyzed for mtCOI and 28S rRNA with information of sex of individuals, sampling sites, date of collections, and GenBank accession numbers.

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