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Paradoxapseudes shimojiensis sp. nov. (Crustacea: Tanaidacea: Apseudidae) from a submarine limestone cave in Japan, with notes on its chelipedal morphology and sexual system

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ABSTRACT

We describe *Paradoxapseudes shimojiensis* sp. nov. from a submarine limestone cave at Shimoji-jima Island, Ryukyu Islands, southwestern Japan. This species resembles five species (*P. basibidens*, *P. bassoprofundo*, *P. bermudeus*, *P. edgari*, and *P. heroae*, among 17 congeners) that bear a long pleotelson, but differs from them in having i) a naked antennal article 1, ii) the maxillipedal basis with one inner distal plumose seta, iii) the chelipedal basis with one dorsodistal and one ventro-subproximal simple setae, iv) the pereopod-1 basis with four dorsal simple setae longer than the width of the pereopod-1 basis, but without ventrodistal spiniform setae, v) the pereopod-1 merus with three mid-inner ventral simple setae, and vi) the pleopodal protopod with two inner plumose setae. We determined partial nucleotide sequences for the cytochrome *c* oxidase subunit I (COI) and 18S rRNA (18S) genes in *P. shimojiensis* for future use in DNA barcoding and phylogeny. *Paradoxapseudes shimojiensis* has serial ridges on the inner surfaces of the left and right chelipedal bases that quite resemble the stridulatory organs in harvestmen (Opiliones); by analogy, we speculate that these ridges may be stridulatory sound-producing organs. Two specimens had both a fully-developed marsupium and genital cone, suggesting that *P. shimojiensis* is simultaneously hermaphroditic.

KEYWORDS: Malacostraca; Peracarida; stygophilic; hermaphrodite; acoustic; benthos

Introduction

Since the pioneering work by Băcescu (1980), 17 species of tanaidaceans in 15 genera have been reported from submarine caves (Kakui and Fujita 2018; Kakui et al. 2019), although most of these species are not restricted to caves (García-Herrero et al. 2019). For species that have been reported only from caves, it remains unclear whether they are obligate cave dwellers, both because they lack obvious external adaptations to cave life and because there are insufficient data from the benthic areas outside the caves (Kakui and Fujita 2018). As submarine caves are difficult to access and investigate, and minute animals like tanaidaceans can easily be overlooked, research on submarine-cave tanaidaceans, including their taxonomy, is still in its infancy.

The apseudid genus *Paradoxapseudes* Guţu, 1991, consisting of 17 species (Tzeng and Hsueh 2014; Bird 2015), is the only tanaidacean genus with multiple submarine-cave dwellers, including *P. bermudeus* (Băcescu, 1980), *P. intermedius* (Hansen, 1895), and *P. mortoni* (Bamber, 1997) (Guţu and Iliffe 1985; Bamber 2000; Gerovasileiou et al. 2016). Only one congener, *P. littoralis* (Shiino, 1952), has been reported from Japanese waters, but not as a cave dweller (Shiino 1952). In 2018, our faunal survey of a submarine limestone cave at Shimoji-jima Island, Miyako Island Group, southwestern Japan, yielded one *Paradoxapseudes* species, which turned out to be undescribed. Here we describe this species as new, provide partial sequences for the cytochrome *c* oxidase subunit I (COI) and 18S rRNA (18S) genes, and discuss the possible function of unusual serial ridges on the chelipeds, as well as indications that the species is simultaneously hermaphroditic.

Materials and methods

All tanaidaceans were collected by SCUBA diving on 26 October 2018 in the submarine limestone cave Akuma-no-Yakata (“Devil’s Palace” in Japanese), located on a reef slope at Shimoji-jima Island, Miyako Island Group, southwestern Japan (24°49'22.51"N, 125°08'07.84"E), with the entrance at a depth of about 35 m; see Osawa and Fujita (2019) for detailed information on the cave. Mud deposited in holes or fissures in the cave wall was collected with a commercially made aquatic suction sampler (yabby pump), from the “middle zone” of the cave (50–80 m from the entrance, ca. 20 m depth, no light, ca. 28‰ salinity; rocky or rubble-covered substrate) (Osawa and Fujita, 2019). Tanaidaceans were sorted from the mud sample and fixed and preserved in 99% ethanol. The specimens studied were deposited in the University Museum Fujukan, University of the Ryukyus (RUMF), Okinawa, Japan, and in the Invertebrate Collection of the Hokkaido University Museum (ICHUM), Sapporo. The methods used for dissection, preparation of slides, light microscopy, scanning electron microscopy (SEM), and drawing were as described by Kakui and Angsupanich (2012).

Orientation and terminology here follow Larsen (2003), except that the term “plumose sensory seta” (PSS; Bird 2011) is used instead of “broom seta” and the term “protopod” is used instead of “basal article” for pleopods and uropods. Body length (BL) was measured from the base of the antennules to the tip of the pleotelson, and body width at the widest portion of the cephalothorax (CW, cephalothorax width). Pleotelson length (PL) was measured between the anterior and posterior edges of the pleotelson, and pleotelson width (PW) at the widest portion of the segment (in many specimens, the width across the lateral processes on the pleotelson). Appendages were measured in the holotype. Measurements were made axially from digital images by using ImageJ (Rasband 2019): dorsally on the body, antennules, antennae, and uropods; laterally on the chelipeds, pereopods, and pleopods. The length and width of congeners were measured from original illustrations if these measurements were not provided in descriptions.

Total DNA was extracted from the left cheliped of the holotype by using a NucleoSpin Tissue XS Kit (TaKaRa Bio, Japan). Table I lists the primers used for DNA amplification and sequencing. PCR amplification conditions for COI with TaKaRa Ex Taq DNA polymerase (TaKaRa Bio) were 94°C for 1 min; 35 cycles of 98°C for 10 s, 62°C for 30 s, and 72°C for 50 s; and 72°C for 2 min. Conditions for 18S amplification with KOD FX Neo polymerase (Toyobo, Japan) were 94°C for 2 min; 45 cycles of 98°C for 10 s, 65°C for 30 s, and 68°C for 90 s; and 68°C for 3 min. Nucleotide sequences were determined by direct sequencing with a BigDye Terminator Kit ver. 3.1 and a 3730 Genetic Analyzer (Life Technologies, California, USA), and segments were concatenated by using MEGA7 (Kumar et al. 2016). All sequences we determined were deposited in the International Nucleotide Sequence Database (INSD) through the DNA Data Bank of Japan (DDBJ).

The determined COI sequence (658 nt, encoding 219 amino acids) was aligned with that of *P. intermedius* obtained from the INSD (accession number HM016216; Drumm 2010; originally identified as *Apseudes* cf. *bermudeus*) by using CLUSTAL W (Thompson et al. 1994); the aligned sequences were trimmed in MEGA7 to the shortest length between them (402 nt). Our 18S sequence (2176 nt) was aligned with those of *P. bermudeus* and *P. littoralis* obtained from INSD (accession numbers GQ175865 and AB618175; Wilson 2009; Kakui et al. 2011) by using MAFFT ver. 7 (Katoh and Standley 2013) with the Q-INS-i strategy (Katoh and Toh 2008); the aligned sequences were trimmed to the shortest length among them (2036 nt). Kimura (1980) 2-parameter (K2P) distances among the aligned sequences in each dataset were calculated with MEGA7.

Systematics

Family Apseudidae Leach, 1814

Genus *Paradoxapseudes* Guţu, 1991

Paradoxapseudes Guţu, 1991: 349. Type species: *Paradoxapseudes cubensis* Guţu, 1991.

Amended diagnosis modified after Guţu (2008)

Apseudinae with small sized, dorsoventrally flattened body. Carapace longer than wide; lateral margins without spiniform processes; posterior lateral expansions slight or absent (= branchial regions not evident in dorsal view); rostrum prominent, acuted anteriorly; ocular lobes well defined, generally with pigmented visual elements; epistome single, thin, spiniform. Pereonites 3–6 similar and approximately equal; anterior half with at most one pair of lateral processes. Pleon with five short pleonites having some lateral circumplumose setae. Antennular article 1 with or without inner proximal fine denticulation; inner flagellum with two or three articles (accidentally, with only one). Antennal articles 4 and 5 long and thin; squama with 3–6 setae. Mandibles with triarticulate palp; article 1 with 3–6 simple setae. Labium palp ovate, slightly narrower distally, with three distal slender spiniform setae. Maxillule with biarticulate palp. Maxilliped generally with inner distal long plumose seta on basis and palp-article 1; palp-article 2 with spiniform or simple seta on outer distal corner. Epignath cup-shaped; terminal seta well developed, slender, setulate in distal half. Cheliped with exopod. Pereopod 1 fossorial, with exopod; coxa with small anterior rounded process bearing 2–5 setae; basis with 3–5 dorsal plumose setae (apparently simple in many cases);

propodus with 3–4 ventral spiniform setae. Propodus of pereopods 5 and 6 with inner ventral row of blade-like spiniform setae. Pleopods biramous, in five pairs. Uropodal exopod with five articles; endopod with at most 24 articles. Oostegites in five pairs.

Remarks

Since Guţu (2008) provided the latest diagnosis of *Paradoxapseudes*, five species were added to the genus (Bird 2015), requiring some minor amendments to the diagnosis (e.g., the condition/number of setae on the pereopod-1 coxa and the maxillipedal basis), which are reflected in the above diagnosis. And, as Guţu and Iliffe (1989) suggested the similarity between *Paradoxapseudes bermudeus* and *Falsapseudes bowmani* (Guţu and Iliffe, 1989), we added two characters to distinguish them: “epistome single, thin, spiniform” and “anterior half [of pereonites 3–6] with at most one pair of lateral processes”. The characters “lateral margins [of carapace] without spiniform processes; posterior lateral expansions [on carapace] slight or absent (= branchial regions not evident in dorsal view)” were also added.

***Paradoxapseudes shimojiensis* sp. nov.**

[New Japanese name: *Shimoji-apuseudesu*]

(Figures 1–5)

Diagnosis

Pleotelson long (PL/PW 2.57–2.61), with two pairs of slight lateral processes. Antennal article 1 naked. Maxillipedal basis with inner distal plumose seta. Chelipedal basis with inner serial ridges and one dorsodistal and one ventro-subproximal simple setae. Chelipedal merus with ventrodistal spiniform seta. Pereopod-1 basis with four dorsal simple setae, each longer than width of pereopod-1 basis; ventrodistal region without spiniform setae. Pereopod-1 merus with three mid-inner ventral simple setae. Pleopodal protopod with two inner plumose setae.

Etymology

The specific name is an adjective referring to the type locality.

Material examined

Holotype: ovigerous simultaneous hermaphrodite, RUMF-ZC-6081 (BL 2.27 mm, CW 0.35 mm), dissected, 8 slides and 1 vial; INSD accession number LC510354 (COI) and LC510355 (18S); Akuma-no-Yakata (Devil's Palace), Shimoji-jima Island, Miyako Island Group, southwestern Japan, northwestern Pacific Ocean (24°49'22.51"N, 125°08'07.84"E), 20 m depth, mud, 26.x.2018, collected by Y. Fujita.

Paratype: simultaneous hermaphrodite with empty, fully-developed marsupium, ICHUM6029 (CW 0.34 mm), dissected, 4 slides, 1 SEM stub, and 1 vial; same collection information as for holotype.

Description of simultaneous hermaphrodite, based primarily on holotype, with observation of epignath from paratype

Body (Figures 1, 2A, a1, B) dorsoventrally flattened, 6.73 times as long as CW, translucent, whitish when alive (Figure 1A, B); body wall not heavily calcified. Cephalothorax 0.17 times as long as BL, 1.16 times as long as wide, with pair of mid-lateral simple setae; rostrum hastate; eyes white when alive (Figure 1A, B); large, acute keel (hyposphenium) present posterior to maxillipeds (Figure 1B). Pereonites 1–6 with length ratio 1.00:1.14:1.63:1.85:1.77:1.46; pereonites 1 and 2 wider than long; pereonites 3–6 almost as long as wide; all pereonites with 1–3 pairs of simple setae;

pereonites 3–6 with pair of slight lateral processes in anterior half; pereonite 6 with genital cone (Figures 1C, 2B). Pleon 0.31 times as long as BL. Pleonites narrower than pereonite 6; all wider than long, similar in shape, with triangular epimeron bearing several plumose setae. Pleotelson 2.57 times as long as wide, slightly narrower than pleonite 5, with two pairs of slight lateral processes and several pairs of simple setae.

Antennule (Figure 2C, D, d1) with seven-articulate outer flagellum and triarticulate inner flagellum. Combined length of peduncle and outer flagellum 2.06 times as long as cephalothorax. Peduncular articles 1–4 with length ratio of 1.00:0.30:0.27:0.11; article 1 with one mid-outer, one outer distal, and four inner simple setae, eight outer PSS, and numerous inner fine setae; article 2 with three outer distal, one inner subproximal, and three inner distal simple setae, and four distal PSS; article 3 with one outer distal and three inner distal simple setae; article 4 with two PSS at insertion of inner flagellum. Outer flagellum 0.63 times as long as peduncle; articles 1 and 3 naked; articles 2, 4, 5, 6 with three, three, one, two simple setae, respectively; articles 4 and 6 each with aesthetasc; article 7 with two middle and four distal simple setae, and distal PSS. Inner flagellum 0.46 times as long as outer flagellum; articles 1 and 3 with two and three simple setae, respectively; articles 1–3 each with distal PSS. Antenna (Figure 2E) with ten articles, 0.58 times as long as antennule; articles 1–10 with length ratio 1.00:2.35:0.52:1.74:1.62:1.01:0.96:1.21:0.69:0.85. Article 1 with inner distal triangular process, naked. Article 2 with one outer subproximal, one outer distal, and one mid-inner simple setae, and two inner distal spines. Article 3 with inner distal simple seta and two (one small and one large) inner distal spines. Article 4 with two inner PSS. Article 5 with two distal simple setae and six distal PSS. Article 6 with outer distal simple seta. Articles 7–9 each with one outer distal and one inner distal simple setae; article 8 with distal PSS. Article 10 with five distal simple setae. Squama 0.13 times as long as antenna, narrow, with five simple setae.

Epistome thin, spiniform (Figures 1B, 2B). Labrum (Figure 2F) bipartite, with lateral fine setae and distal serrations. Mandibles (Figure 2G–J) with serrations on body and well-developed molar process. Left mandibular incisor (Figure 2G) with four teeth; setiferous lobe with several complex setae; lacinia mobilis with four teeth. Right mandibular incisor (Figure 2H) with five teeth; setiferous lobe with trifurcate seta and several complex setae. Palp (Figure 2J, j1, j2) with three articles; articles 1–3 with length ratio 1.00:2.61:1.43; article 1 with four ventral simple setae; article 2 with mid-ventral simple seta and seven ventral blade-like spiniform setae (Figure 2j1); article 3 with three simple setae, four serrate setae, and pectinate seta (Figure 2j2) in distal region. Labium (Figure 2K) with lobe bearing inner and outer setation. Palp setulate, with three distal spiniform setae. Maxillule (Figure 3A–C, c1) with biarticulate palp bearing four biserrate-tipped setae (Figure 3c1) at end. Outer endite (Figure 3A) with twelve distal spiniform setae, two subdistal setae, and outer and inner setation. Inner endite (Figure 3B) with distal simple seta, two distal plumose setae, distal trifurcate seta, outer clumps of fine setae, and outer process. Maxilla (Figure 3D, d1, d2) with outer and inner serrations on body. Inner lobe of fixed endite with serrate spiniform seta and 17 basally swollen setae. Outer lobe of fixed endite (Figure 3D, d1, 2) with six simple setae (one broken), five upswept spiniform setae (one pinnate), three trifurcate spiniform setae, branched seta (Figure 3d2), and serrate spiniform seta; outer margin serrate. Inner lobe of movable endite with five setae (one pinnate). Outer lobe of movable endite with eight simple setae and two basally setulate setae. Maxilliped (Figure 3E, F, f1) with naked coxa. Basis with (right) or without (left) two outer distal spiniform processes; inner distal region with plumose seta. Endite with outer region serrate and setulate; inner region with two (right) or one (left) coupling hooks, five basally swollen setae (two plumose); distal region with ventral simple seta, ventral pinnate spiniform seta, and eight complex spiniform setae. Palp article 1 with outer distal simple seta and inner distal plumose seta; article 2 with one outer distal, one inner ventrodistal, and 17 inner simple setae, and two inner ventral plumose setae; article 3 with nine inner simple setae; article 4 with one outer ventrodistal and two outer distal simple setae, and four inner distal spiniform setae. Epignath (Figure 3G) cup-shaped, with setulate terminal seta.

Cheliped (Figures 4A, B, b1, 5) with triarticulate exopod bearing four plumose setae at tip. Basis 2.06 times as long as wide, with one dorsodistal, one ventro-subproximal, one mid-ventral, and two ventrodistal simple setae, and inner serial ridges (Figure 5). Merus with one dorsodistal, one outer distal, and two ventro-subdistal simple setae, and ventrodistal spiniform seta. Carpus 1.37 times as long as basis, 2.50 times as long as wide, with six dorsal, two outer ventral, and six ventral simple setae. Propodus with three outer ventral, five ventral, and two inner ventral simple setae, and triangular claw; dorsal region of palm with three simple setae; three inner simple setae and inner short plumose seta at insertion of dactylus; cutting surface with three proximal and six outer distal simple setae, proximal small triangular process, subproximal large triangular process bearing three denticles, and several tiny spiniform setae. Dactylus (Figure 4b1) longer than fixed finger, with three inner subdistal simple setae, four ventral small triangular processes, and several ventral spiniform setae; unguis pointed.

Pereopods 1–6 cylindrical, with length ratio 1.00:0.93:0:90:0.83:0.91:1.00. Pereopod 1 (Figure 4C, c1) 0.35 times as long as BL, with length ratio of basis, ischium, merus, carpus, propodus, and dactylus–unguis 1.00:0.11:0.45:0.47:0.35:0.38. Coxa with anterior process bearing three simple setae; inner region with several plumose setae.

Basis cylindrical, narrow, 4.57 times as long as wide, with four dorsal simple setae each longer than width of pereopod-1 basis, one ventro-subproximal, one ventro-subdistal, and three ventrodistal simple setae, and two subproximal PSS. Ischium with three ventrodistal simple setae. Merus with three dorsodistal, three mid-inner ventral, two ventral, and two ventrodistal simple setae, and one dorsodistal and one ventrodistal spiniform setae. Carpus with seven dorsal, three long ventral, and three short ventral simple setae, and one dorsodistal and two ventral spiniform setae. Propodus with two dorsal, one mid-outer, and four ventral simple setae, two dorsal and three ventral spiniform setae, mid-dorsal PSS, and ventrodistal pectinate spiniform seta (Figure 4c1). Dactylus with one dorsal and two ventrodistal simple setae, and ventral serration; unguis half of dactylus length, naked. Exopod triarticulate; article 3 with five plumose setae. Pereopod 2 (Figure 4D) with length ratio of articles from basis to dactylus–unguis 1.00:0.14:0.25:0.43:0.46:0.56. Coxa with simple seta. Basis cylindrical, narrow, 4.69 times as long as wide, with one inner subproximal, one ventro-subproximal, one ventro-subdistal, and three ventrodistal simple setae, and three dorsal PSS. Ischium with two ventrodistal simple setae. Merus with two dorsodistal, one outer distal, and one ventral simple setae, and ventrodistal spiniform seta. Carpus with four dorsodistal and two ventral simple setae, and one mid-outer ventral, one outer distal, and one ventrodistal spiniform setae. Propodus with two dorsal and two ventral (one tiny) simple setae, two dorsal, one mid-outer, and two ventral spiniform setae, and mid-dorsal PSS. Dactylus with one dorsal and two ventrodistal simple setae; unguis slightly shorter than dactylus, naked. Pereopod 3 (Figure 4E, e1) with length ratio of articles from basis to dactylus–unguis 1.00:0.15:0.20:0.36:0.43:0.52. Similar to pereopod 2, except: basis without ventro-subproximal simple seta; basis with two ventrodistal simple setae; merus with dorsodistal simple seta; carpus with three dorsodistal simple setae; carpus without mid-ventral simple seta; carpus with two outer distal spiniform setae; propodus with three dorsal spiniform setae; propodus without mid-outer spiniform seta. Pereopod 4 (Figure 4F, f1) with length ratio of articles from basis to dactylus–unguis 1.00:0.12:0.26:0.40:0.40:0.42. Coxa with simple seta. Basis cylindrical, narrow, 3.52 times as long as wide, with one outer-subproximal, one inner-subproximal, and two ventrodistal simple setae, and three dorsal and one ventral PSS. Ischium with two ventrodistal simple setae. Merus with one dorsodistal and two ventrodistal simple setae, and two ventrodistal spiniform setae. Carpus with two outer distal and two inner distal simple setae, and two ventral, two outer distal, and two inner distal spiniform setae. Propodus with dorsodistal long simple seta, mid-dorsal PSS, dorso-subdistal row of five pectinate setae, and dorsodistal row of six pectinate setae. Dactylus with one dorsal and one ventrodistal simple setae; unguis as long as dactylus, naked. Pereopod 5 (Figure 4G, g1) with length ratio of articles from basis to dactylus–unguis 1.00:0.12:0.32:0.44:0.41:0.55. Coxa, basis, ischium, merus, and dactylus–unguis similar to those of pereopod 4, except: basis without inner subproximal simple seta; basis with mid-inner ventral simple seta; ischium with three ventrodistal simple setae. Carpus with three dorsodistal and one ventro-subdistal simple setae, and three ventral spiniform setae. Propodus with two dorsal simple setae, one dorsodistal, one outer subdistal, and two ventral spiniform setae, mid-dorsal PSS, and inner ventral row of nine blade-like spiniform setae. Pereopod 6 (Figure 4H, h1–4) with length ratio of articles from basis to dactylus–unguis 1.00:0.12:0.42:0.56:0.48:0.57. Coxa with simple seta and plumose seta. Basis with one ventro-subproximal, one ventro-subdistal, and two ventrodistal simple setae, and four dorsal plumose setae; proximal region with four PSS. Ischium with three ventrodistal simple setae. Merus with two ventrodistal simple setae and three dorsal plumose setae. Carpus with two outer distal and two ventral simple setae, ventrodistal spiniform seta, and three dorsal plumose setae. Propodus with mid-dorsal simple seta, two outer subdistal, one ventro-subproximal, and one inner subdistal spiniform setae, mid-dorsal PSS, two dorsodistal serrate setae (Figure 4h1), one outer subdistal and four inner dorsodistal pectinate setae (Figure 4h2), and inner ventral row of eleven blade-like spiniform setae (Figure 4h3). Dactylus–unguis similar to pereopod 5.

Pleopods (Figure 4I, i1) five pairs, all similar. Protopod biarticulate, narrow, with two inner plumose setae. Exopod uniarticulate, 1.27 times as long as protopod, with eight plumose setae. Endopod uniarticulate, 1.23 times as long as exopod, with six plumose setae and mid-inner distally-hooked plumose seta (Figure 4i1).

Uropod (Figures 1B, 4J) with protopod bearing one inner distal and four outer simple setae. Exopod with article 1 bearing simple seta; other articles lost before fixation. Endopod nearly twice as long as pleotelson (Figure 1B); article 1 naked; other articles lost before fixation.

Variation and stability

In addition to the holotype (RUMF-ZC-6081), one paratype (ICHUM6029) was dissected, and its antennule, antenna, maxilliped, cheliped, pereopods 1–6, and pleopod 1 were observed (as with the holotype, most uropodal articles were lost before fixation). The numbers of setae, aesthetascs, and processes on these appendages were identical between the two specimens, with the following exceptions (ranges in parentheses; the state in the holotype in bold). Antennule: inner distal simple setae (**3**–4) and distal PSS (**4**–5) on article 2. Antenna: outer simple setae on article 6 (**1**–2); PSS on article 8 (0–**1**). Maxilliped: outer distal spiniform processes on the basis (**0** or **2**); distal complex spiniform setae on the endite (**8**–9); inner simple setae on palp articles 2 and 3 (17–**18**, 8–**9**, respectively). Cheliped: ventral simple setae on the carpus (5–**6**); proximal simple setae on the cutting surface of the fixed finger (**3**–4); dorsal simple setae on the palm (**3**–4). Pereopod 1: dorsal simple setae on the carpus (6–**7**); inner ventral simple setae proximal to the most proximal spiniform seta on the carpus (**1**–2). Pereopod 2: ventrodistal simple setae on the basis (**3**–4); ventral simple setae on the merus (**1**–2); dorsodistal simple setae (**4**–5) and mid-outer ventral spiniform setae (0–**1**) on the carpus. Pereopod 3: ventroproximal PSS on the basis (**0**–1); ventral simple setae on the carpus (**0**–1). Pereopod 4: ventro-subdistal simple setae on the basis (**0**–1); ventral spiniform setae on the propodus (**0**–1). Pereopod 5: outer distal simple setae (**0**–1) and ventro-subdistal simple setae (0–**1**) on the carpus. Pereopod 6: dorsal plumose setae on the basis (**4**–5); dorsal plumose setae (2–**3**) and inner distal simple setae (**0**–1) on the carpus; inner ventral blade-like spiniform setae (**11** or 13) and inner dorsodistal pectinate setae (**4**–5) on the propodus.

Inner serial ridges on the chelipedal bases, a fully-developed marsupium, and a genital cone were observed on both specimens. The PL/PW ratio of the holotype and paratype were 2.57 and 2.61, respectively.

Genetic information

The partial COI sequence (658 nt, encoding 219 amino acids) and the nearly complete 18S sequence (2176 nt) were determined from the holotype specimen; their INSD accession numbers are LC510354 and LC510355, respectively. For COI (402 nt in the aligned dataset), the K2P distance between *Paradoxapseudes shimojiensis* and *P. intermedius* was 34.3%. For 18S (2036 nt in the aligned dataset), K2P distances between *P. shimojiensis* and two congeners (*P. bermudeus* and *P. littoralis*) were 5.7% and 5.5%, respectively.

Remarks

Paradoxapseudes shimojiensis sp. nov. is the 18th species described in this genus and the fourth *Paradoxapseudes* species found in submarine caves. Five congeners share a long pleotelson, defined here as one with PL/PW greater than 1.7, with *P. shimojiensis*: *P. basibidens* (Guţu, 2007) from Tanzania; *P. bassoprofundo* Bamber and Błażewicz-Paszkowycz, 2013 from Australia; *P. bermudeus* from Bermuda (submarine cave); *P. edgari* Guţu, 2008 from the Cook Islands; and *P. heroae* Sieg, 1985 from Argentina.

Paradoxapseudes shimojiensis can be distinguished from these five species by the combinations of six character states presented in Table II. In addition to the features in the table, *P. shimojiensis* differs from *P. basibidens* in having more-setose maxillipedal palp articles 2 and 3 (eleven and five simple setae on the two articles in *P. basibidens*), the chelipedal merus with one ventrodistal spiniform seta (absent in *P. basibidens*), the pereopod-1 carpus with six or seven dorsal simple setae (four in *P. basibidens*), the bases of pereopods 4 and 5 bearing ventrodistal simple setae (lacking in *P. basibidens*), and the ischia of pereopods 1–6 without dorsal setae (present in *P. basibidens*) (Guţu 2007); from *P. bassoprofundo* in having the chelipedal basis with a single ventro-subproximal simple seta (two in *P. bassoprofundo*), the chelipedal merus with one ventrodistal spiniform seta (absent in *P. bassoprofundo*), the chelipedal carpus with several dorsal simple setae (absent in *P. bassoprofundo*), and the ischia of pereopods 4–6 without dorsal setae (present in *P. bassoprofundo*) (Bamber and Błażewicz-Paszkowycz 2013); from *P. bermudeus* in having the ventro-subproximal seta on the pereopod-1 basis simple (plumose in *P. bermudeus*), the chelipedal merus with one ventrodistal spiniform seta (absent in *P. bermudeus*), and the ischia of pereopods 5 and 6 without dorsal setae (present in *P. bermudeus*) (Băcescu 1980; Guţu 2008); from *P. edgari* in the pleotelson having two pairs of slight lateral processes (lateral margins of pleotelson straight in *P. edgari*), the chelipedal basis with one dorsodistal simple seta (two in *P. edgari*), the chelipedal merus with one ventrodistal spiniform seta (absent in *P. edgari*), and the ventro-subproximal seta on the pereopod-1 basis simple (plumose in *P. edgari*) (Guţu 2008); and from *P. heroae* in having the chelipedal basis without dorsal processes (present in *P. heroae*), the inner distal seta on article 1 of the maxillipedal palp plumose (simple in *P. heroae*), the pereopod-1 basis with one ventro-subproximal simple seta (absent in *P. heroae*), the pereopod-1 carpus with six or seven dorsal simple setae (11 in *P. heroae*), and the ischia of pereopods 4 and 5 without dorsal setae (present in *P. heroae*) (Sieg 1986).

Paradoxapseudes shimojiensis differs from another Japanese species, *P. littoralis*, in having a long pleotelson (PL/PW = 1.2 in *P. littoralis*), antennal article 1 naked (with one inner seta in *P. littoralis*), the chelipedal merus with one ventrodistal spiniform seta (absent in *P. littoralis*), the pereopod-6 basis with four or five dorsal plumose setae (eight in *P. littoralis*), and the dorsal setae on the pereopod-6 carpus plumose (simple in *P. littoralis*) (Shiino 1952).

Discussion

Paradoxapseudes shimojiensis sp. nov. is the 18th tanaidacean species reported from submarine caves worldwide, and the second from Japan—the other being the pseudozeuxid *Haimormus shimojiensis* Kakui and Fujita, 2018, originally described from the same cave as *P. shimojiensis*. Submarine caves are extreme environments under dark, food scarce, and hypoxic conditions; thus morphological, behavioral, and physiological adaptations to improve food finding capability, to resist starvation, and to reduce energy demand via reduced metabolism may be required for life in caves (Iliffe and Bishop 2007). Although cave endemic species are known to exist (e.g., Okanishi and Fujita 2018), as caves open to the surrounding marine environment, animals thriving in caves can also be found in suitable habitats outside of caves. In addition, organisms which can survive in caves for only a short time can accidentally invade caves (Iliffe and Bishop 2007). Two of our *P. shimojiensis* individuals were collected from the completely dark, middle zone of the cave, and both had a fully-developed marsupium, implying this species may be thriving in the caves (= stygophilic taxon). But, since we lack faunal data from the surrounding benthic environment outside the cave, it remains unclear whether *P. shimojiensis* is restricted to submarine caves. Furthermore, while cave-dwelling animals often lose eye pigments or eyes (Iliffe and Bishop 2007), the lack of eye pigments (Figure 1A, B) in *P. shimojiensis* is not necessarily an adaptation to cave dwelling. Species in *Paradoxapseudes*, including *P. shimojiensis,* have a fossorial-type pereopod 1 (Guţu and Sieg 1999), indicating that they are burrowers (or tube-dwellers; cf. Kakui and Hiruta 2017). Non-cave-dwelling congeners thus also likely live in dim or dark microhabitats, and the loss of eye pigments in *P. shimojiensis* could be related either to cave dwelling, or to a burrowing or tube-dwelling mode of life.

We found inner serial ridges on the left and right chelipeds of *P. shimojiensis* (Figure 5), which is the first case known in *Paradoxapseudes*. The ridges form an arc on the inner surface of the basis, and those on the left and right chelipeds are opposed to each other; each ridge is orthogonal to the swing path of the basis. This face-to-face relationship of serial ridges or hatching on chelipeds has been found in some other tanaidacean genera (*Apseudomorpha* Miller, 1940, *Nesotanais* Shiino, 1968, and *Tanaopsis* Sars, 1899), but the location of the ridges in these taxa is different from that in *P. shimojiensis*: the ridges occur on the carpi in *Apseudomorpha* (Menzies 1953); on the propodi and dactyli in *Nesotanais* (Kakui et al. 2010); and on the dactyli in

Tanaopsis (Kakui and Shimada 2017). The location of the serial ridges in *P. shimojiensis* is quite similar to that of the ridges in *Histricostoma* harvestmen (Nemastomatidae, Opiliones; Juberthie 1957), where they form an arc on the inner surface of the basal segment of the chelicerae and are considered to be a stridulatory organ. This similarity suggests that the paired serial ridges in *P. shimojiensis* may also be a stridulatory organ and function in producing sound. As possible stridulatory organs have also been found in tanaidaceans not dwelling in submarine caves (e.g., Kakui et al. 2010), and no other submarine cave species bear these ridges, the serial ridges may not an adaptation to cave dwelling.

The two specimens of *P. shimojiensis* we observed bear external female and male reproductive features in the form of a fully-developed marsupium and genital cone (Figure 1). This indicates that *P. shimojiensis* is simultaneously hermaphroditic. *Paradoxapseudes* contains three possibly hermaphroditic species (*P. bermudeus, P. intermedius*, and *P. shimojiensis*; Băcescu 1980; Guţu 2006; this study), which are three of the four congeners reported from submarine caves. Simultaneous or sequential hermaphroditism has so far been confirmed or inferred for about 30 tanaidacean species (Rumbold et al. 2015; Kakui et al. 2019), or about 2% of the tanaidacean species currently known worldwide (ca. 1400 species; Anderson 2017). Among taxa reported from submarine caves, however, six of 18 species (ca. 33%) have been confirmed or suggested to be hermaphrodites: *Apseudopsis latreilli* (Milne-Edwards, 1828), the three *Paradoxapseudes* species mentioned above, *Falsapseudes bowmani* (Guţu and Iliffe, 1989), and *Chondrochelia savignyi* (Krøyer, 1842) (Masunari 1983; Esquete et al. 2012; Kakui et al. 2019). As tanaidaceans are benthic animals and lack a planktonic larval stage (obligate dispersal phase) in their life cycle, they have fewer opportunities to colonize submarine caves than organisms with planktonic larvae. In the case of two random individuals reaching the inside of a cave, gonochoristic species require both a male and a female for propagation; in comparison, protandrous or protogynous species have a twofold chance of propagation, and simultaneous hermaphrodites have a threefold chance. For simultaneous hermaphrodites that can self-fertilize, such as one species of *Apseudes* (Kakui and Hiruta 2013), only one individual is needed to establish a population. These advantages of hermaphrodites in colonization may be reflected in the larger proportion of hermaphroditic species in submarine caves.

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Table I. List of PCR and cycle sequencing (CS) primers used in this study

Marker	Primer	Sequence	Reaction	Source
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	PCR & CS	Folmer et al. (1994)
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	PCR & CS	Folmer et al. (1994)
18S	SR-1	TACCTGGTTGATCCTGCCAG	PCR	Nakayama et al. (1996)
	18S-b3F	CCTGAGAAACGGCTACCACAT	CS	Kakui and Shimada (2017)
	18S-b4R	TCCAACTACGAGCTTTTTAACC	CS	Kakui et al. (2011)
	18S-b8R	TCTAAGGGCATCACAGACCTG	CS	Kakui et al. (2011)
	18S-b8F	GGTCTGTGATGCCCTTAGATG	CS	Kakui et al. (2011)
	SR-12	CCTTCCGCAGGTTCACCTAC	PCR & CS	Nakayama et al. (1996)

Table II. Comparison of selected characters for six *Paradoxapseudes* species having a long pleotelson (PL/PW greater than 1.7). *, hermaphroditic (others, gonochoristic). [a]Long, as long as or longer than width of pereopod-1 basis; short, shorter than width of pereopod-1 basis. –, no data. Abbreviations: pl.seta, plumose seta; s.seta, simple seta; sp.seta, spiniform seta

	Antenna	Maxilliped	Pereopod 1			Pleopod
	Article 1	Basis	Basis		Merus	Protopod
	Inner s.seta	Inner distal seta	Dorsal seta[a]	Ventrodistal sp.seta	Mid-inner ventral s.seta	Inner pl.seta
P. shimojiensis sp. nov.*	0	1 pl.seta	4 long s.setae	0	3	2
P. basibidens	0	1 pl.seta	5 long pl.setae	1	0	2
P. bassoprofundo	1	0	1 long and 3 short s.setae	0	3	1
*P. bermudeus**	0	–	4 long s.setae	0	3	0
P. edgari	0	1 pl.seta	4 long s.setae	1	4	2
P. heroae	1	2 s.setae	3 short s.setae	0	4	2

Figure 1. *Paradoxapseudes shimojiensis* sp. nov.: A, B, holotype in living state, left dorsal (A) and left (B) views; C, paratype, fixed, in glycerine, showing genital cone with two male gonopores (arrow) on pereonite 6, and empty fully-developed marsupium; right pereopods detached, right ventral view. Abbreviations: *p6*, pereonite 6; *pl1*, pleonite 1.

Figure 2. *Paradoxapseudes shimojiensis* sp. nov., holotype: A, body, dorsal view; a1, pleotelson, dorsal view; B, body, left view; C, right antennule, articles 1 and 2, ventral view; D, right antennule, articles 3 and 4, and outer and inner flagella, ventral view; d1, outer flagellum, article 7, ventral view (most setae omitted); E, right antenna, ventral view; F, labrum; G, H, mandible, left and right distal portions, respectively; I, left mandibular molar; J, right mandibular palp; j1, blade-like spiniform seta; j2, pectinate seta; K, labium. Arrows, left slight lateral processes.

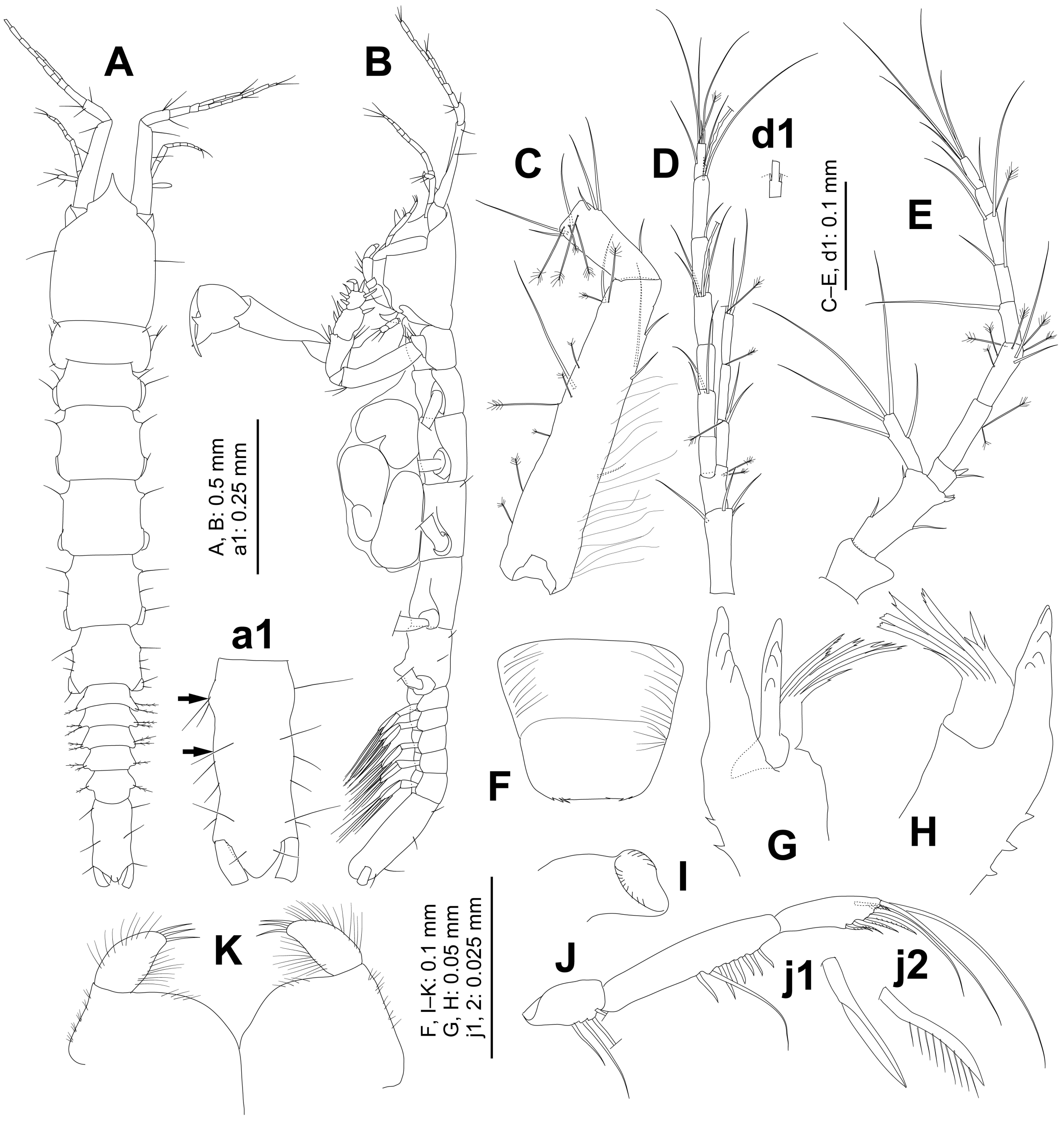
Figure 3. *Paradoxapseudes shimojiensis* sp. nov. (A–F, holotype; G, paratype): A, B, outer and inner endites of left maxillule, respectively; C, right maxillular palp; c1, distal portion of biserrate-tipped seta; D, left maxilla (most setae on outer lobe of fixed endite omitted), anterior view; d1, same, outer lobe of fixed endite, anterior view; d2, branched seta; E, left maxillipedal endite; F, right maxilliped (setae on endite omitted); f1, same, palp article-4; G, right epignath.

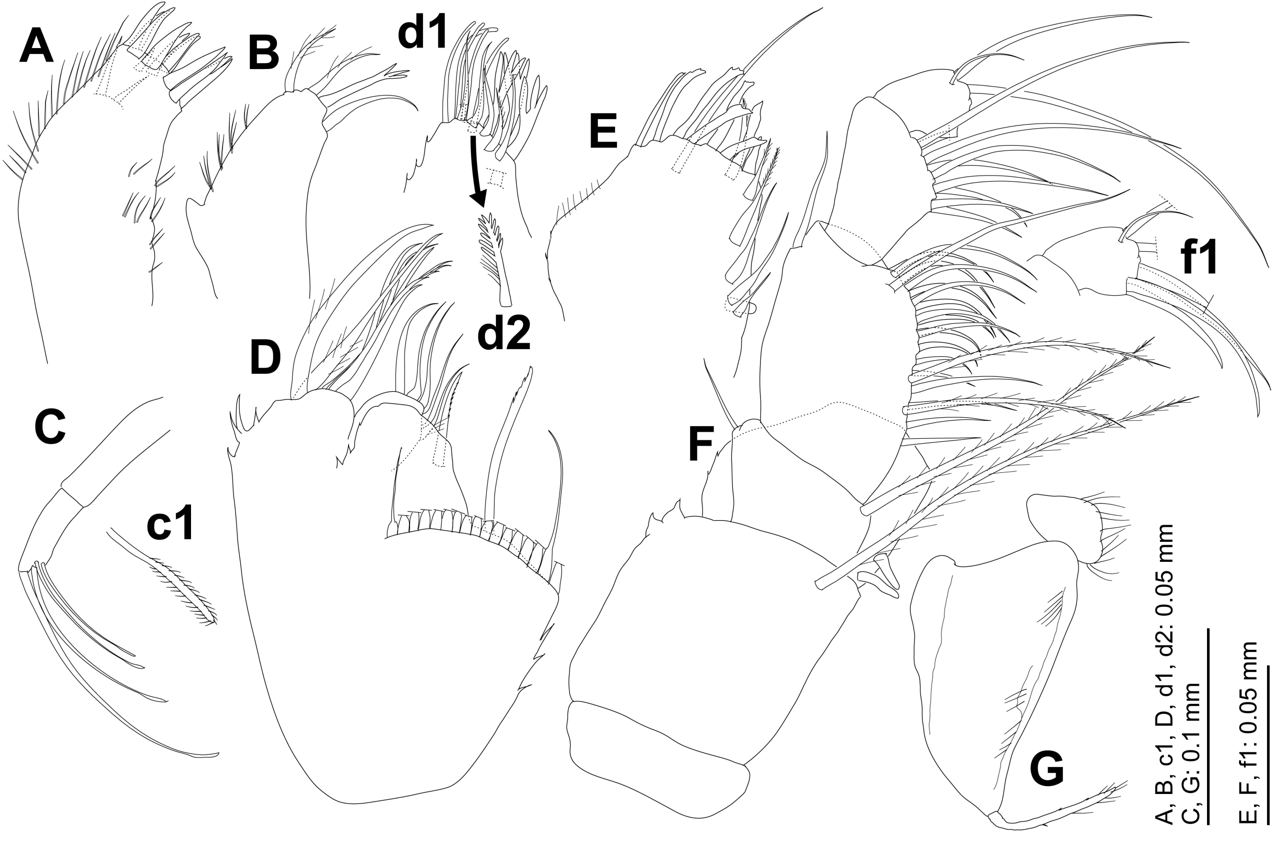
Figure 4. *Paradoxapseudes shimojiensis* sp. nov., holotype: A, left cheliped, outer view (inner serial ridges omitted); B, right chela, inner view (dactylus and most setae omitted); b1, same, dactylus, inner view; C–H, right pereopods 1–6, outer view; c1, pectinate spiniform seta; e1, dactylus (part) and unguis of right pereopod 3, outer view;

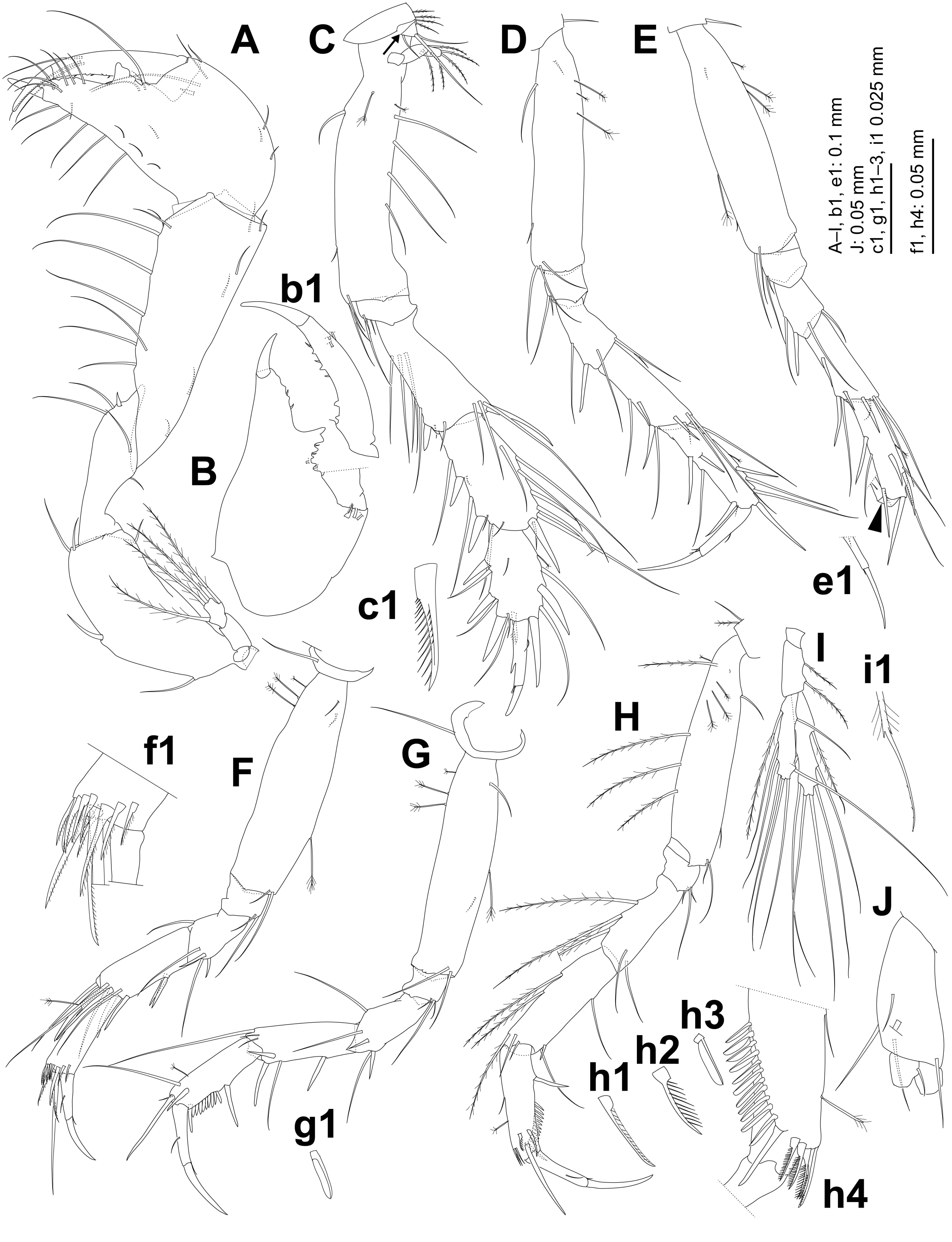
f1, distal portion of right pereopod-4 propodus, outer view; g1, blade-like spiniform seta; h1, serrate seta; h2, pectinate seta; h3, blade-like spiniform seta; h4, distal portion of right pereopod-6 propodus, inner view; I, right pleopod 1 (most setal ornamentation omitted); i1, distally-hooked plumose seta; J, right uropod (most articles of endopod and exopod lost). Arrow, broken portion on pereopod-1 coxa; arrowhead, artificially bent point on pereopod-4 dactylus.

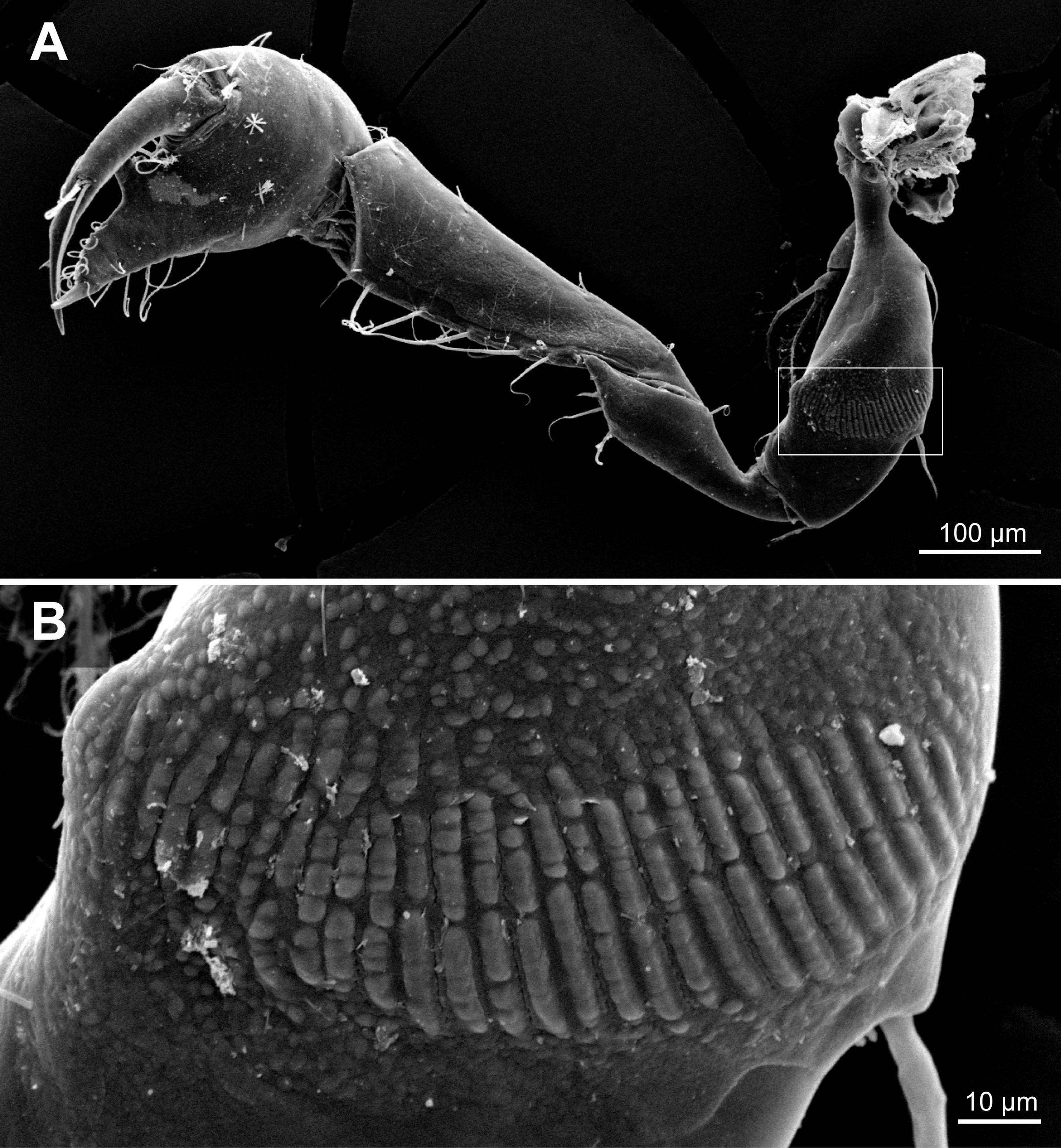
Figure 5. *Paradoxapseudes shimojiensis* sp. nov., paratype, SEM image: A, right cheliped, inner view, with rectangle indicating position of enlargement in B; B, inner serial ridges on basis.


A
B
A, B: 0.5 mm
C
p6
pl1
0.1 mm


A
B
C
D
d1
E
C–E, d1: 0.1 mm
A, B: 0.5 mm
a1: 0.25 mm
a1
F
G
H
I
J
j1
j2
K
F, I–K: 0.1 mm
G, H: 0.05 mm
j1, 2: 0.025 mm


A
B
d1
E
f1
C
c1
D
d2
F
G
A, B, c1, D, d1, d2: 0.05 mm
C, G: 0.1 mm
E, F, f1: 0.05 mm


A
C
D
E
B
b1
c1
e1
f1
F
G
H
I
i1
J
g1
h1
h2
h3
h4
A–I, b1, e1: 0.1 mm
J: 0.05 mm
c1, g1, h1–3, i1 0.025 mm
f1, h4: 0.05 mm


A
100 µm
B
10 µm