Some cryptic Korean karst creatures: revalidation of the pseudoscorpion genus *Spelaeochthonius* (Pseudoscorpiones: Pseudotyrannochthoniidae) and description of two new species from Korea

JoonYong You[1,5], **Jung-Sun Yoo**[2], **Mark S. Harvey**[3,4] and **Danilo Harms**[1]: [1]Zoological Museum Hamburg, Leibniz Institute for the Analysis of Biodiversity Change (LIB), Center for Morphology and Taxonomy, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany. E-mail: danilo.harms@uni-hamburg.de; [2]National Institute of Biological Resources, Biological and Genetic Resources Utilization Division, Environmental Research Complex, Hwangyeong-ro 42, Seo-gu, Incheon, 22689 Republic of Korea; [3]Western Australian Museum, Collections & Research, 49 Kew Street, Welshpool, Western Australia 6106, Australia; [4]University of Western Australia, School of Animal Biology, Crawley, Western Australia 6009, Australia. [5]Universität Hamburg, Fachbereich Biologie, Ohnhorststraße 18, 22609 Hamburg.
Orcid Identifier, D. Harms: 0000-0002-7189-5345

Abstract. South Korea is a country with more than 1000 caves that support a high diversity of invertebrate species. Here we review the pseudoscorpion genus *Spelaeochthonius* Morikawa, 1954 (family Pseudotyrannochthoniidae) that is exclusive to caves in Japan and South Korea and reinstated here as a valid taxon. Based on recent field collections, three species in this genus are described from South Korea: *S. dentifer* (Morikawa, 1970), comb. nov., *S. cheonsooi* sp. nov., and *S. seungsookae* sp. nov. Based on present-day knowledge about range sizes and morphological variability in this fauna, three Japanese taxa currently classified as subspecies are elevated to species rank: *Pseudotyrannochthonius kobayashii akiyoshiensis* (Morikawa, 1956) = *Spelaeochthonius akiyoshiensis* Morikawa, 1956, **stat. nov.**, *Pseudotyrannochthonius kobayashii dorogawanesis* (Morikawa, 1956) = *Spelaeochthonius dorogawaensis* Morikawa, 1956, **stat. nov.**; and *Pseudotyrannochthonius undecimclavatus kishidai* (Morikawa, 1960) = *Spelaeochthonius kishidai* (Morikawa, 1960), **stat. nov.** We emphasize that no epigean *Spelaeochthonius* have ever been found despite considerable search effort in the forests of Japan and Korea, and that past glacial cycling may have resulted in the total extirpation of surface species in this lineage. We also note that all species are narrow-range endemics that may require conservation management.

Keywords: karst, South Korea, systematics, taxonomy, troglobite.

Korea is a country with a karstic geomorphology, and recent surveys suggest there are at least 1000 caves and many more to be explored (Woo & Kim 2018). Considering this diversity but also the past climatic history of the country, that includes significant biome changes during the glacial periods (Kim et al. 2015; Chung et al. 2017), it is not surprising that there is a high diversity of karst invertebrates, including arachnids (Namkung 1980; Yoo et al. 2015), hexapods (e.g., Cho et al. 2003; Lee & Park 2016) and molluscs (e.g., Choi & Park 2020). Of these, many have a troglomorphic appearance, meaning that they lack eyes, have elongated body appendages, and modified sensory systems (Howarth & Moldovan 2018). The majority of these seem to be narrow-range endemics that have been recorded from either a single or only very few caves. Considering the contribution of this fauna to Korea's biodiversity, surprisingly few cave surveys have been carried out and the species known are probably just a small fraction of the actual diversity.

The Korean pseudoscorpion fauna has been studied in moderate detail (e.g., Morikawa 1970; Lee 1981, 1982; Hong & Kim 1993, 1996, 1998; Kim & Hong 1994; Lee & Seo 1995; Hong 1996; Hong et al. 1996, 1997; Choi & Hwang 2009; Ohira et al. 2018; Harvey et al. 2020) and a total of 21 species are presently known, although a recent barcoding study (Ohira et al. 2018) has shown that there are several cryptic species and therefore the total count after detailed taxonomic review will be higher. The subterranean fauna of pseudoscor-

pions in Korea is poorly known and the only study is by Morikawa (1970), who described three species from caves based on a survey undertaken by the National Science Museum, Tokyo (now the Museum of Nature and Science) in 1966. Of these, only the species *Allochthonius* (*Spelaeochthonius*) *dentifer* Morikawa, 1970 [now *Pseudotyrannochthonius dentifer* (Morikawa, 1970)] is a real troglobite without eyes and it was recorded from three caves in the Gangwon-do and Gyeongsangbuk-do provinces in eastern South Korea. The other two species, *Allochthonius* (*A.*) *opticus coreanus* Morikawa, 1970 [now *A. coreanus* Morikawa, 1970] and *Neobisium* (*Parobisium*) *magnum chejuense* Morikawa, 1970 [now *Parobisium magnum chejuense* (Morikawa, 1970)] have eyes, and at least the latter species has also been collected from outside caves (Morikawa 1970). Two of these three species belong to the pseudoscorpion family Pseudotyrannochthoniidae, with *P. magnum chejuense* belonging to the Neobisiidae.The Pseudotyrannochthoniidae in Asia comprises three genera. *Centrochthonius* Beier, 1931 includes four species from high-altitude habitats in China, Kyrgyzstan and Nepal, and one fossil species from Bitterfeld amber in Germany (Schwarze et al. 2021; Harvey & Harms 2022). *Allochthonius* Chamberlin, 1929 is by far the most diverse genus of the family in eastern Asia and includes 20 valid species from China, Japan, far-eastern Russia (Primorsky-Krai) and South Korea (Harvey 2013; Gao et al. 2016; Viana & Ferreira 2021), as well as a fossil species from Baltic amber in northern Europe (Schwarze

et al. 2021). Most species of *Allochthonius* occur in leaf litter throughout warm and cold temperate forest systems, but in Japan there are also several troglomorphic species (Morikawa 1960; Viana & Ferreira 2021). The genus *Pseudotyrannochthonius* Beier, 1930 presently includes species from Australia, Japan, Korea, western U.S.A. and Chile (Harvey 2013), including three species and several subspecies from karstic caves in Japan and *P. dentifer* (Morikawa, 1970) from South Korea. In Japan and Korea, it is only known from subterranean habitats

These species of Japanese and Korean *Pseudotyrannochthonius* have had a checkered taxonomic history. The first species to be described was *Spelaeochthonius kubotai* Morikawa, 1954 from Shimizu-Cave in the Nagasaki Prefecture of Japan. It was included in the new genus *Spelaeochthonius* which was defined by the absence of eyes (e.g., Figs. 1B, D), the slender body appendages and cuticle setae (e.g., Figs. 6A, B; 12A, B), the presence of an intercoxal tubercle (Fig. 4C), and the shape of the coxal spines that are arranged as a row of 11 blades that are thin and terminate distally into a "writing-brush" or "tassel" (Morikawa 1954: 83; Figs. 2A–C). They differ substantially from those of *Allochthonius* species that have much shorter, distally spatulate or clavate coxal spines that sit on a common protuberance, also termed "spray" or "fan" by Chamberlin (1929) (Fig. 2D). Morikawa (1954) did not delineate this genus from any other genera known at that time that were included in the family such as *Afrochthonius* Beier, 1931, *Pseudotyrannochthonius* and *Centrochthonius*. However, in a subsequent paper Morikawa (1960) listed *Spelaeochthonius* as one of three subgenera of *Allochthonius*: *Allochthonius* (*Allochthonius*) Chamberlin, 1929 for epigean species with eyes and 26 or 28 carapaceal setae (e.g., Fig. 1A); *Allochthonius* (*Urochthonius*) Morikawa, 1954 for subterranean species with reduced eyes, at least 18 setae on the carapace, and coxal spines with clavate processes; and *Allochthonius* (*Spelaeochthonius*) Morikawa, 1960 for species with 16 carapaceal setae and penicillate coxal spines (Figs. 1B, D; 2A–C). No reference was made to *Centrochthonius* from central Asia whose species also have 16 setae on the carapace (Redikorzev 1918, 1934; Schwarze et al. 2021; Harvey & Harms 2022) and similar-shaped (although fewer and shorter) coxal spines as *Spelaeochthonius* (Redikorzev 1918; Gao et al. 2016; Schwarze et al. 2021; Harvey & Harms 2022).

Morikawa's classification remained in place until Muchmore (1967) reviewed the North American fauna then included in Pseudotyrannochthoniinae and included all species from the U.S.A. in *Pseudotyrannochthonius*, but also synonymised *Spelaeochthonius* with the latter genus. He cited the original diagnosis of *Pseudotyrannochthonius* by Beier (1930), who had mentioned that the coxal spines in this genus are inserted individually as a row on coxa I, and that the carapace has 16–18 setae (see Beier 1930, figs. 15a, b). Muchmore (1967) correctly noted that the Asian *Spelaeochthonius* were indeed more similar to *Pseudotyrannochthonius* than to *Allochthonius sensu* Chamberlin (1929) but, again, he failed to reference *Centrochthonius* and also overlooked that Beier had actually illustrated 20 carapaceal setae for *Pseudotyrannochthonius* in his original paper. It should be noted here that Beier's generic diagnosis is problematic, as only 18 setae are actually present on the carapace in all species of *Pseudotyrannochthonius* from Chile

(Fig. 1C), including the type species *P. silvestrii* (Ellingsen, 1905) from Santiago (DH, MSH, pers. obs.). The same pattern of 18 setae is also found in *Afrochthonius* and *Selachochthonius* Beier, 1929 from South Africa, and appears to be consistent across species from the Southern Hemisphere, including all species from Australia (Harms & Harvey 2013; Harms 2013, 2018). *Centrochthonius* might have been overlooked as a genus by both Morikawa (1954, 1960) and Muchmore (1967) because the original descriptions are brief and contradictory. Redikorzev (1918) did not describe the carapace setation of *C. kozlovi*, the type species of the genus, and Beier (1931) listed 20 carapaceal setae for this species which clearly is a lapsus because a recent re-examination of the three syntypes revealed the presence of only 16 setae (Harvey & Harms 2022). Redikorzev (1934) correctly recorded 16 setae in his description of the second species of *Centrochthonius*, *C. schnitnikovi*, which is the same pattern as in all species of *Spelaeochthonius*. Importantly though, Muchmore (1967) clearly stated that the synonymy of *Spelaeochthonius* with *Pseudotyrannochthonius* was provisional until a detailed examination of coxal spine morphology in all genera had been carried out.

Overall, the rather confusing state of taxonomy for the Asian species evidently results from errors in the original descriptions and the inaccessibility of original specimens or previous literature to several workers. A prime example is *Centrochthonius* that was omitted from any subsequent descriptions for Asian species, perhaps because the original publications by Redikorzev (1918, 1934) remain difficult to access and are poorly illustrated. For example, a recently described species from high-altitude habitats in China was named *Pseudotyrannochthonius cheni* Gao, Zhang & Zhang, 2016 although it shares with *Centrochthonius* from similar habitats the presence of 16 setae on the carapace and an almost identical shape of the coxal spines (four or five short tripartite spines on the anterior margin of the coxa). Schwarze et al. (2021) recently transferred this species to *Centrochthonius* and diagnosed the genus as having 16 setae on the carapace, a small and usually bisetose intercoxal tubercle, and four or five short and tripartite coxal spines with acute tips.

With regards to the Korean species treated here, it is evident from careful restudy of the coxal spines and carapace setae in several species, that the Asian cave species of *Pseudotyrannochthonius* have significant differences compared to the type species of either *Pseudotyrannochthonius* or *Allochthonius* (see Fig. 2), but rather resemble *Centrochthonius* although they differ in both the number and shape of the coxal spines, next to the obvious troglomorphic features (e.g., lack of eyes and elongated legs and pedipalps) that were excessively used by Morikawa (1954) in his original description of the genus.

The present paper has three aims: First, we reinstate *Spelaeochthonius* as a valid genus for those Japanese and Korean species with 16 setae on the carapace and provide an updated diagnosis that delineates this taxon from all other genera of the family. Second, we redescribe *S. dentifer* based on a recent targeted survey and also describe two additional species in this genus from Korea that were collected in nearby karst systems. Third, we review distributional data for the Japanese species described by Morikawa (1954, 1956, 1960, 1970) and elevate his three currently classified subspecies to species level because our understanding of distribution ranges
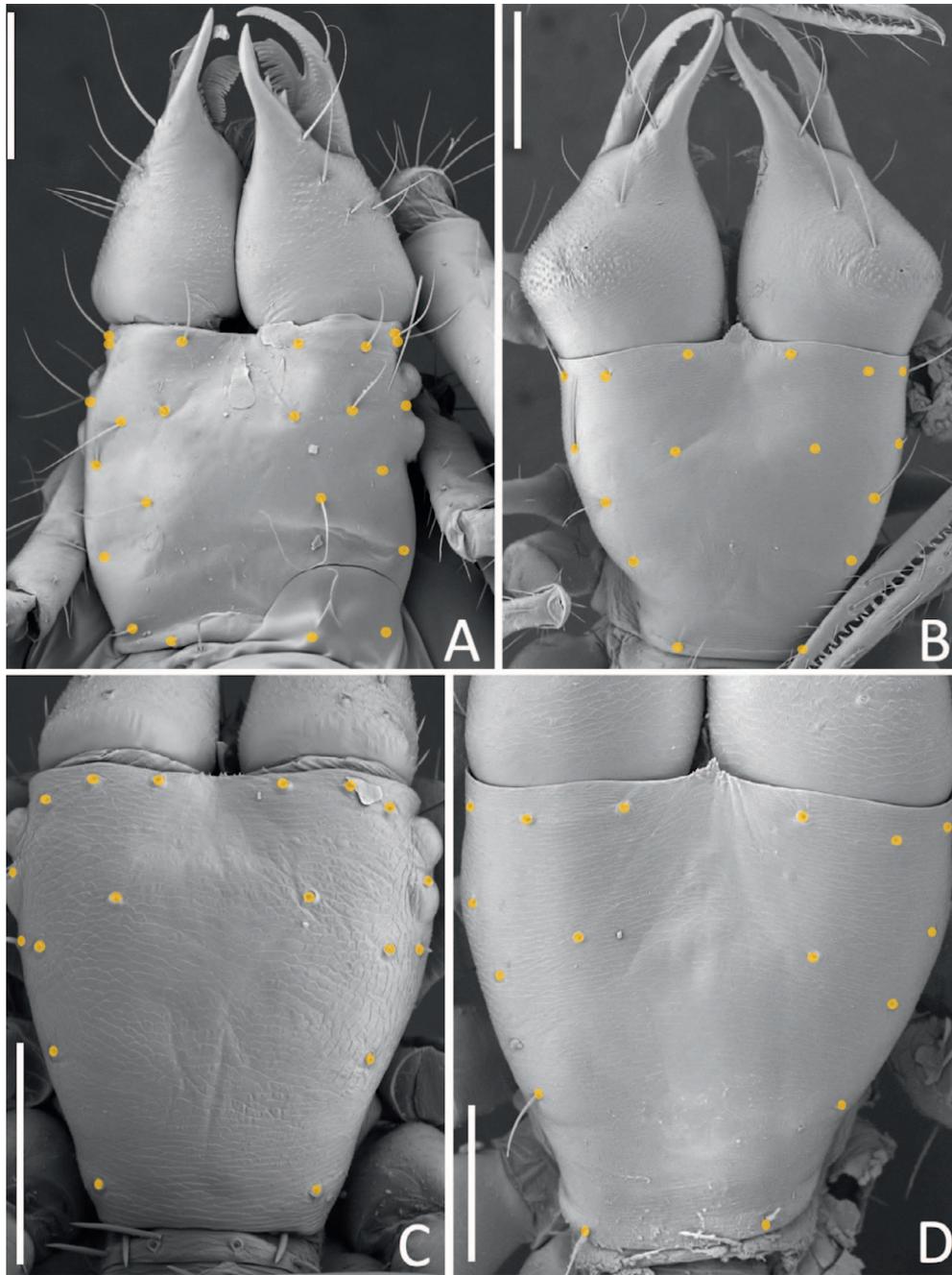
Figure 1.—Scanning electron micrographs showing carapace setation of Pseudotyrannochthoniidae genera: A, *Allochthonius opticus* (WAM T146482); B, *Spelaeochthonius dentifer* (WAM T146409) from the type locality; C, *Pseudotyrannochthonius* sp. indet. from Chiloé, Chile (WAM T146599); D, *Spelaeochthonius kobayashii* from the type locality (WAM T1246408). Note the differences in the number of setae (bases highlighted with yellow shading), notably 16 (*Spelaeochthonius*), 18 (*Pseudotyrannochthonius*) or more than 20 (*Allochthonius*). Scale bars = 200 μm.

in cave pseudoscorpions has advanced significantly since the 1950s, and there are several morphological differences between these subspecies and the nominate forms.

METHODS

This paper is based on a targeted field survey for subterranean pseudoscorpions carried out in June 2010 by Y.G. Choi, J.S. Yoo, D. Harms & M.S. Harvey with the material lodged at the Western Australian Museum (WAM) in Perth, the Zoological Museum in Hamburg (ZMH), and the National Institute of Biological Resources (NIBRI) in Incheon. The syntypes of *Centrochthonius kozlovi* at the Zoological Museum of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg (ZISP) were also re-examined, but a full description of this species is
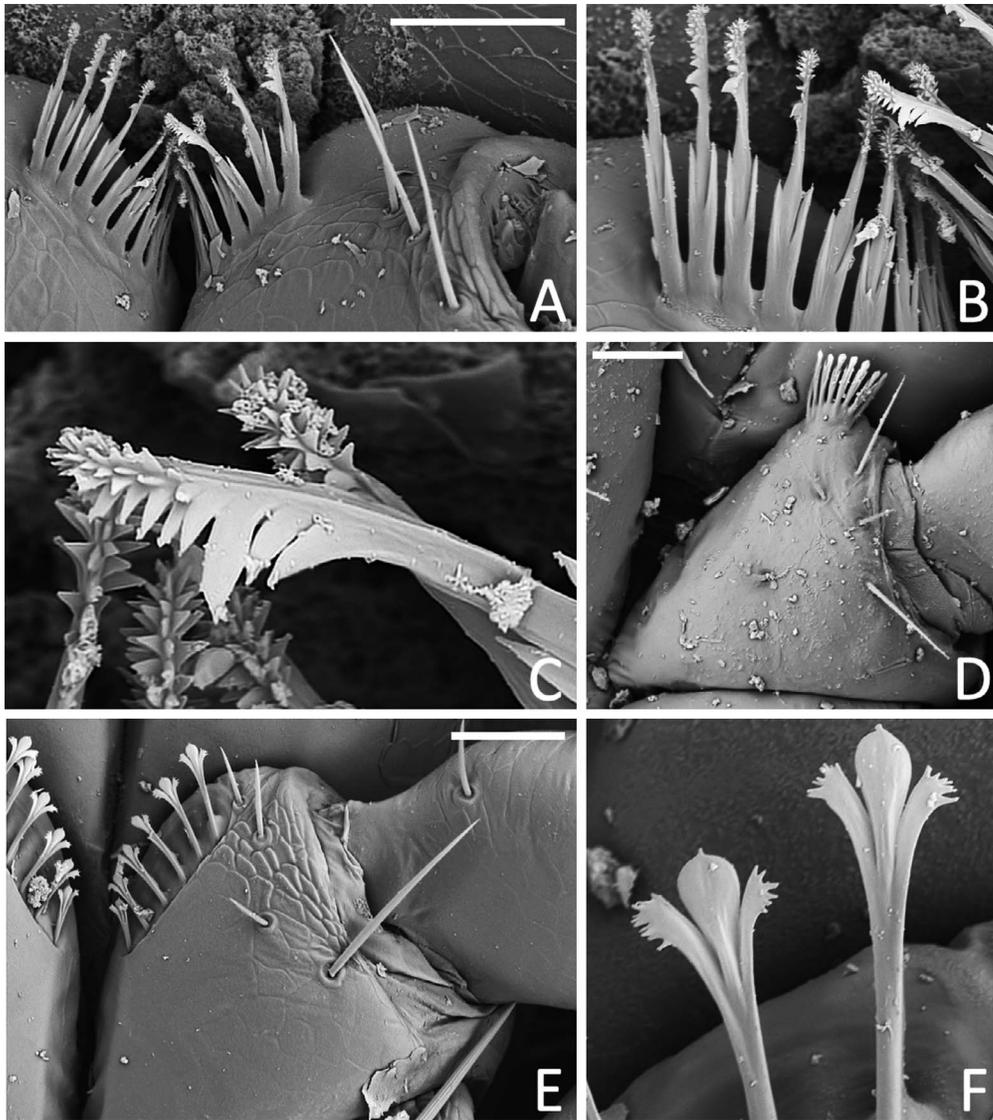
Figure 2.—Scanning electron micrographs showing comparative coxal spine morphology of Pseudotyrannochthoniidae genera: A–C, *Spelaeochthonius dentifer* (WAM T146409) from the type locality; D, *Allochthonius ussuriensis* from far-eastern Russia (WAM T146405); E–F, *Pseudotyrannochthonius* sp. indet. from Chiloé, Chile (WAM T146599). Note major differences between *Pseudotyrannochthonius* sp. indet. from Chile and *S. dentifer* (previously classified as *Pseudotyrannochthonius* following the established synonymy of *Spelaeochthonius* with *Pseudotyrannochthonius* by Muchmore, 1967), but also *Allochthonius* where the coxal spines are short, spatulate and are situated on a common protuberance. Scale bars = 50 μm.

published elsewhere (Harvey & Harms 2022). All specimens were preserved in 75–100% ethanol, then sorted, sexed and identified using a Leica M125 stereomicroscope and a Leica DMC4500 (Leica Microsystems GmbH, Germany). Measurements were taken with an ocular graticule at the highest possible magnification with a Leica DMC4500 and are expressed in millimeters (mm). All measurements were taken in dorsal or lateral view except for the carapace, legs and the pedipalps. Total length measurements of the body exclude the legs and chelicerae. K-Y Lubricating Jelly Sterile Water-based lubricant was used to fix specimens for measurements and illustrations. Line drawings were made using a digital pen tablet (Gaomon S620). Digital images were taken with a custom-made BL Plus Lab System by Dun, Inc. with integrated Canon EOS 7D Mark II, microscopic lens (5x, 10x, 20x magnifications) and the BK stacking software. Scanning electron microscope (SEM) images were produced with Hitachi Tabletop microscopes (models TM4000 Plus at ZMH and Hitachi TM3030 Plus at WAM) and mounting the specimens on copper wire and sputter-coated with gold. Maps were created using QGIS Version 3.16.0 (online at https://www.qgis.org). Cave localities were derived from Google Earth and are rounded to the minute. Images and maps were all edited with Adobe Photoshop Version 13.0.1 x64 and Autodesk Sketchbook version 8.7.1 (online at https://sketchbook.com). Terminology and measurements follow Chamberlin (1931), except for modifications to the nomenclature of the segments of the pedipalps and legs
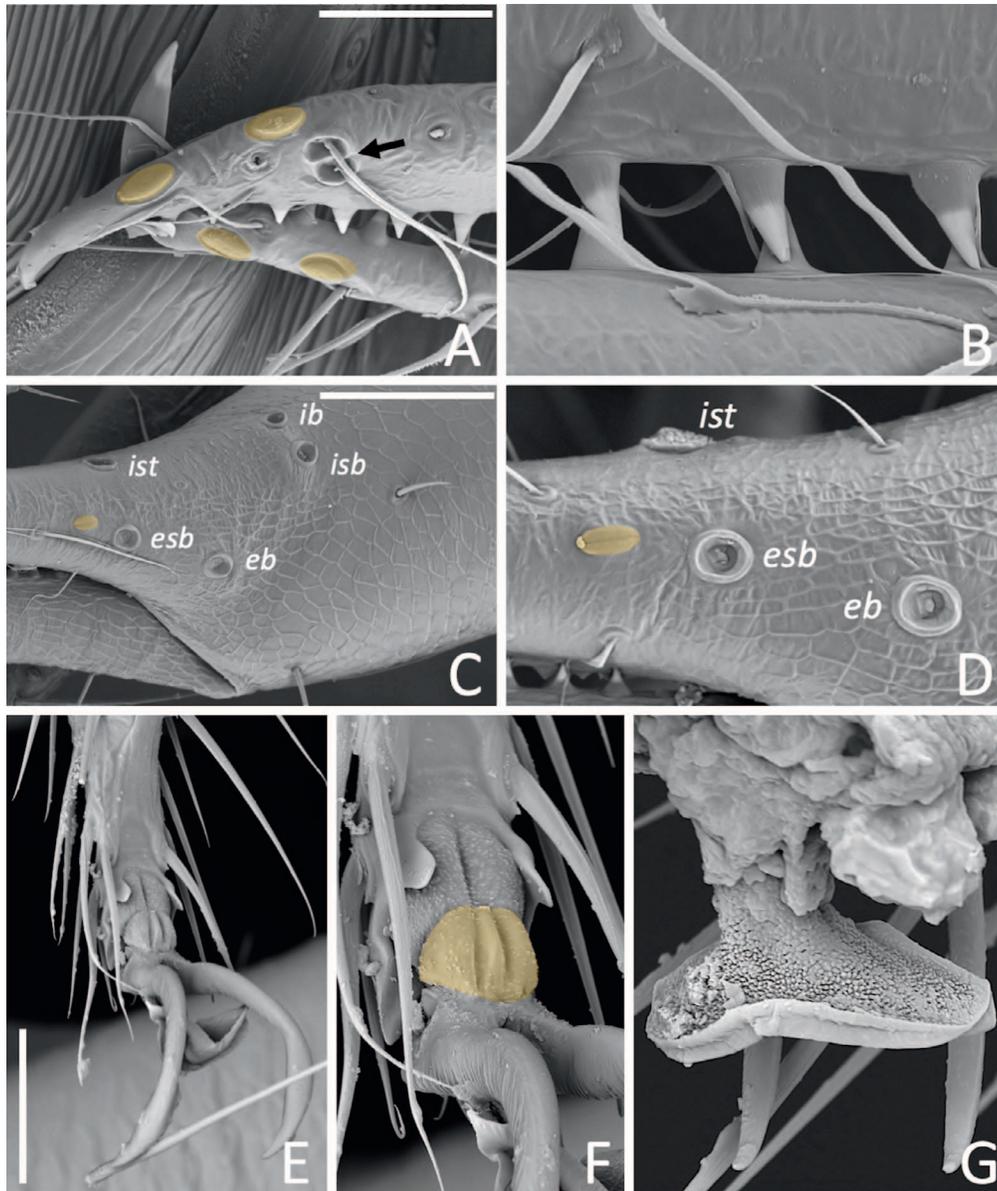
Figure 3.—Scanning electron micrographs showing the pedipalp and leg morphology in *Spelaeochthonius* (example *S. dentifer*, WAM T146409): A, tip of the pedipalp chela showing the duplex trichobothria *dt* (see arrow) and two pairs of sensory organs (in yellow shading) that are found in all Pseudotyrannohthoniidae; B, example of chela dentition in *Spelaeochthonius* where teeth are usually acuminate and widely spaced; C, distal section of pedipalp hand in dorsolateral view showing the dorsal position of trichobothria *ib* and *isb* as well as lyrifissure *fb* (yellow shading) that is found in all adults of *Spelaeochthonius*; D, same, magnified in lateral view; E, leg IV tarsus showing the long but simple claws without teeth and the arolium that is shorter than the claws; F, detailed view of the same showing grooves for the retraction of claws (yellow shading) and scales in a lateral position on the tarsus; G, arolium in ventral view showing granulate surface structure. Scale bars = 50 μm

(Harvey 1992), the trichobothria (Harvey 1992; Harms 2013; Harms & Harvey 2013) and cheliceral setation (Edward & Harvey 2008). The term 'rallum' is used for the cheliceral blades (Judson 2007).

Molecular methods.—To facilitate further characterisation exemplar species of all three specimens were also barcoded for a 694bp fragment of the cytochrome *c* oxidase subunit 1 (*COI*) gene according to the protocols in Harms (2018) and Harms et al. (2019). These sequences are deposited in GenBank.

SYSTEMATICS

Family Pseudotyrannochthoniidae Beier, 1932
Genus *Spelaeochthonius* Morikawa, 1954, stat. rev.

Spelaeochthonius Morikawa, 1954: 83–84. Type species: *S. kubotai* Morikawa, 1954, by original designation.
Allochthonius (*Spelaeochthonius*): Morikawa, 1960: 104–105.
Pseudotyrannochthonius Beier, 1930 (in part): Muchmore, 1967: 132.

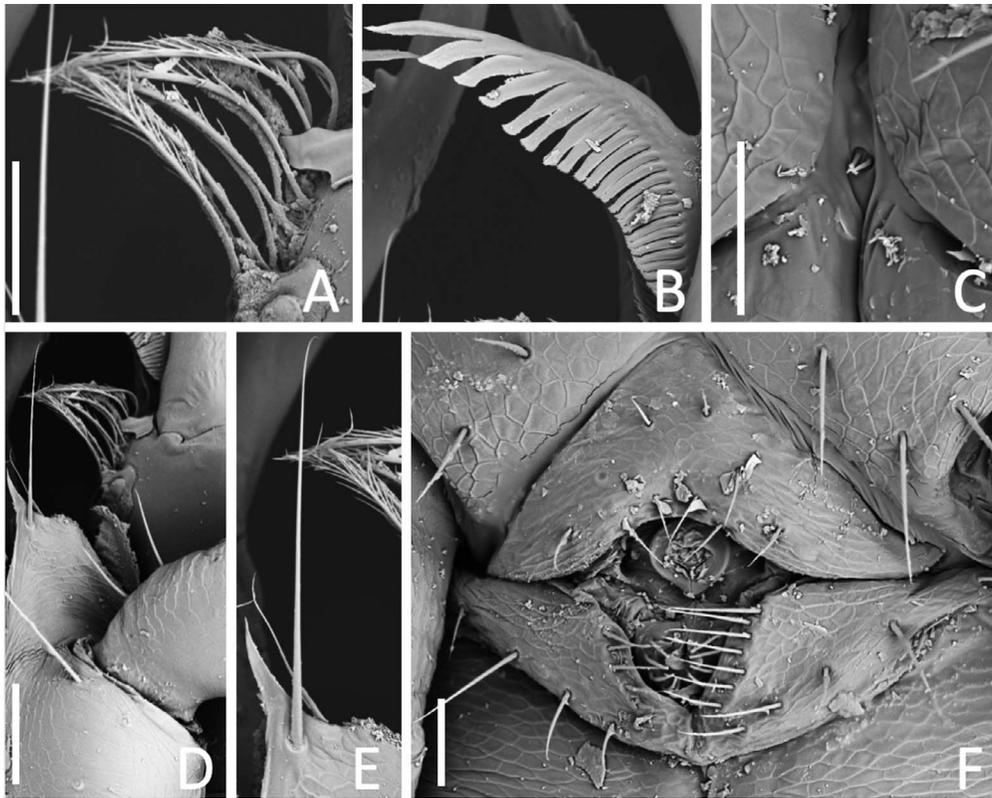**Diagnosis.**—*Spelaeochthonius* is most similar to *Centroch-*

Figure 4.—Scanning electron micrographs showing the chelicerae and ventral morphology of *Spelaeochthonius* (example *S. dentifer*, WAM T146409): A, rallum; B, lamina exterior; C, bisetose intercoxal tubercle which is small; D, coxa I and manducatory process; E, setation of manducatory process with the apical seta being long and straight and the subapical seta being much shorter; F, male genital opening with outer valves and general setation patterns. Scale bars = 50 μm.

thonius Beier, 1931 in having 16 setae on the carapace (Figs. 1 B, D), a small, bisetose intercoxal tubercle (Figs. 4C, 11C), and coxal spines that are tripartite and terminally acute (Figs. 2A–C). It differs from *Centrochthonius* in the number and shape of the coxal spines (more than 7 in *Spelaeochthonius* that are also longer and distally pinnate or serrate; fewer than 6 in *Centrochthonius* that are also shorter and terminally acute). It differs from the other south-east Asian pseudotyrannochthoniid genus *Allochthonius* in the number of carapaceal setae (16 vs. 18–28 in *Allochthonius*) and the shape of the coxal spines (a "spray" or short, spatulate spines on a common protuberance in *Allochthonius*; Fig. 2D), the shape of the intercoxal tubercle (generally larger in *Allochthonius*) and from *Pseudotyrannochthonius* by the number of carapaceal setae (16 vs. 18; see Fig. 1) and the arrangement of the coxal spines that are terminally spatulate and inserted individually on coxa I in the latter genus (Figs. 2 E, F). *Spelaeochthonius* is also similar to the North American species presently misplaced in *Pseudotyrannochthonius* by sharing 16 setae on the carapace. However, they differ in coxal spine morphology, with the species from the U.S.A. having fewer spines that are shorter and distally spatulate (e.g., Muchmore 1967; Benedict & Malcolm 1970).

Description (amended from Morikawa 1954).—Color (live specimens): pale to reddish but never brown or black (Figs. 6, 9, 12). Chelicera (Figs. 7A–B, 10 A–B): Cuticle of hand squamate, generally with 5 setae, movable finger with 1 seta in medial position, fixed finger with 1 seta near basal position, all setae acuminate; movable finger with basal serrations, some medial teeth and a subapical tooth; movable finger with some serrations, serrula exterior with 14–25 blades, serrula interior with an equal number, rallum with 16–20 pinnate blades (Figs. 4 A–B), galea present as a very low mound. Pedipalp (Figs. 3A–C, 7C–F): Fixed and movable fingers straight or distally curved; both fingers with acute and spaced teeth, trichobothria as for family, venom glands absent. Cephalothorax (Figs. 1B, D): longer than broad and constricted posteriorly, eyes absent, epistome (sub) triangular and with some serrations, 16 setae arranged 6: 4: 2: 2: 2, with seta *Mm* absent, cuticle with scales, lyrifissures present but number variable. Coxae: as for family, manducatory process of pedipalp coxa with 1 large apical and 1 smaller subapical seta (Figs. 4D–E), coxae I–IV with 4–9 setae, coxal spines on coxa I only and comprising 8–12 long and basally tripartite spines that are situated individually on anterior inner margin of coxa, never on a common protuberance, tips of spines plumose, slightly serrate or with a short plumose tassel as in the type species *S. kubotai* (Morikawa 1954, fig. 1F; also Figs. 2A–C); intercoxal tubercle present and usually bisetose (Fig. 4C). Abdomen: Pleural membrane papillostriate; tergites and sternites undivided (Fig. 6E), setae uniseriate and acuminate; tergal chaetotaxy often 2:4:4:6:6:6:8:8:8:6:6:4:2:0. Legs: elongate but otherwise typical for the family (Figs. 7G– H); claws simple, without teeth and

Figure 5.—Habitats of *Spelaeochthonius* in Korea: A, Entrance to Sinryeong Cave, the type locality of *S. cheonsooi* and *Allochthonius coreanus*. Note the leaf litter accumulations at the entrance from which *A. coreanus* was sampled in large numbers. B, Rock Massif in which Wooro Cave is located showing the local geomorphology; C, microhabitat of *S. seungsookae* in Hogye Cave (ca. 10 m from the entrance) where the pseudoscorpions live under rocks and boulders on the cave floor and were quite abundant; D, cave habitat in the main chamber of Sinryeong Cave where *S. cheonsooi* was found under rock boulders.

long, retractable in shafts; arolium shorter than claws, simple and undivided but with surface granulation (Figs. 3E–G).

Distribution.—*Spelaeochthonius* is presently known only from subterranean habitats in Japan and South Korea (Figs. 8, 16).

Remarks.—The Morikawa collection held at the Ehime University is difficult to access and the type material of the type species *S. kubotai* could not be re-examined for this study. Note here that most of the original specimens were mounted in Hoyer's solution that has dried and contracted. That said, Morikawa's illustrations are precise enough to align this species with those we have examined here in all the important features. Another Japanese species (*S. kobayashii* Morikawa, 1956) was examined in this study for coxal spine and carapace morphology. It matches all the diagnostic characters mentioned above.

REVIEW OF THE SOUTH KOREAN FAUNA

Spelaeochthonius dentifer (Morikawa, 1970), comb. nov.
(Figs. 1B, 2A–C, 3, 4, 6, 7, 8)

Allochthonius (Spelaeochthonius) dentifer Morikawa, 1970: 144–146, figs. 2c–e, 3.

Pseudotyrannochthonius dentifer (Morikawa): Harvey, 1991: 198.

Material examined.—SOUTH KOREA: *Gangwon-do*: 3 ♂, Yongyeon Cave off Route 38, Changseong-eub, 6.4 km NW. of Taebaek (37°12′33.0″N 128°56′29.0″E), dark zone, 944 m, 17 June 2010, Y.G. Choi, D. Harms, M.S. Harvey (WAM T120618, T146408, T146409).

Diagnosis.—*Spelaeochthonius dentifer* differs from *S. cheonsooi* sp. nov. by having slightly diastemodentate chelal teeth (strongly spaced in *C. cheonsooi* sp. nov.), more teeth on both the movable and fixed chelal fingers (33–37 vs. 17/21), a longer chela (>1.8 vs. 1.5 mm), and both chelal fingers almost straight (distally curved in S. *cheonsooi* sp. nov.). It differs from *S. seungsookae* sp. nov. by its shorter chela (*S. dentifer* ♂ 1.60–1.67 vs. 1.71–2.00 mm), more teeth on the movable pedipalp finger (37 vs. 33–35), serrula exterior with more blades (24 vs. 21), and the shape of the coxal spines (pointed and plumose tips vs. spatulate and plumose). Differs from all Japanese species by the high number of teeth on both chelal fingers (<31 in the Japanese fauna).

Description.—Adult male, WAM T146408. Color (in 75% ethanol): uniformly light orange-brown except chelicera which is darker brown.
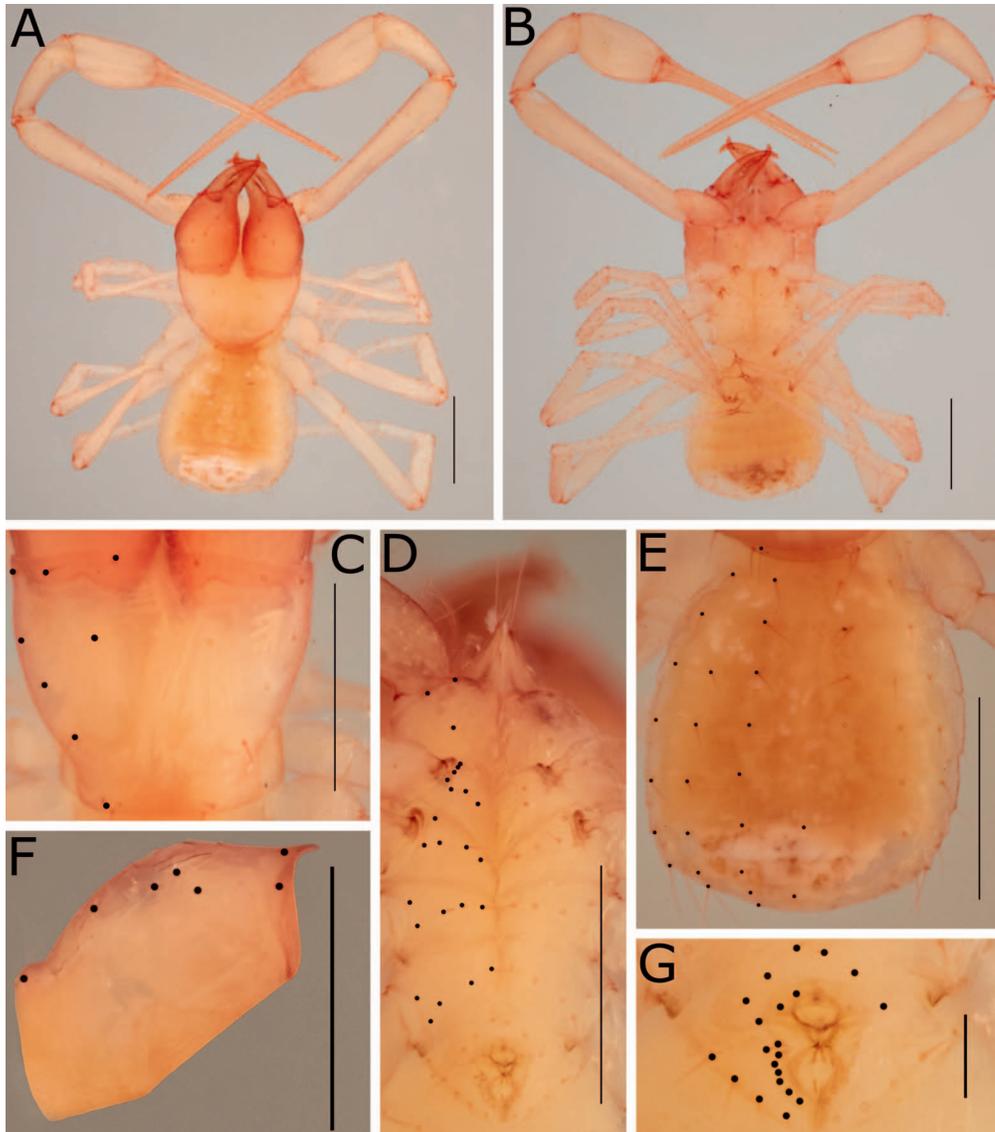
Figure 6.—*Spelaeochthonius dentifer* (Morikawa 1970) (A–C, E: WAM T146408, male; D, F, G: WAM T120618, male): A, habitus in dorsal view; B, same in ventral view; C, carapace in dorsal view; D, coxal area in ventral view; E, abdomen in dorsal view; F, carapace in lateral view; G, male genitalia. Black dots indicate positions of setae. Scale bars: A–F = 0.5 mm; G = 0.1 mm.

Chelicera (Figs. 7A–B): Broad hand 0.68/0.71 (in mm). Cuticle of hand squamate, with 5 setae, movable finger with 1 seta in medial position, fixed finger with 1 seta near basal position, all setae acuminate; movable finger with small 25 teeth; subapical tooth distinctively bigger, medial apical teeth progressively larger than basal teeth, fixed finger with 14 teeth, distal teeth progressively larger than basal teeth except 3 most distal teeth; rallum (Fig. 4A) with 11 blades, distal blades progressively longer feathered, serrula exterior (Fig. 4B) with 24 blades, distal blades progressively larger than basal blades.

Pedipalp (Figs. 3A–D; 7C, E, F): All setae acuminate; trochanter 1.59, femur 5.84, patella 2.83, chela 7.27, hand 2.36 x longer than broad, movable finger 2.17 x longer than hand, without large basal apodeme; both fingers straight in lateral view, but both distal ends curved inwards; venom apparatus absent; chelal finger homodentate, fixed finger with 34, movable finger with 37 broad and close-standing teeth,

intercalary and accessory teeth absent, distance between teeth of movable finger and fixed finger 0.02 mm to 0.04 mm. 7–8 basal serrations at the base of the fixed finger. External and internal chelal condyles small and rounded; fixed chelal finger and hand with 8 trichobothria plus duplex trichobothrium (*dt*), trichobothria *ib* and *isb* distally on dorsum of palm, *esb*, *ist* and *eb* forming an oblique row sublaterally to dorsally at base of fixed chelal finger, *it* and *est* medial and forming a pair, *it* slightly more distal than *est*, *et* subdistal and *dt* distal, *dt* slightly closer to *et* than fingertip; movable finger with 4 trichobothria, triplet *sb*, *b* and *t* distomedial to distal, *st* subproximal, *b* in medial position of *t* and *sb*.

Carapace (Figs. 1B, 6C, F): Subquadrate, as long as it is broad, without furrows; lateral margins constricted posteriorly, eyes absent completely; epistome small, lightly sclerotized and lightly cuspid; with 16 setae arranged 6: 4: 2: 2: 2, seta *Mm*
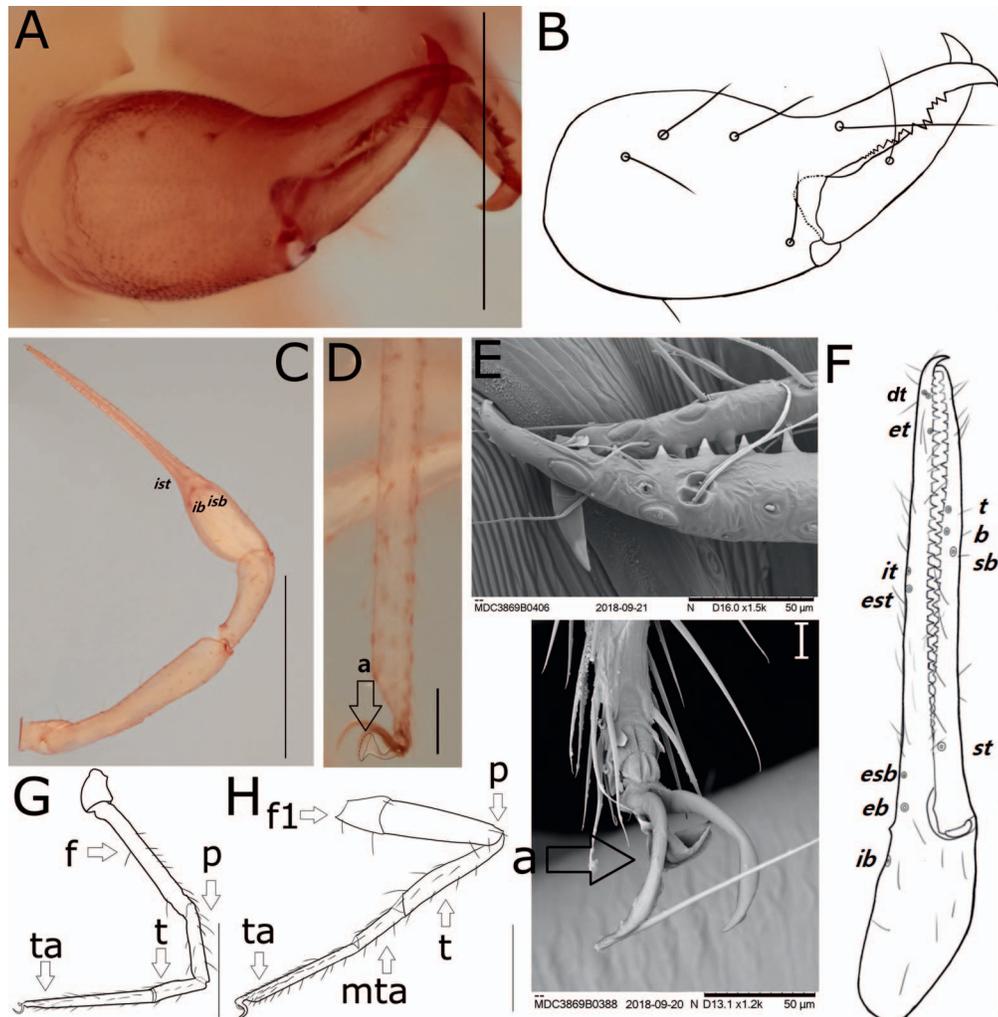
Figure 7.—*Spelaeochthonius dentifer* (Morikawa, 1970) (A–D, F, G: WAM T120618, paratype male; E, I: WAM T146409, paratype male): A, B, chelicera in lateral view; C, pedipalp in dorsal view; D, tarsus of leg IV; E, scanning electron micrograph showing tips of chelal fingers; F, pedipalp chela in lateral view; G, leg I segmentation; H, leg IV segmentation; I, scanning electron micrograph showing arolium and claws of leg I. Scale bars: A, B, C, F, G, H = 0.5 mm, D = 0.1 mm. Abbreviations: a = arolium; f = femur; f1 = femur 1; mta = metatarsus; p = patella; t = tibia; ta = tarsus.

absent, all setae comparably long; with 4 lyrifissures at the apical margin.

Abdomen (Fig. 6E): Pleural membrane papillostriate; tergites and sternites undivided, setae uniseriate and acuminate; tergal chaetotaxy 4: 4: 6: 6: 6: 7: 7: 5: 4: 2: 2: 0, sternal chaetotaxy 12: 10: 13: 10: 9: 8: 5: 5: 4: –: 2.

Coxal area (Fig. 6D): Manducatory process (Figs. 4D, E) with 2 acuminate distal setae, apical seta straight, about 3 times longer than subapical seta and extending to about half of the rallum (Fig. 4A), subapical seta dwarfed and bent towards interior margin, pedipalpal coxa with 3 setae, 2 at distal margin and 1 more medial near center, with 1 medial lyrifissure. Coxae I with 9 tripartite coxal spines with medio-distal and distal serrations but without spatulate tips (Figs. 2A–C), spaces between coxal spines equal, all blades arranged in an oblique row at apical, internal margin of the coxa; apical process of coxa I broadly rounded; coxal chaetotaxy: 7:5:5:5; intercoxal tubercle (Fig. 4C) present, bisetose.

Legs (Fig. 7D): Typical of family. Leg I and IV, trochanter and femur with squamous sculpture, arolium (Figs. 3E, G, 7D, I) shorter than claws (Fig. 7D, I), undivided, claws hook-shaped.

Male genitalia (Figs. 4F, 6G): genital opening subtriangular, flanked by 2 valves with 2 rows of glandular setae; inner row with 5–6 setae and outer row with 4 setae; each valve with 1 oblique lyrifissure; anterior to opening another valve with 10 setae.

Dimensions (in mm). Body length 1.83. Pedipalp: trochanter 0.29/0.16, femur 1.11/0.19, patella 0.51/0.18, chela 1.60/0.22, fixed finger length 1.11, hand length 0.52, movable finger length 1.13; Chelicera total 0.76/0.34, fixed finger length 0.34, movable finger length 0.38; cephalothorax 0.68/0.71 (anterior)/0.49 (posterior). Leg I: femur 0.69/0.10; patella 0.39/0.09; tibia 0.31/0.09; tarsus 0.68/0.05. Leg IV: femur 1 0.31/0.13; patella 0.66/0.12; tibia 0.72/0.12; metatarsus 0.27/0.09; tarsus 0.69/0.06.
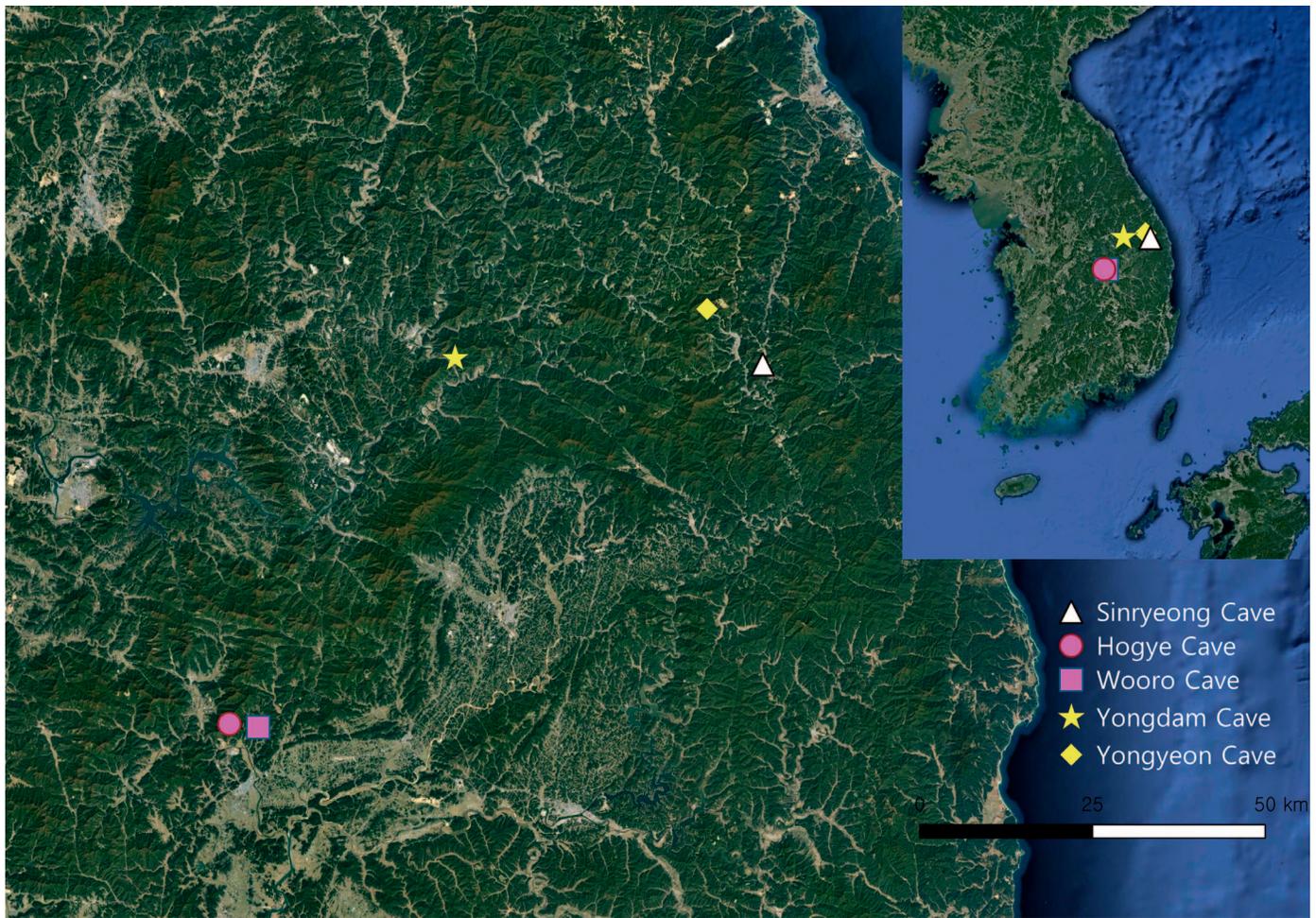
Figure 8.—Records of *Spelaeochthonius* in Korea: *S. dentifer* (Yongyeon Cave and Yongdam Cave); *S. cheonsooi* sp. nov. (Sinryeong Cave); and *S. seungsookae* sp. nov. (Hogye and Wooro Caves). Note that the record of *S. dentifer* from Yongdam Cave (Morikawa 1970) is questionable.

Sequence data.—GenBank Accession No. MZ394006 for specimen WAM T120618. It differs from *S. cheonsooi* sp. nov. by 15.1% pairwise divergence and from *S. seungsookae* by 13.9% in the *COI* data.

Distribution & ecology.—*Spelaeochthonius dentifer* is likely to be endemic to the Yongyeon karst near the town of Taebek in Gangwon-do Province (Fig. 8). All specimens were from a chamber deep within the cave and found under flat rocks near calcite formations. The ground and rocks were moist. The abundance of pseudoscorpions was low.

Remarks.—Morikawa (1970) described this species from the type specimens that are deposited at the National Museum of Nature and Science in Tokyo. They have not been re-examined for this study because recently collected specimens from the type locality were available. Also note that the original paratypes from Yongdam Cave likely represent a distinct species, similar to the paratypes from Hogye-hangtigi Cave that are described as a new species below. Yongdam is 37 km from the type localities and represents a different karst system; however no recently collected specimens are available for sequencing or morphological study and future assessment is necessary.

Spelaeochthonius cheonsooi, sp. nov.
ZooBank Registration: http://zoobank.org/
NomenclaturalActs/4BF9A5FA-D515-47E3-898C-
D61E3190F79C
(Figs. 8–11)

Type material.—*Holotype female*. SOUTH KOREA: *Gangwon-do*: Baegsan-ri, Changseong-eub (SE. of Taebaek), Sinryeong Cave (37°08′44.0″N 129°02′03.0″E), final chamber, dark zone, 641 m altitude, 17 June 2010, Y.G. Choi, D. Harms & M.S. Harvey (NIBRIV0000883004).

Etymology.—This species is named after the first author's father, CheonSoo You, for being a great teacher and guiding his son in the right direction.

Diagnosis.—*Spelaeochthonius cheonsooi* sp. nov. differs from its congeners in South Korea by having strongly diastemodentate (widely spaced) chelal teeth, fewer teeth on both the movable and fixed fingers (17/21, 33–37/33–38 in *S. dentifer* and *S. seungsookae* sp. nov.), a smaller pedipalp chela (♀ 1.49 mm, others > 1.6 mm), and both chela fingers strongly curved distally (almost straight to slightly curved in *S. dentifer* and *S. seungsookae* sp. nov.). Differs from all congeners from
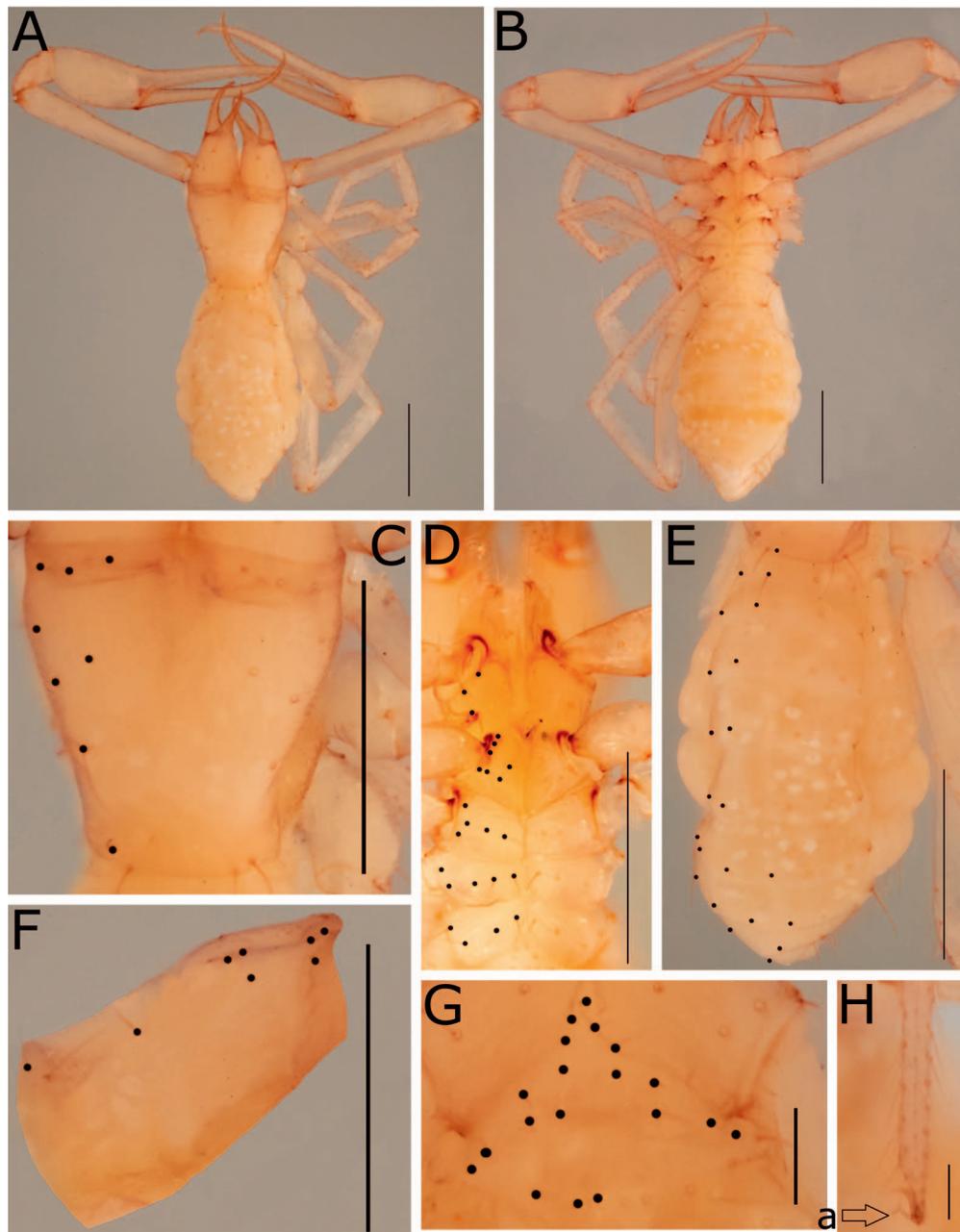
Figure 9.—*Spelaeochthonius cheonsooi* sp. nov. (WAM T120621 holotype female): A, habitus in dorsal view; B, same in ventral view; C, carapace in dorsal view; D, coxal area in ventral view; E, abdomen in dorsal view; F, carapace in lateral view; G, female genitalia; H, arolium (arrow, "a") and claws of leg II. Black dots indicate positions of setae. Scale bars: A–F = 0.5 mm; G, H = 0.1 mm.

Japan except *for S. kishidai* by the low number of teeth on both chelal fingers (fixed finger with more than 23 teeth, movable finger with more than 20 teeth in the Japanese fauna). Also differs from these species, including *S. kishidai*, by the strongly diasteomdentate chelal teeth and the distal curvature of the chelal fingers.

Description.—Color (in 75% ethanol): uniformly bright orange except chelicera which is orange brown.

Chelicera (Figs. 10A, B): hand broad 0.31/0.21 (in mm). Cuticle of hand squamate, with 5 setae, movable finger with 1 seta in medial position, fixed finger with 1 seta near basal position, all setae acuminate; movable finger with 15 teeth; 4 small teeth in distal position but distal teeth progressively larger, fixed finger with 13 teeth, distal teeth progressively sharper than basal teeth; rallum with 10 blades, serrula exterior (Figs. 10D, E) with 19 blades, medial blades progressively larger than basal and apical blades.

Pedipalp (Figs. 10C, 11A–B): All setae acuminate; trochanter 1.44, femur 7.33, patella 2.42, chela 5.32, hand 1.96 x longer than broad, movable finger 1.67 x longer than hand, without large basal apodeme; both fingers curved inwards on both ends in lateral view; chelal teeth diastemodente (Fig.
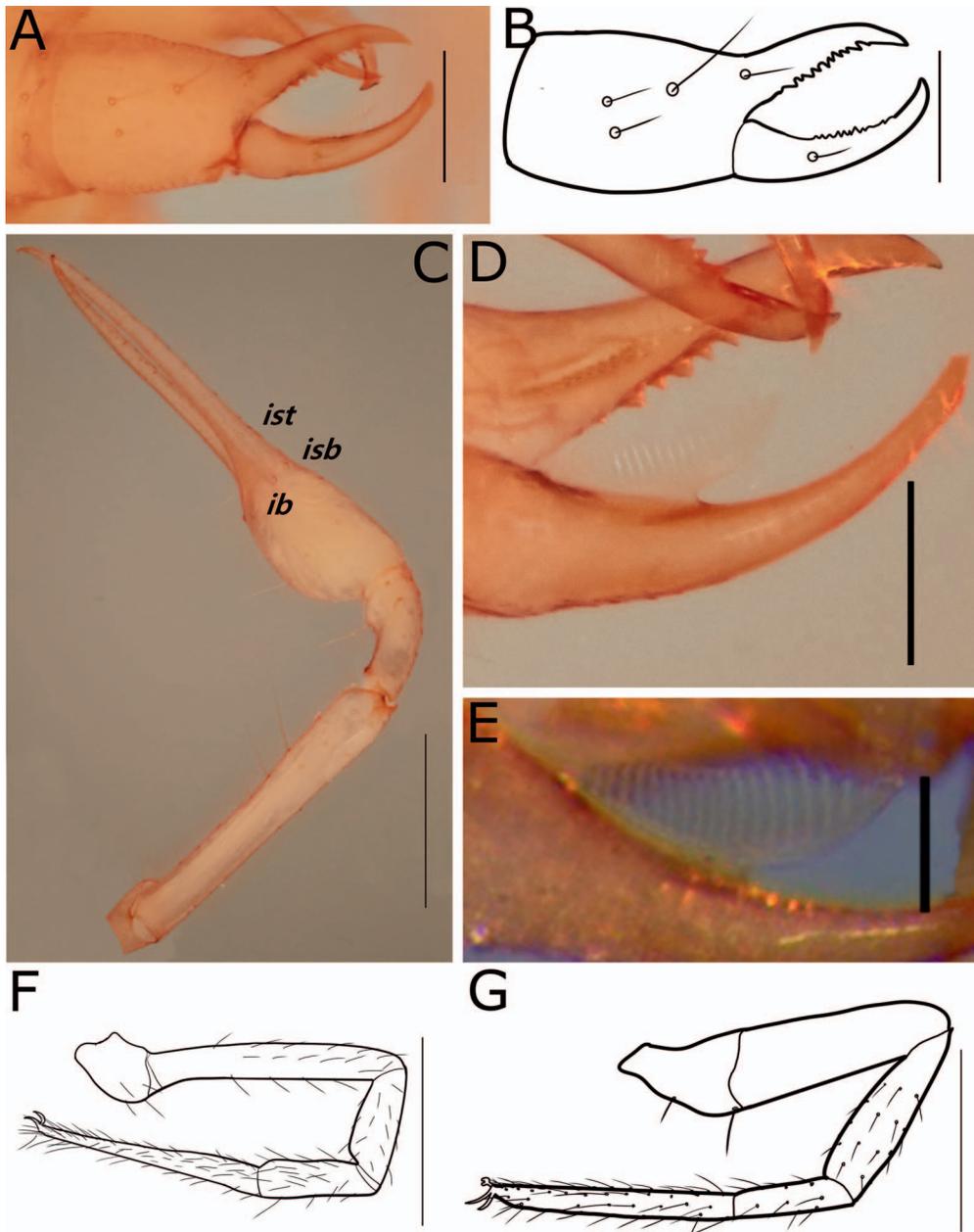
Figure 10.—*Spelaeochthonius cheonsooi* sp. nov. (WAM T120621 holotype female): A, B, chelicera in lateral view; C, pedipalp in dorsal view; D, E serrula exterior; F, leg I; G, leg IV in lateral view. Scale bars: A, B = 0.2 mm; C, E, G = 0.5 mm; D = 0.1 mm.

11B), fixed finger with 21, movable finger with 17 acute and broad teeth, widely spaced with distances ranging from 0.02 to 0.12 mm, fixed finger with 6 serrations basally, intercalary and accessory teeth absent, distance between teeth of movable finger and fixed finger 0.01 mm to 0.012 mm, distances between medial teeth larger than basal and apical. External and internal chelal condyles small and rounded; fixed chelal finger and hand with 8 trichobothria plus duplex trichobothrium (*dt*), trichobothria *ib* and *isb* distally on dorsum of palm, *esb, ist* and *eb* forming an oblique row sublaterally to dorsally at base of fixed chelal finger, *it* and *est* medial and forming a pair, *it* slightly more distal than *est, et* subdistal and *dt* distal, *dt* slightly closer to *et* than fingertip; movable finger with 4

trichobothria, triplet *sb*, *b* and *t* distomedial to distal, *st* subproximal, *b* equally close to *sb* and *t*.

Cephalothorax (Figs. 9C, F): Subquadrate, slightly longer than broad 0.62/0.5 (in mm), without furrows; lateral margins constricted posteriorly, eyes absent completely; epistome small, lightly sclerotized and lightly cuspid; with 16 setae arranged 6: 4: 2: 2: 2, seta *Mm* absent, all setae comparably long.

Abdomen (Fig. 9E): Pleural membrane papillostriate; tergites and sternites undivided, setae uniseriate and acuminate; tergal chaetotaxy: 4: 4: 6: 6: 8: 8: 8: 5: 6: 4: 2: 0, sternal chaetotaxy: 10: 12: 12: 10: 12: 12: 6: 4: 4: –: 2.
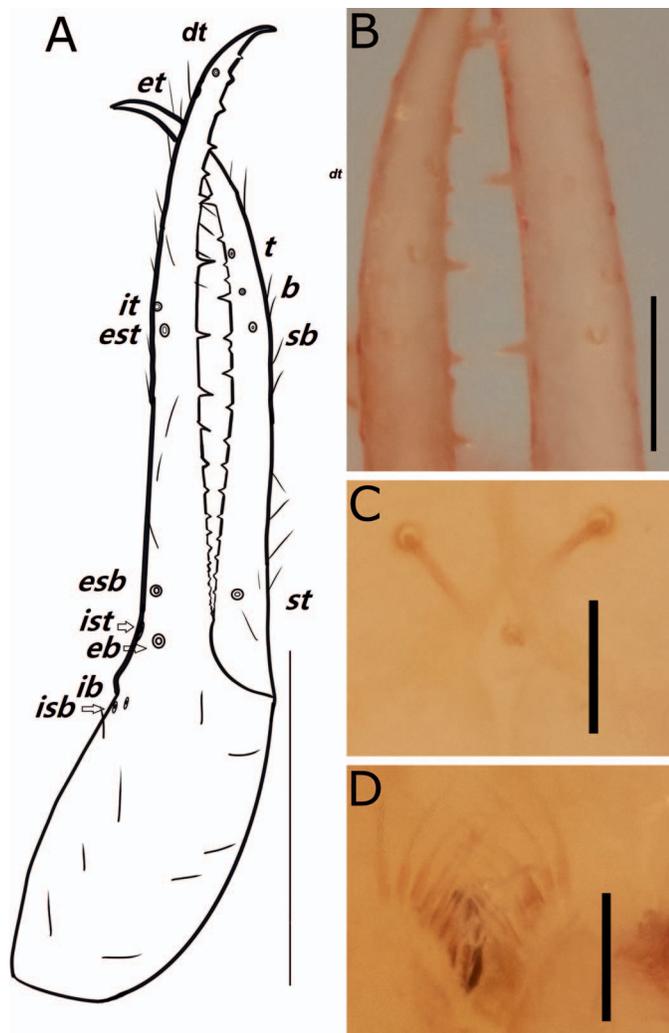
Figure 11.—*Spelaeochthonius cheonsooi* sp. nov. (WAM T120621 holotype female): A, pedipalp chela; B, teeth of pedipalp chela; C, intercoxal tubercle; D, coxal spines. Scale bars: A = 0.5 mm; B = 0.1 mm; C, D = 0.05 mm.

Coxal area (Fig. 9D): Manducatory process with 2 acuminate distal setae, apical seta straight, about 3 times longer than subapical seta and extending to about half of the rallum, subapical seta dwarfed and bent towards interior margin, pedipalpal coxa with 3 setae, 2 at distal margin and 1 more medial near center, with 1 medial lyrifissure. Coxae I with 9 coxal spines (Fig. 11D), spaces between coxal spines equal, all spines arranged in an oblique row at apical, internal margin of the coxa (the tips of the spines are not visible because the holotype was not used for scanning electron microscopy). Apical process of coxa I broadly rounded; coxal chaetotaxy: 7: 5: 5: 4. Intercoxal tubercle (Fig. 11C) present, unisetose.

Legs (Figs. 10F–G): Typical of family. Leg I and IV, trochanter and femur with squamous sculpture, arolium (Fig. 9H) shorter than claws, undivided, claws (Fig. 9H) hook-shaped.

Female genitalia: genital opening slit-shaped, with 15 setae situated proximal and 9 setae distal to opening.

Dimensions (in mm). Body length 1.70. Pedipalp: trochanter 0.26/0.18, femur 0.88/0.12, patella 0.34/0.12, chela 1.49/0.28, fixed finger length 0.98, hand length 0.55, movable finger length 0.92; Chelicera total 0.57/0.21, fixed finger length 0.26, movable finger length 0.29; cephalothorax 0.62/0.54 (anterior)/0.35 (posterior). Leg I: femur 0.65/0.09; patella 0.38/0.1; tibia 0.28/0.08; tarsus 0.64/0.06. Leg IV: femur 1 0.22/0.18; patella 0.57/0.17; tibia 0.65/0.11; metatarsus 0.3/0.07; tarsus 0.73/0.06

Sequence data.—GenBank Accession No. MZ394005 for the holotype. It differs from its congeners by 13.9% and 15.1% pairwise divergence in the *COI* data respectively**.**

Distribution and ecology.—This species is only known from the type locality, which is in Sinryeong cave near the town of Taebek in Gangwon-do Province (Figs. 5A, 8). The single female was collected from the final (dark) chamber under a moist rock (Fig. 5C). *Allochthonius coreanus* was also found in this cave but closer to the entrance and in leaf litter outside the cave entrance.

Remarks.—Sinryeong Cave is also the type locality of *Allochthonius* (*Allochthonius*) *coreanus* Morikawa, 1970 that was originally collected during a cave survey conducted by Shun-Ichi Uéno in 1966. This species was re-collected here in numbers from near the cave entrance and is not a troglobite because it has prominent eyes with lenses. The species is widespread in South Korea and easily recognizable by virtue of the dark-brown chela (Fig. 17).

Spelaeochthonius seungsookae, sp. nov.
ZooBank Registration: http://zoobank.org/
NomenclaturalActs/648F021D-E597-4D13-8341-
6D115D1B6B3B
(Figs. 8, 12–15)

Type material.—*Holotype male.* SOUTH KOREA: *Gyeongsangbuk-do*: Hogye Cave, Byeolam-ri, Hogye-myeon NNW. of Mungyeong (36°39′41.0″N, 128°10′25.0″E), first chamber, dark zone, 286 m, 18 June 2010, Y.G. Choi, D. Harms, J.S. Yoo & M.S. Harvey (NIBRIV0000883005).

Paratypes. SOUTH KOREA: *Gyeongsangbuk-do*: 1 ♀ (allotype), same data as holotype (NIBRIV0000883006); 1 ♀, same data as holotype (NIBRIV0000883007); 2 ♂, 2 ♀, 1 tritonymph (WAM T120620, T120626, T124507, T124406); 2 ♂, 1 ♀, same data as holotype (ZMH-A0014708-10).

Other material examined.—SOUTH KOREA: *Gyeongsangbuk-do*: 1 ♂, Wooro Cave, South of Uro-ri, Hogye-myeon (36°39′36″N, 128°12′34″E), dark zone, 165 m, 18 June 2010, Y.G. Choi, D. Harms, J.S. Yoo & M.S. Harvey (WAM T146483).

Etymology.—This species is named for the first author's mother, SeungSook Lee, for supporting her son in every aspect of life.

Diagnosis.—*Spelaeochthonius seungsookae* sp. nov. differs from *S. cheonsooi* sp. nov. by having slightly diastemodentate chelal teeth (strongly spaced in *S. cheonsooi* sp. nov.), more chelal teeth on both the movable and fixed chelal fingers (33–35 vs. 17/21), a larger pedipalp chela (>1.9 vs. 1.5 mm), and both chelal fingers almost straight (distally curved in S. *cheonsooi* sp. nov.). It differs from *S. dentifer* sp. nov. by its longer pedipalp chela (> 1.71–2.00 vs. 1.60–1.67 mm); less teeth on the movable pedipalp finger (33–35 vs. 37), serrula
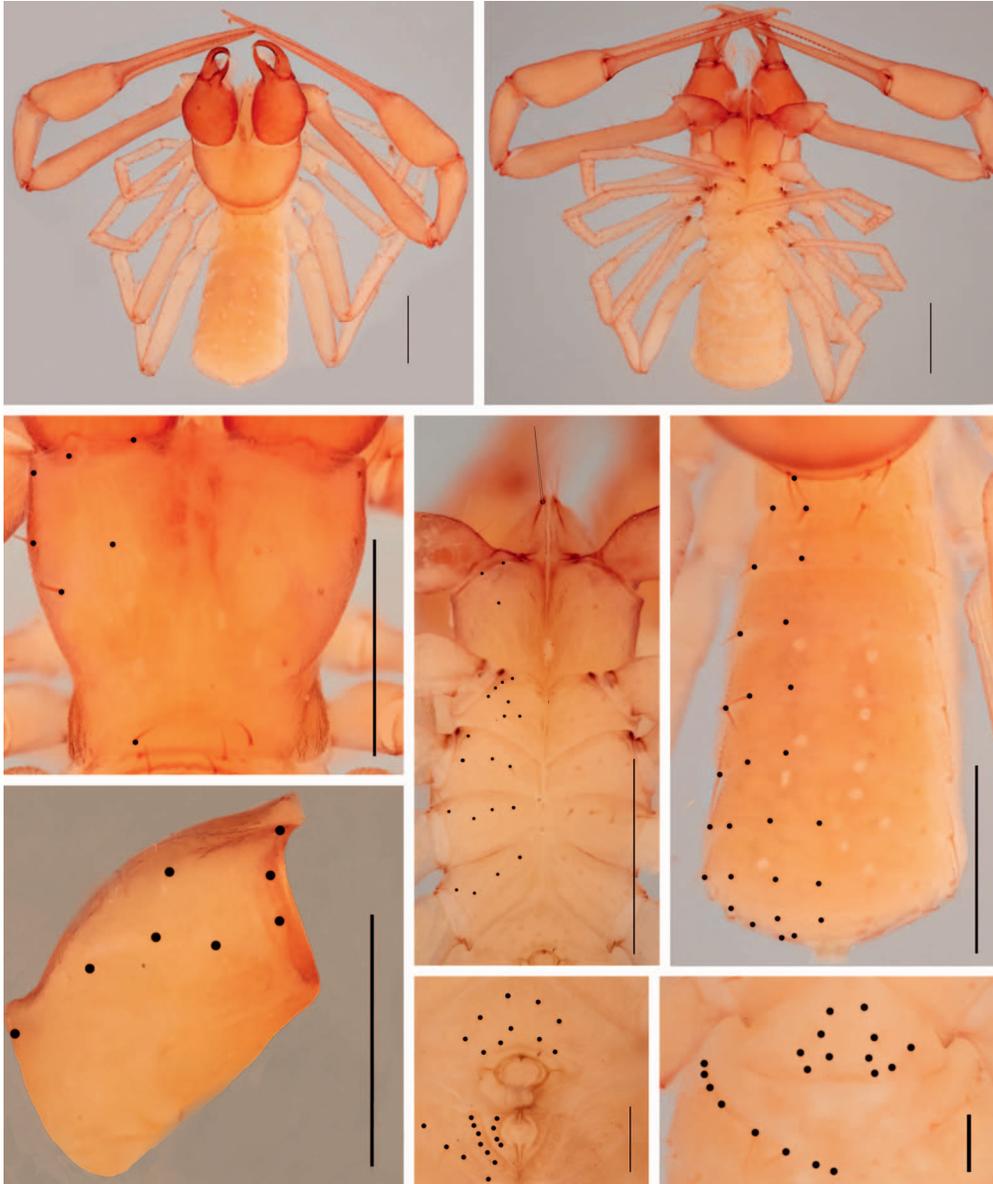
Figure 12.—*Spelaeochthonius seungsookae* sp. nov. (A–C, E, H: WAM T124507 paratype female; D, F, G: WAM T120626 holotype male): A, habitus in dorsal view; B, same in ventral view; C, carapace in dorsal view; D, coxal area in ventral view; E, abdomen in dorsal view; F, carapace in lateral view; G, male genitalia; H, female genitalia. Black dots indicate positions of setae. Scale bars: A–F = 0.5 mm; G–H = 0.1 mm.

exterior with fewer blades (21 vs. 24), and shape of the coxal spines (tips spatulate and plumose vs. pointed and plumose). Differs from all Japanese species by the high number of teeth on both chelal fingers (<31 in the Japanese fauna).

Description.—Adult male, holotype (WAM T120626). Color (in 75% ethanol): uniformly orange brown except chelicera which is darker brown.

Chelicera (Figs. 13A, B): hand broad 0.47/0.34 (in mm). Cuticle of hand squamate, with 5 setae, movable finger with 1 seta in medial position, fixed finger with 1 seta near basal position, all setae acuminate; movable finger with 14 teeth; 4 small teeth in distal position but distal teeth progressively larger, fixed finger with 13 teeth, distal teeth progressively larger than basal teeth except the most distal tooth; rallum (Fig. 14F) with 11 blades, distal blades progressively longer and feathered, serrula exterior (Fig. 14E) with 21 blades, distal blades progressively larger than basal blades.

Pedipalp (Figs. 13C–D; 15C–D): All setae acuminate; trochanter 2, femur 7.9, patella 3.7, chela 7.07, hand 2.3 x longer than broad, movable finger 2.01 x longer than hand, without large basal apodeme; both fingers straight in lateral view but both distal ends curved inwards; chelal finger homodentate, fixed finger with 35, movable finger with 35 acute and broad teeth that are slightly spaced, fixed finger with 3–7 more serrations basally, intercalary and accessory teeth absent, distance between teeth of movable finger and fixed finger 0.03 mm to 0.036 mm. External and internal chelal condyles small and rounded; fixed chelal finger and hand with 8 trichobothria plus duplex trichobothrium (*dt*), trichobothria *ib* and *isb* distally on dorsum of palm, *esb, ist* and *eb* forming
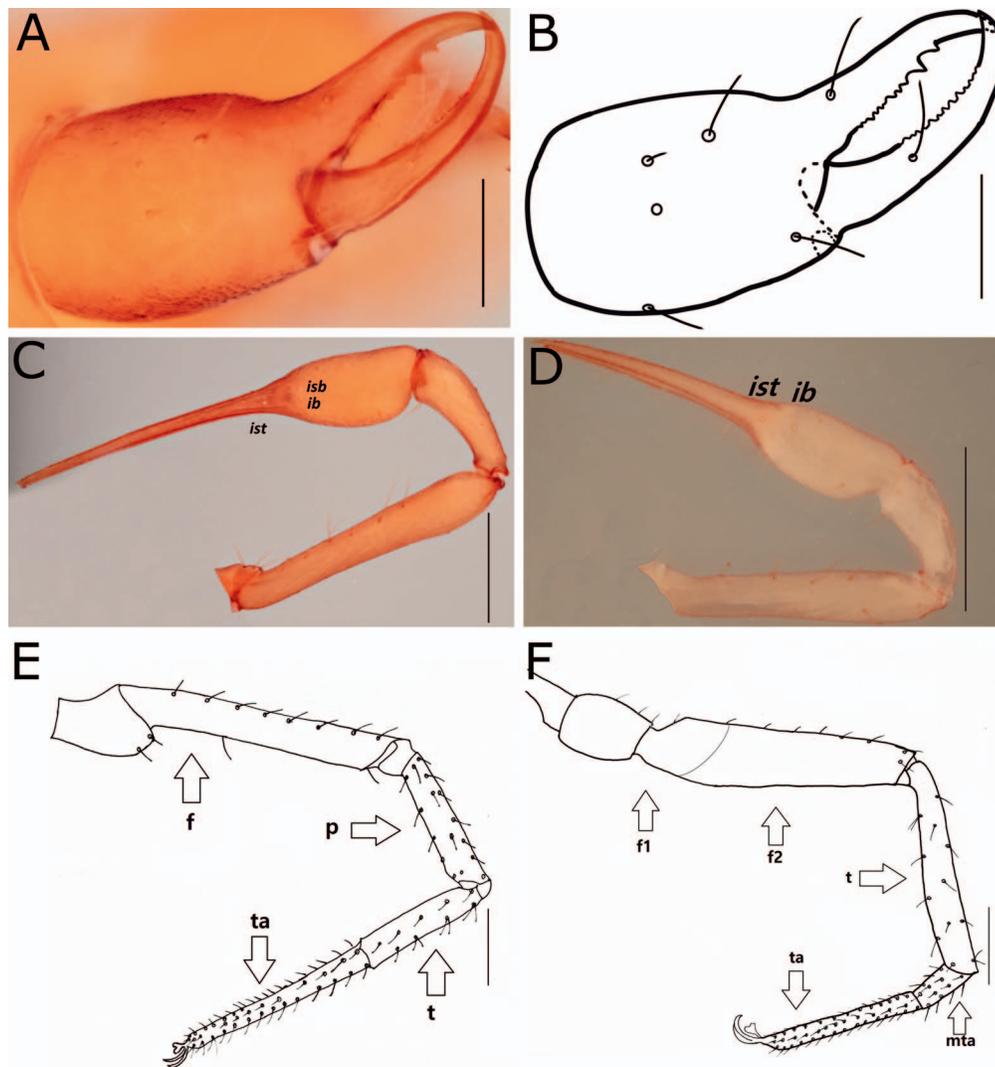
Figure 13.—*Spelaeochthonius seungsookae* sp. nov. (A–C, E, F: WAM T120626 holotype male; D: WAM T124406 paratype tritonymph): A, B, chelicera in lateral view; C, D, pedipalp in dorsal view; E, leg I in lateral view; F, leg IV in lateral view. Scale bars: A, B, E, F = 0.2 mm; C, D = 0.5 mm.

an oblique row sublaterally to dorsally at the base of the fixed chelal finger, *it* and *est* medial and forming a pair, *it* slightly more distal than *est*, *et* subdistal and *dt* distal, *dt* slightly closer to *et* than fingertip; movable finger with 4 trichobothria, triplet *sb*, *b* and *t* distomedial to distal, *st* sub-proximal, *b* closer to *t* than to *sb*.

Cephalothorax (Figs. 12C, F): Subquadrate, as long as broad, without furrows; lateral margins constricted posteriorly, eyes completely absent; epistome small, lightly sclerotized and lightly cuspid; with 16 setae arranged 6: 4: 2: 2: 2, seta *Mm* absent, all setae comparatively long.

Abdomen (Fig. 12E): Pleural membrane papillostriate; tergites and sternites undivided, setae uniseriate and acuminate; tergal chaetotaxy: 4: 4: 6: 6: 7: 7: 7: 5: 4: 2: 2: 0, sternal chaetotaxy: 16: 12: 12: 10: 12: 12: 6: 6: 4: –: 2.

Coxal area (Fig. 12D): Manducatory process with 2 acuminate distal setae, apical seta straight, about 3 times longer than subapical seta and extending to about half of the rallum (Fig. 14F), subapical seta dwarfed and bent towards interior margin; pedipalpal coxa with 3 setae, 2 at distal margin and 1 more medial near center, with 1 medial lyrifissure. Coxae I with 9 coxal spines (Figs. 14A, B), tripartite and distally spatulate with feathered margins, spaces between coxal spines equal, all spines arranged in an oblique row at apical, internal margin of the coxa; apical process of coxa I broadly rounded; coxal chaetotaxy: 7:4:4:5. Intercoxal tubercle (Figs. 14C; 15B) present, bisetose.

Legs (Figs. 13E, F): Typical of family. Leg I and IV, trochanter and femur with squamous sculpture, arolium (Figs. 14D; 15A) shorter than claws (Figs. 14D; 15A), undivided, claws hook-shaped.

Male genitalia (Fig. 12G): genital opening subtriangular, flanked by 2 valves with 2 rows of glandular setae; inner row with 5–6 setae and outer row with 4 setae; each valve with 1 oblique lyrifissure; anterior to opening another valve with 10 setae.

Dimensions (in mm): Body length 1.90. Pedipalp: trochanter 0.36/0.18, femur 1.27/0.16, patella 0.63/0.17, chela 1.9/0.28,
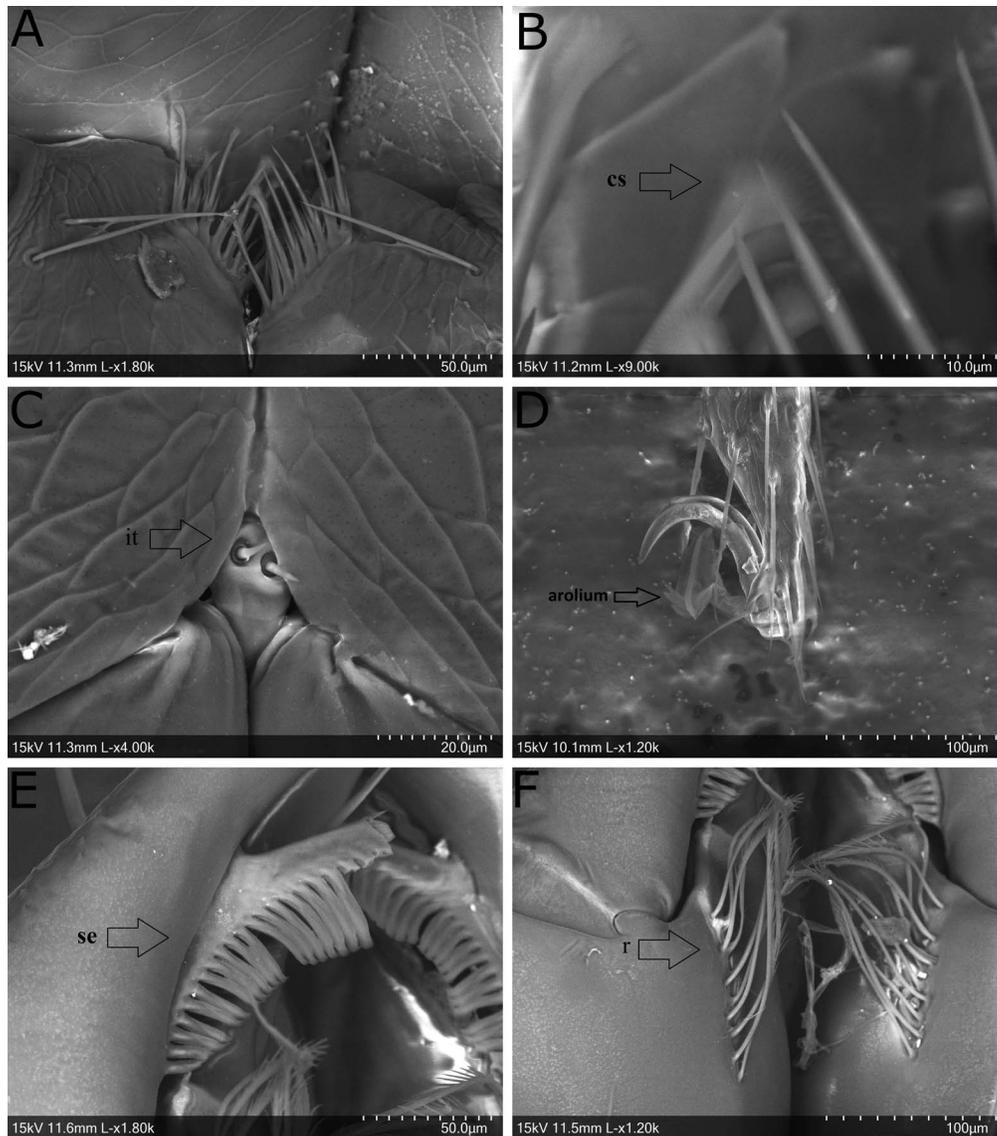
Figure 14.—*Spelaeochthonius seungsookae* sp. nov. (A–C, E, F: WAM T124406 paratype male; D: WAM T 124507 paratype female) scanning electron micrographs: A, coxal spines in overview; B same in detailed view; C intercoxal tubercle; D, arolium and claws of leg IV; E, serrula exterior; F, rallum. Abbreviations: cs = coxal spine; it = intercoxal tubercle; r = rallum; se = serrula exterior.

fixed finger length 1.25, hand length 0.63, movable finger length 1.27; Chelicera total 0.77/0.34, fixed finger length 0.34, movable finger length 0.4; cephalothorax 0.70/0.71 (anterior)/ 0.53 (posterior). Leg I: femur 0.75/0.09; patella 0.42/0.07; tibia 0.35/0.07; tarsus 0.75/0.05. Leg IV: femur 1 0.29/0.14; patella 0.68/0.13; tibia 0.59/0.11; metatarsus 0.31/0.07; tarsus 0.69/ 0.07

Adult female (WAM T124406, WAM T124507): As for male except as follows: larger body size (2.05–2.36 mm; 1.90–1.99 mm in males) and cuticle darker, genital opening (Fig. 12H) slit-like, with 11–14 glandular setae; fewer teeth of fixed finger (32–34).

Dimensions (in mm): body length 2.19; pedipalp: trochanter 0.28/0.22, femur 1.29/0.20, patella 0.59/0.19, chela 1.92/0.31, hand length 0.60, movable finger length 1.34; chelicera 0.90/ 0.33, movable finger length 0.44; cephalothorax 0.70/0.77.

Tritonymph (WAM T124406): Cuticle paler. Teeth on chela movable finger (25) and fixed finger (27).

Variation: Males (*n* = 4): Body length 1.90–1.99 mm, carapace 0.96–1.20 x longer than broad, chelicera 2.26–2.43 x longer than broad, 11–13 teeth on fixed finger of chelicera, teeth on palpal fixed finger (34–35). Females (*n* = 5): Body length 2.05–2.36 mm, carapace 0.80–1.20 x longer than broad, chelicera 2.20–2.38 x longer than broad, teeth on chela movable finger (33–35) and fixed finger (32–34).

Sequence data.—GenBank Accession No. MZ394007 for the holotype. It differs from its congeners by 13.9% and 15.1% pairwise divergence in the *COI* data respectively.

Distribution and ecology.—*Spelaeochthonius seungsookae* sp. nov. is most likely to be endemic to the Hogye karst-system near MunGyeong (Munkyung) College in Gyeongsangbuk-do Province. It is presently known from two caves. Specimens in Hogye Cave were relatively abundant and were collected from
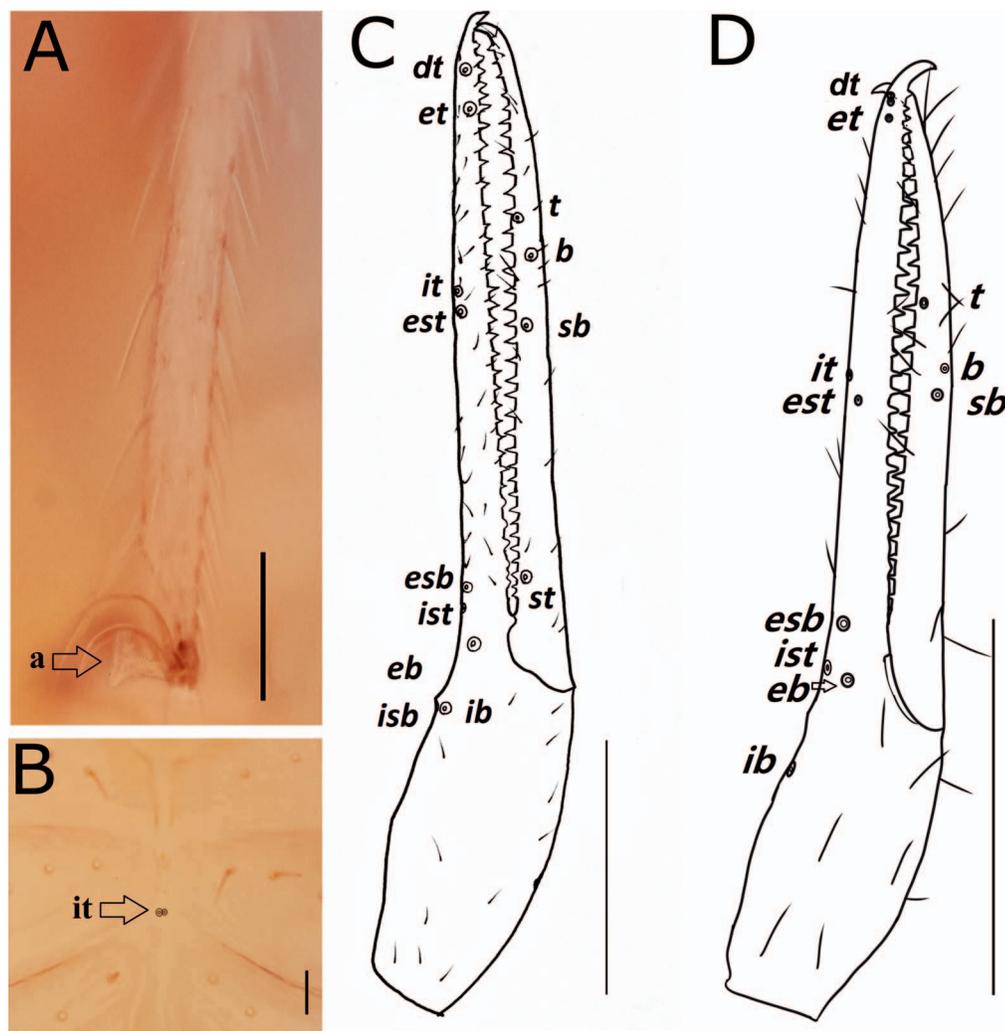
Figure 15.—*Spelaeochthonius seungsookae* sp. nov. (A, B, C: WAM T120626 holotype male; D: WAM T124406 paratype tritonymph): A, arolium and claws of leg I; B, intercoxal tubercle; C, D, pedipalp chela. Scale bars: A = 0.1 mm; B = 0.05 mm; C, D = 0.5 mm. Abbreviations: a = arolium; it = intercoxal tubercle.

under moist boulders and rocks on the cave floor in the first (dark) chamber (Fig. 5C). Wooro Cave is located at the base of a rock formation (Fig. 5B) and the specimen was collected deep within the cave. Note that Hogye Cave is also used as a shrine and seems to be visited frequently which increases the yield of organic materials in this cave, potentially explaining the abundance of pseudoscorpions.

Remarks.—The male specimen from Hogye-hangtigi Cave identified as *A. (S.) dentifer* by Morikawa (1970) undoubtedly belongs to *S. seungsookae*. This cave is situated 92 km from the type locality of *S. dentifer* and belongs to a different, geologically separate karst system (Fig. 8).

REASSESSMENT OF THE JAPANESE FAUNA

Our knowledge of range sizes in troglomorphic pseudo-scorpions has advanced significantly since Morikawa (1954, 1956, 1960) and it is now understood that most if not all subterranean pseudoscorpions have small distribution ranges and are typically confined to single karst systems or geological formations (e.g., the calcretes or mesas of Western Australia, see Harvey & Edward 2007, Edward & Harvey 2008; table mountains of South Africa, see Harvey et al. 2016; or karst formations across the world, e.g., see Beier 1939; Mahnert 2001; Kolesnikov & Turbanov 2018). This is also the case for all subterranean species of Pseudotyrannochthoniidae for which detailed data are available (Lawrence 1935; Dartnall 1970; Harms & Harvey 2013). A number of subspecies of nominate forms in the Japanese fauna have been described by Morikawa (1956) and these make little sense from the current perspective because there are major geographical distances between the nominal species and each subspecies, always spread across multiple prefectures and referring to separate karst systems (Table 1). Although he originally described each Japanese taxon of *Spelaeochthonius* as a distinct species (Morikawa 1954, 1956), he later relegated many of them to subspecies level, as well as describing a new subspecies (Morikawa 1960). These subspecies also differ morphologi-cally and were diagnosed in a key given in Morikawa (1960). We take the opportunity to update Morikawa's taxonomy and
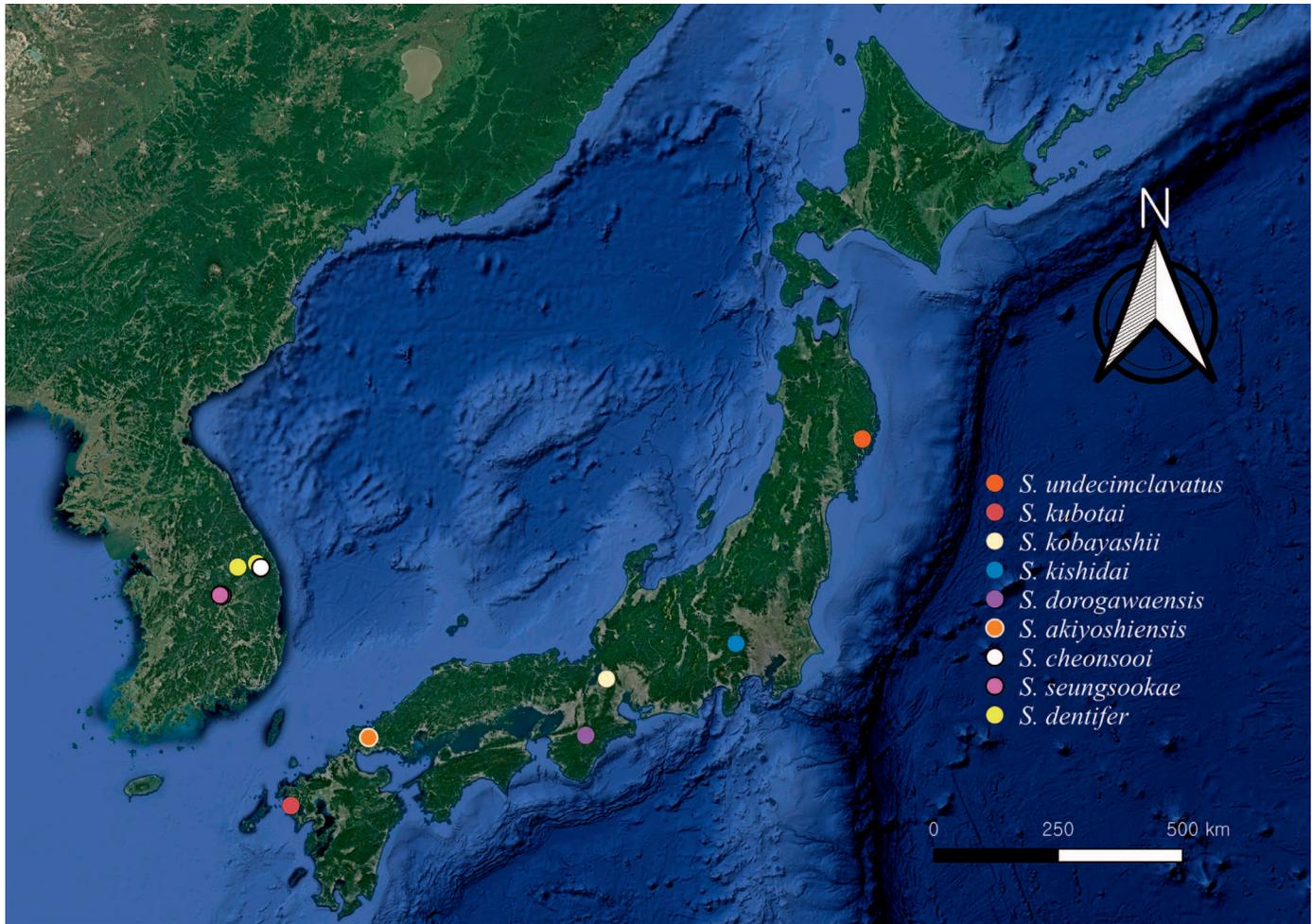
Figure 16.—Distribution of *Spelaeochthonius* species in Korea and Japan following this study.

elevate these taxa to species rank, even though the original material has not been studied for this manuscript (see above).

Spelaeochthonius kobayashii subsp. *akiyoshiensis* Morikawa, 1956 was originally described as a subspecies of *Spelaeochthonius kobayashii* based on two male specimens that were collected in Tanuki-ana Cave, Yamaguchi Prefecture. It was listed as a subspecies of *Allochthonius* (*Spelaeochthonius*) *kobayashii* by Morikawa (1960) following the revised ranking of *Spelaeochthonius* as a subgenus of *Allochthonius* that was established in the same publication (Morikawa, 1960). The species is currently named *Pseudotyranochthonius kobayashii akiyoshiensis* (Morikawa, 1956) following synonymy of *Spelaeochthonius* (or *Allochthonius* subgenus *Spelaeochthonius*) with *Pseudotyrannochthonius* by Muchmore (1967). The type locality of the nominal subspecies is from two caves in the Shiga Prefecture more than 470 km away (Fig. 16). According to Morikawa (1960: 107) it differed from the nominal subspecies by having 8–9 coxal spines vs. 7. It is here elevated to full species rank as *S. akiyoshiensis* Morikawa, 1956 **stat. nov.**

The type locality of *Spelaeochthonius kobayashii* subsp. *dorogawaensis* Morikawa, 1956 (currently *P. kobayashii dorogawaensis*) is also more than 117 km away from the type locality of the nominate subspecies (and 425 km away from the type locality of *S. akiyoshiensis*) and this form is similarly considered a unique species as *S. dorogawaensis* Morikawa, 1956 **stat. nov.** It differs from *S. kobayashii* by having 11 coxal spines and more blades on the flagellum (13 vs. 11).

Spelaeochthonius undecimclavatus Morikawa, 1956 was described from several caves in the Iwate Prefecture but the subspecies *Allochthonius* (*Spelaeochthonius*) *undecimclavatus kishidai* Morikawa, 1960 (currently *Pseudotyrannochthonius undecimclavatus kishidai*) was described from two caves in the Tokyo and Gifu Prefectures, more than 450 km away, hence its treatment here as the distinct species *S. kishidai* (Morikawa, 1960) **stat. nov.** The two species differ in carapace ratios, with *S. kishidai* being more slender and smaller (Morikawa 1956: 274). We note that for some taxa a similar situation as for *S. dentifer* is encountered and specimens from multiple caves and localities are listed in the original description, such as specimens from Tokyo Prefecture (Kurasawado-Cave) and Gifu Prefecture (Hotoke-ana) in the case of *S. kishidai*. A thorough revision of the Japanese fauna is therefore warranted but is beyond the scope of this study.

DISCUSSION

The family Pseudotyrannochthoniidae in South Korea & Japan.—Pseudotyrannochthoniid pseudoscorpions of the ge-
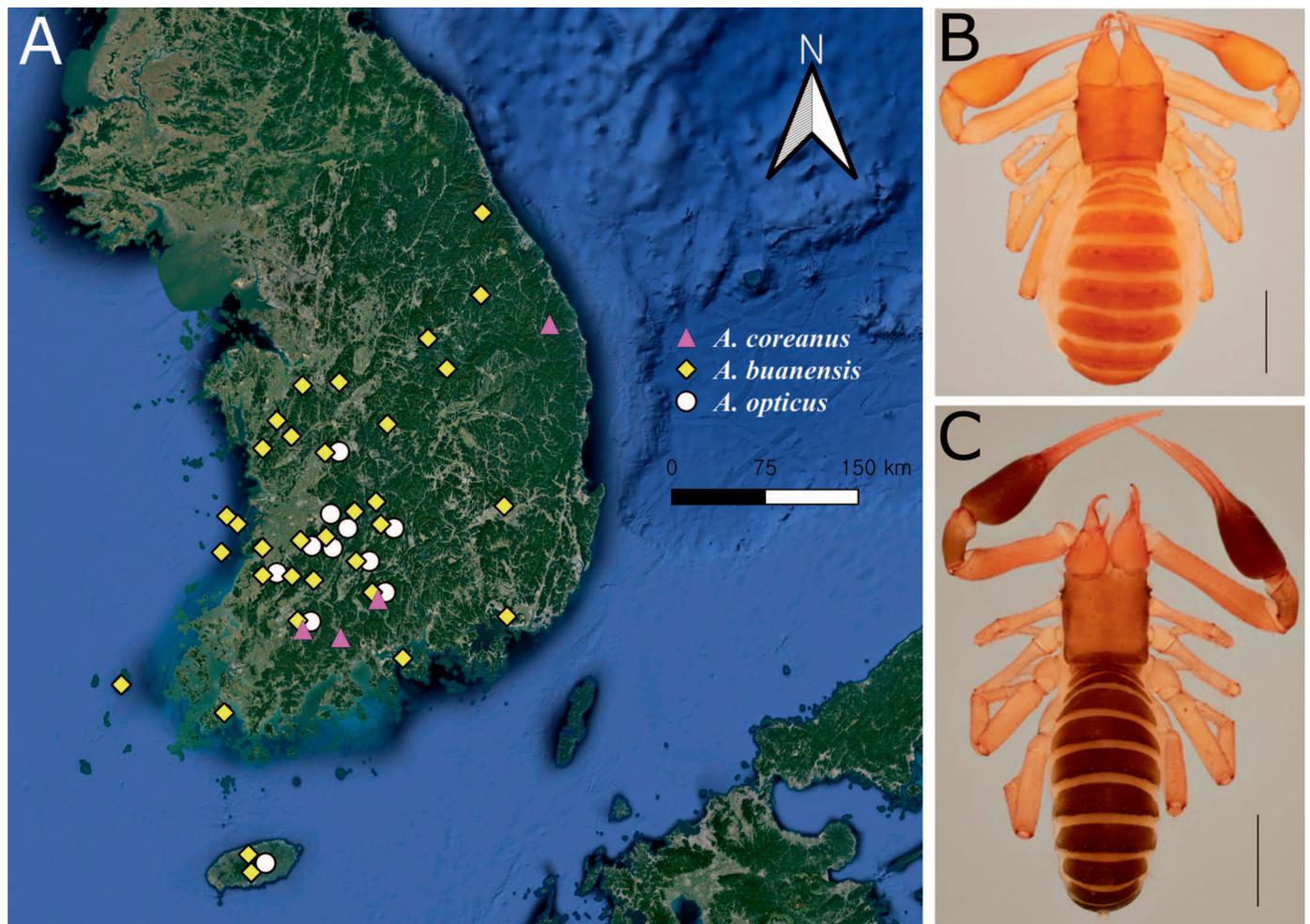
Figure 17.—Distribution of *Allochthonius* species in Korea and images of exemplar species: A, distributions mapped from available taxonomic literature and field collections by the authors; B, *Allochthonius* "*opticus*" from Korea; and C, *Allochthonius coreanus* from Korea (note the dark brown pedipalps that are diagnostic for this species). Scale bars: B, C = 0.5 mm.

nus *Allochthonius* are common and abundant in Korean forest ecosystems and past studies (e.g., Lee 1982; Lee & Seo 1995; Hong et al. 1996, 1997) suggest that the three species recorded from Korea, namely *A. buanensis* Lee, 1982, *A. coreanus* Morikawa, 1970 and *A. opticus* (Ellingsen, 1907), are widespread across the country and occur in a variety of ecosystems, including lowland forest and high-altitude habitats (Fig. 17). In contrast, all species of *Spelaeochthonius* are confined to subterranean habitats and have narrow ranges that seem to correspond to discrete units (e.g., limestone caves) in the karstic geomorphology (Fig. 8). From these data there seems to be niche-partitioning between these two genera with *Allochthonius* dominating surface habitats and *Spelaeochthonius* the karstic landscape. It should be noted here that *A. coreanus* may occasionally be found in caves (Morikawa 1970) but it is actually a surface species with eyes (Fig. 17), similar to some examples of troglophiles in the Australian fauna of Pseudotyrannochthoniidae (Harms & Harvey 2013).

In assessing species diversity for the family, it is important to note that the new species recorded here were collected in only four days of targeted survey visiting five caves. Korea has more than 1000 caves that are spread across discrete karst

systems and we suggest that many more species of *Spelaeochthonius* will occur in Korea. We also emphasize that not even the surface fauna of *Allochthonius* appears to be fully known. A recent barcoding study (Ohira et al. 2018) has highlighted cryptic speciation in *A. buanensis* which can be explained by the variety of habitats from which this species has been collected (Lee 1982; Hong et al. 1996). Moreover, the presence of *A. opticus* in Korea is doubtful since this species was originally described from Okayama, Japan (Ellingsen 1907) and the Korean specimens were matched based on the literature (Lee & Seo 1995; Hong et al. 1996) but without reference to Japanese material. In short, *Allochthonius* in Korea needs a thorough taxonomic review and *Spelaeochthonius* needs additional field surveys.

Comparing diversity across countries, we note that species diversity is higher in Japan where 17 species of *Allochthonius* and several subspecies have been recorded to date (Gao et al. 2016; Viana & Ferreira 2021) but many more undescribed species are known to occur (DH, unpublished data). The lists of material examined given by Morikawa (1956, 1960) also suggest that more species exist in karst systems across the country but no detailed studies have been conducted since the

Table 1.—Classification and localities for *Spelaeochthonius* species in Japan.

Previous classification	Type locality	Revised classification
Pseudotyrannochthonius kobayashii (Morikawa, 1956)	Honshū: Shiga Prefecture: Taga-chô, Samé-no-kômori-ana Cave (ca. 35°14′N, 136°18′E)	*Spelaeochthonius kobayashii* Morikawa, 1956
Pseudotyrannochthonius kobayashii akiyoshiensis (Morikawa, 1956)	Honshū: Yamaguchi Prefecture: Akiyoshi-dai, Tanuki-ana Cave (=Akiyoshidō Limestone Cave in Mine-shi) (ca. 34°14′N, 131°18′E)	*Spelaeochthonius akiyoshiensis* Morikawa, 1956 **stat. nov.**
Pseudotyrannochthonius kobayashii dorogawaensis (Morikawa, 1956)	Honshū: Nara Prefecture: Tenkawa-mura, near Dorogawa, Menfundô-no-iwaya Cave (ca. 34°15′N, 135°51′E)	*Spelaeochthonius dorogawaensis* Morikawa, 1956 **stat. nov.**
Pseudotyrannochthonius kubotai (Morikawa, 1954)	Kyūshū: Nagasaki Prefecture: Nishisonoki-gun: Nanatsugama-mura (Nanatsugama Limestone Cave), Shimizu-do (33°02′N, 129°39′E)	*Spelaeochthonius kubotai* Morikawa, 1954
Pseudotyrannochthonius undecimclavatus (Morikawa, 1956)	Honshū: Iwate Prefecture: Tōno-shi, Kamigomura, Sennin-togé Pass, Kutsukake, Kwannoniwa-no-ana Cave (ca. 39°16′N, 141°42′E)	*Spelaeochthonius undecimclavatus* Morikawa, 1956
Pseudotyrannochthonius undecimclavatus kishidai (Morikawa, 1960) [NB. listed as "*Spelaeochthonius* sp." on page 274 of Morikawa, 1956]	Honshū: Tokyo Prefecture: Okutama, Kurasawa-dô Cave (ca. 35°48″N, 139°6′E)	*Spelaeochthonius kishidai* (Morikawa, 1960) **stat. nov.**

1960s. Interestingly, the strict niche-partitioning in Korea between surface (*Allochthonius*) and subterranean (*Spelaeochthonius*) species is partly abandoned in Japan where three subterranean *Allochthonius* and six subspecies (that require taxonomic review, see above) are known to occur (Hu & Zhang 2012; Viana & Ferreira 2021) of which at least one (*A. biocularis* Morikawa, 1956) still retains rudimentary eye lenses. Importantly, subterranean *Allochthonius* and *Spelaeochthonus* do not seem to occur in sympatry. Considering the varying degrees of troglomorphism in these subterranean *Allochthonius*, one could hypothesize that the colonization of karst by *Allochthonius* is more recent than in the strongly-adapted *Spelaeochthonius,* but a phylogenetic framework is required to test this hypothesis.

Interestingly, no species of *Spelaeochthonius* have yet been recorded from China despite the abundance of karst habitats in this country and the ongoing discovery of troglomorphic pseudoscorpions in several provinces (Gao et al. 2018, 2020; Feng et al. 2019, 2020). Recent studies indicate that *Allochthonius* is diverse in forest habitats throughout China, with nine species already described (Gao et al. 2016) but, again, no subterranean species has been collected there to date and all troglobiontic species belong to the Chthoniidae (genera *Lagynochthonius* Beier, 1951 and *Tyrannochthonius* Chamberlin, 1929) and the Neobisiidae (*Bisetocreagris* Ćurčić, 1983 and *Parobisium* Chamberlin, 1930) (Feng et al. 2020) that have no known troglobiontic species in Korean caves.

Spelaeochthonius: systematics, ecology and biogeography.—*Spelaeochthonius* represents an interesting example of subterranean radiations without epigean species which is rather unusual amongst the pseudoscorpion taxa of Asia that otherwise comprise epigean species as well as subterranean species. All species in this genus are highly troglomorphic, with completely reduced eyes, long legs (a feature originally used by Morikawa 1954 to diagnose the genus), reduction of body pigment, and long cuticular setae (also emphasized by Morikawa 1954, 1956). This raises interesting questions about when and how subterranean habitats were colonized and when the surface fauna went extinct. Timing and mode of speciation are difficult to infer in the absence of a phylogenetic

framework but some hypotheses can be evoked by suggesting *Spelaeochthonius* as the sister-genus to *Centrochthonius*. The latter is poorly known but both genera share the presence of 16 setae on the carapace (e.g., Redikorzev 1934, fig. 19; Harvey & Harms 2022) and a similar (albeit discrete) morphology of the coxal spines (Gao et al. 2016; Schwarze et al. 2021; Harvey & Harms 2022). All occurrences of *Centrochthonius* are from high-altitude habitats in central Asia (China, Nepal and Kyrgyzstan) with regular snow, frost and long winters (Harvey & Harms 2022). Species have been collected from leaf litter during summer and spring (Redikorzev 1918, 1934; Schawaller 1991; Gao et al. 2016; Harvey & Harms 2022) but survival during extreme climates is probably by vertical migration within the soil during winter. *Spelaeochthonius* also favours cold habitats, and it is possible that both taxa represent an ancient radiation with some species persisting in high-altitude habitats (*Centrochthonius*) and *Spelaeochthonius* in caves. Both genera are quite distinct from *Allochthonius*, which is diverse in forested lowland habitats, primarily in the warm temperate forests of eastern Asia with some outliers in cool temperate regions [e.g., *A. ussuiensis* (Beier, 1979) from far-eastern Russia]. The recent discovery of both fossil *Allochthonius* and *Centrochthonius* species in succinite ambers from the Paleogene of Europe (Schwarze et al. 2021) is indicative of significant past extinction in this fauna and supports a relictual hypothesis for present-day distributions. It is easy to perceive that a lineage preadapted to cool conditions survived glacial cycling by colonizing cave habitats (or persisting in cool habitats; see *Centrochthonius*) whereas other pseudoscorpion lineages common in European ambers such as the Pseudogarypidae and Feaellidae were driven to extinction in the Palearctic by climate cycling (Harms & Dunlop 2017). When exactly karst was colonized by surface fauna within this lineage cannot be inferred but the degree of troglomorphism suggests that this is not a Pleistocene radiation and almost certainly older. The relictual hypothesis also has implications for *Allochthonius,* because this taxon may have responded to past glacial cycling, not with *in situ* persistence in caves, but rather local extinction and retreat to the southern Korean coast when temperate forests

were replaced by boreal systems or cold steppe elsewhere on the Korean Peninsula (Chung et al. 2017). The recent notion of cryptic speciation in *A. buanensis* (Ohira et al. 2018) could be explained this way, but also the general diversity of *Allochthonius* at the species level. Repeated range changes in temperate forest systems certainly have created the chance for vicariance (and therefore speciation) in this genus.

A second aspect to consider here is ecology rather than climate, specifically competition between mesopredator lineages in soil and even between the pseudoscorpion taxa that share this type of habitat. Benedict & Malcolm (1970) suggested out-competition as a reason for the rarity of American pseudotyrannochthoniids relative to other pseudoscorpions and this is also a likely scenario for the diverse eastern Asian fauna that includes a variety of chthoniid and neobisiid genera in leaf litter. Competition and niche-partitioning between *Allochthonius* and *Spelaeochthonius* but also the present neobisiid and chthoniid genera may play a role concerning the extinction of surface fauna in *Spelaeochthonius*.

Finally, at the morphological level our study highlights the importance of two morphological features that have not received significant attention in studies on Pseudotyrannochthoniidae, namely the coxal spines and the number of carapaceal setae, with the loss of seta *Mm* (Harvey & Harms 2022). The importance of the latter character had not been fully realised by past authors, probably because the number of setae was incorrectly noted by Beier (1930, 1931, 1932) for several genera (e.g., he noted 20 setae for *Centrochthonius* and *Pseudotyrannochthonius* but the correct numbers are 16 and 18 respectively). The presence of 16 setae is shared by all species of *Centrochthonius*, *Spelaeochthonius* and the North American pseudotyrannochthoniids (presently misclassified as *Pseudotyrannochthonius*) (Harvey & Harms 2022). All "Gondwanan" pseudotyrannochthoniids from Australia, South America, southern Africa, Madagascar and Sri Lanka have 18 setae. *Allochthonius* has variable and usually high numbers, typically between 18 and 28 (Gao & Zhang 2013), with only two species having fewer setae: *A. brevipes* Hu & Zhang, 2021 from China and *A. montanus* Sakayori, 2000 from Japan both have 16 setae but at least *A. brevipes* shares the typical coxal spine morphology of *Allochthonius,* and sequence data of a specimen of *A. montanus* indicates its correct placement in *Allochthonius* (Harvey & Harms 2022). The second important character is the coxal spines that differ drastically between taxa if methods other than light microscopy (e.g., scanning electron microscopy) are used. Again, past descriptions lack detail because technical possibilities did not allow an examination at the fine detail but both characters have phylogenetic signal and take precedence over other characters (e.g., setation of the tergites and sternites, shape of the chela) that have frequently been used.

Karst conservation and diversity in South Korea.—Korea has an extremely diverse karstic landscape that includes both limestone karst and lava tube caves on Jeju Island (Woo & Lee 2021), the latter even being listed as a World Heritage site by the UNESCO. New invertebrate species are being described from these systems each year, with recent discoveries including mainly stygofauna (e.g., Lee et al. 2020; Lee & Min 2021) but also some troglofauna. The latter includes climate relics

amongst the insect fauna such as the Grylloblattidae, that in Korea includes species in both mountain and cave habitats. This taxon follows the niche concept of persistence *in situ* over long periods of climatic change that we have proposed above for *Spelaeochthonius* (Schoville & Kim 2011). Amongst the arachnofauna, several spiders are known to be local cave endemics in Korea [e.g., Paik & Namkung (1967) for an example in the Cybaeidae; Kim & Lee (2004) for Pholcidae; and Namkung (1987) for Leptonetidae]. In all of these families, the subterranean species are part of larger radiations with many surface species in mixed forest habitats (e.g., Lan et al. 2021) and past climate cycling has not resulted in extinction of the surface fauna. Although the ecology and biology of most cave species remains poorly understood, it is possible that increasing temperature under global warming could have an impact, at least on glacial relics in Korean karst, such as Grylloblattidae and *Spelaeochthonius*. Small distribution ranges, local endemism and strong adaptation to the subterranean habitat together render this fauna particularly vulnerable, and informed conservation decisions should address climate change as well as the usual threats to cave fauna such as direct habitat destruction, dewatering, unsustainable agriculture and tourism (Niemiller et al. 2018). So far there is a lack of survey effort in Korea addressing subterranean fauna, and more field studies—embedded into a solid taxonomic framework—are needed to establish the baseline data for a legislative framework that insures protection of this fauna. A start could be to list such species in the Korean Red List of Threatened Species (2014) where this fauna is not currently considered.

ACKNOWLEDGMENTS

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