

A New Species of *Eudactylopus* (Copepoda: Harpacticoida) from the South Coast of Korea Based on Morphological and Molecular Evidence

Dae Hyun Cho¹, Jin Hee Wi², Hae-Lip Suh^{1,*}

¹Department of Oceanography, Chonnam National University, Gwangju 61186, Korea

²School of Earth Sciences and Environmental Engineering, Gwangju Institute of Science and Technology, Gwangju 61005, Korea

ABSTRACT

A new species of *Eudactylopus* Scott A., 1909 is described from the southern coast of Korea. The specimens were collected using a light trap set overnight at the entrance near a pier. *Eudactylopus yokjidoensis* n. sp. is similar to *E. andrewi* Sewell, 1940 and *E. spectabilis* (Brian, 1923) in two key respects: similar length of proximal and distal inner setae on female P2 enp-2, and modification of two subapical setae on male P2 endopod. However, *E. yokjidoensis* can be differentiated from the two species by following morphological characteristics: in females, the length ratio of cephalothorax/2nd-4th thoracic somites combined is smaller in *E. yokjidoensis* than other two species (1 : 0.8 vs. 1 : 1); antennule has nine segments (vs. 7-segmented in *E. andrewi*); P2 to P4 each bears a process in medial distal margin of basis, while it is just smooth in *E. spectabilis*; in males; the length ratio of cephalothorax to 2nd-4th thoracic somites combined is smaller in *E. yokjidoensis* than other two species (1 : 0.6 vs. 1 : 1 in *E. andrewi* and 1 : 0.8 in *E. spectabilis*); and P5 exopod has a comb-like innermost seta, while it is bipinnate seta in *E. spectabilis*. To prove the Korean species of *Eudactylopus* to be new, full descriptions of both sexes are given here, and the claim is supported by distinct genetic differences between *E. yokjidoensis* and *E. spectabilis* (22.3–22.7%) in the mitochondrial gene cytochrome oxidase subunit I (mtCOI) sequence.

Keywords: meiobenthos, barcoding, marine, Thalestridae, taxonomy

INTRODUCTION

The family Thalestridae Sars, 1905 contains 25 genera and five subfamilies (Boxshall and Halsey, 2004). Thalestrid harpacticoids inhabit various environments including macroalgae (Boxshall and Halsey, 2004). According to Hicks (1980), in the harpacticoid fauna of algal samples, the thalestrid species are the second highest in abundance after the family Harpacticidae Dana, 1846. Certain species in the family Thalestridae have been reported as causes of algae infections, as follows: *Ameonophia orientalis* Ho and Hong, 1988 and *Parathalestris infestus* Ho and Hong, 1988 infected the brown algae *Undaria pinnatifida* (Harvey) Suringar and *Thalestris hokkaidoensis* Takemori and Iwasaki, 2009 infected the red algae *Palmaria palmara* (Linnaeus) Kuntze.

The collection of the genus *Eudactylopus* Scott A., 1909

was conducted using diverse sampling methods such as washing (Itô, 1974; Sewell, 1940), dredging (Nicholls, 1941), sledging (Geddes, 1969), and the light trap (Chang and Song, 1995). The light trap is a sampling device for the collection benthic copepods in aquatic systems (Holmes and O'Connor, 1988). *Eudactylopus spectabilis* (Brian, 1923) and *E. andrewi* Sewell, 1940 from the South Korea have been described through using a harbor-based light trap by Chang and Song (1995); for a direct comparison with the previous South Korea results, the same sampling method was used in this study.

The systematic position and the species composition of the family have been controversial subjects over several decades (Lang, 1936, 1944; Hicks, 1988; Willen, 2000). The subfamily Eudactylopusiinae Willen, 2000 is characterized by a unique feature of enp-2 of P2–P3 with its two inner

© This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/3.0/>) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

***To whom correspondence should be addressed**

Tel: 82-62-715-3523, Fax: 82-62-715-3314
E-mail: suhhl@chonnam.ac.kr

setae that includes two genera of *Eudactylopus* and *Neodactylopus* Nicholls, 1945. They are separated by the relative length of exp of P1 (shorter than the enp in *Eudactylopus* vs. longer than the enp in *Neodactylopus*) (Vervoort, 1964).

The genus *Eudactylopus* was erected by Scott A. (1909), designating *Dactylopus latipes* Scott T., 1894 as the type species, which was characterized by 2-segmented enp of the antennae and well developed P5 of the female. However, *E. latipes*, a name that was later rejected by Vervoort (1964) due to its homonymy with *Dactylopus latipes* Boeck, 1865 [= *Paradactylopodia latipes* (Boeck, 1865)], was subdivided by Sewell (1940) into the two forms of *E. latipes* f. *typica* and *E. latipes* f. *andrewi*. These two forms were revised as the two subspecies, *E. andrewi atlanticus* and *E. andrewi andrewi* by Vervoort (1964) and then Itô (1974) subsequently defined them as the two distinct species *E. atlanticus* Vervoort and *E. andrewi* Sewell. *Eudactylopus robustus* was originally described as *Thalestris robusta* from Nice, France by Claus (1863) and later changed to *E. robustus* by Lang (1936). Brady (1905) recorded *Thalestris robusta* Brady, 1905 from tidal pools at Cullercoats, UK, but Wilson (1925) changed the specific name to *T. valida* Wilson, 1925, according to the nomenclature rule. *Eudactylopus spectabilis* (Brian, 1923) was formerly described as *Parathalestris clausi* var. *spectabilis* from the Mediterranean Sea, but Brian (1928) assigned it as the distinct species, *Parathalestris spectabilis*. It was then moved under the genus *Eudactylopus* by Monard (1928). Nicholls (1941) reported a new species based on the female of *E. australis* in the southwestern Pacific. A large genital-double somite, which is almost equal to the combined length of the remaining three urosomal segments, characterizes this species. This species was considered as a synonym of *E. robustus* by Noodt (1955), but Lang (1965) defined it as a distinct species. Geddes (1969) reported *E. lucayosi* that was characterized by a peculiar caudal-rami structure in the northwestern Atlantic. However, of the above-mentioned species, only a few species were nominated. Brian (1928) established the genus *Plesiothalestris* with the description of the new species *P. opima* from Symi Island in Greece, but the genus was relegated to the synonymy of *Eudactylopus* by Sewell (1940). Later, *E. opima* was regarded as a synonym of *E. robustus* by Lang (1965). *Eudactylopus fasciatus*, and *E. striatus* Sewell, 1940 described from the Indian Ocean, were each considered as a subspecies or another junior synonym of *E. robustus* by Noodt (1955). However, Vervoort (1964) and Lang (1965) followed the definition of Sewell (1940). Currently, it remains *incertae sedis* in terms of the genus *Eudactylopus* since the intervention of Bodin (1997). The distinction of *E. krusadensis* Krishnaswamy, 1950, questioned by Lang (1965) due to incomplete descriptions and drawings, and it

has been considered as a misidentification for a Diosaccidae species. Currently, the genus *Eudactylopus* contains the following six species: *E. andrewi*, *E. atlanticus* Vervoort, 1964, *E. australis* Nicholls, 1941, *E. lucayosi* Geddes, 1969, *E. robustus* (Claus, 1863), and *E. spectabilis*.

In this study, we comprehensively compare the new species of *Eudactylopus* and other described species of the genus, based on diagnostic characteristics utilized in the previous literatures. Full descriptions of the morphological characteristics of the new species and the mitochondrial cytochrome oxidase subunit I (mtCOI) sequences are provided.

MATERIALS AND METHODS

The specimens of *Eudactylopus yokjidoensis* were collected from the macroalgal beds on the sandy bottoms of the four stations of Donghang-ri, Yokji-myeon, Tongyeong-si, and Gyeongsangnam-do, Korea, in Apr 2016. The specimens were collected using a light trap and fixed in 99% ethanol. The specimens were then dissected under a dissecting microscope (SMZ645; Nikon, Tokyo, Japan), placed in a mounted CMC-10 aqueous mounting medium (Maters Company, Inc., Wood Dale, IL, USA), mounted on slides, and sealed with high-quality nail varnish. Drawings were made with the Nikon Eclipse Ci differential-interference-contrast microscope equipped with a drawing tube. For scanning electron microscopy, copepods were dehydrated through a series of graded ethanol, acetone, and hexamethyldisilazane concentrations, mounted on aluminum stubs, and sputtered with gold and then observed using the Hitachi S-3000N (Tokyo, Japan).

The total length of each specimen was measured from the tip of the cephalothorax to the posterior end of the anal somite in the lateral view. The scale bars in the figures were marked in micrometers (μm). The terminologies of the body and appendages morphologies were based on Huys and Boxshall (1991). The type materials were deposited in the collections of the Marine Biodiversity Institute of Korea (MABIK) in Seocheon, Korea.

The following abbreviations are used in this text: Ae, aesthetasc; benp, baseoendopod; enp, endopod; enp-1 (2, 3), proximal (middle, distal) segment of the endopod; exp, exopod; exp-1 (2, 3), proximal (middle, distal) segment of the exopod; and P1–P6, first to sixth thoracopod.

Ethanol-preserved specimens were rehydrated in distilled water for 2 h before the DNA-extraction procedure. The DNA was extracted using the Chelex 100 Bio-Rad method (hereafter referred to as “Chelex”), which is a protocol adapted from the utilization of Walsh et al. (1991). In this

procedure, the specimen is dissolved in 200 μ L of a 10% (w/v) solution of Chelex and 10 μ L of proteinase K (10 mg/mL), and then it is incubated at 56°C for 120 min with thorough mixing for 60 min. Following this incubation, the tubes are centrifuged at 6,000 \times g for 1 min, and the supernatant containing the genomic DNA is used directly as a template in the downstream polymerase chain reaction (PCR) analysis. The DNA sequences were accomplished using the mitochondrial COI gene. The gene was amplified through the PCR using a PCR premix (Bioneer Co., Daejeon, Korea) in an Eppendorf PCR thermal cycler (Eppendorf Inc., Hamburg, Germany). The amplification primers that were used are the “universal” primers LCO1490 and HCO2198 (Folmer et al., 1994). The amplification protocol is as follows: initial denaturation of 94°C under 300 s, 34 cycles of denaturation under 94°C for 30 s, annealing at 42°C for 120 s, extension at 72°C for 60 s; final extension at 72°C for 600 s, and storage of the final product at 4°C.

The PCR results were checked using the electrophoresis of the amplification products on 1% agarose gel with ethidium bromide. The PCR products were purified with a LaboPass PCR-purification kit and sequenced in both directions using the 3730xl DNA analyzer (Macrogen, Korea). Multiple-sequence alignments were made using Chromas version 2.5.1 (Technelysium Pty Ltd., Tewantin, Queensland, Australia). Pairwise distance measures and a phylogenetic analysis were conducted using MEGA 6 software (Tamura et al., 2013). Any ambiguous sites were eliminated from the dataset. The mtCOI sequence for *Eudactylopus spectabilis* (Brian, 1923) and *Parathalestris parviseta* Chang and Song, 1997 was obtained from the NCBI database (<http://www.ncbi.nlm.nih.gov>) for the phylogenetic analysis.

SYSTEMATIC ACCOUNTS

Subclass Copepoda Milne Edwards, 1830
 Order Harpacticoida Sars, 1903
 Family Thalestridae Sars, 1905
 Subfamily Eudactylopusiinae Willen, 2000
 Genus *Eudactylopus* Scott A., 1909

Eudactylopus yokjidoensis n. sp. (Figs. 1–7)

Material examined. Holotype. ♀, collected from Yokjido Island in the south coast of Korea (34°38'5.24"N, 128°15'59.42"E, 4 m depth, collector: Cho DH) on 14 Apr 2016, dissected and mounted on five slides (MABIK CR00240677).

Allotype. ♂, dissected and mounted on four slides (MABIK CR00240678), same data as holotype.

Additional paratypes. 1♂, partially dissected and mounted

on one slide (MABIK CR00240679), 8♀ (MABIK CR00235328–CR00235333, MABIK CR00240680–CR00240681) and 8♂ (MABIK CR00235334–CR00235338, MABIK CR00240682–CR00240684) in 70% ethanol, respectively.

Etymology. The species is named after its type locality, Yokjido Island, in the south coast of Korea.

Description of the adult female. Body (Figs. 1A, B, 6A, B) fusiform, total length 1500 μ m (range, 1,500–1,663; mean, 1,597; n=9). Maximum width measured at posterior margin of cephalic shield: 433 μ m (range, 433–455; mean, 445; n=9). All somite with distal hyaline membrane except fifth pedigerous somite and anal somite. Prosome (Figs. 1A, B, 6A, B) comprising cephalothorax with completely fused first pedigerous somite and three free pedigerous somites, 1.2 times as long as urosome excluding caudal rami, similar length including caudal rami. Urosome (Figs. 1A, B, 6A, B) 5-segmented, comprising fifth pedigerous somite, genital double-somite (fusion of genital and first abdominal somites) and three abdominal somites. Genital and third abdominal, and posterior part of genital double-somite and second abdominal somite with 1 or 2 oblique rows of spinules on both lateral surfaces, respectively. Genital double-somite (Figs. 1A, 6A) as long as wide in dorsal view, partly fused in ventral view, with gonopore ventromedially (Figs. 1C, 6G). Penultimate somite forming pseudoperculum (Fig. 1A) with protrusion at middle dorsal end. Anal somite (Fig. 1A) approximately half as long as preceding somite. Caudal rami (Figs. 1A, D, 6A) truncate, about twice as long as anal somite, approximately 1.3 times as long as wide, inner margin unornamented, with 7 setae: seta V covered with fringed setules basally at dorsal view (Fig. 6B, D, F), seta VI bulbous basally and with setules along inner margin. Rostrum (Figs. 1A, B, 2A, 6E) not fused to cephalothorax, nearly triangular, with mid-dorsal paired sensilla and dorsal pore anteriorly.

Antennule (Fig. 2A) 9-segmented, approximately 0.4 times as long as cephalothorax, gradually tapering apically, relative lengths (%) of segments measured from proximal end along caudal margin 26.5 : 13.3 : 14.5 : 15.7 : 6.0 : 7.8 : 5.4 : 3.6 : 7.2; first segment large, bearing 1 seta on posterior margin and 2 rows of spinules on anterior margin; second segment with 7 simple setae on posterior margin, 2 naked setae on anterior margin and 2 setae on outer distal margin; third segment with 2 setae on posterior margin and 6 setae on outer distal margin; fourth segment with 2 setae on posterior margin, long slender apical aesthetasc fused basally to 1 apical seta, and 1 seta on outer distal margin; fifth segment with 1 long seta on outer distal margin; proximal 5 segments stronger than distal 4 segments; sixth segment with 3 simple setae on outer distal margin; seventh and eighth segments with 1 apical and 1 inner marginal setae, respectively; ninth

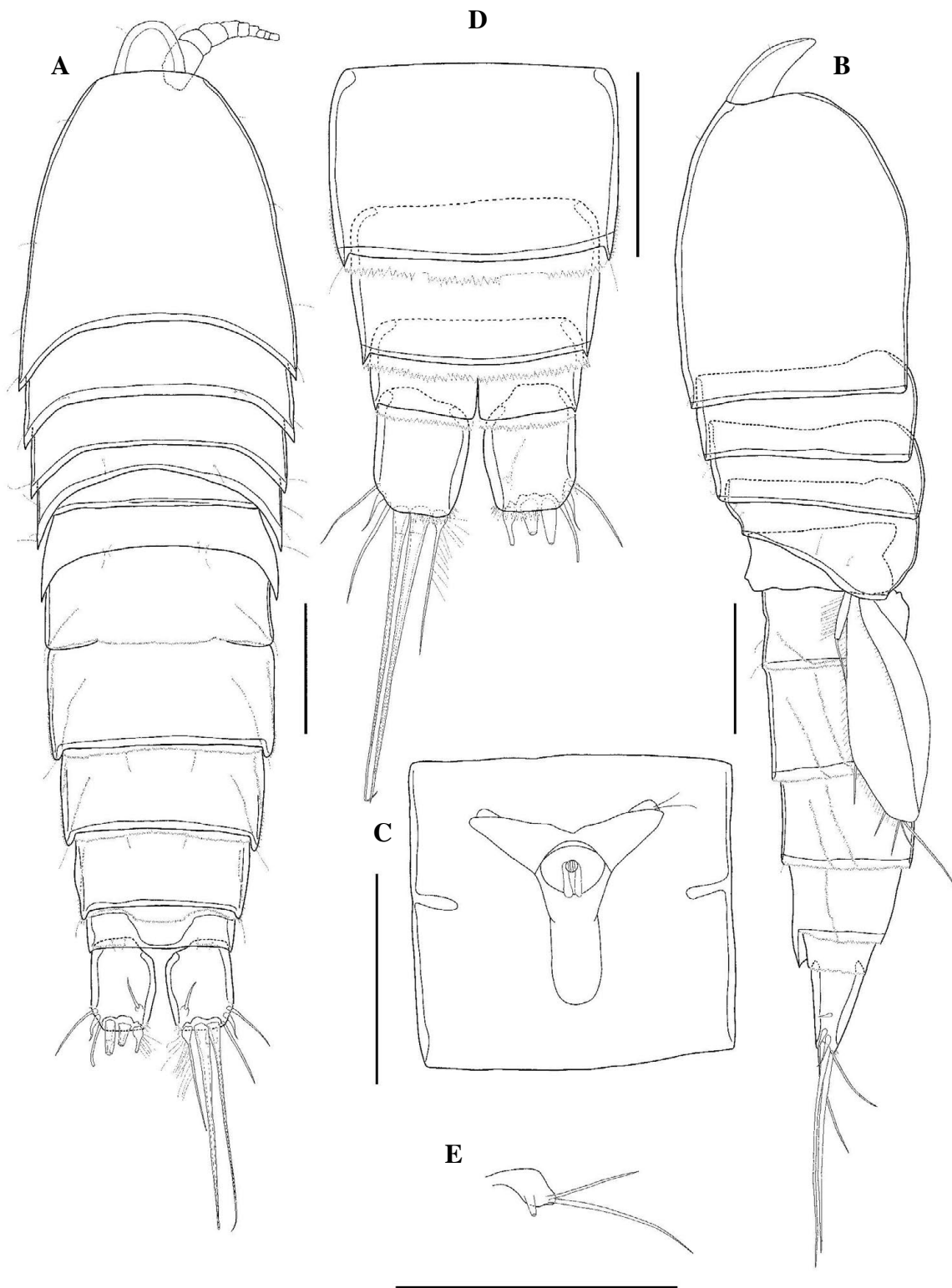


Fig. 1. *Eudactylopus yokjidoensis* n. sp., female (holotype). A, Habitus, dorsal view; B, Habitus, lateral view; C, Genital double-somite, ventral view; D, Urosome, ventral view; E, P6. Scale bars: A-D=200 μ m, E=100 μ m.

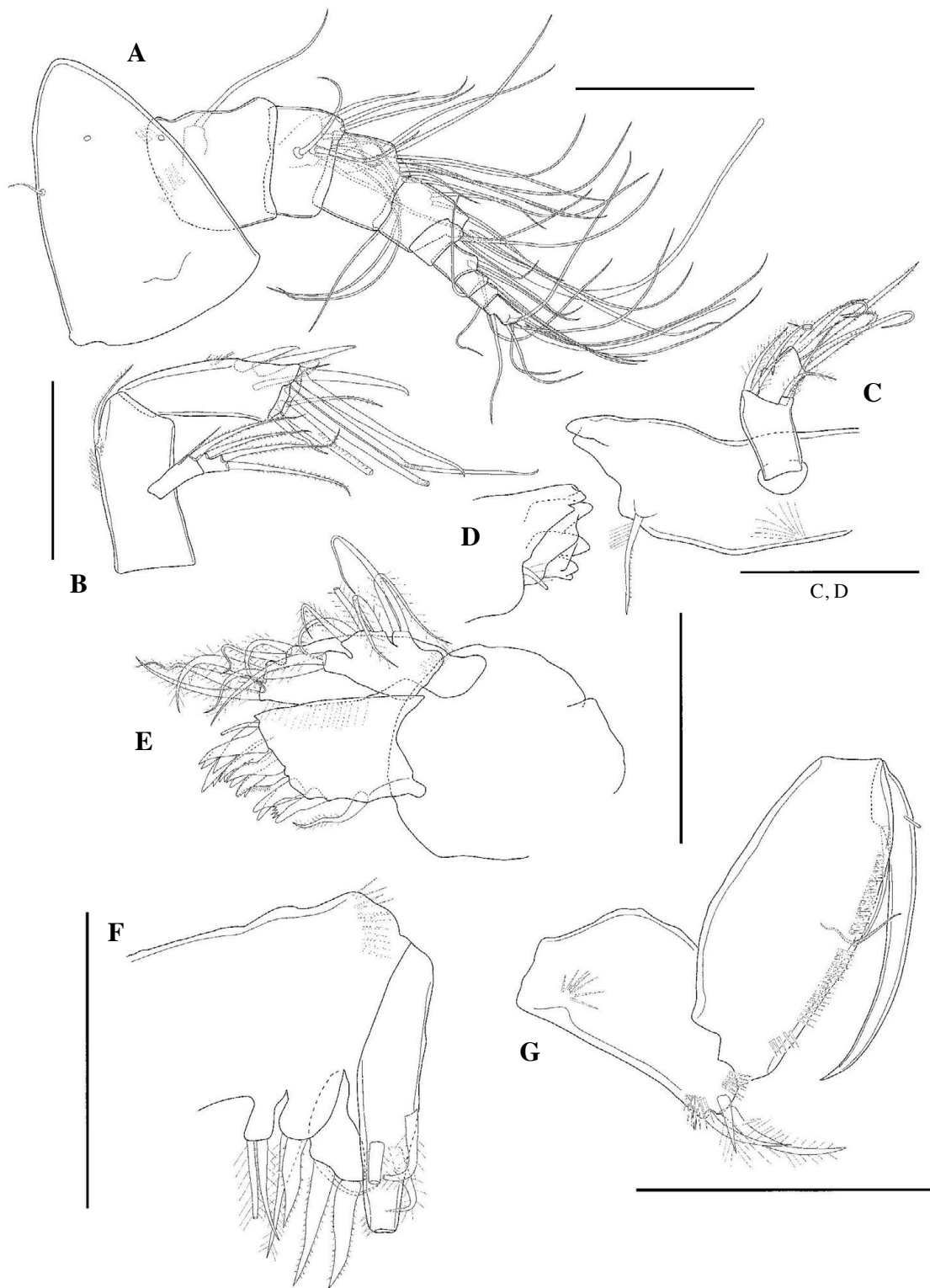


Fig. 2. *Eudactylopus yokjidoensis* n. sp., female (holotype). A, Rostrum and antennule; B, Antenna; C, Mandible; D, Gnathobase of mandible; E, Maxillule; F, Maxilla; G, Maxilliped. Scale bars = 100 μ m.

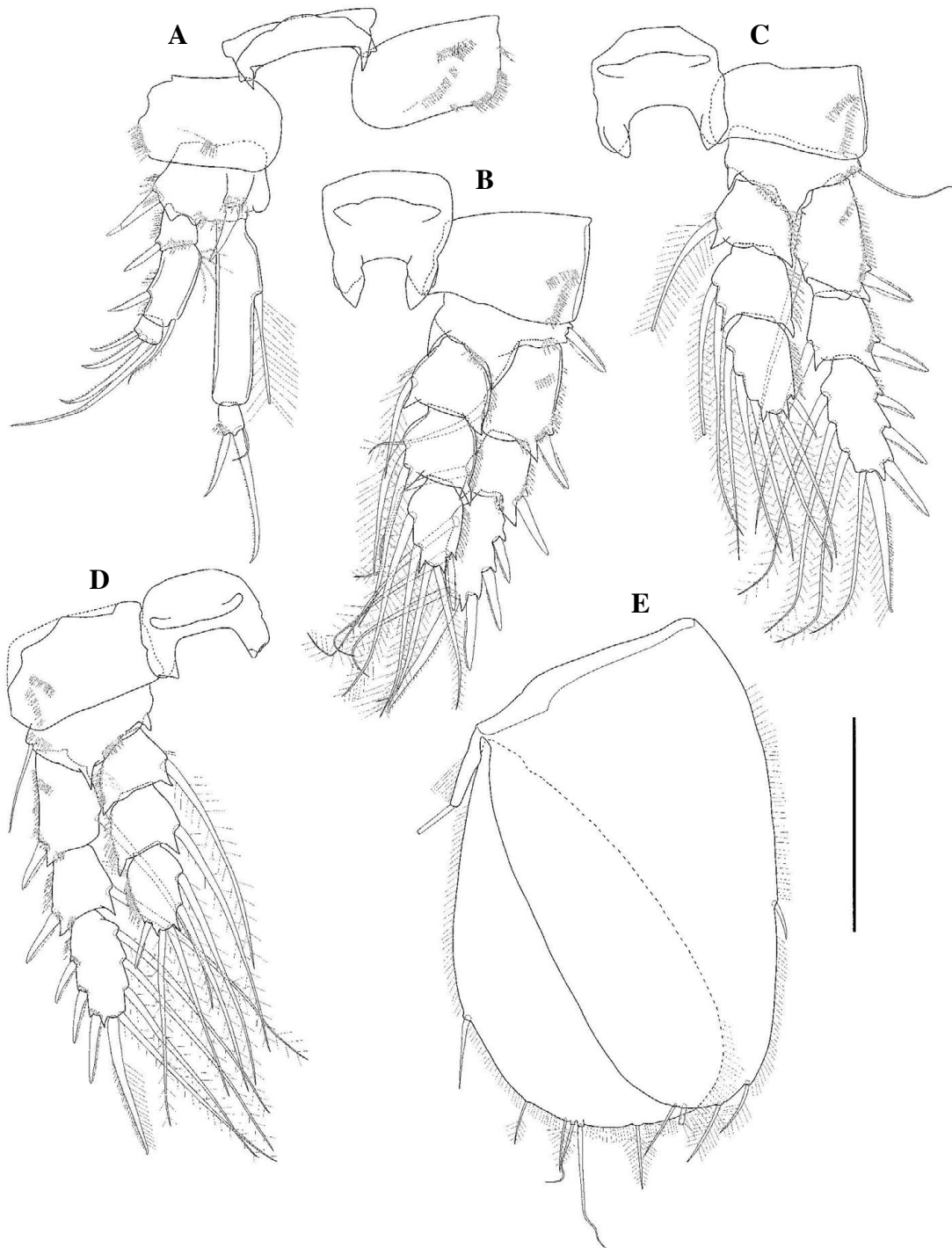


Fig. 3. *Eudactylopus yokjidoensis* n. sp., female (holotype). A, P1, anterior view; B, P2, anterior view; C, P3, anterior view; D, P4, anterior view; E, P5, anterior view. Scale bar=200 μ m.

segment with 1 subapical seta on inner margin, 5 long setae and aesthetasc fused basally to 1 seta apically. Armature formula as follows: 1/11/8/3 + (1 + Ae)/1/3/2/2/6 + (1 + Ae).

Antenna (Fig. 2B) with allobasis and free 1-segmented enp. Allobasis elongate with 1 unipinnate abexopodal seta in distal quarter, and with some spinules along abexopodal

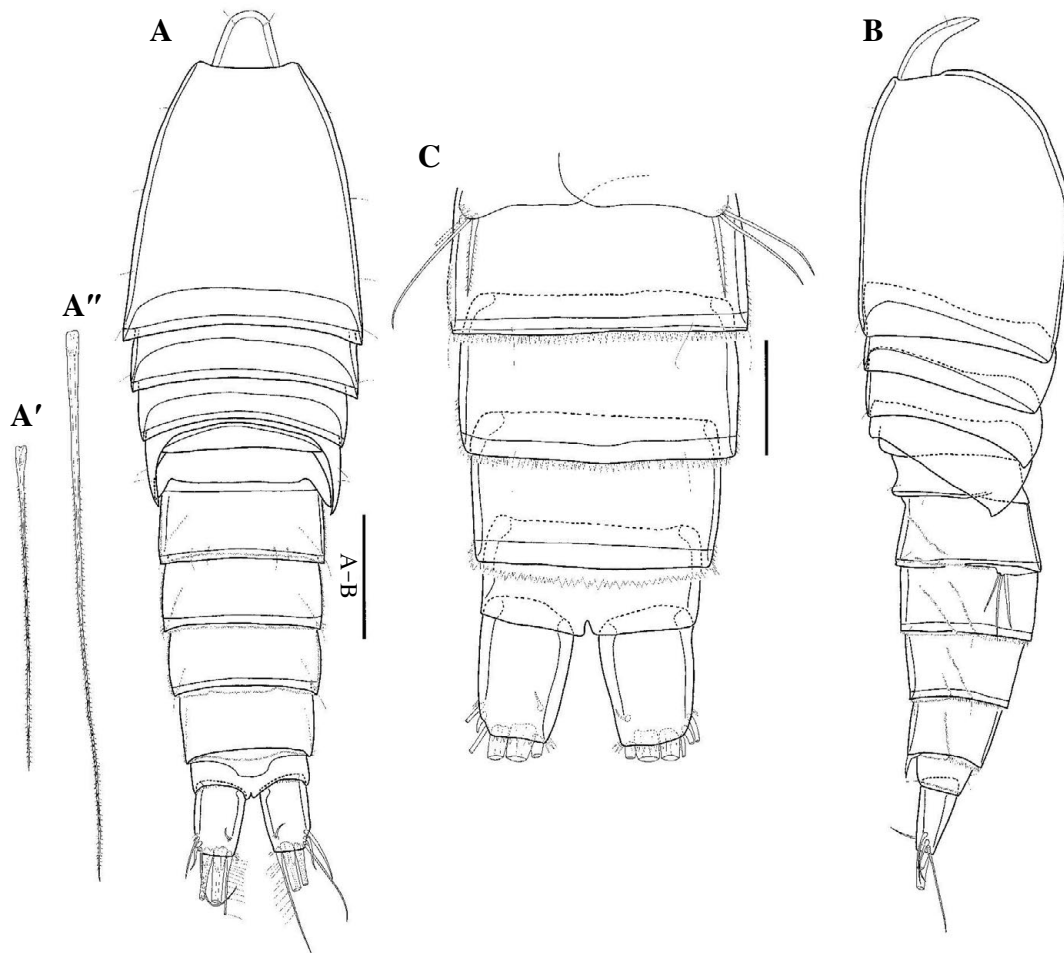


Fig. 4. *Eudactylopus yokjidoensis* n. sp., male (allotype). A, Habitus, dorsal view; A', Partial view of seta IV; A'', Partial view of seta V; B, Habitus, lateral view; C, P6 and urosome. Scale bars: A, B=200 μ m, C=100 μ m.

margin. Exp 2-segmented; exp-1 longer than exp-2, with 1 naked subdistal seta and 1 bipinnate distal seta; exp-2 with 1 bipinnate subapical seta and 2 bipinnate apical setae. Endopodal segment ornamented with spinules along inner margin, inner medial margin with 2 robust spines ornamented with crenulations along medial margin and 2 simple setae, distal margin with 1 spine and 5 setae.

Mandible (Fig. 2C, D) coxa with some setules near base of basis. Gnathobase well-developed, with 4 blunt teeth and 1 long seta distally. Palp biramous comprising basis, 1-segmented endopod and 1-segmented exopod (fused to basis basally). Basis with 2 setae. Exp represented by lobe, with 2 setae. Enp with 1 bipinnate seta on lateral margin and 2 bipinnate, 1 naked, and 1 bipinnate setae fused basally to 1 simple seta on distal margin.

Maxillule (Fig. 2E). Arthrite of precoxa with 1 bipinnate seta on lateral margin, 7 spines, and 1 seta along distal mar-

gin. Coxa elongate, with 2 bipinnate subapical setae and 3 bipinnate apical setae. Basis with 2 apical setae. Exp and enp 1-segmented, fused to basis and represented by lobe armed with 2 and 4 bipinnate setae, respectively.

Maxilla (Fig. 2F) with several spinules on outer margin, and 3 endites on syncoxa; proximal endite armed with 2 slender bipinnate setae; middle endite with 1 bipinnate spine and 1 bipinnate seta; distal endite with 2 bipinnate spines and 1 naked seta; basis drawn into strong, unipinnate claw, with 2 bipinnate setae near base; enp fused to basis, represented by 1 seta on outer distal margin of basis.

Maxilliped (Fig. 2G) subchelate, comprising syncoxa, basis, and enp. Syncoxa with 3 spinulose setae on inner distal margin and 2 rows of spinules on proximal and distal margins. Basis elongate with 1 simple seta on inner medial margin, and row of spinules along inner margin. Enp shorter than basis, drawn into strong claw, concave, with 2 setae on

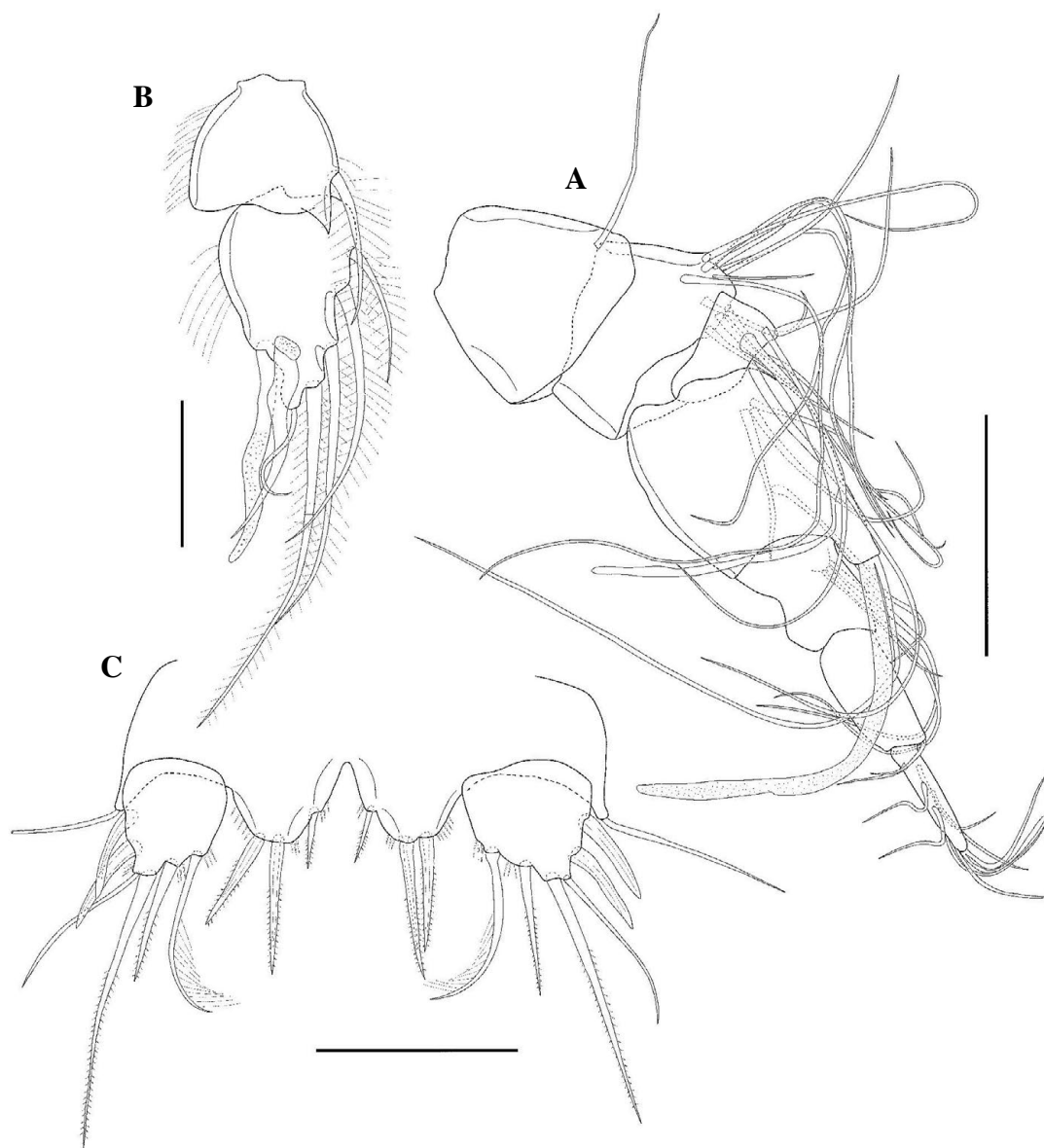


Fig. 5. *Eudactylopus yokjidoensis* n. sp., male (A and C, allotype; B, paratype). A, Right antennule; B, enp of P2, anterior view; C, P5, Anterior view. Scale bars=100 μ m.

proximal margin.

P1 (Fig. 3A). Intercoxal sclerite transversely elongate, bare. Coxa with 2 rows of spinules on anterior surface and some spinules along outer distal margin. Basis with 1 strong inner spine, accompanied with some spinules basally, 1 long outer spine, 2 transverse rows of spinules (1 on outer distal side, 1 on distal middle side). Exp shorter than enp, 3-segmented: exp-1 with some spinules along outer and distal margins and armed with 1 outer spine; exp-2 longer than sum of others, with some long spinules along proximal inner margin, 1 long unipinnate inner seta subdistally, several

spinules along outer margin, and armed with 1 outer spine subdistally; exp-3 shortest, with 3 unipinnate spines and 1 geniculate seta. Enp 2-segmented: enp-1 slightly longer than exp, approximately 4.1 times as long as wide, with 1 long bipinnate seta on proximal one-third of inner margin; enp-2 short, narrower than enp-1, with some spinules on outer margin, armed with 2 long unipinnate spines and 1 simple seta apically, inner apical spine about twice as long as outer apical spine.

Armature formula of P2 to P4 is as follows (Roman numbers mean spine, and arabic numerals setae):

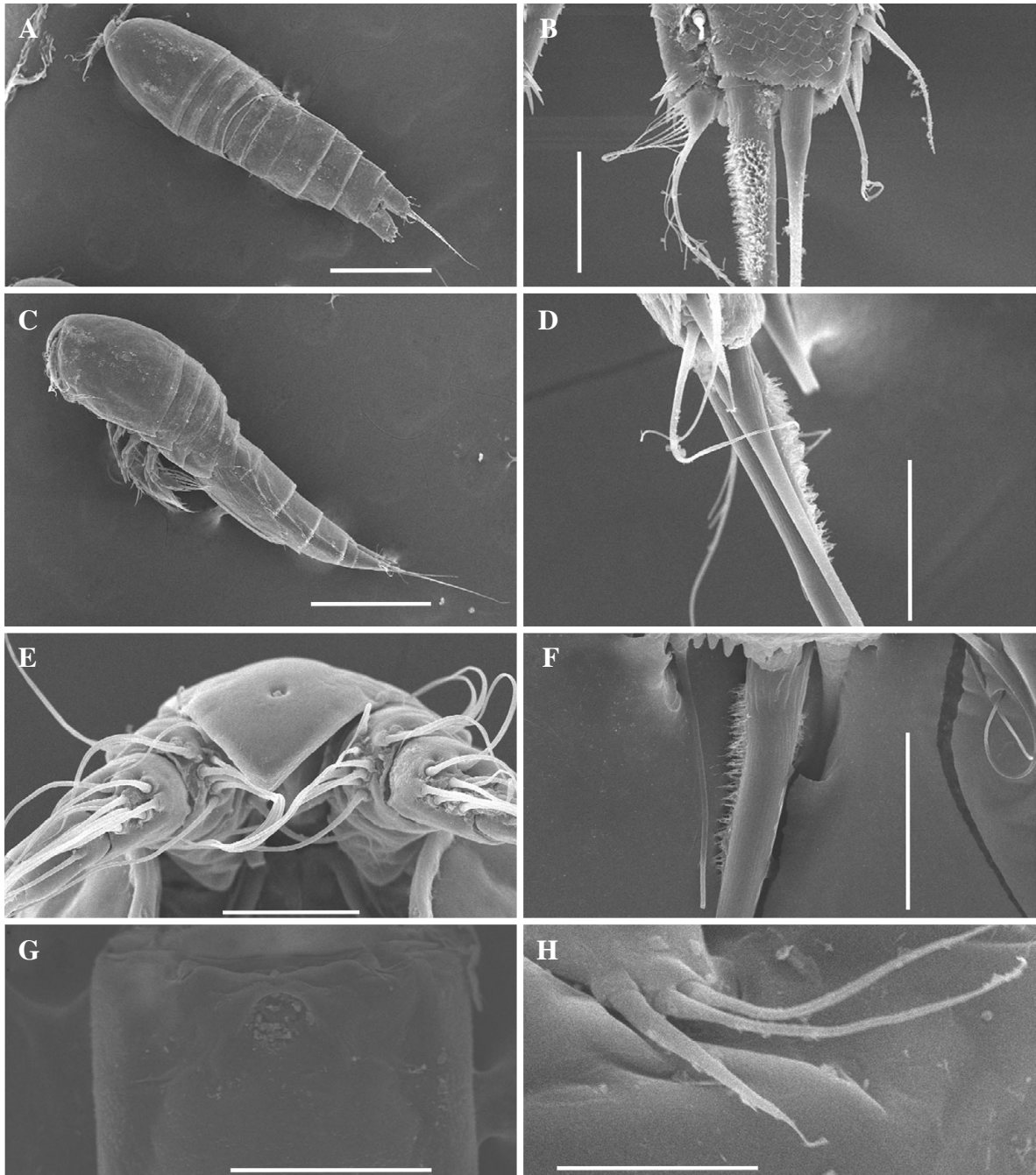


Fig. 6. Scanning electron micrographs of *Eudactylopus yokjidoensis* n. sp., female. A, Habitus, dorsal view; B, Right caudal ramus, dorsal view; C, Habitus, lateral view; D, Inner and outer terminal seta, lateral view; E, Rostral area, ventral view; F, Inner terminal seta, ventral view; G, H, Genital double-somite, ventral view. Scale bars: A, C= 500 μ m, B, D-F= 50 μ m, G= 200 μ m, H= 20 μ m.

	Exp	Enp
P2	I-1;I-1;III,I1,2	0-1;0-2;I,2,2
P3	I-1;I-1;III,I1,3	0-1;0-2;I,2,3
P4	I-1;I-1;III,I1,3	0-1;0-1;I,2,2

P2 (Fig. 3B) intercoxal sclerite smooth, rostrocaudally

elongate. Coxa approximately 0.7 times as long as wide, with 2 transverse rows of spinules near outer margin. Basis narrower than coxa, with 2 sharp processes between both rami and at inner distal margin, 2 rows of spinules near base of exp and enp, and armed with 1 outer spine. Both rami tapering toward distal segment, 3-segmented. Exp approxi-

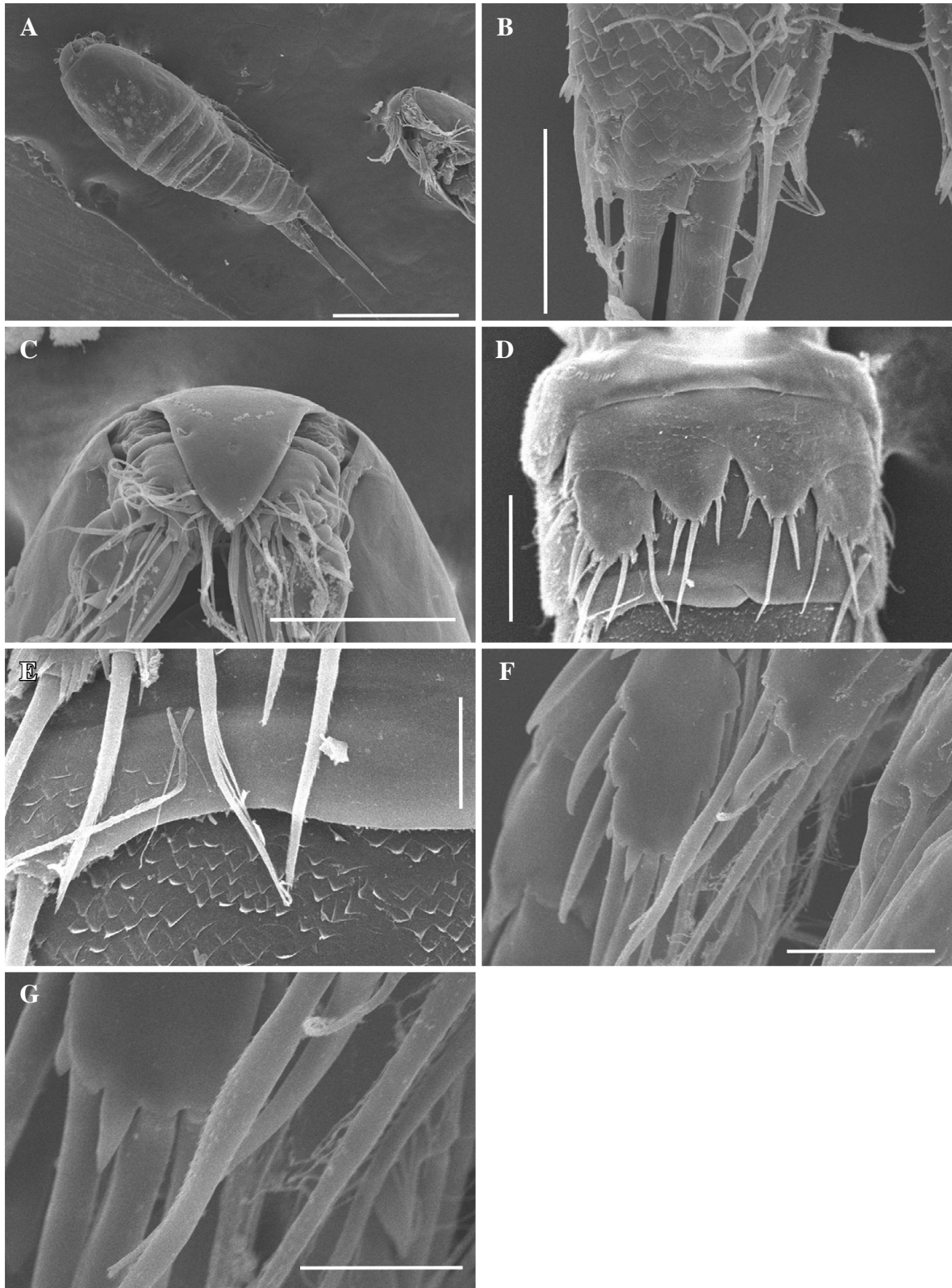


Fig. 7. Scanning electron micrographs of *Eudactylopus yokjidoensis* n. sp., male. A, Habitus, dorsal view; B, Left caudal ramus, dorsal view; C, Rostral area, ventral view; D, E, P5, ventral view; F, G, enp of P2, ventral view. Scale bars: A=500 μ m, B, F=50 μ m, C, D=100 μ m, E, G=25 μ m.

mately 1.2 times as long as enp: exp-1 with triangular protuberance at outer distal margin, some spinules near anterior surface, base of outer spine, and exp-2, rows of spinules on outer margin, and armed with 1 outer spine and 1 bipinnate subdistal inner seta; exp-2 shorter than exp-1, with triangular protuberance at inner and outer distal margin, some spinules near base of outer spine and exp-3, row of spinules on outer margin, and armed with 1 outer spine and 1 bipinnate subdistal inner seta; exp-3 similar to length of exp-1, 3 outer spines, 1 long outer spine (armed with spinules on outer margin and setules on inner margin), and 1 long inner apical bipinnate seta, and 2 bipinnate inner setae. Enp with row of spinules along outer margin of each segment: enp-1 approximately 0.9 times as long as wide, with triangular protuberance at inner and outer distal corners, row of spinules and 1 long plumose seta on inner margin; enp-2 approximately 0.9 times as long as wide, with triangular protuberance on each of inner and outer distal margins, 2 long bipinnate inner setae; enp-3 1.3 times as long as wide, with 1 outer spine, 2 apical and 2 inner setae.

P3 (Fig. 3C) intercoxal sclerite smooth, rostrocaudally elongated, with deeply concave distal margin. Coxa approximately half as long as wide, with 2 transverse rows of spinules near outer margin. Basis narrower than coxa, with 2 sharp processes between both rami and at inner distal margin, 2 rows of spinules near base of exp and enp, and armed with 1 long outer seta. Both rami tapering toward distal segment, 3-segmented. Exp approximately 1.2 times as long as enp: exp-1 with triangular protuberance at outer distal margin, some spinules near proximal outer margin and near base of outer spine, rows of spinules on outer margin, and armed with 1 outer spine and 1 subdistal inner seta; exp-2 shorter than exp-1, with triangular protuberance on each of inner and outer distal margins, some spinules near base of outer spine, rows of spinules on outer margin, and armed with 1 outer spine and 1 subdistal inner seta; exp-3 similar to length of exp-1, with some spinules on proximal outer margin, 3 outer spines, 1 long outer spine (armed with spinules on outer margin and setules on inner margin), and 1 long inner apical bipinnate seta, and 3 bipinnate inner setae. Enp with row of spinules along outer margin of each segment: enp-1 with triangular protuberance at inner and outer distal margin, some spinules and 1 long bipinnate subdistal seta on inner margin; enp-2 with triangular protuberance on each of inner and outer distal margins, 2 long bipinnate inner setae; enp-3 1.3 times as long as wide, with 1 outer spine, 2 apical and 2 inner setae.

P4 (Fig. 3D) intercoxal sclerite, coxa, and basis as in P3. Both rami tapering toward distal segment, 3-segmented. Exp approximately 1.5 times as long as enp: exp-1 with triangular protuberance at outer distal margin, some spinules

near medial outer margin, 3 rows of spinules on outer margin, near bases of outer spine and exp-2, and armed with 1 outer spine and 1 subdistal inner seta; exp-2 shorter than exp-1, with triangular protuberance at inner and outer distal margins, 3 rows of spinules on outer margin, near bases of outer spine and exp-3, and armed with 1 outer spine and 1 subdistal inner seta; exp-3 similar to length of exp-1, with some spinules on proximal outer margin and near base of each outer spine, 3 outer spines, 1 long outer spine (armed with spinules on outer margin and setules on inner margin), 1 long inner apical bipinnate seta, and 3 bipinnate inner setae. Enp with row of spinules along outer margin of each segment: enp-1 approximately 0.6 times as long as wide, with triangular protuberance on each of inner and outer distal margins, some spinules and 1 long bipinnate seta on inner margin; enp-2 approximately 0.9 times as long as wide, with triangular protuberance on each of inner and outer distal margins, 1 long bipinnate inner seta; enp-3 approximately 1.5 times as long as wide, with 1 outer spine, 2 apical and 2 inner setae.

P5 (Figs. 3E, 6C) well-developed, foliaceous, composed of benp and separate exp, each ramus (excluding setae) reaching middle of second abdominal somite. Benp with outer peduncle bearing simple seta on basis. Endopodal lobe larger than exp, with 4 setae on distal margin and 1 naked seta on proximal two-third of inner margin; inner margin armed with fine setules. Exp with 5 setae on distal margin and 1 simple seta on outer margin subdistally; outer and distal margins armed with fine setules.

P6 (Figs. 1C, E, 6H) on anterior part of genital double-somite ventrally, represented by protuberance armed with 3 setae.

Description of the adult male. Body (Figs. 4A, B, 7A) fusiform, total length 1,255 μm (range, 1,165–1,307; mean, 1,240; $n=9$). Maximum width measured at posterior margin of cephalic shield: 370 μm (range, 344–375; mean, 360; $n=9$). All somite with distal hyaline membrane except fifth pedigerous somite and anal somite. Prosoma (Figs. 4A, B, 7A) comprising cephalothorax with completely fused first pedigerous somite and three free pedigerous somites, 1.1 times as long as urosome excluding caudal rami, 1.3 times length including caudal rami. Urosome (Figs. 4A, B, 7A) 6-segmented, comprising fifth pedigerous somite, genital somite and 4 free abdominal somites. Abdomen with 1 or 2 oblique rows of spinules on both lateral surfaces of each somite, with exception of anal somite ornamented with row of spinules along distal margin. Anal somite (Figs. 4A, B, 7A) approximately 0.6 times as long as preceding somite. Caudal rami (Fig. 4A) truncate, about 1.8 times as long as anal somite, approximately 1.5 times as long as wide, inner margin unornamented, with 7 setae: seta V longest (Fig. 4A"),

approximately 7.8 times as long as caudal rami. Rostrum (Figs. 4A, B, 7C) as in female.

Antennule (Fig. 5A) 7-segmented, haplocer; first segment bearing 1 seta on anterior margin; second segment with 1 simple seta on posterior margin, 2 naked setae on anterior margin and 8 setae along outer distal margin; third segment small, with 1 aesthetasc and 1 seta on anterior margin and 2 setae on distal margin; fourth segment large, with 4 setae on posterior margin, long apical aesthetasc fused basally to 1 apical seta; fifth segment with 3 setae on posterior margin; sixth segment with 1 simple seta on outer distal margin; seventh segment with 2 setae on posterior margin, 3 setae on anterior margin, 1 subapical seta on inner margin and 1 naked seta and aesthetasc fused basally to 1 seta apically. Armature formula as follows: 1/11/3 + Ae/4 + (1 + Ae)/3/1/7 + (1 + Ae).

Antenna, mouth appendages, and P1, P3, P4 as in female.

P2 (Figs. 5B, 7F, G) enp modified, 2-segmented and with row of spinules along outer margin: enp-1 with 1 long subdistal inner seta and some setules near inner seta; enp-2 strongly modified, longer than enp-1, with 4 bipinnate setae on inner margin, 1 naked apical seta, 1 long spine, rounded at the end and 1 recurved spine on outer margin.

P5 (Figs. 5C, 7D) composed of benp fused medially and separate exp. Benp with 1 outer simple seta on basis. Endopodal lobe with 1 bipinnate subapical inner spine and 2 long bipinnate apical spines, with length ratio (from inner side) 0.5 : 1.2 : 1. Exp 1-segmented, with 1 long slender seta, armed with setules along inner margin (Fig. 7E), 1 bipinnate spine on inner margin, 1 long bipinnate spine and 1 simple seta apically, and 2 outer spines.

P6 (Fig. 4C) represented by wide, short plate, with 1 bipinnate spine and 2 naked setae on outer distal margin, and some spinules near outer seta.

Molecular diversity. The 576-bp region of the mtCOI was obtained for six female and male individuals (GenBank accession Nos: KY694381–KY694383 and KY694387–KY694389 for the female and, KY694384–KY694386 and KY694390–KY694392 for the male) of *Eudactylopus yokjidoensis* n. sp. Individuals of the same species showed only a slight difference in the mtCOI sequence (0.0–1.6%), while individuals of different species showed distinct differences (22.3–22.7%) (Table 1). The pairwise distance of between the *Parathalestris parviseta* and *Eudactylopus* species are between 30.4–31.4%. Divergences within *E. yokjidoensis* and between species of the genus *Eudactylopus* are relatively

Table 1. Pairwise percentage differences for mtCOI sequences between individuals of *Eudactylopus yokjidoensis* n. sp. and *E. spectabilis*

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. <i>Eudactylopus yokjidoensis</i> F1 (GenBank accession No. KY694381)													
2. <i>Eudactylopus yokjidoensis</i> F2 (GenBank accession No. KY694382)	0.8												
3. <i>Eudactylopus yokjidoensis</i> F3 (GenBank accession No. KY694383)	0.4	1.2											
4. <i>Eudactylopus yokjidoensis</i> F4 (GenBank accession No. KY694387)	1.2	0.8	1.6										
5. <i>Eudactylopus yokjidoensis</i> F5 (GenBank accession No. KY694388)	0.0	0.8	0.4	1.2									
6. <i>Eudactylopus yokjidoensis</i> F6 (GenBank accession No. KY694389)	0.0	0.8	1.4	1.2	0.0								
7. <i>Eudactylopus yokjidoensis</i> M1 (GenBank accession No. KY694384)	0.8	0.4	1.2	0.8	0.8	0.8							
8. <i>Eudactylopus yokjidoensis</i> M2 (GenBank accession No. KY694385)	0.0	0.8	0.4	1.2	0.0	0.0	0.8						
9. <i>Eudactylopus yokjidoensis</i> M3 (GenBank accession No. KY694386)	0.8	0.4	1.2	0.8	0.8	0.8	0.0	0.8					
10. <i>Eudactylopus yokjidoensis</i> M4 (GenBank accession No. KY694390)	0.0	0.8	0.4	1.2	0.0	0.0	0.8	0.0	0.8				
11. <i>Eudactylopus yokjidoensis</i> M5 (GenBank accession No. KY694391)	0.0	0.8	0.4	1.2	0.0	0.0	0.8	0.0	0.8	0.0			
12. <i>Eudactylopus yokjidoensis</i> M6 (GenBank accession No. KY694392)	0.0	0.8	0.4	1.2	0.0	0.0	0.8	0.0	0.8	0.0	0.0		
13. <i>Eudactylopus spectabilis</i> (GenBank accession No. KR049015.1)	22.4	22.7	22.7	22.5	22.4	22.4	22.7	22.4	22.7	22.4	22.4	22.4	
14. <i>Parathalestris parviseta</i> (GenBank accession No. KT030280.1)	32.2	31.6	31.9	31.4	32.2	32.2	31.6	32.2	31.6	32.2	32.2	32.2	31.9

mtCOI, mitochondrial gene cytochrome oxidase subunit I.

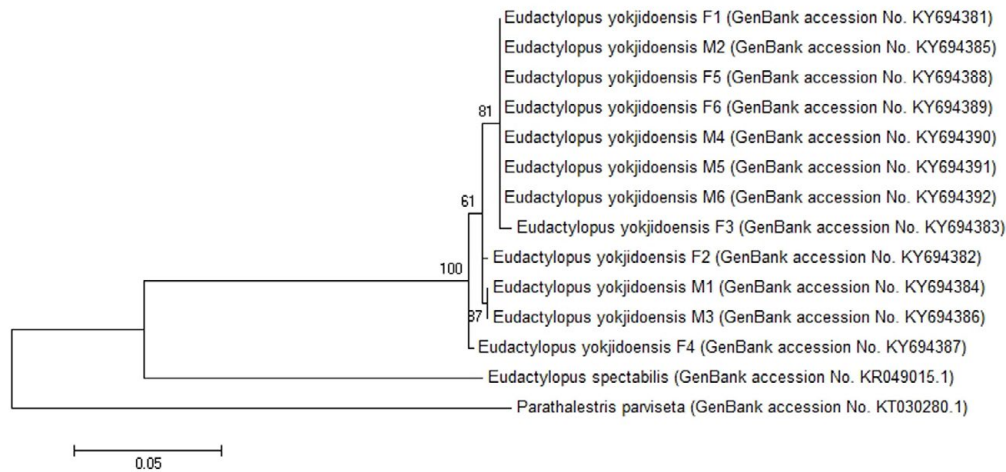


Fig. 8. Gene tree for mitochondrial gene cytochrome oxidase subunit I (mtCOI) showing proportional differences between individual samples of *Eudactylopus yokjidoensis* n. sp. and *E. spectabilis* on south coast of Korea. The numbers at the branch points are bootstrap values (i.e., percentage of trees with that branch point among the 1,000 subreplicates). The gene sequences for *Parathalestris parivseta*, downloaded from the NCBI database, were used as an outgroup. The specimen numbers correspond to those in Table 1.

indicative of intra-specific and inter-specific variabilities (Lefébure et al., 2006). Additionally, the mtCOI gene tree also showed that *E. yokjidoensis* is clearly separated from *E. spectabilis* (Fig. 8).

DISCUSSION

The new species, *Eudactylopus yokjidoensis* n. sp. closely resembles *E. andrewi* and *E. spectabilis* in terms of the lengths of 2 inner setae on the P2 enp-2 of the female and 2 subapical modified setae on the P2 endopod of the male (Itô, 1974; Chang and Song, 1995). *Eudactylopus yokjidoensis*, however, differs from the latter two species with respect to the following characteristics: In the female, (1) the length ratio of the cephalothorax to 2nd–4th thoracic somites is smaller than those of the other two species (1 : 0.8 vs. 1 : 1); (2) 9-segmented antennule in *E. yokjidoensis* (vs. 7-segmented in *E. andrewi*); (3) the number of apical setae on the maxillular coxa (3 vs. 4); (4) 2 setae on the maxillular basis in *E. yokjidoensis* (vs. 1 in *E. spectabilis*); (5) the presence of an accompanying seta on the maxilliped claw, while it is absent in *E. spectabilis*; and (6) the process in the medial outer margin of P2–P4 basis, unlike the smooth medial outer margin of *E. spectabilis*; and in the male (1) the length ratio of the cephalothorax/2nd–4th thoracic somites is smaller than those of the other two species (1 : 0.6 vs. 1 : 1 in *E. andrewi* and 1 : 0.8 in *E. spectabilis*); (2) the aesthetascs are on the 3rd–4th and the last segments of antennules, while *E. andrewi* has two aesthetascs on the 4th segment and *E. spectabilis* has one aesthetasc on each of the 4th and 5th

segments; (3) the baseoendopod and exopod of P5 are separated in *E. yokjidoensis*, whereas they are fused in *E. andrewi*; and (4) a comb-like innermost seta applies to the P5 exopod, while a bipinnate seta is applicable in *E. spectabilis*. Additionally, *E. yokjidoensis* can be separated from the other species in terms of the morphological combination of the setal number on the coxa and the maxillule basis in the female. The numbers of subapical and apical setae on the coxa and seta on the basis of the maxillule (2, 3, and 2, respectively) differ in *E. yokjidoensis* (vs. 2, 4, and 2 in *E. andrewi*, 2, 4, and 1 in *E. spectabilis*, 1, 4, and 2 in *E. lucayosi*, and 0, 2, and 6 in *E. atlanticus*). *Eudactylopus australis* differs from *E. yokjidoensis* in 6 setae on the maxillular basis. *Eudactylopus robustus* shows some discrepancies between synonymized species, which can be identified using these characteristics (0, 4, and 2 in *E. striatus* vs. 0, 3, and 3 in *E. fasciatus*).

The above-mentioned species of *Eudactylopus* should be considered with caution in morphological studies owing to the insufficient descriptive content for each species (Wells, 2007). To date, a number of researchers have tried to solve these problems through detailed descriptions or reviews (Lang, 1965; Itô, 1974; Wells and Rao, 1987; Chang and Song, 1995). Lang (1965) reported the occurrence of *E. atlanticus* females (as *E. latipes* f. *typica*), previously known as an Atlantic species, for the first time in the Pacific, with detailed descriptions and illustrations of the morphological parts. Itô (1974) reported *E. andrewi* from Oshoro, Japan, mentioning the presence of two subspecies of *E. latipes*. However, Vervoort (1964) raised a question for the presence of the two subspecies of *E. latipes* based on sufficient de

Table 2. Morphological comparison of species in the genus *Eudactylopus* Scott A., 1909

Characters	<i>E. andrwei</i> Sewell, 1940	<i>E. atlanticus</i> Vervoort, 1964	<i>E. australis</i> Nicholls, 1941	<i>E. lucayosi</i> Geddes, 1969	<i>E. robustus</i> (Claus, 1863)	<i>E. spectabilis</i> (Brian, 1923)	<i>E. yokjidoensis</i> n. sp.
Female							
Body size (µm)	1,280 ^a 1,500 ^b	1,250 ^c 1,500 ^d	1,260–1,380 ^e	1,200 ^f	1,500 ^g	1,000–1,500 ^h 1,350 ⁱ	1,500
Cephalothrax : 2nd–4th thoracic somites	1 : 0.9 ^a 1 : 1 ^b	1 : 1 ^d	1 : 1 ^e	1 : 0.75 ^f	1 : 0.63 ⁱ 1 : 0.7 ^a	1 : 0.92 ^h 1 : 1 ⁱ	1 : 0.8
Genital double-somite : 2nd–4th abdominal somites	0.7 : 1 ^b	0.7 : 1 ^d	1 : 1 ^e	0.8 : 1 ^f	1 : 1 ^a	0.8 : 1 ⁱ	0.8 : 1
Antennular segmentation	7 ^b	7 ^d	9 ^e	9 ^f	9 ^g	9 ⁱ	9
Number of seta on basis of mandible	2 ^b	2 ^d	1 ^e	2 ^f	2 ^a	2 ⁱ	2
Number of seta on exp of mandible	2 ^b	2 ^d	1 ^e	2 ^f	1 ^a	2 ⁱ	2
Basis and exp of mandible	Fused ^b	Distinct ^d	Fused ^e	Distinct ^f	Fused ^a	Fused ⁱ	Distinct
Number of apical seta on maxillular coxa	4 ^b	2 ^d	Unknown	4 ^f	3 ^g	4 ⁱ	3
Number of seta on maxillular basis	2 ^b	6 ^d	6 ^e	2 ^f	3 ^g	4 ⁱ	3
Endopod and basis of maxilla	Fused ^b	Distinct ^d	Fused ^e	Fused ^f	Unknown	Fused ⁱ	Fused
Number of accompanied seta on maxillipedal claw	1 ^b	2 ^d	1 ^e	1 ^f	1 ^g	0 ⁱ	1
Process in medial outer margin on basis of P2–P4	Y ^b	Y ^d	Y ^e	Y ^f	Y ^g	N ⁱ	Y
Relative length of proximal seta to distal seta of P2 enp-2	Similar ^b	Shorter ^d	Unknown	Shorter ^f	Shorter ^g	Similar ⁱ	Similar
Shape of P5 exp	Square ^b	Droplet ^d	Droplet ^e	Track ^f	Droplet ^g	Droplet ⁱ	Droplet
Ratio of maximum length to maximum width of P5 exp	1.4 ^b	1.5 ^d	1.6 ^e	2.3 ^f	2.2 ^g	1.8 ⁱ	1.8
Male							
Body size (µm)	1,300 ^a 900 ^b	–	1,350 ⁱ	Unknown	1,125 ⁱ 1,162 ^a	1,000 ^h 1,520 ⁱ	1,255
Cephalothrax : 2nd–4th thoracic somites	1 : 0.9 ^a 1 : 1 ^b	–	Unknown	Unknown	1 : 0.73–0.8 ^a	1 : 0.7 ^h 1 : 0.8 ⁱ	1 : 0.6
Antennular segmentation	7 ^b	–	9 ⁱ	Unknown	9 ^a	7 ⁱ	7
Benp and exp of P5	Fused ^b	–	Fused ⁱ	Distinct ^f	Distinct ^g	Distinct ⁱ	Distinct
Inner seta of P5 exp	Long, comb-like ^b	–	Short ⁱ	Short ^f	Short ^g	Long, bipinnate ⁱ	Long, comb-like

^aSewell (1940). ^bIto (1974). ^cScott T. (1893). ^dLang (1965). ^eNicholls (1941). ^fGeddes (1969). ^gClaus (1863). ^hBrian (1923). ⁱChang and Song (1995). ^jNicholls (1942). ^kNoodt (1955). ^lBrian (1928).

criptions of the developmental stages for *E. andrewi* and an *E. atlanticus* review. Wells and Rao (1987) recorded *E. robustus* from the Indian Ocean and reviewed its synonymized species (i.e., *E. opima*, *E. striatus*, *E. fasciatus*, and *E. australis*). The authors raised some doubts about the taxonomic status of these species, suggesting some morphological differences in the exopod segmentation of the antenna, abdominal ornamentation, setation of the exp of the male P5, shape of the female P5, and endopod of the male P2. Despite these differences, however, the authors failed to separate these synonymized species into independent species, due to the limited descriptions of these species. Subsequently, Chang and Song (1995) first recorded two thalestrid harpacticoids (*E. andrewi* and *E. spectabilis*) in Korea. The authors found the morphological differences between *E. spectabilis* of Korean water and the Mediterranean Sea, as follows: the number of inner seta on the P2 enp-2 of the male and the length-to-width ratio of the caudal ramus of the female. However, the authors concluded that the differences could be caused by the different fixation.

Through the comprehensive comparison of each species in this study, we could confirm that the following characteristics are important parameters to identify the species of *Eudactylopus* (Table 2): Lang (1965) described a basally bulbous caudal seta VI with setules along the inner margin to define the female of *E. atlanticus* (Lang, 1965: 218 and Figs. 121b, c, 122a, as *E. latipes* f. *typica*). This character is evident in *E. lucayosi*, *E. spectabilis* and *E. yokjidoensis* n. sp., but not in the normal seta with the setules in *E. andrewi* and the normal seta without the setules in *E. australis* and *E. robustus* (as *E. opima* sensu Sewell, 1940). That of the *E. spectabilis* female from the Black Sea is bipinnate (Marcus and Por, 1960: TAFEL III Ab. 17). Additionally, *E. spectabilis* shows a distinction by the absence of a process in the medial outer margin (vs. the presence in the others), as well as its separation by the male antennule 7-segmented, which overlaps in *E. andrewi* and *E. yokjidoensis* (vs. 9-segmented in the others and unknown in *E. lucayosi*). A long and comb-like innermost seta on the exopod of the male P5 is a unique character overlap between *E. andrewi* and *E. yokjidoensis* (vs. the long and bipinnate in *E. spectabilis*, long and naked in *E. robustus* (as *E. opima* sensu Brian, 1928), the short in *E. australis* and *E. robustus* (as *E. opima* sensu Sewell 1940, *E. striatus* and *E. fasciatus*), and unknown in *E. atlanticus*). *Eudactylopus lucayosi* is distinguished from the other species of the genus by the peculiar structure of the caudal rami and the truncated form of the benp of the female P5 as presented by Geddes (1969). This species is also unique due to the absence of seta at the middle of the inner margin of the maxilliped (vs. 1 seta in the others), which is found in the *E. spectabilis* (Monard, 1928, Fig. XXI. 2) and the syn-

onymized species of *E. robustus* (as *E. fasciatus* Sewell, 1940, Text-Fig. 38F). In particular, these morphological differences that are evident between the synonymized species and the original specimen, suggest the need of a further examination for specific variations or differences among these species.

DNA barcoding is an efficient tool to identify species, especially morphologically similar species (Floyd et al., 2002). The mtCOI sequence provides molecular markers that can be used to confirm taxonomic identifications in Crustacea (Costa et al., 2007). In previous molecular studies of harpacticoid copepods, the inter-specific difference is in the region of 21.2–23.2% regarding the genus *Nitokra* (Karanovic et al., 2015), the region of 20.2–26.7% regarding the genus *Wellstenhelia* (Karanovic et al., 2014). *Eudactylopus yokjidoensis* and *E. spectabilis* represent genetic differences from 22.4–22.7%, providing that these two species are genetically isolated and distinct (Lefébure et al., 2006).

ACKNOWLEDGMENTS

We need to thank the anonymous referees who made constructive and invaluable suggestions. This study was a part of the project titled ‘Long-term change of structure and function in marine ecosystems of Korea’, funded by the Ministry of Oceans and Fisheries, Korea. This work was supported by National Marine Biodiversity Institute Research Program (2018M01200), funded by National Marine Biodiversity Institute of Korea (MABIK).

REFERENCES

- Bodin P, 1997. Catalogue of the new marine harpacticoid copepods (1997 edition). Documents du travail de l’Institut Royal des Sciences Naturelles de Belgique, 8:1-304.
- Boxshall GA, Halsey SH, 2004. An introduction to copepod diversity. The Ray Society, London, pp. 1-966.
- Brady GS, 1905. On Copepoda and other Crustacea taken off Northumberland and Durham in July, 1904. Transactions of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne, 1:210-223.
- Brian A, 1923. Elenco di copepodi marini bentonici provenienti da Rovigno e descrizione di una n. varietà di *Parathalestris clausi* Norm. Monitore Zoologico Italiano, 34:126-135.
- Brian A, 1928. Descrizione di specie nuove o poco conosciute di copepodi bentonici del mare Egeo. Bollettino dei Musei di Zoologia e Anatomia Comparata della Università di Genova, 7:1-37.
- Chang CY, Song SJ, 1995. Marine harpacticoid copepods of genus *Eudactylopus* (Harpacticoida, Thalestridae) in Korea. Korean Journal of Systematic Zoology, 11:379-388.

- Claus C, 1863. Die frei lebenden Copepoden mit besonderer Berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres. Wilhelm Engelmann, Leipzig, pp. 1-230.
- Costa FO, deWaard JR, Boutillier J, Ratnasingham S, Dooh RT, Hajibabaei M, Hebert PDN, 2007. Biological identifications through DNA barcodes: the case of the Crustacea. Canadian Journal of Fisheries and Aquatic Sciences, 64:272-295. <https://doi.org/10.1139/f07-008>
- Floyd R, Abebe E, Papert A, Blaxter M, 2002. Molecular barcodes for soil nematode identification. Molecular Ecology, 11:839-850. <https://doi.org/10.1046/j.1365-294X.2002.01485.x>
- Folmer O, Balck M, Hoeh W, Lutz R, Vrijenhoek R, 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3:294-299.
- Geddes DC, 1969. Marine biological investigations in the Bahamas. 9. Harpacticoid copepods belonging to the family Thalestridae. Sarsia, 39:1-16. <https://doi.org/10.1080/00364827.1969.10411154>
- Hicks GRF, 1980. Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. Journal of Experimental Marine Biology and Ecology, 44:157-192. [https://doi.org/10.1016/0022-0981\(80\)90151-3](https://doi.org/10.1016/0022-0981(80)90151-3)
- Hicks GRF, 1988. Systematics of the Donsiellinae Lang (Copepoda, Harpacticoida). Journal of Natural History, 22:639-684. <https://doi.org/10.1080/00222938800770441>
- Holmes JMC, O'Connor JP, 1988. A portable light-trap for collecting marine crustaceans. Journal of the Marine Biological Association of the United Kingdom, 68:235-238. <https://doi.org/10.1017/S0025315400052140>
- Huys R, Boxshall GA, 1991. Copepod evolution. Publication No. 159. The Ray Society, London, pp. 1-468.
- Itô T, 1974. Descriptions and records of marine harpacticoid copepods from Hokkaido, V. Journal of the Faculty of Science, Hokkaido University, Series VI, Zoology, 19:546-640.
- Karanovic T, Eberhard S, Cooper SJB, Guzik MT, 2015. Morphological and molecular study of the genus *Nitokra* (Crustacea, Copepoda, Harpacticoida) in a small palaeochannel in Western Australia. Organisms Diversity and Evolution, 15:65-99.
- Karanovic T, Kim K, Lee W, 2014. Morphological and molecular affinities of two East Asian species of *Stenhelia* (Crustacea, Copepoda, Harpacticoida). Zookeys, 411:105-143. <https://doi.org/10.3897/zookeys.411.7346>
- Lang K, 1936. Copepoda Harpacticoida. Further Results of the Swedish Antarctic Expedition 1901-1903, 3:1-68.
- Lang K, 1944. Monographie der Harpacticiden (Vorläufige Mitteilung). Almqvist and Wiksells Boktryckeri, Uppsala, pp. 1-39.
- Lang K, 1965. Copepoda Harpacticoida from the Californian Pacific coast. Kungl. Svenska Vetenskapsakademiens Handlingar, 10:1-560.
- Lefébure T, Douady CJ, Gouy M, Gibert J, 2006. Relationship between morphological taxonomy and molecular divergence within Crustacea: proposal of a molecular threshold to help species delimitation. Molecular Phylogenetics and Evolution, 40:435-447. <https://doi.org/10.1016/j.ympev.2006.03.014>
- Marcus A, Pór F, 1960. Die Copepoden einer Probe aus dem Felsbiotop von Yalt a (Krimhalbinsel). "Grigore Antipa" National Museum of Natural History, 2:145-163.
- Monard A, 1928. Les harpacticoides marins de Banyuls. Archives de Zoologie Expérimentale et Générale, 67:259-443.
- Nicholls AG, 1941. Littoral Copepoda from South Australia. (I) Harpacticoida. Records of the South Australian Museum, 6:381-427.
- Nicholls AG, 1942. Marine Copepoda from Western Australia. I. Littoral harpacticoids from Rottnest Island. Journal of the Royal Society of Western Australia, 27:135-141. <https://doi.org/10.2988/10-36.1>
- Noodt W, 1955. Marine Harpacticoiden (Crust. Cop.) aus dem Marmara Meer. Istanbul Üniversitesi Fen Fakültesi Mecmuası, 20B:49-94.
- Scott A, 1909. The Copepoda of the Siboga Expedition. Part I. Free-swimming, littoral and semi-parasitic Copepoda. Siboga Expedition Monographs, 29a:1-323.
- Scott T, 1893. Report on Entomostraca from the Gulf of Guinea, collected by John Rattray, B.Sc. Transactions of the Linnean Society of London, 6:1-161. <https://doi.org/10.1111/j.1096-3642.1894.tb00660.x>
- Sewell RBS, 1940. Copepoda Harpacticoida. Scientific Reports of the John Murray Expedition, 7:117-382.
- Tamura K, Stecher G, Peterson D, Filipksi A, Kumar S, 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. Molecular Biology and Evolution, 30:2725-2729. <https://doi.org/10.1093/molbev/mst197>
- Vervoort W, 1964. Free-living Copepoda from Ifaluk Atoll in the Caroline Islands with notes on related species. Bulletin of the United States National Museum, 236:1-431. <https://doi.org/10.5479/si.03629236.236.1>
- Walsh PS, Metzger DA, Higuchi R, 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. Biotechniques, 10:506-513.
- Wells JBJ, 2007. An annotated checklist and keys to the species of Copepoda harpacticoida (Crustacea). Zootaxa, 1568:1-872.
- Wells JBJ, Rao GC, 1987. Littoral Harpacticoida (Crustacea: Copepoda) from Andaman and Nicobar Islands. Memoirs of the Zoological Survey of India, 16:1-385.
- Willen E, 2000. Phylogeny of the Thalestridomorpha Lang, 1944 (Crustacea, Copepoda). Cuvillier Verlag, Göttingen, pp. 1-233.
- Wilson CB, 1925. New North American parasitic copepods, new hosts, and notes on copepod nomenclature. Proceedings of the United States National Museum, 64:1-22. <https://doi.org/10.5479/si.00963801.64-2507.1>

Received December 4, 2017
Revised April 30, 2018
Accepted June 8, 2018