European Journal of Taxonomy 1039: 70–115
https://doi.org/10.5852/ejt.2026.1039.3181

europeanjournaloftaxonomy.eu
ISSN 2118-9773
2026 · Kim G. *et al.*

Received: 4 June 2025 • Accepted: 18 November 2025 • Published: 5 February 2026

Topic editor: Magalie Castelin • Section editor: Nesrine Akkari • Desk editor: Kristiaan Hoedemakers

Research article

urn:lsid:zoobank.org:pub:39074DC2-B53C-49CE-B63E-0B73C4E5E586

The family Xystodesmidae in the Korean Peninsula (Diplopoda: Polydesmida)

Gyeongmin KIM [1], Zoltán KORSÓS [2,*] & Ui Wook HWANG [3,*]

[1] School of Life Sciences, Graduate School, Kyungpook National University, Daegu 41566, Republic of Korea
[2] Department of Zoology, University of Veterinary Medicine Budapest, Rottenbiller u. 50, H-1077 Budapest, Hungary.
[2] Department of Zoology, Hungarian Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary.
[3] Department of Biology Education, Teachers College, and Institute for Phylogenomics and Evolution, Kyungpook National University, Daegu 41566, Republic of Korea.
[3] Department of Biomedical Convergence Science and Technology, Kyungpook National University, Daegu 41566, Republic of Korea.
[3] Department of Advanced Bioconvergence, Kyungpook National University, Daegu 41566, Republic of Korea.
[3] Institute for Korean Herb-Bio Convergence Promotion, Kyungpook National University, Daegu 41566, Republic of Korea.
[3] Phylomics Inc., Daegu 41910,Republic of Korea.

[*] Corresponding authors: zkorsos@gmail.com, uwhwang1@gmail.com
[1] Email: koungmin94@gmail.com

Abstract. The polydesmidan family Xystodesmidae is reviewed with respect to the millipede fauna of the Korean Peninsula. It encompasses eight species in four genera: *Xystodesmus* Cook, 1895; *Riukiaria* Attems, 1898; *Levizonus* Attems, 1898; and *Parafontaria* Verhoeff, 1936. We redescribe five species of *Xystodesmus* including *Xystodesmus pallidus* (Verhoeff, 1937) and *Xystodesmus amoenus* (Takakuwa, 1942). *Xystodesmus shirozui* (Takakuwa, 1942) is new to the fauna of Korea. The enigmatic *Pachydesmus bazanensis* Takakuwa, 1942 is transferred to *Xystodesmus* as *X. bazanensis* comb. nov. A new species is described, *X. bifurcus* sp. nov. Of the other three genera, only one species of each is known from Korea, and they are as follows: *Riukiaria koreana* sp. nov. (from *R. semicircularis* (Takakuwa, 1941)), *Levizonus circularis* (Takakuwa, 1942) and *Parafontaria koreana* (Paik, 1963). Their validity and taxonomic position, based partly on new material, is discussed. Our maximum likelihood phylogeny, estimated based on concatenated sequences of mitochondrial *COI* and nuclear *EF1-α*, supported the monophyly of these four genera. Furthermore, the presence of subclades within these clades suggests potential genetic differentiation at the population level.

Keywords. *Levizonus*, North and South Korea, *Parafontaria*, *Riukiaria*, *Xystodesmus*.

Kim G., Korsós Z. & Hwang U.W. 2026. The family Xystodesmidae in the Korean Peninsula (Diplopoda: Polydesmida). *European Journal of Taxonomy* 1039: 70–115. https://doi.org/10.5852/ejt.2026.1039.3181

Introduction

The polydesmidan millipede family Xystodesmidae Cook, 1895 is represented by two tribes in the Korean Peninsula: Xystodesmini Hoffman, 1980 and Parafontariini Hoffman, 1980 (Means *et al.* 2021). Xystodesmini in East Asia has three genera: *Xystodesmus* Cook, 1895, *Riukiaria* Attems, 1938, and *Levizonus* Attems, 1898. The position of the fourth genus of Xystodesmidae, *Parafontaria* Verhoeff, 1936, is in its own tribe Parafontariini, based on the phylogenetic classification of Means *et al.* (2021).

Currently, six species in five genera of the family Xystodesmidae have been recorded on the Korean Peninsula (Kim *et al.* 2023): *Xystodesmus pallidus* (Verhoeff, 1937), *X. amoenus* (Takakuwa, 1942), *Riukiaria semicularis* (Takakuwa, 1941), *Levizonus circularis* Takakuwa, 1942, *Pachydesmus bazanensis* Takakuwa, 1942, and *Parafontaria koreana* (Paik, 1963).

The first record of a xystodesmid species on the Korean Peninsula was reported by Verhoeff (1937), with a species initially named *Koreoaria pallida* (currently recognized as *X. pallidus*). Subsequently, additional species were described: *Riukiaria semicularis* by Takakuwa (1941b), *Levizonus circularis* by Takakuwa (1942a), *Koreoaria amoena* (currently *X. amoenus*) and *Pachydesmus bazanensis* by Takakuwa (1942b), *Japonaria koreana* (currently *Parafontaria koreana*) by Paik (1963), and *Levizonus variabilis* by Mikhaljova *et al.* (2000).

After these records, several taxonomic revisions have occurred. The genus *Japonaria* was synonymized with *Parafontaria* by Hoffman (1978b) and Tanabe (2002), resulting in the reclassification of *J. koreana* as *P. koreana*. The genus *Koreoaria* was synonymized with *Xystodesmus* by Korsós & Nakamura (2025), thereby reassigning *K. pallida* and *K. amoena* to *Xystodesmus*. Within the genus *Levizonus*, *L. variabilis* was synonymized with *L. circularis* by Mikhaljova (2021). Furthermore, the genus *Pachydesmus* is generally recognized as a North American genus within Xystodesmidae, and its taxonomic validity had already been questioned in previous studies (Tanabe & Shinohara 1996; Kim *et al*. 2023), highlighting the need for further taxonomic re-examination.

The genus *Xystodesmus* has been reviewed by Tanabe & Shinohara (1996), who already suggested moving the two Korean species previously known in *Koreoaria* Verhoeff, 1937 (*Koreoaria pallida* Verhoeff, 1942 and *K. amoena* Takakuwa, 1942) to *Xystodesmus*. More recently, Korsós & Nakamura (2025) established the synonymy of these two species as *Xystodesmus pallidus* and *X. amoenus*, respectively. With our decision to move the enigmatic *Pachydesmus bazanensis* Takakuwa, 1942, our description of the new species *Xystodesmus bifurcus* sp. nov., and the occurrence of *X. shirozui* (Takakuwa, 1942) in Korea, we now deal with five species of *Xystodesmus* altogether in the Korean Peninsula. *Riukiaria*, *Levizonus*, and *Parafontaria* have one species each, of which we separate *Riukiaria* from the Japanese *Riukiaria semicircularis* (Takakuwa, 1941) as new: *R. koreana* sp. nov. Our phylogeny using a maximum likelihood algorithm (ML) based on concatenated *COI* and *EF1-α* sequences supports the five species, indicating the distinct genetic lineages within each genus.

Material and methods

Millipedes were collected during 2023 and 2024 in seven provinces of South Korea from the southern islands of Jindo, Wando and Geoje, to the north in Gangwon Province. They are stored in 70% ethanol in the Molecular Phylogenetics Laboratory in the Department of Biology Education, Teachers College of Kyungpook National University, Daegu. Specimens were studied and dissected using a Nikon SMZ445 stereo microscope. Measurements and photographs were made with a Leica M205C stereo microscope equipped with a Leica MC190 HD digital camera. Images were processed with Helicon Focus 8.1.15 focus stacking software and Adobe Photoshop 7.0 CE for Windows. The habitus pictures were made with a Nikon D750 SLR camera and Nikon R1C1 wireless close-up speedlight system. The terminology of the morphology follows Hoffman (1956), Tanabe & Shinohara (1996), Tanabe (2002), and Korsós *et al*. (2011). Maps were obtained from a free map source (https://d-maps.com) and were modified using Adobe Illustrator ver. 22.2 (https://www.adobe.com).

DNA extraction and sequencing

To perform a molecular analysis, we selected a total of 29 specimens including eight of *X. pallidus*, ten of *X. shirozui*, six of *X. bifurcus* sp. nov., two of *R. koreana* sp. nov., and three of *P. koreana*. Genomic DNA was extracted from the right legs of the 13–16th rings of each individual using a DNeasy Blood and Tissue Kit (Qiagen, United States). The concentration of extracted DNA was measured using NanoDrop 2000 (Thermo Fisher Scientific, United States), and integrity was checked with a 1% agarose gel electrophoresis.

For the present study, we employed two genetic markers: mitochondrial cytochrome c oxidase subunit I (*COI*) and elongation factor 1-alpha (*EF1-α*), which were primarily used for the phylogeny of the family Xystodesmidae in previous studies (Sota & Tanabe 2010; Tanabe & Sota 2014; Means *et al*. 2021). To amplify and sequence the two genetic markers, primers were as follows: LCO1490 (forward primer, 5’-GGT CAA CAA ATC ATA AAG ATA-3’) and HCO2198 (reverse primer, 5’-TAA ACT TCA GGG TGA CCA AAA AAT CA-3’) (Folmer *et al*. 1994) for *COI*, and DiploEF1aF (forward primer, 5’-GCC TGG GTT TTG GAT AAA CTT AAG GC-3’), DiploEF1aR3 (reverse primer, 5’-CCT CCA ATC TTG TAA ACG TC-3’) (Sota & Tanabe 2010) for *EF1-α*. Polymerase chain reaction (PCR) was conducted to amplify each gene fragment with a 50 µL total volume of PCR mix comprising 25–100 ng genomic DNA, 10 mM dNTP, and 10 pM of forward and reverse primers, with the addition of 0.25 units of Taq DNA polymerase (Solgent, South Korea). To amplify *COI*, the following thermal cycling conditions were used: denaturation at 94°C for 1 min, followed by 5 amplification cycles of 94°C for 1 min, 45°C for 1 min 30 s, and 72°C for 1 min, 30 amplification cycles of 94°C for 1 min, 50°C for 1 min 30 s, and 72°C for 1 min, and a final extension at 72°C for 5 min. Amplification of *EF1-α* was conducted with the following thermal cycling conditions: denaturation at 94°C for 2 min, followed by 35 amplification cycles of 94°C for 30 s, 48° C for 50 s, and 72°C for 1 min, and a final extension at 72°C for 5 min. To confirm the amplification, 1 µL of each PCR product was electrophoresed on a 1% agarose gel containing eco-dye and observed under UV light. The confirmed PCR bands were purified using a QIAquick PCR Purification Kit (QIAGEN, Germany) and directly sequenced with an ABI Prism 3730 DNA sequencer (PerkinElmer, United States) using a Big Dye Termination Sequencing Kit (PerkinElmer, United States).

Genetic distance and phylogenetic analysis

The nucleotide sequences of the partial mitochondrial *COI* and nuclear *EF1-α* from eight specimens of *X. pallidus*, six of *X. bifurcus* sp. nov., ten of *X. shirozui*, two of *R. koreana* sp. nov., and three of *P. koreana* were confirmed by BLAST searches (Altschul *et al*. 1990). All sequences were aligned using Clustal X2, and ambiguous regions where homology could not be identified at the 5’ and 3’ ends in sequences were trimmed by BioEdit ver. 7.2.5 (Hall 1999; Larkin *et al*. 2007). In the case of *EF1-α*, some poorly aligned blocks which may be caused by intronic regions were removed using Gblock ver. 0.91b (Castresana 2000). All novel sequences discovered in this study were deposited in NCBI GenBank (Supp. file 1: Table S1). Genetic distance was calculated for all three genera (*Xystodesmus*, *Riukiaria*, *Parafontaria*) based separately on *COI* and *EF1-α* by the Kimura 2-Parameter method using MEGA ver. 11 (Kimura 1980; Tamura *et al*. 2021). To perform the analysis, we obtained several additional *COI* and *EF1-α* sequences of each genus from NCBI GenBank, and the detailed information is provided in Supp. file 1: Table S2.

Phylogenetic analyses were performed using maximum likelihood (ML) and Bayesian inference (BI) algorithms with unrooted and rooted topologies based on concatenated sequence sets: 29 sequences obtained in the present study, and two sets of *COI* and *EF1-α* sequences, which are *Xystodesmus* sp. PM-2015 and *R. holstii* MTX0191, retrieved from NCBI GenBank, were also included in the phylogenetic analysis (National Library of Medicine 1988; www.ncbi.nlm.nih.gov/genbank) (Supp. file 1: Table S3). To reconstruct the phylogeny with a rooted topology, *COI* and *EF1-α* sequences of *Melaphe vestita* Hoffman & Lohmander, 1968 were selected as an outgroup and retrieved from NCBI GenBank (Supp. file 1: Table S3). Before conducting the phylogenetic analyses, model selection was conducted using Modelfinder in the IQ-TREE software package (http://www.iqtree.org). For reconstructing an unrooted phylogeny, TIM3+F+I (*COI*) and K2P+I (*EF1-α*) were selected as best-fit substitution models, while the substitution models TIM3+F+G4 (*COI*) and K2P+G4 (*EF1-α*) were selected as the optimal models for the rooted phylogeny under the Bayesian information criterion (Schwarz 1978). The ML tree was reconstructed on the IQ-TREE webserver (http://iqtree.github.io) (Trifinopoulos *et al.* 2016). The bootstrap values for the analysis were computed by ultrafast bootstrap approximation with 1000 bootstrap alignments. Each sequence dataset was set to 1000 maximum iterations with 1000 replicates. For BI phylogenetic tree reconstruction, the best-fit substitution models were determined under a Bayesian information criterion using jModeltest ver. 2.2 (Darriba *et al.* 2012). As a result, GTR+F+I (*COI*) and K80+F+I (*EF1-α*) for the unrooted tree, and GTR+F+I (*COI*) and HKY+F+G4 (*EF1-α*) for the rooted tree were selected as the optimal models, respectively. The BI tree was reconstructed using MrBayes ver. 3.22 under two parallel runs for 10 million iterations with a sampling frequency of 1000 iterations (Ronquist *et al.* 2012). After determining that the Markov chain Monte Carlo (MCMC) generations reached a stationary level, the initial 15% of the generations were removed as burn-in. All phylogenies were visualized using FigTree ver. 1.4.2 (Rambaut 2012).

Acronyms of collections

HIBR	=	Honam National Institute of Biological Resources, Mokpo, Republic of Korea
HNHM	=	Hungarian National History Museum, Budapest, Hungary
LEGOA	=	Laboratory of Evolutionary Genomics for Organelles, Arthropod, Daegu, Republic of Korea
SNSB-ZSM	=	Bavaria State Collection of Zoology, Munich, Germany

Results

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Polydesmida Leach, 1815
Family Xystodesmidae Cook, 1895
Subfamily Xystodesminae Hoffman, 1978
Tribe Xystodesmini Hoffman, 1980

Genus ***Xystodesmus*** Cook, 1895

Takakuwaia Verhoeff, 1936a: 152–153 (with type species *T. furculigera* Verhoeff, 1936), synonymized by Hoffman (1956: 96).
Cyphonaria Verhoeff, 1936a: 160–161 (with type species *Fontaria* (*Cyphonaria*) *scabra* Verhoeff, 1936, originally as a subgenus), synonymized by Hoffman (1980: 156).
Koreoaria Verhoeff, 1937: 319 (with type species of *K. palllida* Verhoeff, 1937), synonymized by Korsós & Nakamura (2025: 193).
Phrurodesmus Takakuwa, 1943: 604 (with type species *P. gracilipes* Takakuwa, 1943), synonymized by Tanabe & Shinohara (1996: 1472).
Nikkonus Chamberlin & Wang, 1953: 9 (with type species *N. nikkoensis* Chamberlin & Wang, 1953), synonymized by Tanabe & Shinohara (1996: 1472).

Type species

Polydesmus (*Fontaria*) *Martensii* Peters, 1864, by original designation.

Diagnosis

A typical xystodesmid which differs from the closely related *Riukiaria* Attems, 1938 by a smaller body size (usually under 30 mm), brownish or greyish tergites with conspicuous red, orange or yellow paranotal spots, and the gonopod conformation, especially the two well-developed processes (prefemoral and acropodite) with various additional appendages (Korsós & Nakamura 2025).

Species included

The genus includes 20 species: *Xystodesmus amoenus* (Takakuwa, 1942), *X. bazanensis* (Takakuwa, 1942) comb. nov., *X. bifurcus* sp. nov., *X. fasciatus* Korsós & Nakamura, 2025, X. *gracilipes* (Takakuwa, 1943), *X. keramae* Korsós & Nakamura, 2025, *X. kumamotoensis* Korsós & Nakamura, 2025, *X. kumeensis* Korsós & Nakamura, 2025, *X. martensii* (Peters, 1864), *X. nikkoensis* (Chamberlin & Wang, 1953), *X. pallidus* (Verhoeff, 1937), *X. parvus* Korsós & Nakamura, 2025, *X. rebekae* Korsós & Nakamura, 2025, *X. saltuosus* (Haga 1968), *X. serrulatus* (Miyosi, 1952), *X. sesokoensis* Korsós & Nakamura, 2025, *X. shirozui* (Takakuwa, 1942), *X. tokaiensis* Tanabe & Shinohara, 1996, *X. variatus* (Pocock, 1895), *X. yamamiensis* Masuda, 2001.

Distribution

The genus *Xystodesmus* is distributed predominantly on the Japanese islands of Honshu, Shikoku, and Kyushu, and in the northern and central Ryukyu Islands (Kagoshima and Okinawa Prefectures). Two species of *Koreoaria* (*Koreoaria amoena* and *K. pallida*) have recently been allocated to *Xystodesmus* (Korsós & Nakamura 2025), and with the present paper, three more (*Xystodesmus bazanensis* comb. nov., *X. bifurcus* sp. nov., *X. shirozui*) are confirmed for the Korean Peninsula, increasing the number of species occurring there to five.

Xystodesmus pallidus (Verhoeff, 1937)
Figs 1–2, 10A, 12A–B, 15–16

Koreoaria pallida Verhoeff, 1937: 319–320, fig. 8.

Koreoaria pallida – Tanabe & Shinohara 1996: 1487 (“species possibly belonging to *Xystodesmus*”). — Lim 2001: 128–129, figs 142–144. — Marek *et al*. 2014: 71.
Xystodesmus pallidus – Korsós & Nakamura 2025: 216–218, figs 11a–e, 12a–d, 13a–b.

Diagnosis

A small-sized (total body length up to 30 mm) *Xystodesmus* showing a typical colour pattern with orange or yellow paranotal spots. Differs from congeners by strongly separated femoral and tibiotarsal parts of the male acropodite (Fig. 2: *a*), a curved and pointed solenomere (Fig. 2: *sl*), and a simple, flat prefemoral process (Fig. 2: *pfp*).

Type material

Holotype

SOUTH KOREA • ♂; “Südkorea”; SNSB-ZSM Reg.Nr. A20060019, SNSB-ZSM Reg.Nr. A20033594 (gonopods and legs, respectively).

Paratypes

SOUTH KOREA • 4 ♀♀; SNSB-ZSM Reg.Nr. A20060019.

Other material examined

SOUTH KOREA • 1 ♂; Gyeongsangnam Prov., Gimhae District, Daecheong Town, Mt. Bulmo-san; 35°10′42.4″ N, 128°45′11.6″ E; 9 Apr. 2023; D. Kim leg.; GenBank nos: PX471584 (*COI*), PX516894 (*EF1-α*) LEGOA030010 GH01 • 1 ♂; Gyeongsangnam Prov., Geoje District, Mundong Town, Mundong Recreational forest; 34°51′38.7″ N, 128°40′2.0″ E; 14 May 2023; D. Kim leg.; GenBank nos: PV446385 (*COI*), PV544250 (*EF1-α*); HNHM diplo-04554 GJ01 23 • 1 ♂; same data as for preceding; GenBank nos: PV446388 (*COI*), PV544253 (*EF1-α*); LEGOA030011 GJ04 23 • 1 ♂; Gangwon Prov., Taebaek District, Won Town; 37°17′04.1″ N, 128°57′17.8″ E; 959 m a.s.l.; 4 Jun. 2023, S.J. Suh leg.; LEGOA030012 TB05 • 1 ♂; Gangwon Prov., Taebaek District, Hwangji Town; 37°08′52.2″ N, 128°58′17.1″ E; 740 m a.s.l.; 4 Jun. 2023; S.J. Suh leg.; LEGOA030013 TB08 • 1 ♂; Gyeongsangnam Prov., Geoje District, Mundong Town, Mundong Recreational forest; 34°51′42.9″ N, 128°40′6.4″ E; 19 May 2024; G. Kim and D. Kim leg.; GenBank nos: PV446389 (*COI*), PV544254 (*EF1-α*); LEGOA030014 GJ01 24 • 1 ♂; same data as for preceding; GenBank nos: PV446390 (*COI*), PV544255 (*EF1-α*); LEGOA030015 GJ02 24 • 1 ♂; same data as for preceding; GenBank nos: PV446391 (*COI*), PV544256 (*EF1-α*); LEGOA030016 GJ03 24 • 1 ♂; same data as for preceding; LEGOA030017 GJ04 24 • 1 ♂; same data as for preceding; LEGOA030018 GJ05 24 • 1 ♂; same data as for preceding; LEGOA030019 GJ06 24 • 1 ♂; same data as for preceding; LEGOA030020 GJ09 24 • 1 ♀; same data as for preceding; HNHM diplo-04555 GJ08 24 • 1 ♂; Jellanam Prov., Damyang District, Wolsan-myeon, Yongheung-ri San 86-26; 35°20′22.9″ N, 126°53′25.8″ E; 6 Jul. 2024; G. Kim leg.; GenBank nos: PV446406 (*COI*), PV544271 (*EF1-α*); LEGOA030022 DY08 • 1 ♀; same data as for preceding; GenBank nos: PV446405 (*COI*), PV544270 (*EF1-α*); LEGOA030021 DY07.

Description

Head. Smooth, with 1+1 frontal setae and several smaller ones on clypeus and around antennal sockets; epicranial suture distinct. Antennae bent, article 1 globose, 2 long and clavate, articles 3–5 subequal in length, 6 longest, all setose, 7 small, length equal to width, with 4 apical sensory cones.

Collum. Convex, oval, its length twice as long as metatergite 2, lateral edges pointed, anterior margin circular, with visible ridge, posterior margin straight with lateral parts directed forward (Fig. 12A–B).

Body. Collum and first four rings narrower, gradually widening to ring 5, body sides between rings 5–15 parallel, then gradually tapering towards telson. Proterga and metaterga completely smooth, metaterga with a transverse depression in the middle, without any tubercles or punctation. Posteriolateral edge of paranota 2–4 rectangular, of 5–6 slightly pointed, from 7 onwards triangular in shape, with weak excavation on the posterior edge of each of the metaterga. Pore formula mostly typical for Polydesmida, pores on rings 5, 7, 9, 10, 12–13, and 15–19, positioned laterally on slightly swollen paranota. Rings 16–19 gradually tapering, posterolateral projections becoming more pointed, on 17 triangular, on 18–19 very long, almost as long as length of metaterga.

Telson. Epiproct protruding, in dorsal view triangular and rounded, in lateral view slightly curved downwards, with 4+4 setae sitting on tubercles of sides, and with 2+2 stronger setae apically. Paraprocts (anal valves) smooth, with 2+2 setae on median ridges; hypoproct semitriangular, with 1+1 setae on small tubercles.

Legs. Bases of midbody legpairs well separated in males by 1.2–1.9 mm, in females by 1.7–1.8 mm, sterna smooth and wide, pro- and metasterna well separated. Coxae of legs from ring 7 short, its length subequal to prefemur, which has a well-developed ventral spine, increasingly larger from legs 9 onwards; femur 1.2 times as long as prefemur, slightly clavate; postfemur short, about ⅓ as long as femur; tibia subequal to postfemur, hairy, about same length as tarsus; podomeres distally increasingly hairy; curved claws on all legs.

Measurements. Males (based on 13 specimens): total body length 26–30 mm, midbody width (including paranota) 4.0–6.6 mm, metatergal length 1.0–1.6 mm, midbody prozonite width 2.8–4.2 mm, collum width 3.5–4.9 mm, median collum length 1.5–2.7 mm. Females (based on 2 specimens): total body length 27–29 mm, midbody width (including paranota) 5.5–6.4 mm, metatergal length 1.3–1.4 mm, midbody prozonite width 4.1 mm, collum width 4.4 mm, median collum length 1.9–2.1 mm.

Colouration (Fig. 12A–B). Preserved specimens in ethanol with prozonite and metazonite dorsally equally brown, collum anteriorly with dark stripe, epiproct lighter; all metaterga paramedially with large, marbled patches, adjacent paranota with pale orange or yellow spots, first and last rings excluded. Head brown, antennae, legs, and ventral side light brown, whitish.

Male characters. Coxae of legpairs 2–6 with pair of protruding, cone-shaped processes, those of legpairs 3 and 6 much reduced, those of legpairs 4–5 longer and pointed. Remaining legs and sterna without modifications. Gonopods (Figs 1B–C, 2A–F): with two conspicuous processes, prefemoral process (*pfp*), and acropodite (*a*), which is divided into femoral and tibiotarsal parts (solenomere, *sl*) by a cingulum (*c*). Coxa (*cx*) stout, subcylindrical, about twice as long as wide, without coxal apophysis, but with single apophyseal macroseta (*ms*) on dorsal side. Cannula on mesal side, starting near macroseta, then connected to prefemur and continuing in prostatic groove (*pg*). Prefemur short, stout, bent dorsad, densely setose; prefemoral process (*pfp*) thin and flat, parallel and subequal in length to femoral part of

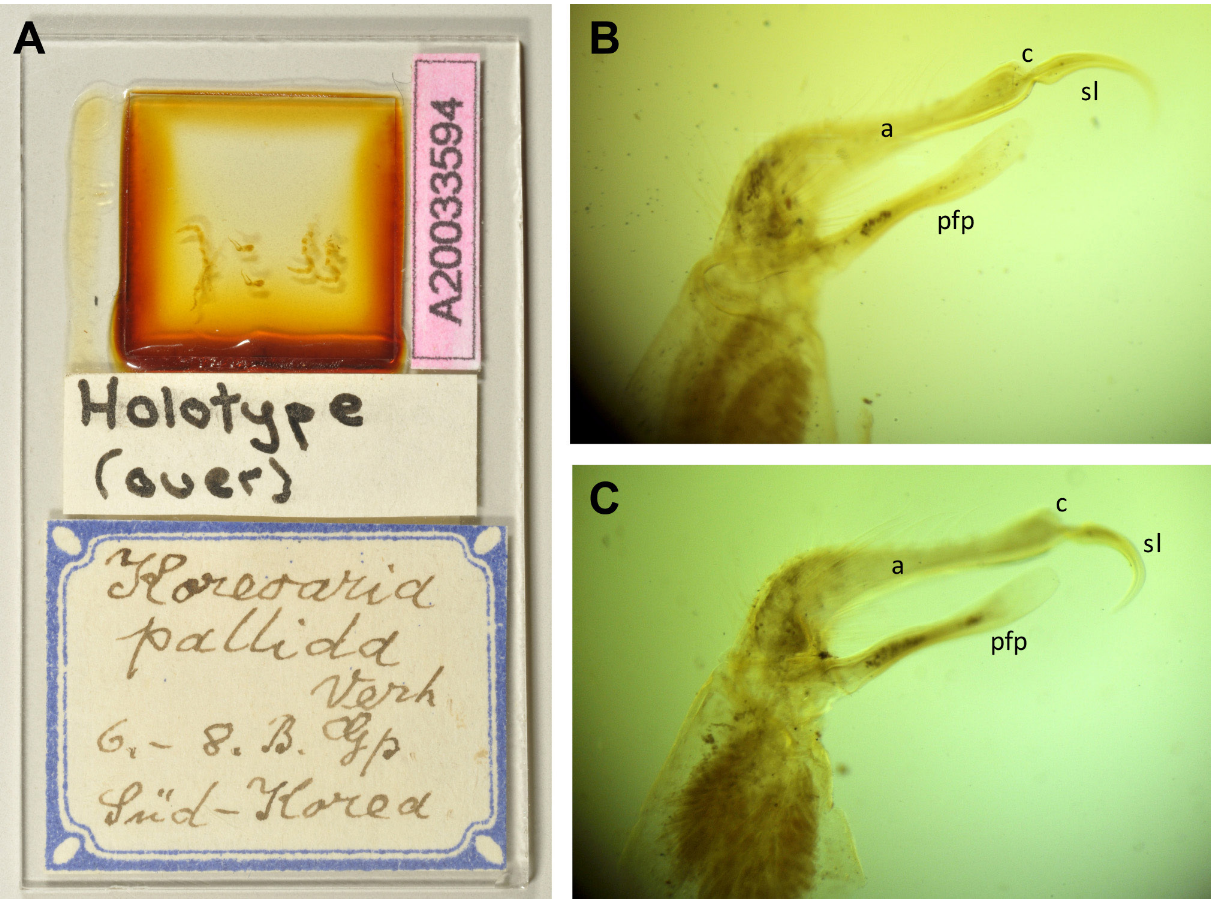

Fig. 1. *Xystodesmus pallidus* (Verhoeff, 1937). **A**. Slide of male gonopods and 6–8th legpairs of holotype from "Süd-Korea" (SNSB-ZSM, Reg.Nr. A20033594). **B**. Left gonopod in mesal view. **C**. Right gonopod in lateral view. Abbreviations: a = acropodite; c = cingulum; pfp = prefemoral process; sl = solenomere.

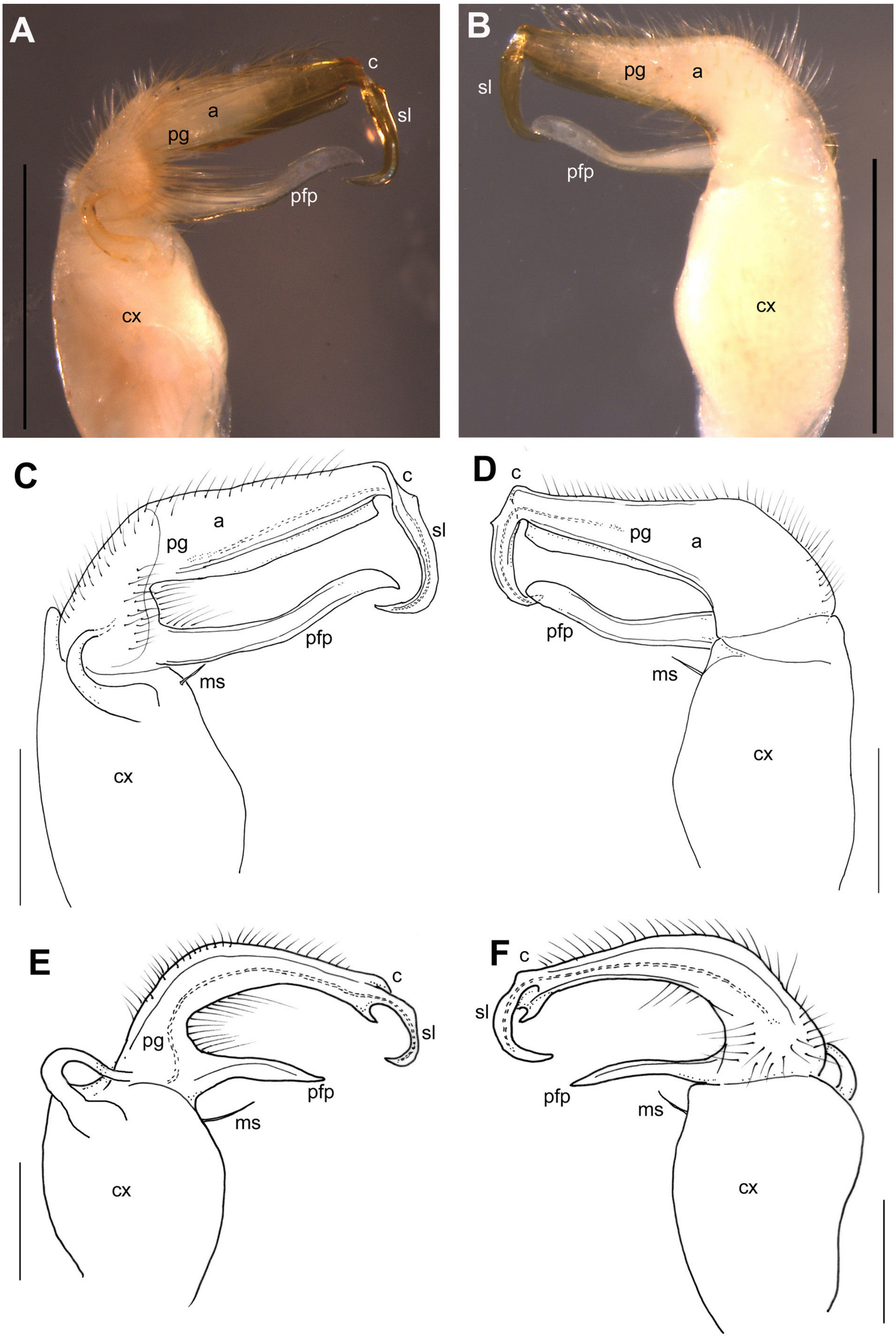

Fig. 2. *Xystodesmus pallidus* (Verhoeff, 1937), ♂♂. **A–D**. Right gonopod of specimen from Geoje District (GJ01). **A, C**. Mesal view. **B, D**. Lateral view. **E–F**. Right gonopod of specimen from Gimhae District (GH01). **E**. Mesal view. **F**. Lateral view. Abbreviations: a = acropodite; c = cingulum; cx = coxa; ms = macroseta; pfp = prefemoral process; pg = prostatic groove; sl = solenomere. Scale bars: A–B = 1 mm; C–F = 0.5 mm.

acropodite, shape variable, sometimes straight and apical part blunt, sometimes slightly bent ventrad and pointed. Acropodite (*a*) continuing from prefemur until a strong contraction called cingulum (see also Marek *et al*. 2014: 5, fig. 2b–c: *cg*). This part considered as femur, densely setose, slightly tapering distally, and with a parallel lamina along dorsal side. Tibiotarsal part (solenomere, *sl*) of acropodite starting after cingulum with thickening, then gradually tapering to pointed tip, which is strongly curved back toward prefemoral process. Prostatic groove (*pg*) runs dorsally on mesal side.

Female characters. Somatic characters similar to those of males, including shape of collum, tergites and epiproct, as well as strong prefemoral ventral spines, starting on legpair 5. Coxae of legpair 2 with protruding, pointed processes (Fig. 10A), similar to males, but subsequent legs without any sternal or coxal modifications. Cyphopods in situ closely behind legpair 2, in joint transversal, semicircular-shaped opening; valves (*v*) of equal size, ventral edges jagged, medially with depression for genital opening, operculum (*op*) laterally closely overlaying, receptacles (*r*) deeply embedded under valves.

Distribution

Xystodesmus pallidus occurs in scattered locations across the entire South Korean Peninsula (Fig. 15).

Remarks

Xystodesmus pallidus was originally described by Verhoeff (1937) as *Koreoaria pallida*, the type species of the genus *Koreoaria* Verhoeff, 1937. When erecting the genus, Verhoeff (1937: 319) compared it to *Pachydesmus* Cook, 1895, at that time considered a large genus of the family Leptodesmidae (Attems 1938). The family was later divided into several families including Xystodesmidae (Hoffman 1978a, 1978b, 1980). *Koreoaria pallida*, together with its sister species *K. amoena* Takakuwa, 1942, was recently transferred to *Xystodesmus*, based only on the original description and examination of its type specimen (Korsós & Nakamura 2025). Having been able to investigate a relatively large number of specimens from different parts of South Korea, we became convinced that the specimens we studied are conspecific with Verhoeff's "*pallida*". The diagnostic separation of the femoral and tibiotarsal part by a cingulum in the male gonopod acropodite can also be observed in the microscopic slides made by Verhoeff (Fig. 1A–C), although the direction of the solenomere has changed to that of a right angle, probably due to the pressure of the microscopic cover glass. In all other aspects, our specimens morphologically agree with the original description, so the identification seems to be well warranted.

Xystodesmus amoenus (Takakuwa, 1942)
Figs 3A, 15

Koreoaria amoena Takakuwa, 1942a: 362–363, 366, fig. 5.

Koreoaria amoea (recte *amoena*) – Tanabe & Shinohara 1996: 1487 ("species possibly belonging to *Xystodesmus*"). — Marek *et al*. 2014: 71.
Koreoaria amoena – Lim 2001: 129–131, fig. 145.
Xystodesmus amoenus – Korsós & Nakamura 2025: 218, fig. 15a.

Diagnosis

A species of *Xystodesmus* as defined by Tanabe & Shinohara (1996) and Korsós & Nakamura (2025) by its small size and colouration already described by Takakuwa (1942a). Without fresh material, the shape of the gonopods can only be studied based on the figure provided by Takakuwa (1942a: 362, fig. 5, redrawn here as Fig. 3A, and in Korsós & Nakamura 2025: 218, fig. 15a). Acropodite (Fig. 3A: *a*) amidst with a broad, leaflike lamina ending in a small point (Fig. 3A: *b*), its distal part bent at almost right angle back to prefemoral process, which is slender and curved.

Type material (not examined)

SOUTH KOREA • 1 ♂; "Taikyu 大邱 (Süd-Korea)" (= Daegu, South Korea); Takakuwa's private collection, including type material of many species, considered lost (Tanabe & Shinohara 1996; Chao & Chang 2008).

Description

Without the type material and fresh specimens, we can only rely on Takakuwa's (1942a: 366) description: "Rücken graulich, Kopf, Antennen und Bauch gelb, Bein proximal etwas graulich, distal gelb. Seitenflügel mit einem deutlich rötlichen Fleck." (= "Back greyish, head, antennae and belly yellow, legs proximally somewhat greyish, distally yellow. Paranota with a clear reddish spot." – translated from German). Female unknown.

Distribution

Known only from its type locality (Daegu, South Korea; Takakuwa 1942a) (Fig. 15).

Remarks

In our present material we did not find any *Xystodesmus* in or around Daegu, which is now a huge metropolis. The original figure is quite schematic, and the description is short (Takakuwa 1942a: 362, fig. 5), but other somatic characters, such as size and colouration, are definitely implying the species' position in *Xystodesmus*, as already stated by Korsós & Nakamura (2025).

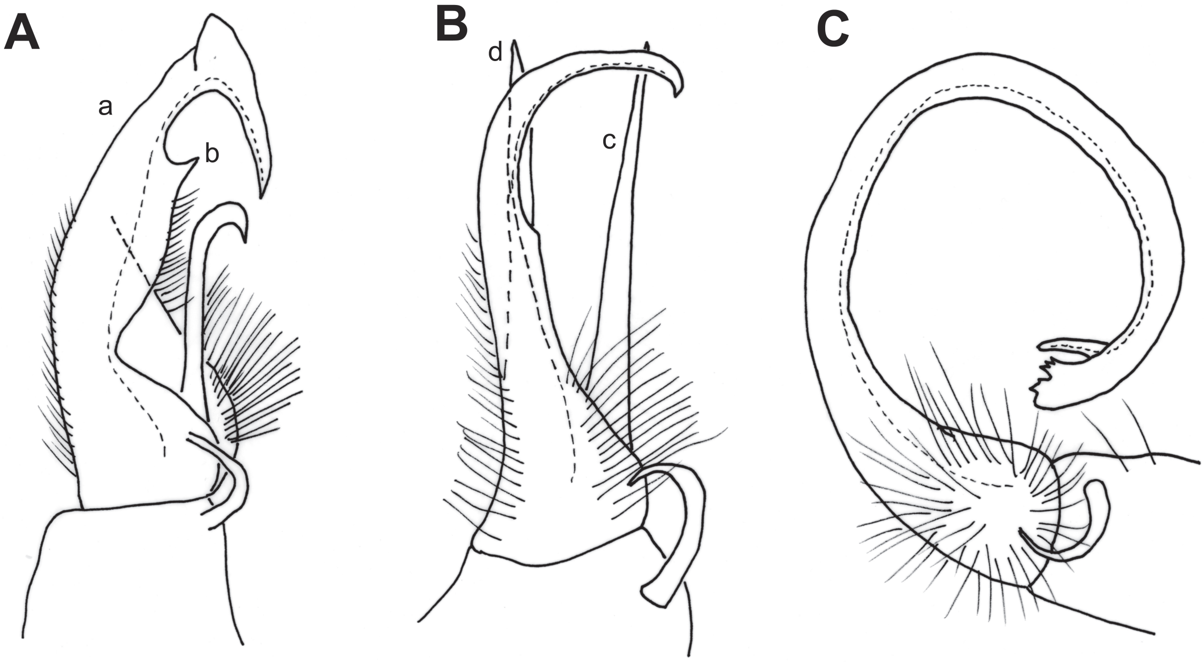

Fig. 3. Right gonopods of species of *Xystodesmus* Cook, 1895 and *Levizonus* Attems, 1898; redrawn from original drawings, mesal views. **A**. *X. amoenus* (Takakuwa, 1942) from Takakuwa (1942a: 362, fig. 5). **B**. *Xystodesmus bazanensis* (Takakuwa, 1942) comb. nov., from Takakuwa (1942a: 363, fig. 6). **C**. *Levizonus circularis* (Takakuwa, 1942) from Takakuwa (1942c: 44, fig. 8). Abbreviations: a = acropodite; b = small tooth; c–d = separate processes. Not drawn to scale.

Xystodesmus bazanensis (Takakuwa, 1942) comb. nov.
Figs 3B, 15

Pachydesmus bazanensis Takakuwa, 1942a: 363, 366, fig. 6.

Nikkonus bazanensis – Chamberlin & Wang 1953: 9. — Marek *et al*. 2014: 81.
Pachydesmus bazanensis – Tanabe & Shinohara 1996: 1487 ("species possibly belonging to *Xystodesmus*"). — Korsós & Nakamura 2025: 228.

Diagnosis

"Mit Ausnahme von Gonopoden stimmt diese Spezies ähnelr [sic] vielmehr der vorigen Koreoariaart (*K. amoena*) besonders stimmt sie im Aussehen und Farbe überein, jedoch ist bei dieser Spezies der rötliche Fleck auf Flügel etwas grösser als bei jener." (Takakuwa 1942a: 366) (= "With the exception of gonopods, this species is more similar to the previous *Koreoaria* species (*K. amoena*), especially in appearance and colour, but in this species the reddish spot on the wing is slightly larger than in that one." – translated from German.)

Type material (not examined)

SOUTH KOREA • 1 ♂; "Bazan馬山(Süd-Korea)" (= Masan, today part of Changwon Distr., Gyeongsannam Prov., South Korea); Takakuwa's private collection, including type material of many species, considered lost (Tanabe & Shinohara 1996).

Description

Without the type material and fresh specimens, we can only rely on Takakuwa's (1942a: 366) description: "Körperlänge 22 mm, Körperbreite 4 mm. An der Hüfte des 2. Beinpaares des ♂ mit rundlichen Höckern, Sternit zwischen den Hüften des 4., 5., und 6. Beinpaares des ♂ mit dreieckigen oder spitzigen Zäpfen versehen, von denen der des 6. das grösste besitzt. Gonopoden: Hüfte breit, ohne Stab. Präfemur breit, dicht lang behaart, mit 2 grossen getrennten Fortsätzen, beide gerade, sind dem Proximalteil des Acropodits fast parallel gerichtet, und erreicht die Höhe sein Ende." (= Body length 22 mm, width 4 mm. Coxae of male 2nd legpair with roundish humps, 4th, 5th and 6th sternites with triangular or pointed cones, of which the 6th the largest. Gonopods: coxae wide, without apophysis. Prefemur (*b*) broad, with dense, long hairs, with two large separate processes (*c*, *d*), both straight, almost parallel with the proximal part of acropodite (*a*) and reaching its end in height." – translated from German.)

Female unknown.

Distribution

Known only from its type locality ("Bazan", South Korea; Takakuwa 1942a) (Fig. 15).

Remarks

This species was considered dubious for a long time (Attems 1938; Chamberlin & Wang 1953; Hoffman 1956), although its relation to the genus *Xystodesmus* was already suspected (Tanabe & Shinohara 1996; Marek *et al*. 2014). Even Verhoeff (1937), when describing his *Koreoaria pallida*, thought that *Pachydesmus* was close to that genus. Later, *Pachydesmus* was restricted to the group of species in the eastern United States (Hoffman 1956), but with a schematic description and without type material the Korean *P. bazanensis* remained enigmatic for a long time (Nguyen *et al*. 2016; Kim *et al*. 2023). Recently, Korsós & Nakamura (2025) speculated about its status, but still abstained from assigning it to a genus. Based on our detailed study of Korean xystodesmids, even without fresh samples of the species at hand, but based on the original diagnostic characters (size and colouration), we here take the opportunity to settle the generic affiliation, and establish the new combination *Xystodesmus bazanensis* (Takakuwa, 1942) comb. nov.

Xystodesmus shirozui (Takakuwa, 1942)
Figs 4, 10B, 12C–D, 15–16

Rhysodesmus shirozui Takakuwa, 1942b: 239, fig. 5.

Rhysolus shirozui – Miyosi 1959: 80, fig. 55.
Riukiaria shirozui – Shinohara 1977: 119.
Xystodesmus shirozui – Tanabe & Shinohara 1996: 1485–1486, figs 3–7, 11m–n, 13c–d, 16c–d, 17o-p.

Diagnosis

A medium-sized *Xystodesmus* with a strong colour pattern typical for the genus. Differs from congeners by male gonopod conformation having three subequal processes: a prefemoral process (*pfp*, with a small accessory spine, *s*), a femoral process (*fp*), and an acropodite with solenomere (*sl*) (Fig. 4A–F).

Type material (not examined)

JAPAN • 1 ♂; "Tusima, 勤馬ヒタカッ擁" (= Japan, Nagasaki Pref., Tsushima Island, Kamiagata Distr., Kamitsushima Town, Hitakatsu, Mt. Gongen-san, see Tanabe & Shinohara 1996); Takasi Shirozu leg.; Takakuwa's private collection, including type material of many species, considered lost (Tanabe & Shinohara 1996).

Other material examined

SOUTH KOREA • 1 ♂; Gyeongsangnam Prov., Geoje District, Mundong Town, Mundong Recreational forest; 34°51′38.7″ N, 128°40′20.0″ E; 14 May 2023; D. Kim leg.; GenBank nos: PV446387 (*COI*), PV544252 (*EF1-α*); HNIBRIV12832 GJ03 23 • 1 ♀; Gyeongsangnam Prov., Geoje District, Mundong Town, Mundong Recreational forest; 34°51′42.9″ N, 128°40′6.4″ E; 19 May 2024; G. Kim and D. Kim leg.; GenBank nos: PV446386 (*COI*), PV544251 (*EF1-α*); LEGOA030023 GJ02 23 • 1 ♂; Jellanam Prov., Hwasun Town, Baega-myeon, Songdan-gil 479-55, Mt. Bakeasan; 35°10′4.8″ N, 127°11′10.3″ E; elev. 480 m; 25 Sep. 2023; G. Kim leg.; HNHM diplo-04556 HS13 23 • 1 ♂; same data as for preceding; GenBank nos: PV446398 (*COI*), PV544263 (*EF1-α*); LEGOA030025 HS11 23 • 1 ♂; same data as for preceding; GenBank nos: PV446399 (*COI*), PV544264 (*EF1-α*); LEGOA030026 HS12 23 • 1 ♂; Jellanam Prov., Damyang Town, Wolsan-myeon, Yongheung-ri, San 86-26; 35°20′22.9″ N, 126°53′25.8″ E; 6 Jul. 2024; G. Kim leg.; GenBank nos: PV446403 (*COI*), PV544268 (*EF1-α*); LEGOA030027 DY05 • 1 ♂; same data as for preceding; GenBank nos: PV446407 (*COI*), PV544272 (*EF1-α*); LEGOA030028 DY10 • 1 ♀; same data as for preceding; GenBank nos: PV446400 (*COI*), PV544265 (*EF1-α*); LEGOA030029 DY01 • 1 ♀; same data as for preceding; GenBank nos: PV446401 (*COI*), PV544266 (*EF1-α*); LEGOA030030 DY02 • 1 ♀; same data as for preceding; GenBank nos: PV446402 (*COI*), PV544267 (*EF1-α*); LEGOA030031 DY03 • 1 ♀; same data as for preceding; GenBank nos: PV446404 (*COI*), PV544269 (*EF1-α*); LEGOA030033 DY06 • 1 ♀; Jellanam Prov., Hwasun Town, Baega-myeon, Songdan-gil 479-55; 35°10′22.1″ N, 127°11′0.6″ E; 6 Jul. 2024; G. Kim leg.; HNHM diplo-04557 HS04 24 • 1 ♂; same data as for preceding; LEGOA030034 HS05 24 • 1 ♀; same data as for preceding; LEGOA030035 HS02 24 • 1 ♀; same data as for preceding; LEGOA030036 HS03 24 • 1 ♀; Jellanam Prov., Gurye District, Ganjeon-myeon, Jungdae-ri, Mt. Baekunsan; 35°07′55.8″ N, 127°36′12.6″ E; 580 m a.s.l.; 2 Sep. 2023; D. Kim leg.; LEGOA030037 GR02.

Description

Head. Smooth, no frontal setae, only small ones on edge of clypeus, and none around antennal sockets; epicranial suture distinct. Antennae bent; article 1 globose; articles 2–6 long, straight, and subequal in length, about 2.5 times as long as article 1, all moderately setose; article 7 small, densely setose, length subequal to width, with 4 apical sensory cones.

Collum. Convex, subtrapeziform, length 1.5 times as large as that of metatergite 2, lateral edges pointed, anterior margin semicircular, with a visible ridge, posterior margin straight with lateral parts directed forward.

Body. Collum and first four rings narrower, gradually widening to ring 5, body sides between rings 5–15 parallel, then gradually tapering towards telson. Proterga and metaterga completely smooth, shiny, metaterga with strong transverse medial depression, without any tubercles or punctation. Posteriolateral edge of paranota 2–4 rounded, of 5 slightly pointed, from 6 onwards triangular in shape, with weak

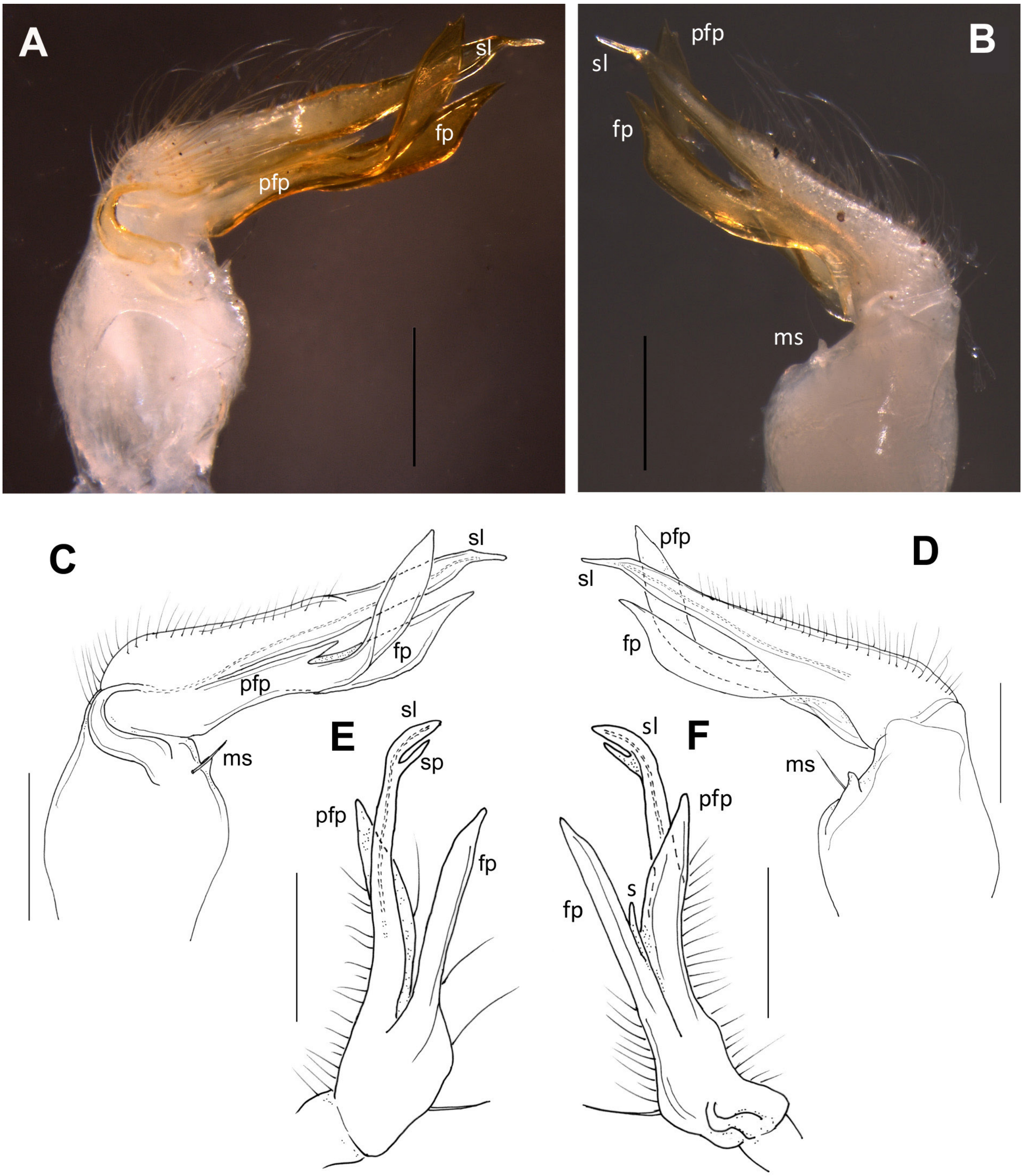

Fig. 4. *Xystodesmus shirozui* (Takakuwa, 1942), ♂♂. **A–D**. Right gonopod of specimen from Hwasun Town (HS11). **A, C**. Mesal view. **B, D**. Lateral view. **E–F**. Telopodite of right gonopod of specimen from Geoje District (GJ03). **E**. Mesoventral view. **F**. Mesolateral view. Abbreviations: fp = femoral process; ms = macroseta; pfp = prefemoral process; s = spine; sl = solenomere; sp = small process. Scale bars: 0.5 mm.

excavation on posterior edge of each of the metaterga, all with strong lateral ridge. Pore formula mostly typical for Polydesmida, pores on rings 5, 7, 9– 10, 12– 13, and 15–19, in lateral position on slightly swollen paranota. Rings 16–19 gradually tapering, posterolateral projections becoming more pointed, on 17 triangular, on 18–19 long, almost as long as length of metaterga.

TELSON. Epiproct protruding, in dorsal view triangular, in lateral view only slightly curved downwards, with 4+4 setae sitting on tubercles of sides, and with 2+2 stronger setae apically; paraprocts (anal valves) smooth, with 2+2 setae on median ridges; hypoproct semitriangular, with 1+1 setae on small tubercles.

LEGS. Bases of midbody legpairs well separated in males by 1.2–1.5 mm, in females by 1.3–1.6 mm, sterna smooth and wide, pro- and metasterna well separated. Coxa of legs from ring 7 short, shorter than prefemur, which has well-developed ventral spine, increasing in size from legs 9 onwards; femur 1.2 times as long as prefemur, clavate; postfemur short, stout; tibia and tarsus of about same length; podomeres distally increasingly setose; curved claws on all legs.

MEASUREMENTS. Males (based on 7 specimens): total body length 24–28 mm, midbody width (including paranota) 4.4–5.4 mm, metatergal length 0.9–1.4 mm, midbody prozonite width 3.0–3.6 mm, collum width 3.3–3.9 mm, median collum length 1.4–1.9. Females (based on 9 specimens): total body length 21–30 mm, midbody width (including paranota) 4.3–5.7 mm, metatergal length 0.9–1.3 mm, midbody prozonite width 3.2–4.3 mm, collum width 3.5–4.2 mm, median collum length 1.4–1.9 mm.

COLOURATION (Fig. 12C–D). Preserved specimens in ethanol. Dorsum of collum, prozonite, metazonite, and proximal part of epiproct equally dark brown, nearly black, tip of epiproct lighter; all metaterga paramedially with large, marbled patches, adjacent paranota with wide bright red or orange spots, collum included, but last ring excluded. Head brown, antennae, legs, and venter white.

MALE CHARACTERS. Coxae of legpair 2 with protruding, pointed processes, of legpair 3 with very small, of legpairs 4–5 with longer and pointed, and of legpair 6 again with small processes. Other legs and sterna without modifications. Gonopods (Fig. 4A–F): coxa stout, about as long as wide, without coxal apophysis, but with small hump next to single apophyseal macroseta (*ms*) on dorsum. Cannula on mesal side, starting near macroseta, then connected to prefemur and continuing in prostatic groove. Prefemur short and wide, densely setose; prefemoral process (*pfp*) long and flat, parallel and nearly as long as acropodite, with small spine on dorsal side halfway (*s*), last ⅓ flattening, slightly twisted, turning ventrad, apical part pointed. Acropodite with two processes, solenomere (*sl*) straight and long, distally slightly tapering, tip abruptly narrow and pointed, sometimes subapically with a small, pointed extra process (*sp*) (Fig. 4E–F); and another process, called femoral (*fp*) after Hoffman (1956: 98, fig. 1), which starts at base of acropodite close to prefemoral process, its shape and length also similar to it, flat and parallel-sided, sometimes gradually tapering, until last ⅓, then ends in pointed tip. Prostatic groove runs dorsally on mesal side of solenomere.

FEMALE CHARACTERS. Total body length generally shorter than males, other measurements and somatic characters similar, including colouration, shape of collum, tergites and epiproct, as well as strong prefemoral ventral spines, starting on legpair 5: coxae of legpair 2 with small triangular projection (Fig. 10B), remaining legs without any sternal or coxal modifications. Cyphopods in situ held closely behind legpair 2, in joint transversal, semicircular opening; valves (*v*) of subequal size, ventral edges jagged, medially with weak depression for genital opening, operculum (*op*) laterally closely overlaying, receptacles (*r*) deeply embedded under valves.

Distribution

Xystodesmus shirozui in South Korea occurs in the southernmost parts, Gyeongsangnam and Jellanam provinces (Fig. 15).

Remarks

First, we have to emphasize that our identification is largely based on the high variability of the species outlined by Tanabe & Shinohara (1996). Some characters, including those mentioned in our diagnosis, slightly differ from those given by them who considered, for instance, all three gonopodal processes "prefemoral". Considering the geographical distribution of our samples, especially that of Geoje Island (Fig. 15), we feel confident that the South Korean populations are within the individual variation of the Japanese *X. shirozui*, the type locality of which, Tsushima Island, is just 80 km away from Geoje Island in the East Sea. *Xystodesmus shirozui* is new to the fauna of Korea.

Xystodesmus bifurcus sp. nov.

urn:lsid:zoobank.org:act:1B1E13DC-453C-4A7E-B483-EA490FC4C1C3

Figs 5, 10C, 11A, 12E–F, 15–16

Diagnosis

A medium-sized *Xystodesmus* with typical colour pattern, i.e., bright orange spots on all paranota. Differs from all other congeners by having a strongly bifurcated acropodite, and by the 2nd legpair of females simple, without coxal projections.

Etymology

Refers to the two-forked acropodite of the male gonopod (*bi* + *furca*, *furcus* = two + fork, forked, in Latin). Adjective, masculine.

Type material

Holotype

SOUTH KOREA • ♂; Gangwon Prov., Pyeongchang District, Yongpyeong Town, Nodong-ri, Mt. Gyebang-san; 37°41′43.1″ N, 128°28′42.7″ E; 850 m a.s.l.; 9 Jun. 2023; G. Kim leg.; GenBank nos: PV446393 (*COI*), PV544258 (*EF1-α*); LEGOA030038 PC10.

Paratypes

SOUTH KOREA • 1 ♂; same collection data as for holotype; GenBank nos: PV446394 (*COI*), PV544259 (*EF1-α*); HNIBRIV8508 PC11 • 1 ♀; same collection data as for holotype; GenBank nos: PV446392 (*COI*), PV544257 (*EF1-α*); LEGOA030039 PC09 • 1 ♂; Gangwon Prov., Pyeongchang Town, Jinbu-myeon, Odaesan-ro, Mt. Odae-san; 37°44′23.3″ N, 128°35′8.9″ E; 14 Apr. 2023; G. Kim leg.; GenBank nos: PV446397 (*COI*), PV544262 (*EF1-α*); HNHM diplo-04558 PC14 • 1 ♀; Gangwon Prov., Inje Town, Gwidun-ri, Mt. Jeombong-san; 38°1′23.0″ N, 128°25′53.8″ E; 940 m a.s.l.; 8 Aug. 2024; H. Yu and D. Kim leg.; HNHM diplo-04559 IJ04 • 1 ♂; same data as for preceding; GenBank nos: PV446395 (*COI*), PV544260 (*EF1-α*); LEGOA030041 IJ02 24 • 1 ♀; same data as for preceding; GenBank nos: PV446396 (*COI*), PV544261 (*EF1-α*); LEGOA030042 IJ03 24 • 1 ♀; same data as for preceding; LEGOA030043 IJ05 24 • 1 ♀; Gangwon Prov., Inje Town, Buk-myeon, Yongdae-ri, Yongdae recreational forest; 38°14′3.0″ N, 128°20′49.2″ E; 480 m a.s.l.; 7 Aug. 2024; H. Yu and D. Kim leg.; LEGOA030044 IJ01 24 • 1 ♀; Gangwon Prov., Inje Town, Girin-myeon, Jindong-ri, Gachilbong Peak; 37°59′17.5″ N, 128°24′27.7″ E; 620 m a.s.l.; 14 Aug. 2023; D. Kim leg.; LEGOA030045 IJ03 23 • 1 ♀; Gangwon Prov., Inje Town, Girin-myeon, Jindong-ri, Gachilbong Peak; 37°59′17.5″ N, 128°24′27.7″ E; 620 m a.s.l.; 9 Aug. 2024; H. Yu and D. Kim leg.; LEGOA030046 IJ06 24 • 1 ♀; same data as for preceding; LEGOA030047 IJ07 24 • 1 ♀; Jellanam Prov., Gurye-gun, Ganjeon-myeon, Jungdae-ri, Mt. Baekunsan; 35°07′55.8″ N, 127°36′12.6″ E; 580 m a.s.l.; 2 Sep. 2023; D. Kim leg.; LEGOA030048 WJ03 • 1 ♀; Gyeonggi Prov., Gapyeong-gun, Dumil-ri, Mt. Daegeumsan; 37°48′31.0″ N, 127°25′45.2″ E; 270 m a.s.l.; 12 Aug. 2023; D. Kim leg.; LEGOA030049 GP05 • 1 ♀; Gyeongsangnam Prov., Geoje District, Mundong Town, Mundong Recreational forest; 34°51′42.9″ N, 128°40′6.4″ E; 19 May 2024; G. Kim and D. Kim leg.; LEGOA030050 GJ07.

Description

HEAD. Smooth, with 1+1 large frontal setae and several smaller ones on clypeus and around antennal sockets; epicranial suture distinct. Antennae slightly bent; article 1 globose; article 2 longer; articles 3–5 subequal in length; article 6 longer, hairy; article 7 small, its length equal to width, with 4 apical sensory cones.

COLLUM. Subtrapezoidal, convex, its length 2.5 times as long as that of metatergite 2, lateral edges directed ventrad, anterior margin with weak ridge.

BODY. Collum and first four rings narrower, body sides between rings 5–14 parallel, then gradually tapering towards telson. Proterga and metaterga completely smooth, metaterga with transverse depression in middle. No trace of tubercles or punctation on metaterga. Posteriolateral edge of paranota 2–4 rounded, of 5–6 slightly pointed, from 7 onwards triangular in shape, with weak excavation on the posterior edge of each of the metaterga. Pore formula mostly typical for Polydesmida, pores on rings 5, 7, 9–10, 12–13, and 15–19, in lateral position on slightly swollen paranota. Rings 15–19 gradually tapering, posterolateral projections becoming more pointed.

TELSON. Epiproct protruding, in dorsal view triangular, in lateral view distinctly curved, with 3+3 setae on sides, and with 1+1 setae apically; paraprocts (anal valves) smooth, with 2+2 setae on median ridges; hypoproct semicircular, with 1+1 setae on small tubercles.

LEGS. Bases of midbody legpairs well separated in males by 1.1–1.7 mm, in females by 1.6–2.0 mm, sterna smooth and wide, pro- and metasterna well separated. Prefemur of legs from ring 7 with well-developed ventral spine, increasingly larger from midbody legs onwards; femur about as long as prefemur, slightly clavate; postfemur short, half as long as femur; tibia slender, setose, as long as postfemur and tarsus; tarsus densely setose; all legs with claws.

MEASUREMENTS. Males (based on 4 specimens): total body length 27–30 mm, midbody width (including paranota) 4.9–5.1 mm, metatergal length 1.2–1.4 mm, midbody prozonite width 3.5–3.7 mm, collum width 4.0–4.4 mm, median collum length 1.9–2.4 mm. Females (based on 11 specimens): total body length 28–33 mm, midbody width (including paranota) 5.3–6.4 mm, metatergal length 1.2–1.6 mm, midbody prozonite width 3.9–4.9 mm, collum width 3.9–5.4 mm, median collum length 1.7–2.2 mm.

COLOURATION (Fig. 12E–F). Specimens preserved in ethanol: dorsum pale brownish, prozonite lighter, metazonite, including epiproct, darker; paranota bright orange on all rings, including collum, except ring 19. Head, antennae, legs, and whole ventral side white.

MALE CHARACTERS. Collum relatively thin and long (see Measurements). Coxae of legpair 2 with pair of small protruding processes, of legpair 3 with small triangular, of legpairs 4 and 5 with long and pointed processes. Other legs and sterna without modifications. Gonopods (Fig. 5A–D): composed of three conspicuous processes, one considered as prefemoral process (*pfp*), and the other one, the acropodite (*a*), strongly bifurcated into two processes subequal in length. Coxa stout, 1.5 longer than wide, without coxal apophysis, but with single apophyseal macroseta (*ms*) on dorsal side. Cannula on mesal side, starting near macroseta, then connected to prefemur and continuing in prostatic groove (*pg*). Prefemur short, stout, bent dorsad, densely setose; prefemoral process (*pfp*) long, broad at base, thin and transparent (often broken), gradually and straight tapering toward pointed tip. Acropodite (*a*) densely setose, distally bifurcate in two parts: solenomere (*sl*), bent ventrad, gradually tapering towards tip and carrying prostatic groove (*pg*), and shorter pointed process (*p*), slightly bent toward solenomere.

FEMALE CHARACTERS. Body of females relatively larger (longer and wider) than that of males; collum, nevertheless, wider and shorter than males (see Measurements); other somatic characters, including colouration and strong prefemoral ventral spines (Fig. 11A: *ps*), similar. All coxae, including those of legpair 2, and sterna without modification (Fig. 10C). Cyphopods in situ held closely behind legpair 2; opening oval; valves (*v*) of subequal size, pentagon-shaped, ventral edges each with small peak (Fig. 10C), operculum (*op*) laterally closely overlaying, receptacles (*r*) deeply embedded under valves.

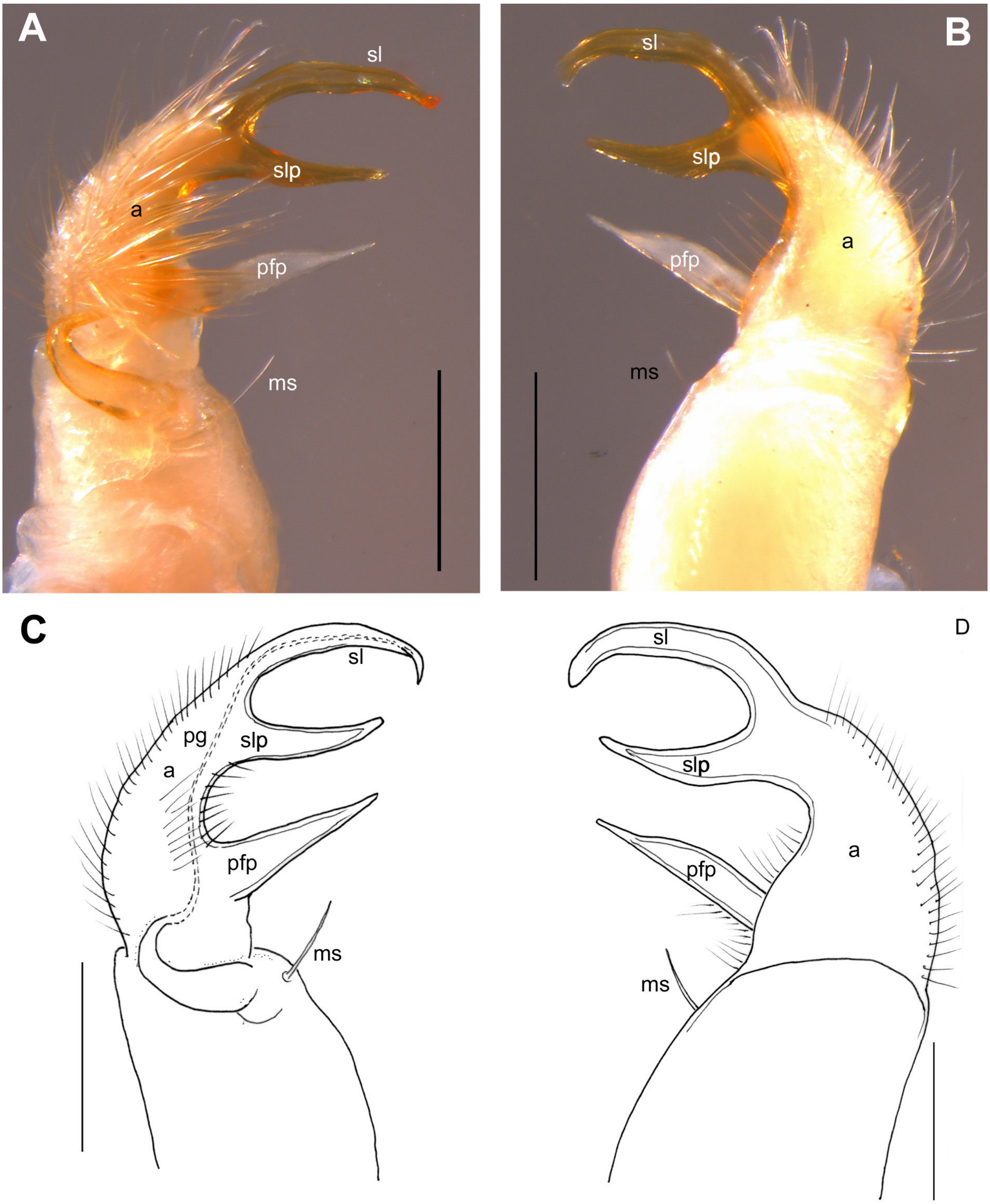

Fig. 5. *Xystodesmus bifurcus* sp. nov., right gonopod of male paratype from Pyeongchang Town (PC11). **A, C**. Mesal view. **B, D**. Lateral view. Abbreviations: a = acropodite; ms = macroseta; pfp = prefemoral process; pg = prostatic groove; sl = solenomere; slp = solenomere process. Scale bars: 0.5 mm.

Genus ***Riukiaria*** Attems, 1938

Riukiaria Verhoeff, 1936b: 298. Unavailable, because type species was not designated (Jeekel 1971).
Rhysolus Chamberlin & Wang, 1953: 8 (with type species: *Rhysolus semicirculatus* Takakuwa, 1941), synonymized by Hoffman (1980: 157).
Sinoria Tanabe, Ishii & Yin, 1996: 13 (with type species: *Sinoria tianmu* Tanabe, Ishii & Yin, 1996), synonymized by Golovatch (2014: 189).
Parariukiaria Nguyen, 2016: 332 (with type species: *Parariukiaria cucfuongensis* Nguyen, 2016), synonymized by Golovatch (2023: 233).

Riukiaria – Attems 1938: 151. — Shinohara 1977: 117–119. — Korsós *et al*. 2011: 56, fig. 1. — Golovatch 2023: 233–234.

Type species

Riukiaria pugionifera Verhoeff, 1936b: 298–299, figs 1–2 (designated by Attems 1938), "Riukiu-Insel Okinawa".

Diagnosis

Xystodesmid typically of length over 30 mm, up to 80 mm, colouration generally dark grey, brown, metallic green, or uniformly light yellow, orange, or with distinct bands and patches on each ring; paranota also dark or with large yellow or white spots in their entire edge (vs *Xystodesmus* with smaller body size, and colouration with small red, orange or yellow paranotal spots). Gonopods with two branches, prefemoral process and acropodite form a simple forceps (Korsós *et al.* 2011), sometimes with different teeth or additional small processes.

According to Golovatch (2023: 233): "Morphologically, *Riukiaria* differs from *Xystodesmus* in the less elaborate and largely forceps-shaped gonopodal telopodite, in which among the two main branches, the solenomere and prefemoral process, the former is always longer to much longer than the latter, if any, while the gap between both is very considerable. In contrast, the solenomere and prefemoral process in *Xystodesmus* are quite variable in length and shape, both lying clearly adjacent and/or clearly appressed to each other, forming no considerable gap between them."

The genus encompasses 37 species (Korsós *et al*. 2011; Golovatch 2023), with a wide distribution including the central and southern Japanese islands, Taiwan, central-east China, and North Vietnam. Only one species was briefly mentioned from South Korea (Takakuwa 1941b), but its occurrence has remained unconfirmed up to now.

Riukiaria koreana sp. nov.

urn:lsid:zoobank.org:act:B67C0886-6A00-4C4D-B69C-0733D70DBDDC
Figs 6–7, 10D, 11B, 13, 15–16

Rhysodesmus semicircularis – Takakuwa 1941b: 413–414, fig. 1 (partim), "Kagosima, Sihusi, Itihata, Miyasima, Kyoto, Hieisan, Yamanaka, Siramine" (= all in Japan), and "Husan (Korea)" (= Busan, South Korea).
Riukiaria semicircularis – Shinohara 1977: 118. — Lim 2001: 126–128, fig. 141.

Diagnosis

Typical species of *Riukiaria* in size, colouration and basic form of gonopods. *Riukiaria koreana* sp. nov. differs from *Riukiaria semicircularis* (Takakuwa, 1941b) by its completely smooth metazonites (vs with coarse row of tubercles in *R. semicircularis*), lacking a row of sawteeth on male tarsus of rings 3–13 (vs present in *R. semicircularis*), having a pair of cone-shaped coxal processes on legpair 2, by a shorter and straight prefemoral process (vs long and flagellum-like, undulating in *R. semicircularis*), and by a curved acropodite not reaching the prefemoral process (vs forming an almost complete circle in *R. semicircularis*).

Etymology

Emphasizing its occurrence in the Korean Peninsula, and its separation from all other species of *Riukiaria*. Adjective, feminine.

Type material

Holotype

SOUTH KOREA • ♂; Jellanam Prov., Jindo Town, Gogun-myeon, Jindo-daero 1320; 34°26′18.6″ N, 126°21′4.3″ E; 10 Jul. 2024; G. Kim leg.; LEGOA030054 JD07.

Paratypes

SOUTH KOREA • 1 ♀; same locality and date as holotype; HNHM diplo-4561 JD03 • 1 ♀; same locality and date as holotype; HNHM diplo-4561 JD04 • 1 ♂; same locality and date as holotype; HNHM diplo-4560 JD06 • 1 ♂; same locality and date as holotype; HNHM diplo-4560 JD08 • 1 ♂; same locality and date as holotype; HNIBRIV12831 JD01 • 1 ♂; same locality and date as holotype; LEGOA030052 JD02 • 1 ♂; same locality and date as holotype; LEGOA030056 JD10 • 1 ♂; same locality and date as holotype; LEGOA030057 JD11 • 1 ♀; same locality and date as holotype; LEGOA030053 JD05 • 1 ♀; same locality and date as holotype; LEGOA030055 JD09 • 1 ♀; same locality and date as holotype; LEGOA030058 JD12 • 1 ♂; Jellanam Prov., Hwasun Town, Baega-myeon, Songdan-gil 479-55; 35°10′22.1″ N, 127°11′0.6″ E; 6 Jul. 2024; G. Kim leg.; LEGOA030059 HS01 24 • 1 ♂; Jellanam Prov., Hwasun Town, Baega-myeon, Songdan-gil 479-55; 35°10′04.8″ N, 127°11′10.3″ E; 25 Sep. 2023; D. Kim leg.; LEGOA030061 HS02 • 1 ♂; same data as for preceding; LEGOA030062 HS03 • 1 ♂; same data as for preceding; LEGOA030063 HS04 • 1 ♂; same data as for preceding; LEGOA030065 HS06 • 1 ♂; same data as for preceding; LEGOA030066 HS07 • 1 ♂; same data as for preceding; LEGOA030066 HS09 • 1 ♀; same data as for preceding; LEGOA030060 HS01 • 1 ♀; same data as for preceding; LEGOA030064 HS05 • 1 ♀; same data as for preceding; LEGOA030067 HS08 • 1 ♀; same data as for preceding; LEGOA030069 HS10 • 1 ♂; Jellanam Prov., Wando Town, Gunoe-myeon, Samdu 1-gil; 34°20′50.7″ N, 126°40′07.7″ E; 27 Jul. 2024; G. Kim leg.; LEGOA030070 WD01 • 1 ♀; same data as for preceding; LEGOA030071 WD02 • 1 ♂; Jellanam Prov., Gurye Town, Sandong-myeon, Jwasa-ri. Nogodan; 35°18′08.0″ N, 127°30′48.8″ E; 25 May 2024; 1160 m a.s.l.; D. Kim leg.; LEGOA030072 GR02 • 1 ♂; same data as for preceding; LEGOA030073 GR03 • 1 ♂; Gyeongsangbuk Prov., Yecheon Town, Hyoja-myeon, Gohang-ri, near Mt. Sobaek-san; 36°50′14.0″ N, 128°27′39.1″ E; 750 m a.s.l.; 24 Jul. 2023; D. Kim leg.; LEGOA030074 YC02 • 1 ♂; same data as for preceding; LEGOA030075 YC03 • 1 ♂; same data as for preceding; LEGOA030076 YC04 • 1 ♂; same data as for preceding; GenBank nos: PV446411 (*COI*), PV544276 (*EF1-α*); LEGOA030077 YC05 • 1 ♂; same data as for preceding; LEGOA030078 YC06 • 1 ♂; same data as for preceding; GenBank nos: PV446412 (*COI*), PV544277 (*EF1-α*); LEGOA030079 YC07 • 1 ♀; same data as for preceding; LEGOA030080 YC10 • 1 ♀; same data as for preceding; LEGOA030081 YC11 • 1 ♂; Gangwon Prov., Wonju Town, Seowon-myeon, Uhyeon-ri, Mt. Baeggun-san; 37°15′40.5″ N, 127°57′48.2″ E; 640 m a.s.l.; 4 Jun. 2023; D. Kim leg.; LEGOA030082 WJ01 • 1 ♀; same data as for preceding; LEGOA030083 WJ02 • 1 ♂; Gyeongsangnam Prov., Sancheong Town, Sicheon-myeon, Dongdang-ri, Mt. Gugok-san; 35°17′49.9″ N, 127°46′58.9″ E; 640 m a.s.l.; 2 Oct. 2023; D. Kim leg.; HNHM diplo-04562 SC13 • 1 ♀; same data as for preceding; HNHM diplo-04562 SC01 • 1 ♂; same data as for preceding; LEGOA030084 SC02 • 1 ♂; same data as for preceding; LEGOA030085 SC03 • 1 ♂; same data as for preceding; LEGOA030086 SC04 • 1 ♂; same data as for preceding; LEGOA030087 SC05 • 1 ♂; same data as for preceding; LEGOA030088 SC06 • 1 ♂; same data as for preceding; LEGOA030089 SC07 • 1 ♂; same data as for preceding;

LEGOA030091 SC09 • 1 ♂; same data as for preceding; LEGOA030092 SC10 • 1 ♂; same data as for preceding; LEGOA030095 SC14 • 1 ♂; same data as for preceding; LEGOA030096 SC15 • 1 ♂; same data as for preceding; LEGOA030097 SC16 • 1 ♀; same data as for preceding; LEGOA030090 SC08 • 1 ♀; same data as for preceding; LEGOA030093 SC11 • 1 ♀; same data as for preceding; LEGOA030094 SC12 • 1 ♀; same data as for preceding; LEGOA030098 SC17 • 1 ♀; same data as for preceding; LEGOA030099 SC18 • 1 ♀; same data as for preceding; LEGOA030100 SC19.

Description

HEAD. Smooth, with 2+2 large frontal setae and several smaller ones on clypeus and around antennal sockets; epicranial suture distinct. Antennae straight; article 1 globose; articles 2–6 long, subequal in length, increasingly setose; article 7 small, globose, length equal to width, with 4 apical sensory cones hidden among dense setae.

COLLUM. Parallelogram-shaped, only slightly convex, its length 2.5 times as large as that of metatergite 2, posterolateral corners directed caudad, anterior margin nearly semicircular, without ridge.

BODY. Collum and first two rings narrow, body sides between rings 4–12 parallel, then gradually tapering towards telson. Proterga and metaterga completely smooth, metaterga with weak transverse depression in middle from ring 5 onwards. Posterolateral edge of paranota 2–4 rectangular, from 5 onwards slightly pointed triangular shape, from 12 triangular, with weak excavation on posterior edge of each of the metaterga. Pore formula mostly typical for Polydesmida, pores on rings 5, 7, 9–10, 12–13, and 15–19, in lateral position on swollen paranota. Rings 13–19 gradually tapering, posterolateral projections becoming more pointed.

TELSON. Epiproct protruding, in dorsal view triangular, in lateral view slightly curved, with 4+4 setae on sides, and with 1+1 setae apically; paraprocts (anal valves) smooth, with 2+2 setae on median ridges; hypoproct semicircular, with 1+1 setae on small tubercles.

LEGS. Bases of midbody legpairs well separated in males by 1.6–2.2 mm, in females by 1.9–2.5 mm, sterna smooth and wide, pro- and metasterna well separated. Prefemur of legs beginning at ring 7 with well-developed ventral spine (Fig. 11B: *ps*) increasing in size from midbody onwards; femur about twice as long as prefemur, slightly clavate; postfemur short, half as long as femur; tibia slender, setose, as long as postfemur; tarsus densely setose, about 1.5 times as long as tibia; all legs with curved claws.

MEASUREMENTS. Males (based on 36 specimens): total body length 29–42 mm, midbody width (including paranota) 5.4–7.7 mm, metatergal length 1.3–2.3 mm, midbody prozonite width 3.8–4.9 mm, collum width 4.6–6.5 mm, median collum length 1.8–2.8 mm. Females (based on 20 specimens): total body length 31–40 mm, midbody width (including paranota) 6.6–7.8 mm, metatergal length 1.6–2.2 mm, midbody prozonite width 4.3–5.6 mm, collum width 5.4–6.6 mm, median collum length 2.0–2.9 mm.

COLOURATION (Figs 7A, 13). Preserved specimens in ethanol: dorsum, prozonites, metazonite, and proximal part of epiproct dark grey, almost blackish, distal part of epiproct lighter. Posterior portion of paranota with bright yellow spots on all rings, including collum. Posterior part of head and proximal part of antennal articles dark grey; clypeus, cheeks and distal end of antennal articles, femur, postfemur and tibia from legs 2 onwards light grey or whitish; legpair 1, other articles of other legs, and ventral side white.

MALE CHARACTERS. Coxae of legpair 2 with pair of protruding, cone-shaped processes, remaining legs and sterna without modifications. Posterior margin of rings 5–13 medially with minute serrated edge (Fig. 7B). Gonopods (Fig. 6A–D): two forceps-like processes as typical of *Riukiaria*; one prefemoral process (*pfp*), and the other acropodite (*a*) (after Korsós *et al.* 2011: 57, fig. 1). Coxa stout, as long as wide, without coxal apophysis, with single apophyseal macroseta (*ms*) on dorsal side. Cannula on mesal side, starting near macroseta, then connected to prefemur and continuing in prostatic groove. Prefemur short, densely setose, prefemoral process straight, directed dorsad, about ⅔ in length compared to

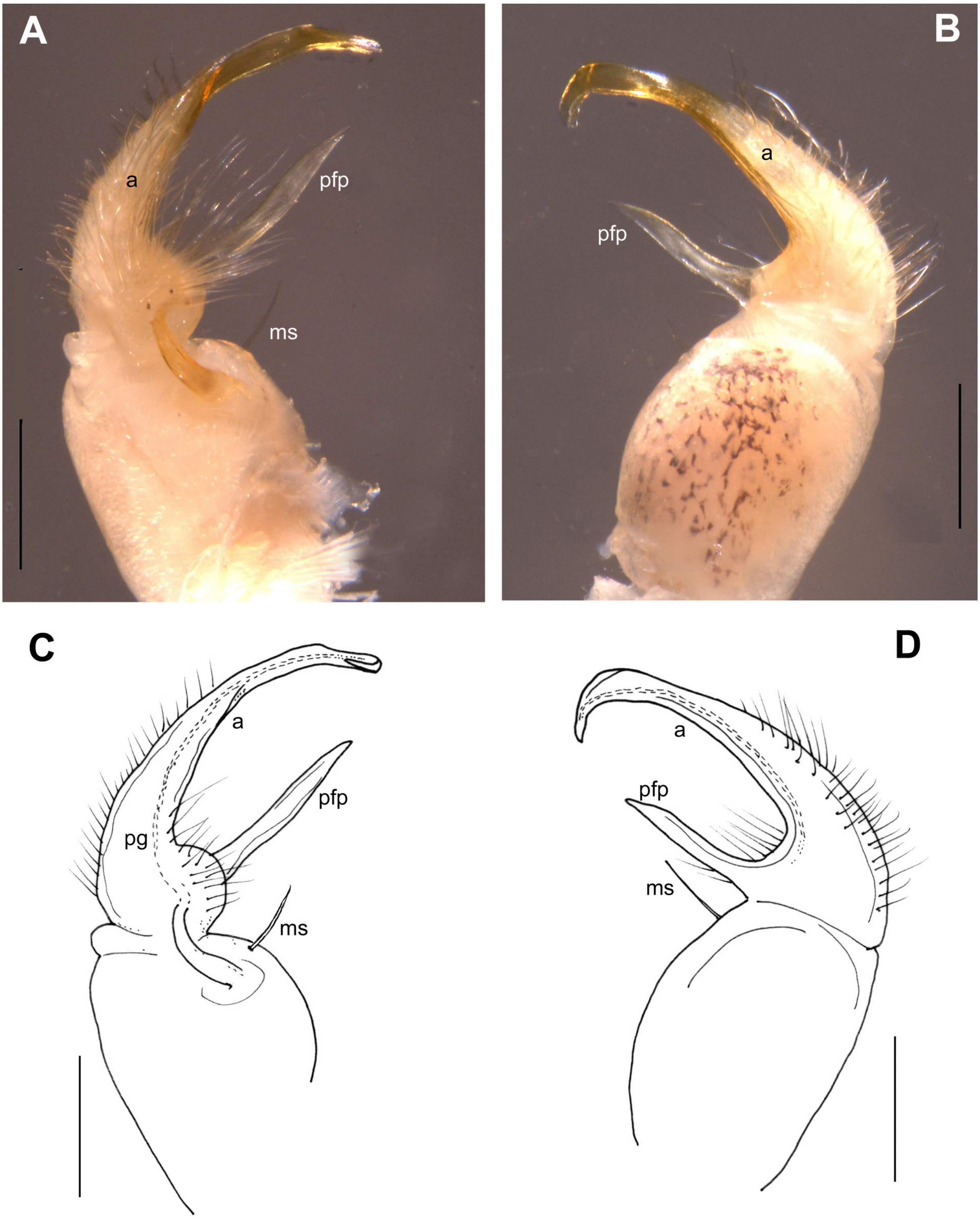

Fig. 6. *Riukiaria koreana* sp. nov., right gonopod of male holotype from Jindo (JD07). **A, C**. Mesal view. **B, D**. Lateral view. Abbreviations: a = acropodite; ms = macroseta; pfp = prefemoral process; pg = prostatic groove. Scale bars: 0.5 mm.

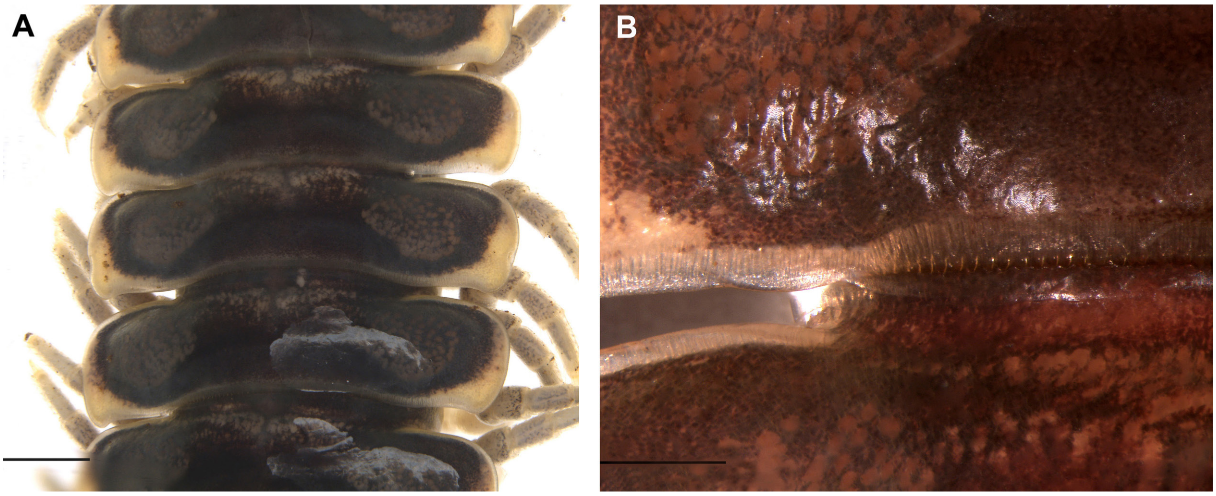

Fig. 7. *Riukiaria koreana* sp. nov. **A**. Midbody rings of male paratype from Gurye Town (GR03). **B**. Serrated metatergite of ring 10, paratype from Wonju (WJ01). Scale bars: A = 1 mm; B = 0.5 mm.

acropodite, gradually tapering to pointed tip. Acropodite (*a*) straight at base, subparallel with prefemoral process (*pfp*), about 1.5 times as thick as prefemoral process, gradually bending dorsally at midpoint, tip curving, directed towards but not reaching end of prefemoral process. Prostatic groove (*pg*) running along dorsal side of acropodite, (*a*) opening at tip.

Female characters. Body of females wider than that of males, subequal in length; other somatic characters, including colouration and strong prefemoral ventral spines, similar. Posterior margin of rings 5–13 medially without serrated edge. Coxae of legpair 2 without projection (Fig. 10D), further legs also without any sternal or coxal modifications. Cyphopods in situ closely behind legpair 2, in common oval-shaped opening; valves of equal size, pentagon-shaped, ventral edges each with a small peak (Fig. 10D), operculum laterally closely overlaying, receptacles deeply embedded under valves.

Distribution

Riukiaria koreana occurs scattered across the entire South Korean Peninsula (Fig. 15).

Remarks

In the original description of *Rhysodesmus* (= *Riukiaria*) *semicircularis*, Takakuwa (1941b) mentioned a single Korean locality, "Husan" (= Busan, South Korea). This record was mentioned by some authors (Miyosi 1952, 1959; Shinohara 1977), based on literature and without examining specimens from Korea. Lim (2001) translated the original description, while mentioning "it is necessary to make a better description based on fresh material" (Lim 2001: 126). Lim Kil-Young (2024 pers. comm.) admitted that his concept of *Riukiaria* in Korea needs re-evaluation. Here, with fresh Korean material of *Riukiaria* at hand, we can clearly establish the differences from the Japanese *R. semicircularis* (see Diagnosis).

Genus ***Levizonus*** Attems, 1898

Levizonus Attems, 1931: 69.
Ezaria Takakuwa, 1941a: 8 (with type species: *Ezaria montana* Takakuwa, 1941), synonymized by Hoffman (1980: 157).
Profontaria Verhoeff, 1941: 411–412 (with type species: *Profontaria takakuwai* Verhoeff, 1941), synonymized by Tanabe (1994: 102).

Hokkaidaria Verhoeff, 1941: 414–415 (invalidly proposed without type species), synonymized by Jeekel (1971: 266).
Ezodesmus Takakuwa, 1942c: 42 (with type species: *Ezodesmus lunatus* Takakuwa, 1942), synonymized with *Profontaria* by Hoffman (1956: 99), synonymized with *Levizonus* by Tanabe (1994: 102).

Levizonus – Tanabe 1994: 102–103. — Mikhaljova 2021: 160–162.

Type species

Sulciferus (*Levizonus*) *thaumasius* Attems, 1898: 352, fig. V.112; "Wladiwostok", by original designation.

Diagnosis

Without the possibility to investigate any material, the diagnosis here is given based on earlier descriptions (Tanabe 1994: 102; Mikhaljova 2021: 162). *Levizonus* differs from all other Palaearctic xystodesmid genera mainly by the arcuate to coiled ring-like gonopod telopodite without prefemoral process, but with a modified apex. The loop makes at most one ring, whereas in *Parafontaria* Verhoeff, 1936 it forms 1.5 to 2 rings. *Levizonus* has a relatively long subcylindrical gonopod coxa (vs oval in *Parafontaria*), and a short solenomere (vs long in *Riukiaria* Attems, 1938).

Species included

At present, eight species are recognized in the genus *Levizonus*: *L. circularis* Takakuwa, 1942, *L. distinctus* Mikhaljova, 1990, *L. laqueatus* Mikhaljova, 1981, *L. malewitschi* Lokschina & Golovatch, 1977, *L. montanus* (Takakuwa, 1941), *L. nakhodka* Mikhaljova, 2021, *L. takakuwai* (Verhoeff, 1941), and *L. thaumasius* Attems, 1898 (Mikhaljova 2021).

Distribution

Members of the genus are only known from the northern part of the Far Eastern region: Russia (Primorskiy krai), North Korea, Japan (Hokkaido), and North-East China.

Levizonus circularis (Takakuwa, 1942)
Figs 3C, 15

Levizonus circularis Takakuwa, 1942c: 43–44, fig. 8; "Zyônanri 上南里 (Korea)" (= North Korea, Pyeongannam-do province, Yeonweon-gun county, Sangnam-ri village, according to Mikhaljova 2021: 167)
Levizonus variabilis Lokshina & Golovatch, 1977: 76–77, fig. 3.

Levizonus circularis – Lim 2001: 131–132, fig. 146.
Levizonus variabilis – Lim 2001: 132–133, figs 147–149. — Mikhaljova 2021: 163–167, figs 1–3 (synonymyzation).

Diagnosis

"The main distinguishing characters are: apex of gonopod telopodite not like two plates placed perpendicular to each other as in *L. malewitschi*; gonopod solenomere, more or less strongly curved mesad (vs not strongly curved mesad in other congeners); the central edge of the gonopod telopodite apex with outgrowths and spinules (vs without outgrowths and spinules in other congeners excluding *L. thaumasius*, *L. nakhodka* and *L. malewitschi*); metaterga with low bosses either everywhere or only laterally (vs smooth in other congeners)." (after Mikhaljova 2021: 165, omitting references to her figures).

Type material (not examined)

NORTH KOREA • 1 ♂; "Zyônanri 上南里 (Korea)"; Takakuwa's private collection, including type material of many species, considered lost (Tanabe & Shinohara 1996; Chao & Chang 2008).

Remarks

Levizonus circularis only occurs in Far East Russia, North-East China and North Korea (Mikhaljova 2021). In addition to the type locality (Sangnam-ri, Yeonweon-gun) Lim (2001: 132) mentioned two females collected by the expedition of the Polish Academy of Sciences in Jueul, Hamgyongbukdo Prov., 5. Sep. 1970, leg. R. Bielawski and M. Mroczkowski (Bańkowska & Sterzyńska 1997). Mikhaljova (2021) added one more in North Korea: Hamgyongnamdo Prov., Lake Čangdžin-ho, 9 Jun. 1965, leg. M. Mroczkowski and A. Riedel (also from the Polish Academy of Sciences). Unfortunately, no material was available for us to study, so in the characterization of *L. circularis*, we can only rely on Mikhaljova (2021) whose Korean specimens (the same as mentioned above) were first considered as *L. variabilis* Lokshina & Golovatch, 1977 (Mikhaljova *et al*. 2000), then later synonymized with *L. circularis* (Mikhaljova 2021). The two female specimens of *L. circularis* mentioned by Lim (2001) from the 1970 Polish expedition is probably a mistake as was clarified by Lim Kil-Young in a personal discussion (2024 pers. comm.). Thus, until new and abundant material from North Korea becomes available, it is difficult to estimate the population variability and hence the taxonomic status of the Korean *L. circularis*, so we keep it as it is, following Mikhaljova (2021).

Tribe Parafontariini Hoffman, 1978

Genus ***Parafontaria*** Verhoeff, 1936

Parafontaria Verhoeff, 1936b: 300–301 (with type species *Fontaria* (*Parafontaria*) *armigera* Verhoeff, 1936, originally erected as a subgenus).
Japonaria Verhoeff, 1936a: 155 (invalidly proposed without type species, see Hoffman 1978b: 216).
Japonaria Attems, 1938: 174 (with type species: *Fontaria* (*Japonaria*) *falcifera* Verhoeff, 1936), synonymized by Hoffman (1978b: 216).
Grayaria Chamberlin, 1943: 16 (with type species: *Grayaria attemsii* Chamberlin, 1943), synonymized by Hoffman (1978b: 216).

Parafontaria – Tanabe 2002: 2144–2149. — Lim 2001: 133–134.

Type species

Fontaria (*Parafontaria*) *armigera* Verhoeff, 1936: 301–303, figs 4–6; "Suwa bei Tokio".

Diagnosis

"Separable from other confamiliars [in the subfamily Xystodesminae] by the following characters: gonopods forming one and a half to two loops; cyphopods with the membranous bellows tube. In some species, the coxae and sternite of segment 3 of females are strongly modified." (Tanabe 2002: 2144).

Species included

At present 14 species of *Parafontaria* are recognized as valid (Tanabe 2002; Sierwald *et al*. 2025): *Parafontaria crenata* Shinohara, 1986, *P. doenitzi* (Karsch, 1880), *P. erythrosoma* (Takakuwa, 1942), *P. falcifera* (Verhoeff, 1936), *P. ishiii* Shinohara, 1986, *P. koreana* (Paik, 1963), *P. laminata* (Attems, 1909), *P. longa* Shinohara, 1986, *P. shiraiwaensis* Shinohara, 1986, *P. spathulata* (Miyosi, 1951), *P. takakuwai* (Shinohara, 1957), *P. terminalis* (Takakuwa, 1942), *P. tokaiensis* Tanabe, 2002, and *Parafontaria tonominea* (Attems, 1899).

Distribution

According to Tanabe (2002), all species of *Parafontaria* are endemic to Japan (Tanabe 2002: 2139). However, he missed the single Korean species, *P. koreana* described by Paik (1963). Here, we confirm its identification based on new material.

Parafontaria koreana (Paik, 1963)

Figs 8–9, 10E–H, 11C, 14–16

Japonaria koreana Paik, 1963: 34, fig. 7; "Mt. Sokkri, July 24, 1960" (= Mt. Songni-san, at the border of Chungcheongbuk Prov. and Gyeongsangbuk Prov., South Korea).

Parafontaria koreana – Lim 2001: 134–135, figs 150–152.

Diagnosis

A medium-sized member of the genus *Parafontaria* as shown by its gonopod telopodite forming a complete circle, without prefemoral process, and with short gonopodal coxa. Telopodite divided into two subequal parts, femur and tibiotarsus ("prefemurs" and "prefemurofemurs" by Paik 1963). Acropodite with two or three small processes.

Type material (not examined)

Holotype

SOUTH KOREA • ♂; Mt. Sokkri; 24 Jul. 1960; Ji-e Choi leg.

Allotype

SOUTH KOREA • 1 ♀; Mt. Sokkri; 21 Jul. 1960; Mok-hong Choi leg.

The type specimen was kept in the author's collection, but unfortunately, all types of Paik's myriapod species are seemingly lost (Lim 2024 pers. comm.).

Other material examined

SOUTH KOREA • 1 ♂; Daegu metropolitan city, Dalseong Town, Gachang-myeon, Ju-ri, Mt. Choejeong-san; 35°45′07.5″ N, 128°35′59.3″ E; 800–850 m a.s.l.; 28 Sep. 2023; D. Kim leg.; GenBank nos: PV446408 (*COI*), PV544273 (*EF1-α*); LEGOA030101 DG01 23 • 1 ♀; same data as for preceding; GenBank nos: PV446409 (*COI*), PV544274 (*EF1-α*); LEGOA030102 DG02 23 • 1 ♀; same data as for preceding; LEGOA030103 DG03 23 • 1 ♀; same data as for preceding; LEGOA030104 DG04 23 • 1 ♀; same data as for preceding; LEGOA030105 DG05 23 • 1 ♀; same data as for preceding; LEGOA030106 DG06 23 • 1 ♂; Daegu metropolitan city, Gunwi Town, Bugye-myeon, Namsan-ri; 36°1′20.4″ N, 128°38′28.2″ E; 560 m a.s.l.; 16 Sep. 2023; G. Kim and D. Kim leg.; HNHM diplo-04563 GN02 • 1 ♂; same data as for preceding; LEGOA030107 GN01 • 1 ♂; same data as for preceding; LEGOA030109 GN04 • 1 ♀; same data as for preceding; LEGOA030108 GN03 • 1 ♂; Gyeongsangbuk Prov., Andong District, Dosan-myeon, Dancheon-ri, near Mt. Cheongyangsan; 36°44′55.0″ N, 128°54′53.3″ E; 600 m a.s.l.; 31 Aug. 2023; D. Kim leg.; GenBank nos: PV446410 (*COI*), PV544275 (*EF1-α*); LEGOA030110 AD03 • 1 ♂; Gyeongsangbuk Prov., Daegu metropolitan city, Chilgok Town, Gasan-myeon, San 117-30; 36°1′50.52″ N, 128°30′40.32″ E; 1 Jun. 2024; G. Kim leg.; LEGOA030111 DG01 24 • 1 ♂; Gyeongsangbuk Prov., Cheongsong Town, Cheongsong-eup, Woroe-ri 216; 36°26′26.0″ N, 129°08′34.3″ E; 16 May 2024; G. Kim leg.; LEGOA030112 CS11 • 1 ♀; Jeollanam Prov., Gurye Town, Ganjeon-myeon, Jungdae-ri, Mt. Baegun-san; 35°07′55.8″ N, 127°36′12.6″ E; 580 m a.s.l.; 2 Sep. 2023; D. Kim leg.; HNHM diplo-04564 GR03 • 1 ♀; same data as for preceding; LEGOA030113 GR04 • 1 ♂; Ulsan metropolitan city, Ulju Town, Dudong-myeon, Weolpyeong-ri, Mt. Mugjang-san; 35°40′47.6″ N, 129°14′27.7″ E; 570 m a.s.l.; 8 Jul. 2023; D. Kim leg.; LEGOA030115 US20 • 1 ♂; same data as for preceding; LEGOA030116 US21 • 1 ♂; Ulsan metropolitan city, Ulju Town, Sangbuk-myeon, Soho-ri, Mt. Goheon-san; 35°39′18.8″ N, 129°05′02.0″ E; 570 m a.s.l.; 8 Jul. 2023; D. Kim leg.; LEGOA030114 US08 • 1 ♀; Gangwon Prov., Inje Town, Girin-myeon, Jindong-ri, Mt. Gachil-bong peak; 37°59′17.5″ N, 128°24′27.7″ E; 620 m a.s.l.; 14 Aug. 2023; D. Kim leg.; LEGOA030117 IJ01.

Description of the type

The original description by Paik (1963) is as follows: "Male: Body length 40 mm, width of postcephalic somites 6.3 mm and somites are 4.4 mm. General colour grayish yellow brown. Distal spines of coxae and prefemurs are seen after 11th pair of legs. Male gonopod makes a circle. Prefemurofemurs of male gonopod with a sharp small projection on its distal end. Prefemurofemurs of male gonopod yellowish white, and the acropodite yellowish brown. The acropodite with a bi- or tri-partited flat internal branch and horn-like shaped external branch. The distal end of acropodite bipartite. Remarks: Differs in the structure of male gonopods from the others."

Description based on present material

Head. Smooth, no frontal setae, only several long ones around antennal sockets and smaller ones on clypeus, thickening at margin; epicranial suture conspicuous. Antennae slightly bent; article 1 globose; articles 2–6 all subequal in length, increasingly setose; article 7 small, somewhat longer than wide, with four apical sensory cones.

Collum. Strongly convex, four times as wide as long, wider and bending more ventrad than terga of ring 2, anterior margin straight, without ridge, posterior margin subcircular with weak, undulate depression in the middle, length about twice as large as metatergite 2.

Body. Entire body almost cylindrical, collum and all rings convex, lateral sides of metaterga directed latero-ventrad, body sides all along parallel, only last three rings narrower and slightly tapering toward telson. Proterga and metaterga completely smooth, and shiny, metaterga medially only with weak, incomplete transverse depression starting on ring 9. Posteriolateral edge of paranota rounded all along until ring 13, then slightly pointed backwards, laterally with visible ridges. Pore formula typical for Polydesmida, pores on rings 5, 7, 9–10, 12–13, and 15–19 in lateral position. Rings 17–19 gradually tapering, posterolateral projections becoming triangular and pointed.

Telson. Epiproct protruding, in dorsal view triangular, in lateral view distinctly curved ventrad, with 3+3 setae on sides, and with 1+1 setae apically, sitting on small tubercles; paraprocts (anal valves) wrinkled, with 2+2 setae on sides and median ridges; hypoproct semicircular, with 1+1 setae on large tubercles.

Legs. Bases of midbody legpairs well separated in males by 1.4–1.8 mm, in females 1.6–2.2 mm, sterna smooth and wide, pro- and metasterna well separated. Prefemur of legs without (Fig. 11C) or with only very small ventral spine, and without any other extra modifications; femur 1.5 times as long as prefemur, slightly clavate; postfemur short, half as long as femur; tibia slender, 1.2 times as long as postfemur, tarsus twice as long; all articles scarcely setose; all legs with long claws.

Measurements. Males (based on 10 specimens): total body length 32–38 mm, midbody width (including paranota) 5.3–6.6 mm, metatergal length 1.4–1.8 mm, midbody prozonite width 3.9–4.6 mm, collum width 5.2–5.9 mm, median collum length 1.9–2.8 mm. Females (based on 9 specimens): total body length 33–38 mm, midbody width (including paranota) 6.2–7.5 mm, metatergal length 1.6–1.9 mm, midbody prozonite width 4.7–5.2 mm, collum width 5.5–6.2 mm, median collum length 2.3–2.8 mm.

Colouration (Fig. 14). Specimens preserved in ethanol: dorsal side of metazonites, including collum and anterior part of epiproct, dark grey, almost black, paramedially with large marbled patches, without any light part of paranotal spots; prozonites pink, with dark, incomplete, transverse medial strip. Head light grey; cheeks, antennae, legs, posterior part of epiproct light brownish grey; ventral side whitish sometimes with pinkish tone.

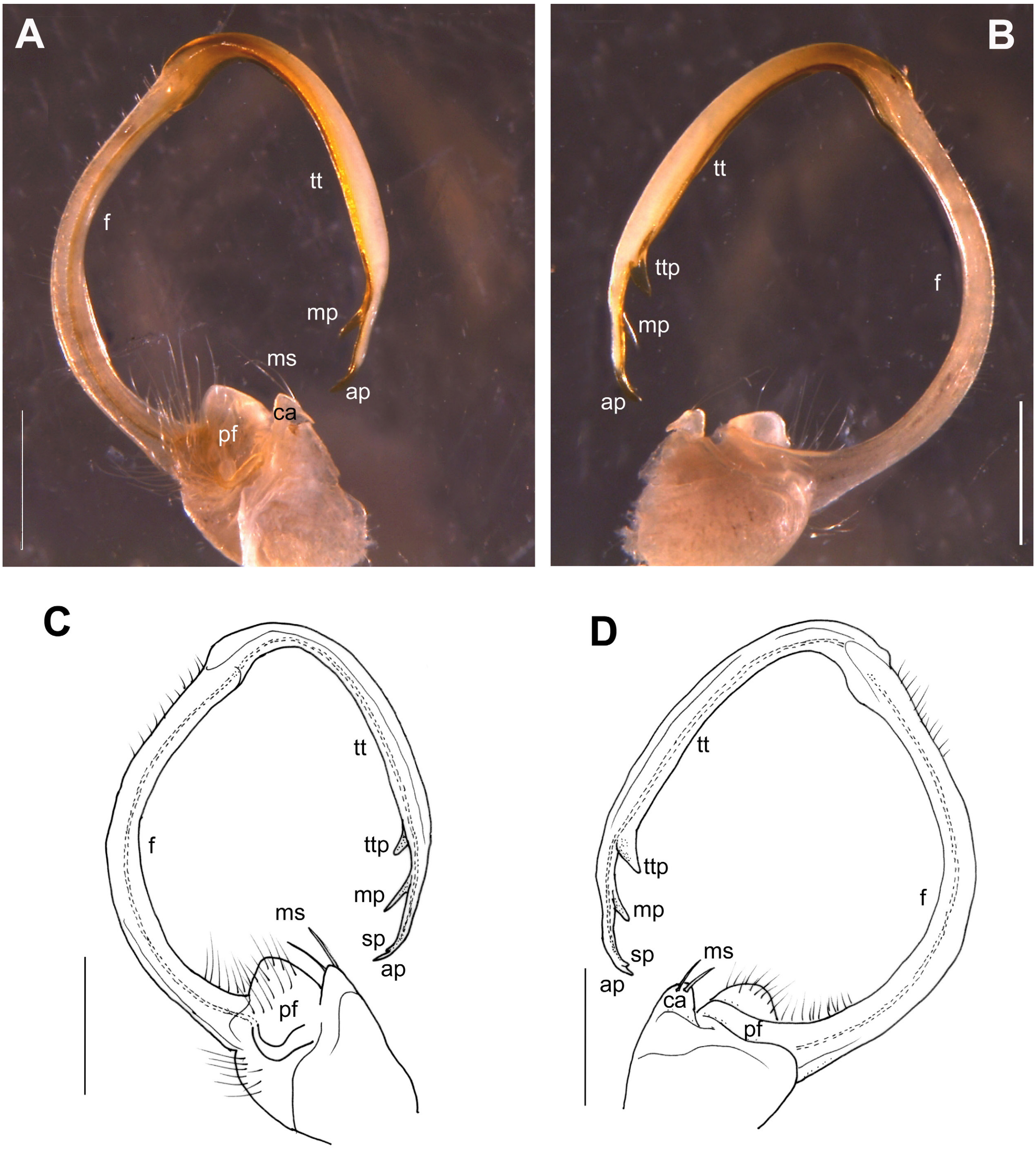

Fig. 8. *Parafontaria koreana* (Paik, 1963), right gonopod of male specimen from Gunwi Town (GN01). **A, C**. Mesal view. **B, D**. Lateral view. Abbreviations: ap = apical process; ca = coxal apophysis; f = femur; mp = mesal process; ms = macrosetae; pf = prefemur; sp = solenomere process; tt = tibiotarsus; ttp = tibiotarsal process. Scale bars: 1 mm.

Male characters. Coxae of legpair 2 with protruding cone-shaped processes, of legpair 3 with small pointed, of legpair 4 with rectangular processes, other legs without modifications. Gonopods (Figs 8–9): typical *Parafontaria*-type, with a single long telopodite, curving into a nearly complete ring. Coxa stout, cubiform, with a blunt apophyseal process (*ca*), and with two large macrosetae (*ms*) on dorsal side. Cannula starts at base of apophysis, turns to telopodite, and continues in prostatic groove, running all along on its mesal side. Prefemur (*pf*) short, densely setose, with a hump dorsally. Telopodite divided into two parts subequal in length, femur (*f*) and tibiotarsus (*tt*), also noticeable by their colour, femur being whitish and tibiotarsus yellowish, darker. Femur bending into quarter circle, rarely bristly on ventral side; tibiotarsus hairless, takes hard turn dorsad and bends back almost reaching coxal apophysis; at ¾ with flat, triangular or sharply pointed tibiotarsal process (*ttp*) pointing ventrad, sometimes with small tooth (*t*) at tip (Fig. 9B, D); after that continues into acropodite. Acropodite with pointed mesal process (*mp*), shorter than tibiotarsal process; and ends in small, pointed apical process (*ap*). Prostatic groove opens on very small solenomere process (*sp*) always below tip of acropodite (names of processes follow Tanabe 2002: 2149, fig. 10e).

Female characters. Somatic characters, including colouration, similar. Coxae of legpair 2 with small triangular projection (Fig. 10H), further legs without any sternal or coxal modifications. Cyphopods (Fig. 10E–G) in situ held closely behind legpair 2, aperture oval, normally deeply embedded; valves (*v*) of equal size, ventral edges smooth, operculum (*op*) laterally closely overlaying, receptacles (*r*) hardly visible or missing, instead long, bellow-like tubes (*b*) under valves. Sometimes these tubes protracted at length, in other cases compressed, compact (Fig. 10E–G); their function probably expressed during copulation, accepting long male solenomere.

Distribution

The species is found scattered across the South Korean Peninsula (Fig. 15).

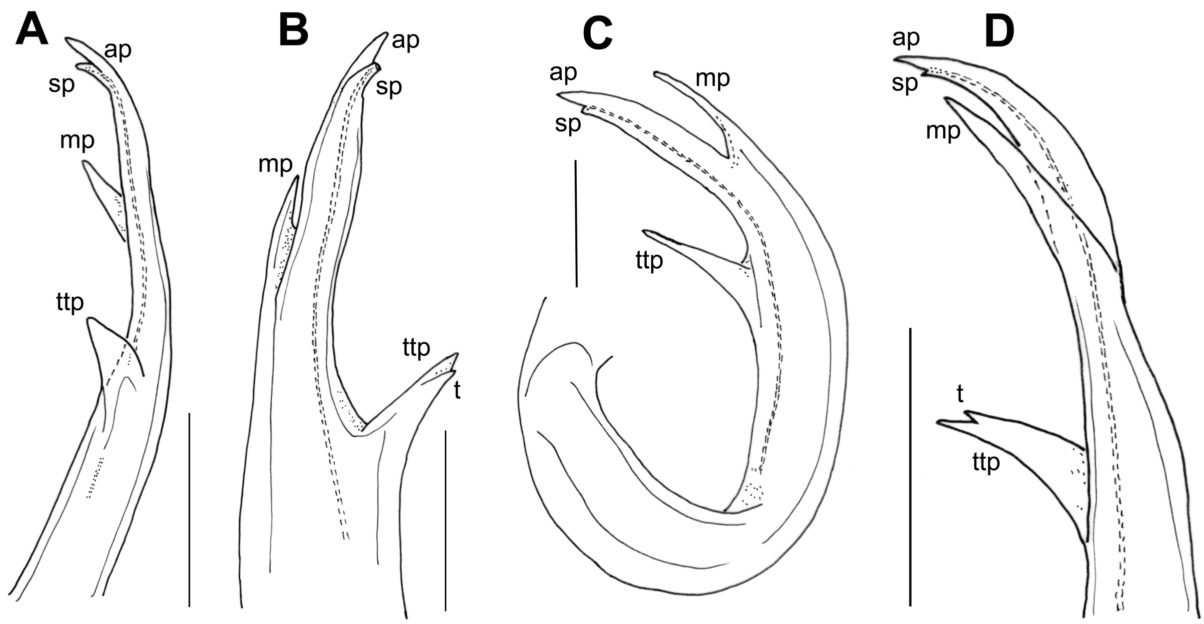

Fig. 9. *Parafontaria koreana* (Paik, 1963), ♂♂, tip of acropodite of right gonopods, apical view. **A–B**. Specimen from Gunwi Town (GN01). **A**. Mesal view. **B**. Lateral view. **C–D**. Specimen from Ulsan City (US08). Abbreviations: ap = apical process; mp = mesal process; sp= solenomere process; t = tooth; ttp = tibiotarsal process. Scale bars: 0.5 mm.

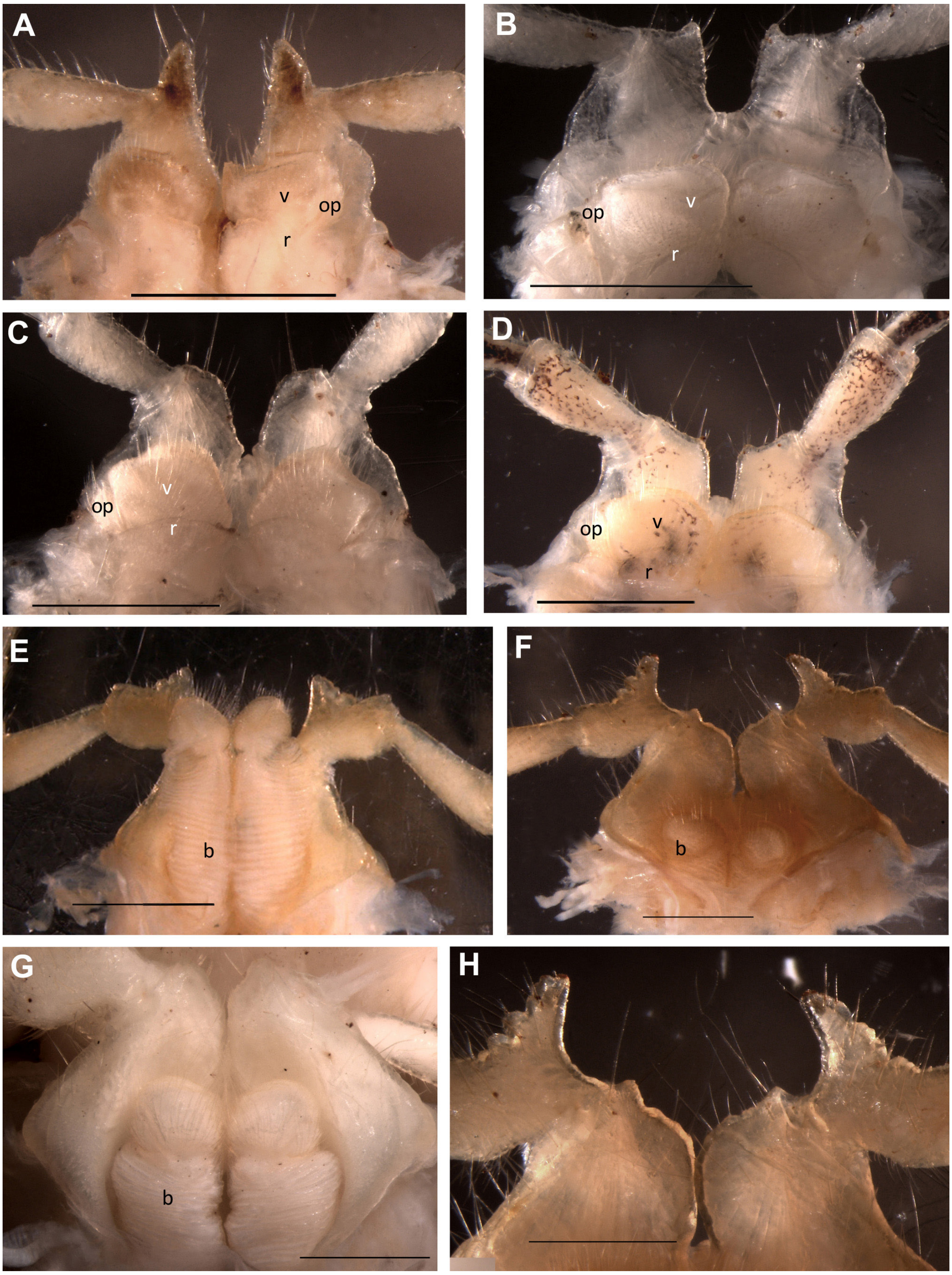

Fig. 10. Female cyphopods with legpair 2 of Korean species Xystodesmidae Cook, 1895, posterior views. **A**. *Xystodesmus pallidus* (Verhoeff, 1937), specimen from Geoje District (GJ08). **B**. *X. shirozui* (Takakuwa, 1942), specimen from Hwasun Town (HS02). **C**. *X. bifurcus* sp. nov., paratype from Inje Town (IJ03). **D**. *Riukiaria koreana* sp. nov., paratype from Hwasun Town (HS01). **E–H**. *Parafontaria koreana* (Paik, 1963). **E**. Cyphopods with extended bellows, specimen from Daegu City (DG04). **F**. Cyphopods with contracted bellows, specimen from Injo Town (IJ01). **G**. Cyphopods with intermediate bellows, specimen from Daegu City (DG05). **H**. Legpair 2 with cyphopods behind, anterior view, specimen from Injo Town (IJ01). Abbreviations: b = bellow; op = operculum; r = receptacle; v = valve. Scale bars: 1 mm.

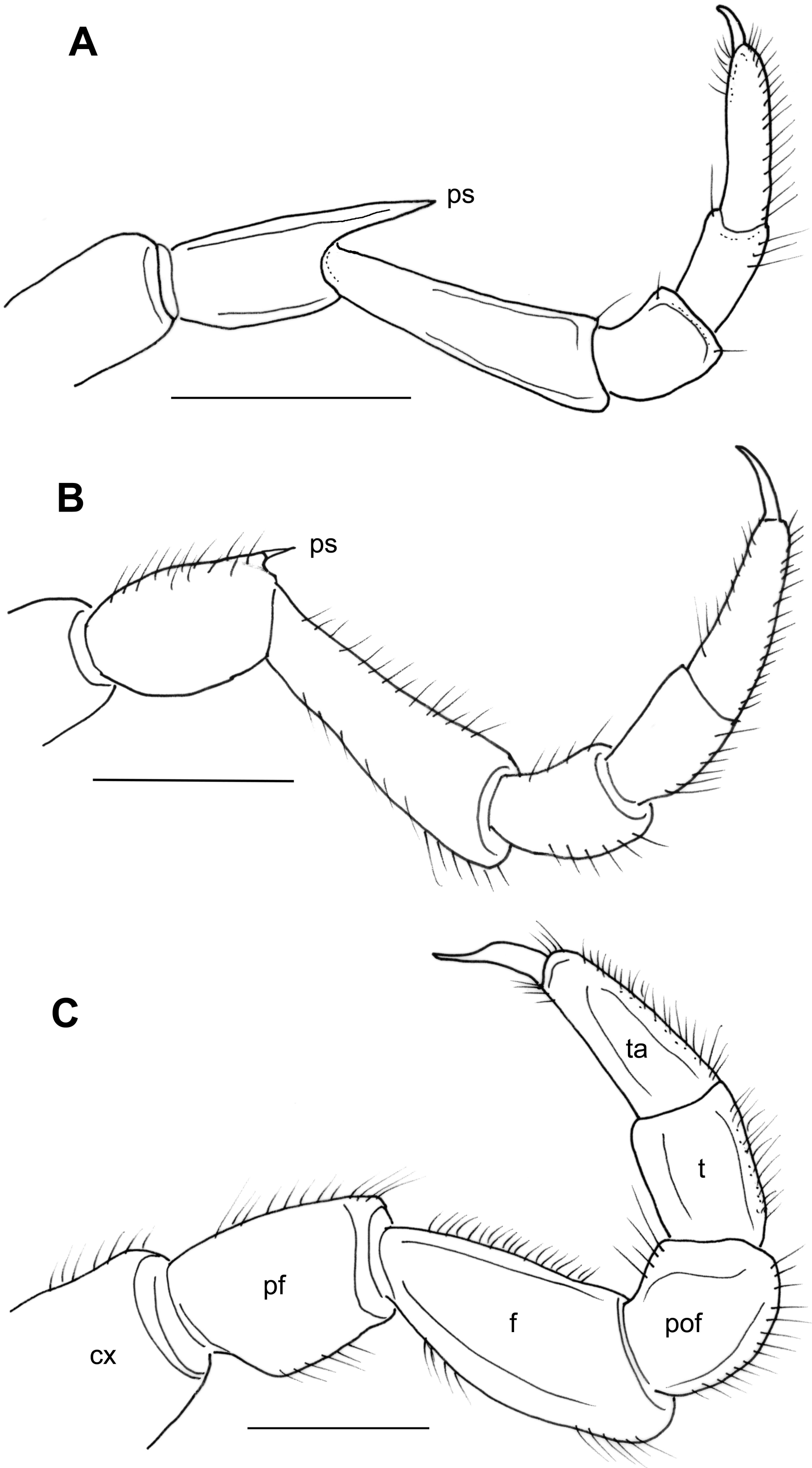

Fig. 11. Legs of Korean Xystodesmidae Cook, 1895. **A**. *X. bifurcus* sp. nov., right leg 15 of female paratype specimen from Geoje District (GJ07), anterior view. **B**. *R. koreana* sp. nov., left leg 17 of male paratype from Gurye Town (GR03), posterior view. **C**. *P. koreana* (Paik, 1963), left leg 10 of male specimen from Daegu City (DG01), posterior view. Abbreviations: cx = coxa; f = femur; pf = prefemur; pof = postfemur; ps = prefemoral spine; t = tibia; ta = tarsus. Scale bars: 1 mm.

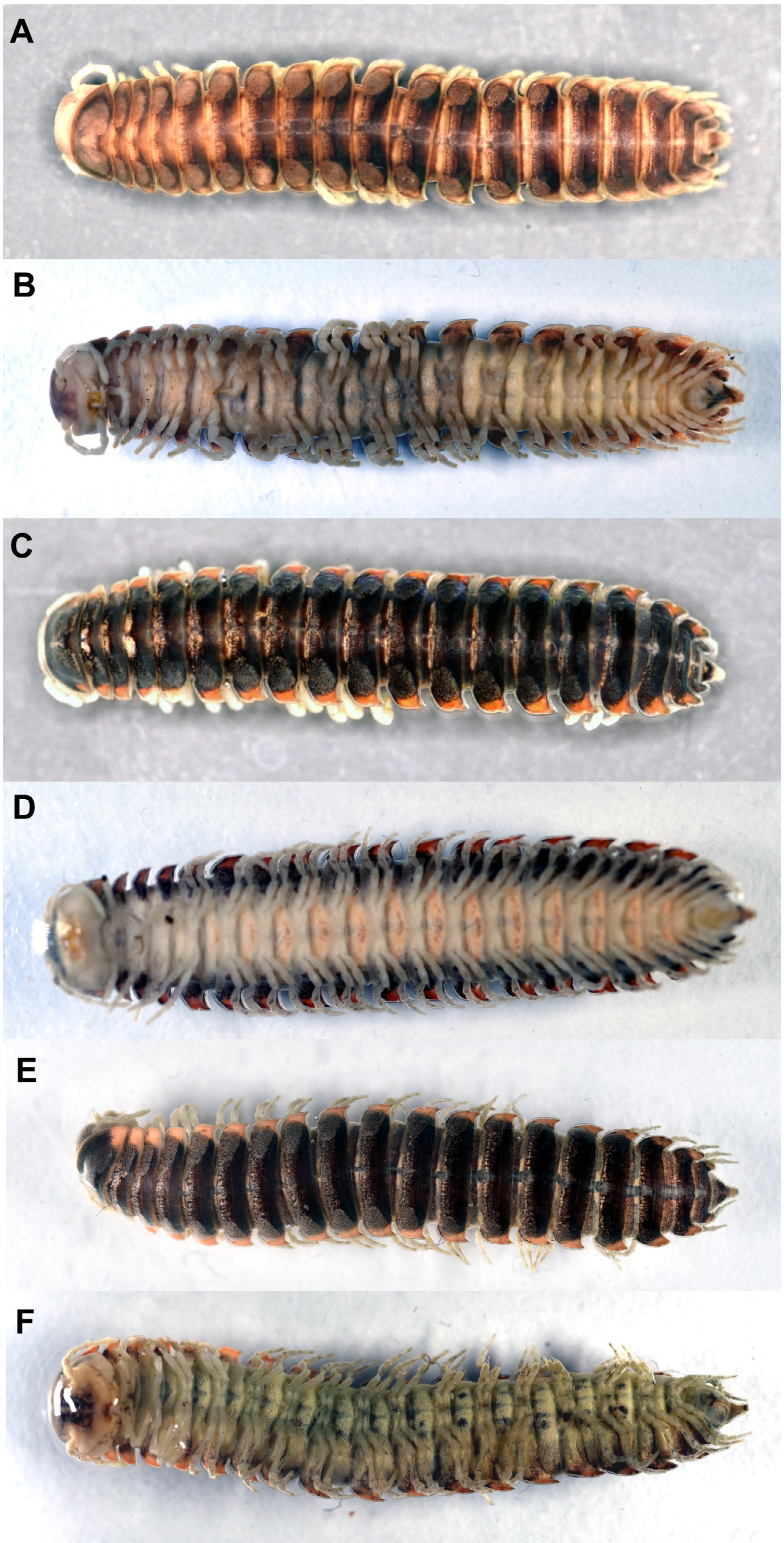

Fig. 12. Habitus of Korean millipedes of the genus *Xystodesmus* Cook, 1895, dorsal and ventral views, respectively. **A–B**. *X. pallidus* (Verhoeff, 1937), ♂ from Geoje District (GJ06). **C–D**. *X. shirozui* (Takakuwa, 1942), ♀ from Gurye District (GR02). **E–F**. *X. bifurcus* sp. nov., female paratype from Inje Town (IJ01). Not to scale.

Remarks

The generic status of this species was unconfirmed because the diagnostic character of *Parafontaria* – the exaggerated female genitalia with bellow tubes (Tanabe & Sota 2008: 2014) – was not mentioned in the original description. Tanabe & Sota (2014: 442–444) hypothesized that *Parafontaria* and *Levizonus* can be differentiated by the structure of the female genitalia: *Parafontaria* possesses fully developed bellow tubes and lacks receptacles (Tanabe 2002: 2154, fig. 15), whereas *Levizonus* exhibits partially developed

Fig. 13. *Riukiaria koreana* sp. nov., male paratype from Hwasun Town. **A**. Dorsal view. **B**. Ventral view. Not to scale.

Fig. 14. *Parafontaria koreana* (Paik, 1963), ♂ from Daegu City (DG01). **A**. Dorsal view. **B**. Ventral view. Not to scale.

bellow tubes and retains receptacles, as observed in two Japanese species, *L. montana* and *L. takakuwai* (Tanabe 1994: 105, figs 2e–f and 5g–e; Tanabe & Sota 2014: 443, fig. 2). In the freshly collected female specimens of *P. koreana*, we could observe both fully and only partially extended bellow tubes, and receptacles were hardly seen (Fig. 10E–H).

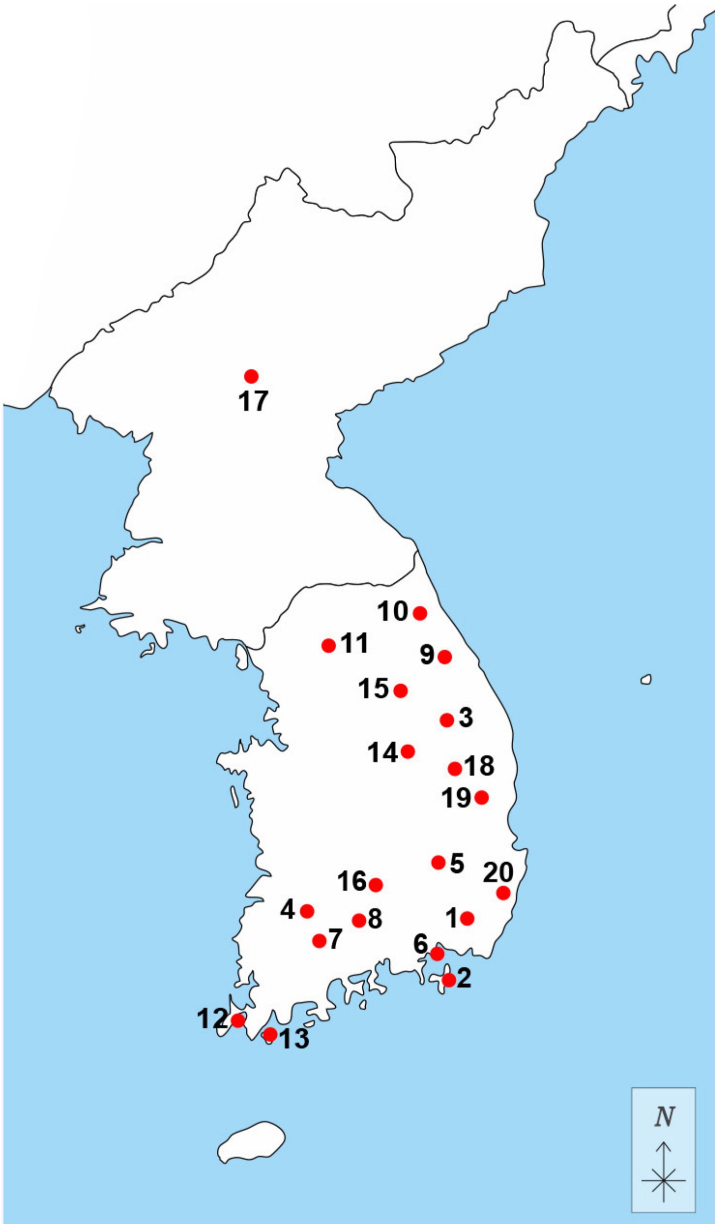

Fig. 15. Distribution of eight species of xystodesmid millipedes in the Korean Peninsula. Locality numbers for *Xystodesmus pallidus* (Verhoeff, 1937): 1, 2, 3, 4; *X. amoenus* (Takakuwa, 1942): 5; *X. shirozui* (Takakuwa, 1942): 2, 4, 7, 8; *X. bifurcus* sp. nov.: 2, 8, 9, 10, 11; *X. bazanensis* (Takakuwa, 1942) comb. nov.: 6; *Riukiaria koreana* sp. nov.: 7, 8, 12–16; *Parafontaria koreana* (Paik, 1963): 5, 10, 18–20; and *Levizonus circularis* (Takakuwa, 1942): 17.

Molecular analysis

This study obtained 529 bp of mitochondrial *COI* and 474 bp nuclear *EF1-α* from eight specimens of *X. pallidus*, ten of *X. shirozui*, six of *X. bifurcus* sp. nov., two of *R. koreana* sp. nov., and three of *P. koreana*. When we calculated the mean pairwise genetic distances based on *COI* and *EF1-α* with the Kimura 2-Parameter (K2P) method, all five species revealed significant genetic differences with the other species in each genus (Tables 1–2). Overall, genetic difference values among the species for each genus are bigger in *COI* than *EF1-α*. In the genus *Xystodesmus*, three species, *X. pallidus*, *X. shirozui*, and *X. bifurcus*, have mean genetic distance values of 7–18% in mitochondrial *COI*, and 1–3% in nuclear *EF1-α* with other species of *Xystodesmus*. In the case of *Riukiaria*, the mean K2P distance values between *R. koreana* and other species of *Riukiaria* are 10–12% in mitochondrial *COI*, and 1–3% in nuclear *EF1-α*. The mean K2P distance values between *P. koreana* and other species of *Parafontaria* are 12–16% in mitochondrial *COI*, and 1–2% in nuclear *EF1-α*. Within species, the genetic distance values are 0 (in *X. bifurcus*, and *R. koreana*) – 3% (in *X. pallidus*) in mitochondrial *COI*, and 0% (in *X. shirozui*, *X. bifurcus*, and *P. koreana*) – 1% (in *X. shirozui*, and *R. koreana*).

The phylogenetic reconstruction was based on the concatenated nucleotide sequences of two genetic loci (*COI* and *EF1-α*), comprising 1003 alignment sites, of which 150 were parsimoniously informative. The analyses contained 31 individuals, 7 species, and 3 genera: out of the 31 individuals, 29 are from the present study, and 2 from NCBI GenBank (Supp. file 1: Tables S1, S3). Both unrooted and rooted phylogenies consist of seven distinct genetic lineages representing the three genera: *Xystodesmus*, *Riukiaria*, and *Parafontaria* (Fig. 16, Supp. file 1: Fig. S1). *Xystodesmus* and *Riukiaria* do not form independent monophyletic groups, but instead cluster in multifurcating clades in the tree. Within the genus *Xystodesmus*, *X. bifurcus* sp. nov. and *X. pallidus* cluster together with high bootstrap values and posterior probabilities (BP 99 and BPP 0.99, respectively, in the rooted phylogeny, and BP 88 and BPP 1.00, respectively, in the unrooted phylogeny), whereas *X. shirozui* forms a sister clade to *Xystodesmus* sp. PM-2015 (BP 74 and BPP 0.69 in the rooted phylogeny, and BP 75 and BPP 0.81 in the unrooted phylogeny). The two specimens of *R. koreana* sp. nov. (YC05, YC07) form a clade (BP 100 and BPP 1.00 in the rooted phylogeny, and BP 100 and BPP 1.00 in the unrooted phylogeny), but are not recovered as monophyletic with *R. holstii* MTX0191. The three specimens of *P. koreana* (DG01, DG02, and AD03) form a distinct monophyletic clade (BP 100 and BPP 1.00 in both the unrooted and the rooted phylogeny). Within each clade of the five species examined in the present study, the existence of subclades may imply potential genetic differentiation at the population level. Due to the limited availability of molecular data – specifically, the two genetic markers derived from a single specimen – data from the genus *Levizonus* could not be included in the phylogenetic analysis.

Discussion

In this study, all five investigated Korean xystodesmid species – *Xystodesmus pallidus*, *X. shirozui*, *X. bifurcus* sp. nov., *Riukiaria koreana* sp. nov., and *Parafontaria koreana* – were confirmed as distinct monophyletic groups in the phylogenetic trees, affirming the taxonomic cohesiveness of each species (Fig. 15). Among the three species of *Xystodesmus*, *X. pallidus* and *X. bifurcus* were identified as sister taxa, forming a well-supported clade with high bootstrap and posterior probability values in both ML and BI phylogenies, respectively. Geographically, these two species are sympatrically distributed in the Geoje District, while outside this region, *X. pallidus* is found further south than *X. bifurcus*. In contrast, *X. shirozui*, whose type locality is Tsushima Island, Japan, is clustered with another Japanese species of *Xystodesmus* (*Xystodesmus* sp. PM-2015), exact locality unknown. Unlike *X. pallidus* and *X. bifurcus*, *X. shirozui* is restricted to the southern region of the Korean Peninsula.

Sympatric distributions of species of *Xystodesmus* were observed in both Geoje District and Damyang Town, with three species (*X. pallidus*, *X. shirozui*, and *X. bifurcus*) present in Geoje and two species

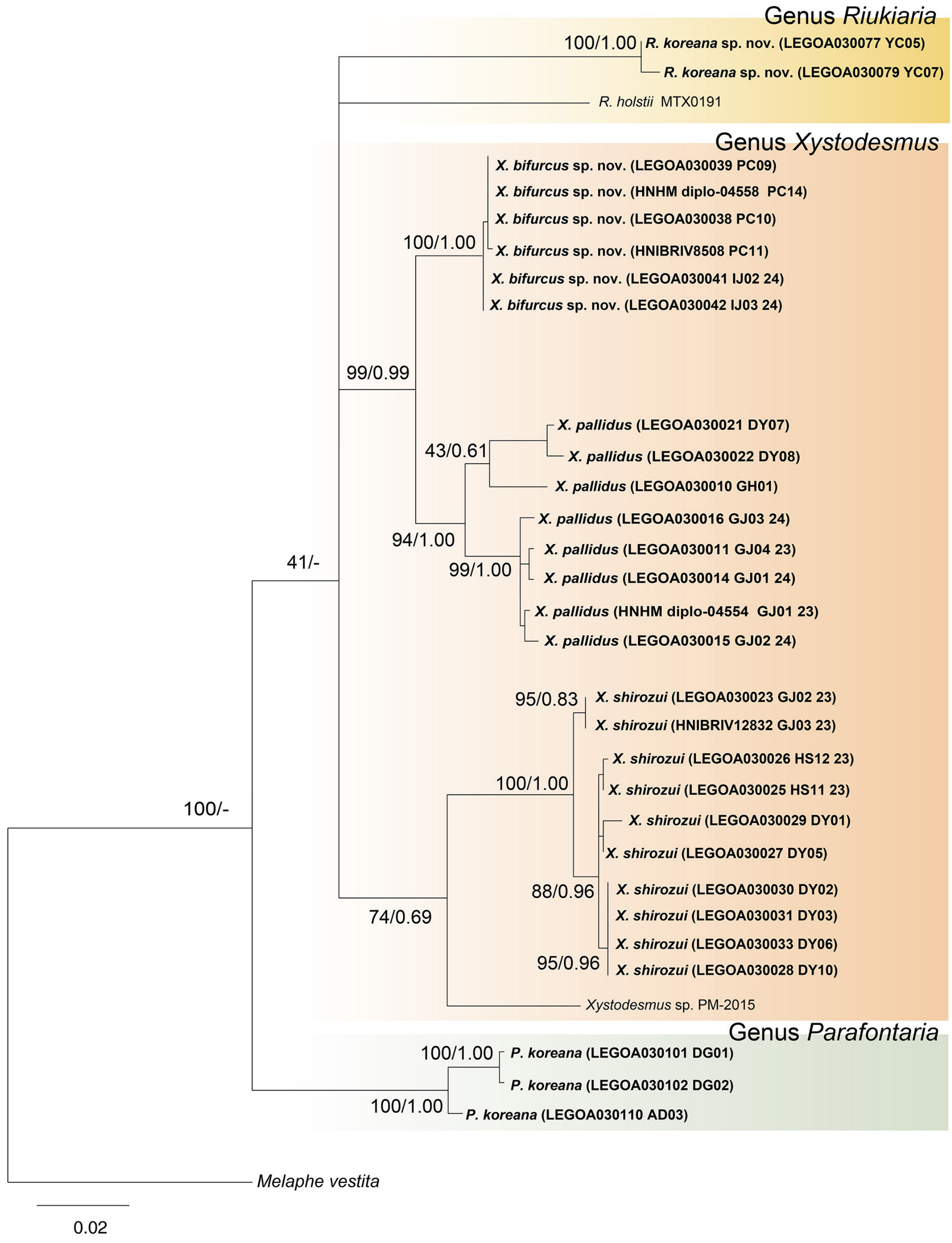

Fig. 16. A rooted maximum likelihood phylogeny based on sequences that combine mitochondrial *COI* and nuclear *EF1-α* including three xystodesmid genera. The phylogeny includes six sequences of *Xystodesmus bifurcus* sp. nov., eight of *X. pallidus* (Verhoeff, 1937), nine of *X. shirozui* (Takakuwa, 1942), two of *Riukiaria koreana* sp. nov., and three of *Parafontaria koreana* (Paik, 1963) obtained in this study, and two sequences of closely related species, *Xystodesmus* sp. PM-2015 and *R. holstii* (Pocock, 1895) which were retrieved from NCBI GenBank. *Melaphe vestita* Hoffman & Lohmander, 1968 was employed as an outgroup which was also retrieved from NCBI GenBank. The detailed information of sequences in the phylogeny is given in Supplementary Tables 1 and 3 (Supp. file 1). The numbers on the branches indicate bootstrap values (BP in ML phylogeny) and posterior probabilities (BPP in BI phylogeny) separated by a slash. The scale bar refers to a phylogenetic distance of 0.02 nucleotide substitutions per site.

Table 1 (continued on next page). Matrix of mean genetic distance with the Kimura 2-Parameter model between species and within each species based on mitochondrial *COI* sequences. **A**. Seven species of *Xystodesmus* Cook, 1895. **B**. Eight species of *Riukiaria* Attems, 1898. **C**. Six species of *Parafontaria* Hoffman, 1980. Genetic distance matrixs within each species marked as bold font. Empty cells marked with '–' indicate that the species is represented by a single sample.

A)	***X. pallidus*** (PV446385, PV446388–PV446391, PV446405, PV446406, PX471584)	***X. shirozui*** (PV446386, PV446387, PV446398–PV446404, PV446407)	***X. bifurcus*** (PV446392–PV446397)	***X. martensii*** (MN699817.1)	***X. serrulatus*** (MN699818.1)	***Xystodesmus* sp.** PM-2015 (KR136041.1)	***Xystodesmus* sp.** YD-2016 (KU721886.1)
X. pallidus (PV446385, PV446388–PV446391, PV446405, PV446406, PX471584)	**0.03**						
X. shirozui (PV446386–PV446387, PV446398– PV446404, PV446407)	0.12	**0.01**					
X. bifurcus (PV446392– PV446397)	0.07	0.12	**0.00**				
X. martensii (MN699817.1)	0.10	0.09	0.10	–			
X. serrulatus (MN699818.1)	0.10	0.09	0.10	0.07	–		
Xystodesmus sp. PM-2015 (KR136041.1)	0.12	0.10	0.11	0.10	0.09	–	
Xystodesmus sp. YD-2016 (KU721886.1)	0.17	0.17	0.14	0.18	0.17	0.17	–

Table 1 (continued). Matrix of mean genetic distance with the Kimura 2-Parameter model between species and within each species based on mitochondrial *COI* sequences. **A**. Seven species of *Xystodesmus* Cook, 1895. **B**. Eight species of *Riukiaria* Attems, 1898. **C**. Six species of *Parafontaria* Hoffman, 1980. Genetic distance matrixs within each species marked as bold font. Empty cells marked with '–' indicate that the species is represented by a single sample.

B)	***R. koreana*** (PV446411, PV446412)	***R. uncata*** (MN699802.1)	***R. semicircularis*** (MN699801.1)	***R. montana*** (MN699800.1)	***R. maculata*** (MN699799.1)	***R. falcifera*** (MN699798.1)	***R. cornuta*** (MN699797.1)	***R. holstii*** (KR136017.1)
R. koreana (PV446411, PV446412)	**0.00**							
R. uncata (MN699802.1)	0.10	–						
R. semicircularis (MN699801.1)	0.10	0.06	–					
R. montana (MN699800.1)	0.12	0.08	0.07	–				
R. maculata (MN699799.1)	0.10	0.10	0.10	0.13	–			
R. falcifera (MN699798.1)	0.10	0.13	0.11	0.13	0.11	–		
R. cornuta (MN699797.1)	0.10	0.07	0.07	0.08	0.11	0.13	–	
R. holstii (KR136017.1)	0.11	0.12	0.12	0.13	0.11	0.12	0.15	–

C)	***P. koreana*** (PV446408–PV446410)	***P. tokaiensis*** (MN699788.1)	***P. longa*** (MN699786.1)	***P. ishiii*** (MN699785.1)	***P. erythrosoma*** (MN699784.1)	***P. crenata*** (MN699783.1)
P. koreana (PV446408– PV446410)	**0.02**					
P. tokaiensis (MN699788.1)	0.12	–				
P. longa (MN699786.1)	0.14	0.09	–			
P. ishiii (MN699785.1)	0.15	0.11	0.10	–		
P. erythrosoma (MN699784.1)	0.16	0.12	0.10	0.08	–	
P. crenata (MN699783.1)	0.12	0.11	0.08	0.11	0.11	–

Table 2 (continued on next two pages). Matrix of mean genetic distance with the Kimura 2-Parameter model between species and within each species based on nuclear *EF1-α* sequences. **A**. Six species of *Xystodesmus* Cook, 1895. **B**. Ten species of *Riukiaria* Attems, 1898. **C**. Ten species of *Parafontaria* Hoffman, 1980. Genetic distance matrix within each species marked as bold font. Empty cells marked with '–' indicate that the sequence is represented by a single sample.

A)	***X. pallidus*** (PV544250, PV544253– PV544256, PV544270, PV544271, PX516894)	***X. shirozui*** (PV544251, PV544252, PV544263– PV544269, PV544272)	***X. bifurcus*** (PV544257– PV544262)	***X. martensii*** (MN719712.1)	***X. serrulatus*** (FJ775333.1)	***Xystodesmus*** sp. PM-2015 (KR136081.1)
X. pallidus (PV544250, PV544253– PV544256, PV544270, PV544271, PX516894)	**0.01**					
X. shirozui (PV544251, PV544252, PV544263– PV544269, PV544272)	0.02	**0.00**				
X. bifurcus (PV544257– PV544262)	0.01	0.03	**0.00**			
X. martensii (MN719712.1)	0.03	0.02	0.03	–		
X. serrulatus (FJ775333.1)	0.03	0.02	0.03	0.01	–	
Xystodesmus sp. PM-2015 (KR136081.1)	0.02	0.01	0.02	0.02	0.02	–

Table 2 (continued). Matrix of mean genetic distance with the Kimura 2-Parameter model between species and within each species based on nuclear *EF1-α* sequences. **A**. Six species of *Xystodesmus* Cook, 1895. **B**. Ten species of *Riukiaria* Attems, 1898. **C**. Ten species of *Parafontaria* Hoffman, 1980. Genetic distance matrix within each species marked as bold font. Empty cells marked with '–' indicate that the sequence is represented by a single sample.

B)	***R. koreana*** (PV544276, PV544277)	***R. semicircularis*** (FJ775330.1, MN719723.1)	***R. montana*** (MN719714.1)	***R. maculate*** (MN719716.1)	***R. falcifera*** (MN719724.1)	***R. cornuta*** (FJ775329.1, MN719722.1)	***R. holstii*** (KR136062.1)	***R. chelifera*** (MN719713.1, FJ775332.1)	***R. mundyi*** (MN719717.1)	***R. puella*** (MN719715.1)
R. koreana (PV544276, PV544277)	**0.01**									
R. semicircularis (FJ775330.1, MN719723.1)	0.03	0.00								
R. montana (MN719714.1)	0.03	0.00	–							
R. maculata (MN719716.1)	0.03	0.01	0.01	–						
R. falcifera (MN719724.1)	0.02	0.01	0.01	0.02	–					
R. cornuta (FJ775329.1, MN719722.1)	0.03	0.01	0.01	0.02	0.02	**0.00**				
R. holstii (KR136062.1)	0.03	0.02	0.02	0.02	0.01	0.02	–			
R. chelifera (MN719713.1, FJ775332.1)	0.03	0.01	0.01	0.02	0.01	0.02	0.02	**0.02**		
R. mundyi (MN719717.1)	0.03	0.02	0.02	0.03	0.02	0.02	0.02	0.02	–	
R. puella (MN719715.1)	0.03	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	—

Table 2 (continued). Mean genetic distance matrix between species and within each species based on nuclear *EF1-α* sequences. **A**. Six species of *Xystodesmus* Cook, 1895. **B**. Ten species of *Riukiaria* Attems, 1898. **C**. Ten species of *Parafontaria* Hoffman, 1980. The values represent using the Kimura 2-parameter model. Genetic distance matrix within each species marked as bold font. Empty cells indicate that the sequence is represented by a single sample.

C)	***P. koreana*** (PV544273–PV544275)	***P. tokaiensis*** (FJ775360.1)	***P. doenitzi*** (FJ775358.1)	***P. ishiii*** (FJ775356.1)	***P. tonominea*** (FJ775524.1)	***P. falcifera*** (FJ775365.1)	***P. erythrosoma*** (FJ775354.1)	***P. crenata*** (FJ775353.1)	***P. laminata*** (FJ775350.1)	***P. longa*** (FJ775342.1)
P. koreana (PV544273–PV544275)	**0.00**									
P. tokaiensis (FJ775360.1)	0.01	–								
P. doenitzi (FJ775358.1)	0.02	0.01	–							
P. ishiii (FJ775356.1)	0.01	0.00	0.01	–						
P. tonominea (FJ775524.1)	0.01	0.01	0.01	0.01	–					
P. falcifera (FJ775365.1)	0.01	0.01	0.02	0.01	0.00	–				
P. erythrosoma (FJ775354.1)	0.01	0.01	0.01	0.00	0.01	0.01	–			
P. crenata (FJ775353.1)	0.01	0.00	0.01	0.00	0.01	0.01	0.01	–		
P. laminata (FJ775350.1)	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	–	
P. longa (FJ775342.1)	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.00	–

(*X. pallidus* and *X. shirozui*) in Damyang. Unlike Damyang Town, which is located further inland, Geoje District – an island in the South Sea of the Korean Peninsula – is geographically closer to Japan, lying approximately 80 km from Tsushima Island, the nearest Japanese island. Seismic and stratigraphic evidence suggests that the Korean Peninsula and Tsushima Island may have been connected during the last glacial period in the Late Pleistocene (Park *et al*. 1996). This historical land bridge may have facilitated the dispersal of *X. shirozui*. However, additional studies with more specimens are required to confirm this hypothesis.

The sister relationships between the genetic lineage including *X. pallidus* and *X. bifurcus* sp. nov. and between the lineage including *X. shirozui* and *Xystodesmus* sp. PM-2015 were consistently observed in both ML and BI phylogenies. The presence of two genetically distinct lineages within the genus *Xystodesmus* suggests that one of them may not be congeneric and could warrant recognition as a separate genus. However, this finding also underscores the need for molecular data from a broader range of species of *Xystodesmus* in future studies. Although the genus includes more than ten species, previous studies have provided limited molecular data, particularly for *X. martensii* and *X. serrulatus* with very limited genetic markers focusing on *COI* and *EF1-α* (Means *et al*. 2021). Further research employing various molecular markers for diverse species of *Xystodesmus* may help bridge the gap between these two genetic lineages.

In this study, we also describe a newly identified species of *Riukiaria*, *R. koreana* sp. nov., from the Korean Peninsula. Morphologically, *R. koreana* differs significantly from *R. semicircularis*, the only other species of *Riukiaria* previously recorded on the Korean Peninsula (Lim 2001; Nguyen *et al.* 2016; Kim *et al.* 2023). Distinguishing characteristics include completely smooth metazonites and a shorter, straight prefemoral process. These morphological differences are corroborated by molecular data: mean pairwise genetic distances between the two species are 10% for mitochondrial *COI* and 3% for nuclear *EF1-α*, values similar to interspecific differences observed in other species of *Riukiaria*. Phylogenetic analyses further support *R. koreana* as an independent species, with its clade receiving strong statistical support in both ML and BI phylogenies. Additionally, *R. koreana* is sympatrically distributed with *X. shirozui* in Hwasun, and *X. shirozui*, *X. bifurcus* sp. nov. and *P. koreana* in Gurye Town.

Previous morphological studies of the family Xystodesmidae in East Asia have highlighted strong similarities between the genera *Xystodesmus* and *Riukiaria*, particularly in gonopodal structure and colouration (Tanabe & Shinohara 1996; Sota & Tanabe 2010; Korsós *et al*. 2011; Golovatch 2023). These morphological parallels align with phylogenetic findings, as both genera consistently form sister groups in earlier studies (Sota & Tanabe 2010; Means *et al*. 2021). The phylogenetic results of this study also reveal a multifurcating branch pattern for these two genera, indicating unresolved phylogenetic relationships between *Xystodesmus* and *Riukiaria*. Further research is needed to clarify these relationships through an in-depth integrative taxonomic study.

The morphological characteristics of *P. koreana* were re-examined in conjunction with its genetic distances and phylogenetic relationships. The analysis provides robust evidence that *P. koreana* exhibits genetic divergences of 12–16% for mitochondrial *COI* and 1–2% for nuclear *EF1-α* in comparison with other *Parafontaria* species. Geographically, *P. koreana* is found in sympatry with *X. shirozui* and *R. koreana* sp. nov. in Gurye Town, and with *X. bifurcus* sp. nov. in Inje Town. Additionally, based on the type locality of *X. amoenus*, it is plausible that *P. koreana* coexists sympatrically with *X. amoenus* in Daegu Metropolitan City.

Our study could not resolve the phylogenetic relationship between the genera *Parafontaria* and *Levizonus*. Tanabe & Sota (2014) suggested the bellows of the female cyphopod as a distinctive character, with well-developed (extended) bellows in *Parafontaria* and less-developed bellows in *Levizonus*. However, we found both fully developed and partially developed bellows in female specimens of *P. koreana*. The observation raises doubts about the separation of the two genera based only on the bellow of the female cyphopod. Unfortunately, molecular analysis could not be included due to the scarce genetic data of the two genera with regards to *COI* and *EF1-α* from the same specimens in NCBI GenBank. Molecular phylogenetic analyses based on genetic markers including *16S rRNA* (Means *et al.* 2021) supported the monophyly of the clades of *Levizonus* and *Parafontaria* as separate lineages. Further study, to understand the taxonomic relationships of the two genera, should incorporate an integrative taxonomic approach for *Levizonus* with a focus on female genetic morphology and various genetic markers such as *16S rRNA* in the mitochondrial genome and *28S rRNA* in the nuclear genome.

Previous population-level genetic studies on millipedes have demonstrated notable intraspecific genetic variation and patterns of genetic isolation driven by geographic barriers, which collectively suggest the presence of structured genetic differentiation among populations (Walker *et al*. 2009; Reip & Wesener 2018; Xu *et al*. 2022). In this study, the phylogenetic analyses further reveal genetic differentiation at the population level for certain species. Notably, populations of both *X. shirozui* and *X. pallidus* from Geoje District and Damyang Town are segregated into distinct subclades, underscoring the existence of population-specific genetic patterns. However, designating these populations as independent species is problematic due to the relatively low average genetic distances within populations compared to those observed between species. This indicates that the observed genetic divergences are more likely reflective of population-level structuring rather than speciation events. Further population-level genetic investigations are necessary to elucidate evolutionary processes such as species divergence and to deepen our understanding of biodiversity patterns within these taxa.

Acknowledgements

We thank the following persons for their contribution to this project: Bia Park, Dooyoung Kim, Hyejeong Yu, and Geonhyeok Kim for collecting samples; Kil Young Lim for his valuable comments and encouragement for the taxonomic history of Korean millipedes. E. Lazányi (HNHM) helped with registration codes for her museum, and S. Friedrich (SNSB-ZSM) kindly arranged the loan of the holotype *Koreoaria pallida*. Furthermore, we are deeply grateful to Dr Elena V. Mikhaljova, Dr Jackson Means, and Dr Paul Marek for their careful reviews and insightful comments that helped us to improve this paper. The work was supported by a grant from the National Institute of Biological Resources (NIBR; NIBRE202405) and the Honam National Institute of Biological Resources (HNIBR; HNIBR202301210, HNIBRIV202401222), funded by the Ministry of Environment of the Republic of Korea.

References

Altschul S.F., Gish W., Miller W., Myers E.W. & Lipman D.J. 1990. Basic local alignment search tool. *Journal of Molecular Biology* 215 (3): 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2

Attems C. 1898. System der Polydesmiden, I. *Denkschriften der Kaiserlichen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Classe* 67: 221–482.

Attems C. 1931. Die Familie Leptodesmidae und andere Polydesmiden. *Zoologica* 30 (3/4): 1–149.

Attems C. 1938. Polydesmoidea II. Fam. Leptodesmidae, Platyrhachidae, Oxydesmidae, Gomphodesmidae. *Das Tierreich* 69: 1–487. Walter de Gruyter & Co., Berlin & Leipzig.

Bańkowska R. & Sterzyńska M. 1997. Faunistic investigations conducted in North Korea by researchers from the Institute of Zoology Polish Academy of Sciences from 1959 to 1990. *Fragmenta faunistica* 40 (20): 247–253. https://doi.org/10.3161/00159301FF1997.40.20.247

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17 (4): 540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Chamberlin R.V. 1943. On some genera and species of American millipeds. *Bulletin of the University of Utah* 34: 3–20.

Chamberlin R.V. & Wang Y.M. 1953. Records of millipeds (Diplopoda) from Japan and other oriental areas, with descriptions of new genera and species. *American Museum Novitates* 1621: 1–13.

Chao J-L. & Chang H-W. 2008. Neotype designation for two centipedes, *Scolopocryptops curtus* (Takakuwa, 1939) and *Cryptops nigropictus* Takakuwa, 1936, and a review of species of Scolopendromorpha (Chilopoda) in Taiwan. *Collection and Research* 21: 1–15. Available from https://libknowledge.nmns.edu.tw/nmns/upload/bulletin/000000177/209000c/200812-1.pdf [accessed 9 Jan. 2026].

Darriba D., Taboada G.L., Doallo R. & Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772. https://doi.org/10.1038/nmeth.2109

Folmer O., Black 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.

Golovatch S.I. 2014. The millipede genus *Riukiaria* Attems, 1938 in continental China, with descriptions of new species (Diplopoda: Polydesmida: Xystodesmidae). *Zootaxa* 3793 (1): 188–200. https://doi.org/10.11646/zootaxa.3793.1.9

Golovatch S.I. 2023. On the synonymy of the millipede genera *Riukiaria* Attems, 1938 and *Parariukiaria* Nguyen, 2016, with records of *Riukiaria* cf. *davidiani* Golovatch, 2014 from Sichuan, southern China (Diplopoda: Polydesmida: Xystodesmidae). *Arthropoda Selecta* 32 (3): 231–238. https://doi.org/10.15298/arthsel.32.3.01

Hall T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.

Hoffman R.L. 1956. Studies on some oriental xystodesmine millipeds (Polydesmida, Chelodesmidae). *Proceedings of the Entomological Society of Washington* 58 (2): 95–104.

Hoffman R.L. 1978a. On the classification and phylogeny of chelodesmoid Diplopoda. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 21/22: 129–134.

Hoffman R.L. 1978b. The taxonomic and nomenclatorial status of the milliped generic names *Parafontaria* Verhoeff, *Cyphonaria* Verhoeff, and *Japonaria* Attems (Polydesmida, Xystodesmidae). *Spixiana* 1: 215–224.

Hoffman R.L. 1980. *Classification of the Diplopoda.* Muséum d'Historie Naturelle, Genève.

Jeekel C.A.W. 1971. Nomenclator generum et familiarum Diplopodorum: A list of the genus and family-group names in the Class Diplopoda from the 10th edition of Linnaeus, 1758, to the end of 1957. *Monografieën van de Nederlandse Entomologische Vereniging* 5: 1–412.

Kim G., Adebimpe A.A., Nguyen A.D., Korsós Z. & Hwang U.W. 2023. An annotated checklist of millipedes (Myriapoda: Diplopoda) inhabiting the Korean Peninsula. *Animal Systematics, Evolution and Diversity* 39 (4): 133–154. https://doi.org/10.5635/ASED.2023.39.4.019

Kimura M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120. https://doi.org/10.1007/BF01731581

Korsós Z. & Nakamura Y. 2025. Review of the millipede genus *Xystodesmus* (Diplopoda: Polydesmida), with seven new species from the southwestern part of Japan. *ZooKeys* 1231: 191–232. https://doi.org/10.3897/zookeys.1231.141443

Korsós Z., Nakamura Y. & Tanabe T. 2011. Two new millipede species of the genus *Riukiaria* (Diplopoda, Polydesmida, Xystodesmidae) endemic to the Ryukyu Archipelago, Japan. *Zootaxa* 2877: 55–68. https://doi.org/10.11646/zootaxa.2877.1.3

Larkin M.A., Blackshields G., Brown N.P., Chenna R., McGettigan P.A. & McWilliam H. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* 23: 2947–2948. https://doi.org/10.1093/bioinformatics/btm404

Lim K.-Y. 2001. *Taxonomy of Millipedes (Arthropoda: Diplopoda) in Korea.* PhD thesis, Chonbuk National University, Jeonju.

Lokshina I.E. & Golovatch S.I. 1977. The new myriapods (Diplopoda) from the USSR. *Byulleten Moskovskogo Obshchestva Ispytateley Prirody, Otdel Biol.* 82 (1): 73–78. [In Russian.]

Marek P., Tanabe T. & Sierwald P. 2014. A species catalog of the millipede family Xystodesmidae (Diplopoda: Polydesmida). *Virginia Museum of Natural History Special Publication* 17: 1–117. Available from https://www.vmnh.net/content/vmnh/uploads/PDFs/research_and_collections/special_publications/vmnhspecialpub17.pdf [accessed 9 Jan. 2026].

Means J.C., Hennen D.A., Tanabe T. & Marek P.E. 2021. Phylogenetic systematics of the millipede family Xystodesmidae. *Insect Systematics and Diversity* 5 (2): 1–26. https://doi.org/10.1093/isd/ixab003

Mikhaljova E.V. 2021. Review of the millipede genus *Levizonus* Attems, 1898, with description of a new species from the Far East of Russia (Diplopoda, Polydesmida, Xystodesmidae). *European Journal of Taxonomy* 751: 159–184. https://doi.org/10.5852/ejt.2021.751.1387

Mikhaljova E.V., Golovatch S. I. & Wytwer J. 2000. On some new or poorly-known millipedes (Diplopoda) from North Korea. *Fragmenta Faunistica* 43 (10): 109–122. https://doi.org/10.3161/00159301FF2000.43.10.109

Miyosi Y. 1952. Beiträge zur Kenntniss japanischer Myriopoden. 4. Aufsatz: Ueber eine neue Art und eine neue Unterart von Diplopoda. *Zoological Magazine* 61 (9): 281–282.

Miyosi Y. 1959. Über japanische Diplopoden. *Arachnological Society of East Asia, Spec. Number*. Osaka. [In Japanese with German summary.]

National Library of Medicine 1988. *National Center for Biotechnology Information (NCBI)*. Bethesda, MD: National Library of Medicine (US). Available from https://www.ncbi.nlm.nih.gov/ [accessed 12 Oct. 2024].

Nguyen A.D. 2016. Discovery of a new millipede species in northern Vietnam, and the proposal of a new genus, *Parariukiaria* (Diplopoda, Polydesmida, Xystodesmidae). *Zootaxa* 4121 (3): 331–336. https://doi.org/10.11646/zootaxa.4121.3.7

Nguyen A.D., Jang K.H., Hyun J.S. & Hwang U.W. 2016. An updated checklist and perspective study of millipedes (Arthropoda: Myriapoda: Diplopoda) in the Korean Peninsula. *Animal Systematics, Evolution and Diversity* 32: 44–48. https://doi.org/10.5635/ASED.2016.32.1.044

Paik K.-Y. 1963. Survey of the myriapods of Mt. Sokkri, Chungcheung-Pookto, Korea. *Kyungpook University Theses Collection* 7: 33–42.

Park J.O., Kimura M. & Taira A. 1996. Late Pleistocene unconformity of the Tsushima and Korea Straits revealed by seismic reflection profiles. *Journal of Geography (Chigaku Zasshi)* 105 (3): 297–305. https://doi.org/10.5026/jgeography.105.3_297

Rambaut A. 2012. FigTree ver. 1.4. Available from https://github.com/rambaut/figtree [accessed 9 Jan. 2026].

Reip H.S. & Wesener T. 2018. Intraspecific variation and phylogeography of the millipede model organism, the Black Pill Millipede *Glomeris marginata* (Villers, 1789) (Diplopoda, Glomeridae, Glomeridae). *ZooKeys* 741: 93–131. https://doi.org/10.3897/zookeys.741.21917

Ronquist F., Teslenko M., Van Der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: e539542. https://doi.org/10.1093/sysbio/sys029

Schwarz G. 1978. Estimating the dimension of a model. *The Annals of Statistics* 6 (2): 461–464. https://doi.org/10.1214/aos/1176344136

Shinohara K. 1977. Revaluation on *Riukiaria* (Diplopoda). *Acta Arachnologica* 27: 115–119. [In Japanese with English synopsis.] https://doi.org/10.2476/asjaa.27.Specialnumber_115

Sierwald P., Decker P. & Spelda J. 2025. MilliBase. https://doi.org/10.14284/370

Sota T. & Tanabe T. 2010. Multiple speciation events in an arthropod with divergent evolution in sexual morphology. *Proceedings of the Royal Society of London B: Biological Sciences* 277: 689–696. https://doi.org/10.1098/rspb.2009.1822

Takakuwa Y. 1941a. Weitere japanische *Lithobius*-Arten und zwei neue Diplopoden. *Transactions of the Sapporo Natural History Society* 17 (1): 1–9.

Takakuwa Y. 1941b. *Rhysodesmus*-Arten aus Japan. *Transactions of the Natural History Society of Formosa* 31: 413–415. [In German with Japanese summary.]

Takakuwa Y. 1942a. Die Myriopoden von Formosa, Philippinien, u. s. w. *Transactions of the Natural History Society of Formosa* 32 (231): 359–367.

Takakuwa Y. 1942b. Einige neue Arten von Diplopoda aus Nippon. *Zoological Magazine* 54: 237–239.

Takakuwa Y. 1942c. Zur Kenntnis der Japanischen Diplopoden. *Annotationes Zoologicae Japonenses* 21: 39–47.

Tamura K., Glen S. & Sudhir K. 2021. MEGA11: Molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution* 38: 3022–3027. https://doi.org/10.1093/molbev/msab120

Tanabe T. 1994. The millipede genus *Levizonus* (Polydesmida, Xystodesmidae) in Japan. *Japanese Journal of Entomology* 62 (1): 101–113.

Tanabe T. 2002. Revision of the millipede genus *Parafontaria* Verhoeff, 1936 (Diplopoda, Xystodesmidae). *Journal of Natural History* 36: 2139–2183. https://doi.org/10.1080/00222930110085610

Tanabe T. & Shinohara K. 1996. Revision of the millipede genus *Xystodesmus*, with reference to the status of the tribe Xystodesmini (Diplopoda: Xystodesmidae). *Journal of Natural History* 30: 1459–1494. https://doi.org/10.1080/00222939600770831

Tanabe T. & Sota T. 2008. Complex copulatory behavior and the proximate effect of genital and body size differences on mechanical reproductive isolation in the millipede genus *Parafontaria*. *American Naturalist* 171: 692–699. https://doi.org/10.1086/587075

Tanabe T. & Sota T. 2014. Both male and female novel traits promote the correlated evolution of genitalia between the sexes in an arthropod. *Evolution* 68 (2): 441–452. https://doi.org/10.1111/evo.12288

Tanabe T., Ishii K. & Yin W.Y. 1996. Two new xystodesmid millipeds [Arthropoda] from the Tian-mu mountains, Zhejiang province, China. *Edaphologia* 57: 13–19.

Trifinopoulos J., Nguyen L.T., von Haeseler A. & Minh B.Q. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Reseach* 44: W232–W235. https://doi.org/10.1093/nar/gkw256

Verhoeff K.W. 1936a. Über Diplopoden aus Japan, Gesammelt von Herrn Y. Takakuwa, *Transactions of the Sapporo Natural History Society* 54: 148–172.

Verhoeff K.W. 1936b. Zur Kenntnis ostasiatischer Strongylosomiden and Fontariiden. 149. Diplopoden-Aufsatz. *Zoologischer Anzeiger* 115 (11–12): 297–311.

Verhoeff K.W. 1937. Zur Kenntnis ostasiatischer Diplopoden. *Zoologischer Anzeiger* 117 (11/12): 309–321.

Verhoeff K.W. 1941. Über Gruppen der Leptodesmiden und neues System der Ordo Polydesmoidea. *Archiv für Naturgeschichte* 10 (3): 399–415.

Walker M.J., Stockman A.K., Marek P.E. & Bond J.E. 2009. Pleistocene glacial refugia across the Appalachian Mountains and coastal plain in the millipede genus Narceus: Evidence from population genetic, phylogeographic, and paleoclimatic data. *BMC Evolutionary Biology* 9: 1–11. https://doi.org/10.1186/1471-2148-9-25

Xu R., Chen J., Pan Y., Wang J., Chen L., Ruan H., Wu Y., Xu H., Wang G. & Liu H. 2022. Genetic diversity and population structure of *Spirobolus bungii* as revealed by mitochondrial DNA sequences. *Insects* 13: 729. https://doi.org/10.3390/insects13080729

Printed versions of all papers are deposited in the libraries of two of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France and Royal Museum for Central Africa, Tervuren, Belgium. The other members of the consortium are: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Meise Botanic Garden, Meise, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.

Supplementary file

Supp. file 1. Supplementary data associated with this study. **Table S1**. Summary of respective *COI* and *EF1-α* sequence information obtained from this study. **Table S2**. Summary of *COI* and *EF1-α* sequence information from NCBI GenBank for genetic distance analysis for respective three Xystodesmid genera, *Xystodesmus*, *Riukiaria*, and *Parafontaria* in this study. **Table S3**. Summary of respective *COI* and *EF1-α* sequence information for Xystodesmid phylogeny from NCBI GenBank and outgroups in this study. **Fig. S1**. An unrooted maximum likelihood phylogeny based on sequences that combine mitochondrial *COI* and nuclear *EF1-α*, including three Xystodesmid genera.
https://doi.org/10.5852/ejt.2026.1039.3181.14137