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Integrative taxonomy reveals multiple lineages of the spider genus *Cybaeus* endemic to the Ryukyu Islands, Japan (Arachnida : Araneae : Cybaeidae)

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Running title: Systematics of Ryukyu Islands *Cybaeus*

Abstract. The epigean spiders of the genus *Cybaeus* L. Koch, 1868 are known to have diversified in western North America and the Japanese Archipelago. To date, ca. 80 species of *Cybaeus* are known from Japan, but they have not previously been recorded from the Ryukyu Islands that harbour a diversity of endemic species. Here we describe eight new species of *Cybaeus* from the Ryukyu Islands, extending the range of *Cybaeus* southward to the central Ryukyus. Both sexes of each of the new species are described, and their phylogenetic relationships are estimated using nuclear and mitochondrial gene markers. Although *Cybaeus okumurai*, sp. nov. and *C. kumadori*, sp. nov. possess genital features that are common in the other Japanese congeners, the other six species (*C. yakushimensis*, sp. nov., *C. kodama*, sp. nov., *C. amamiensis*, sp. nov., *C. aikana*, sp. nov., *C. tokunoshimensis*, sp. nov., and *C. hikidai*, sp. nov.) are characterised by an elongated embolus and tubular spermathecae. These unique genital characteristics and the phylogeny recovered here suggest that these features evolved independently among the Japanese and Ryukyu *Cybaeus* species. Phylogenetic analyses highlight an unusual biogeographical pattern in which *C. yakushimensis* and *C. kodama* endemic to Yakushima Island in the northern Ryukyus are related to species distributed in the central Ryukyus. In contrast, our phylogeny suggests that *C. okumurai* from Tanegashima Island in the northern Ryukyus is sister to *C. ashikitaensis* (Komatsu, 1968) distributed in Kyushu of the Japanese Archipelago. The retreat constructs and sympatric distribution of *Cybaeus* found among the Ryukyus are also briefly discussed.

Additional keywords: island fauna, morphology, phylogenetics

Introduction

Spiders belonging to the genus *Cybaeus* L. Koch, 1868 are epigean species inhabiting moist woodlands in the Holarctic region (Bennett 2017). *Cybaeus* currently consists of 164 species with disjunct distributions from western Europe to the Caucasus, the northern Far East, and the eastern and western Nearctic, and is highly diverse in western North America and the Japanese Archipelago (World Spider Catalog, ver. 21.5, see https://wsc.nmbe.ch/, accessed 10 September 2020). Molecular phylogenetic analyses have revealed that *Cybaeus* spiders endemic to western North America comprise two distinctive lineages, the 'Holarctic' and 'Californian' clades (Copley *et al.* 2009). The Holarctic clade contains species widely distributed in North America and includes the type species of *Cybaeus*, *C. tetricus* (C.L. Koch, 1839), which is endemic to Europe (Bennett *et al.* 2016). By contrast, the species belonging to the Californian clade all have restricted ranges within western North America (Bennett *et al.* 2019). To date, 46 species of *Cybaeus* are known from North America (World Spider Catalog, ver. 21.5).

Japanese *Cybaeus* currently comprises 83 species (World Spider Catalog, ver. 21.5) indicating a high species richness in contrast to other East-Asian regions where only 14 and five species, respectively, are known from the Korean Peninsula, and the Russian Far East and Kuril Islands (Marusik and Logunov 1991; Marusik and Kovblyuk 2011; Seo 2017). Although their phylogenetic relationships remain uncertain, the Japanese *Cybaeus* have been classified by characteristics of the palp and female genitalia (Ihara 2009*a*). Morphology of the patellar apophysis, the retrolateral tibial apophysis, and the proximal arm of the conductor are crucial in male diagnoses. In females, features of the spermathecae are key characters. Each spermatheca of *Cybaeus* generally consists of three distinct parts: the head, stalk and base. The spermathecal heads of *Cybaeus* are distinguished by the presence of primary pores on their surface (Bennett 1992, 2006). Bennett's gland (Ramírez 2014) is typically located between the spermathecal stalk and the base (Bennett 1992). However, with the exception of *Cybaeus daimonji* Matsuda, Ihara & Nakano, 2020, primary pores and Bennett's gland have not been documented in Japanese *Cybaeus* (Matsuda *et al.* 2020).

An interesting evolutionary phenomenon known in Japanese *Cybaeus* is the sympatry between species of different-sized classes (see Ihara 2008). To help

understand their species-richness and sympatric distributions, Japanese *Cybaeus* have been divided into three groups according to the body length of mature individuals as defined by Roth (1993): 'small-sized', with body length less than 5 mm; 'medium-sized', ranging from 5 to 10 mm; and 'large-sized', greater than 10 mm (Ihara 2004).

In addition to the genital and size-related features, ca. 42 of 83 of the Japanese species of *Cybaeus* are known to construct tube-like silken retreats on undersides of stones and woods (Y. Ihara, unpubl. data; see Ihara 2009*b*). The most common form of retreat is 'V-shaped' with two openings, one at each end (Ihara 2006). A similar V-shaped retreat is built by the Appalachian hahniid *Cicurina bryantae* Exline, 1936 (Bennett 1985). However, retreats of *Cybaeus* feature silk signal threads radiating from the openings; no such signal threads are present in the retreats of *Cicurina bryantae* (see Matsuda *et al.* 2020). In addition to the V-shaped form, three less common types of retreats are constructed by the Japanese *Cybaeus*: V-shaped with three openings, 'Y-shaped' with three openings, and hexagonal with three openings (Komatsu 1961, 1968; Ihara 2003, 2009*b*). Retreats with three openings were known previously only from troglobitic species inhabiting northern Honshu Island and Shikoku Island in the Japanese Archipelago (Komatsu 1961, 1968), but recent studies have shown that epigean species distributed in western Honshu and northern Kyushu Island also construct retreats with three openings (Ihara 2003, 2009*b*).

Prior to our work, the southern distributional limit of Japanese *Cybaeus* was documented as Kyushu in the Japanese Archipelago (Ihara 2009*a*). To our knowledge *Cybaeus* spiders have not previously been recorded from the Ryukyu Islands, which form a continental island arc south of Kyushu between the Japanese Archipelago and Taiwan. The Ryukyu Islands are known to harbour a unique biota with a wide variety of endemic species, including various epigean/ground-dwelling spiders (e.g. Shimojana and Haupt 1998; Shimojana 2000; Tanikawa and Miyashita 2008; Xu *et al.* 2019). The Ryukyu Islands are comprised of three major biogeographic divisions: Northern Ryukyus (Tanegashima Island and Yakushima Island, and adjacent islets), Central Ryukyus (Amamioshima Island, Tokunoshima Island, and Okinawa Islands, and adjacent islets), and Southern Ryukyus (Miyako Islands and Yaeyama Islands). The divisions are separated by two tectonic depressions, the Tokara and Kerama Gaps (e.g. Ota 1998; Motokawa 2000). In the present study, *Cybaeus* spiders were collected from

several islands in the Northern and Central Ryukyus. Here we present their systematic accounts including an assessment of their phylogenetic relationships based on nuclear and mitochondrial gene markers.

Materials and methods

Samples and morphological observation

Previously undescribed species of *Cybaeus* spiders were collected from six islands in the Ryukyu Islands, Japan. For comparative purposes for the molecular phylogenetic analyses, specimens of a further nine Japanese species, including *C. ashikitaensis* (Komatsu, 1968), *C. daimonji*, *C. fuujinensis* (Komatsu, 1968), *C. gotoensis* (Yamaguchi & Yaginuma, 1971), *C. itsukiensis* Irie, 1998, *C. kompiraensis* (Komatsu, 1968), *C. kunisakiensis* Ihara, 2003, *C. striatipes* Bösenberg & Strand, 1906, and *C. ishikawai* (Kishida in Komatsu, 1940), were also collected from or near their type localities (Table 1). In addition, one male and two female specimens of *C. ashikitaensis* were examined for morphological comparison: 1 #, 1 @ from the type locality (KUZ Z3675, Z3677); 1 @ from Ebino, Miyazaki, Kyushu Island (KUZ Z3676). Where possible, geographical coordinates for the collection sites were obtained using a GPS unit (eTrex®, Garmin, Olathe, KS, USA). Specimens were preserved in 70% ethanol; legs of some specimens were removed and preserved in 99% ethanol for DNA extraction.

Epigynes were dissected from various female specimens and cleared with proteinase K (100 μg/mL) (see Matsuda *et al.* 2020), or with hot 10% KOH + 3% H_2O_2 (see Komatsu and Yaginuma 1968) to observe the internal structure. When more than one female could be examined per species, several specimens were dissected. Morphological examination of the specimens was conducted using a stereoscopic microscope (models MZ-7.5 and M125C, Leica, Wetzlar, Germany). Images of specimens and their dissected parts were captured with the aid of a digital microscope (VHX-5000, KEYENCE, Osaka, Japan). Measurements were taken to the nearest 0.01 mm. Specimens examined in this study have been deposited in the Zoological Collection of Kyoto University (KUZ).

Terminology of morphological characters follows Bennett (2005, 2017) and Bennett *et al.* (2016, 2019), with the exception of one structure on the bulb, which was

referred to as the 'tegular apophysis' by these studies, but is referred to herein as a 'conductor' (Matsuda *et al*. 2020). The chaetotaxy of leg macrosetae follows Komatsu (1968); abbreviations for macrosetae are: p, prolateral; r, retrolateral; v, ventral. The following abbreviations are also used in the text and figures: AER, anterior eye row; AME, anterior median eyes; BG, Bennett's gland; CD, copulatory duct; CL, carapace length; CP, copulatory pore; CW, carapace width; EM, embolus; FD, fertilization duct; PA, patellar apophysis; PCO, proximal arm of conductor; PER, posterior eye row; PME, posterior margin of epigynal plate; PP, primary pore; RTA, retrolateral tibial apophysis; SB, spermathecal base; SH, spermathecal head; SP, simple pore; SS, spermathecal stalk; TibIL, length of leg I tibia.

PCR and DNA sequencing

The procedure for extraction of genomic DNA from leg muscle was modified from Nakano (2012). Primer sets for the polymerase chain reactions (PCR) and the cycles sequencing (CS) reactions used for nuclear histone H3 (H3), internal transcribed spacer 1 (ITS-1), mitochondrial cytochrome *c* oxidase subunit I (COI), and 16S ribosomal RNA (16S) followed Nakano *et al.* (2017), and those for nuclear 28S ribosomal RNA (28S) and mitochondrial 12S ribosomal RNA (12S) were as indicated in Matsuda *et al.* (2020). In addition to the previously established primer set for COI, a new primer set, COIARAF (5′-ACAAATCATAAAGATATTGC-3′) and COIARAR (5′-ATAGCATAAATTATTCCTAA-3′), was designed using Primer3 (ver. 0.4.0, see http://bioinfo.ut.ee/primer3-0.4.0/; Koressaar and Remm 2007; Untergasser *et al.* 2012).

PCR reactions and DNA sequencing were performed using the method outlined by Matsuda *et al.* (2020). All PCR reactions were performed using a GeneAmp PCR System 9700 (Thermo Fisher Scientific, Waltham, MA, USA), or a GeneAtlas (ASTEC, Shime, Fukuoka, Japan) using an Ex Taq Polymerase Kit (Takara Bio Inc., Kusatsu, Shiga, Japan) The PCR mixtures were heated to 94°C for 6 min, followed by 35 cycles at 94°C (10 s), 40°C for COI and 16S or 50°C for the other markers (20 s), and then 72°C (42 s), with a final extension at 72°C for 6 min. The amplified DNA fragments were purified using polyethylene glycol (20% PEG 6000) precipitation.

All samples were sequenced in both directions. The CS reactions were performed using a BigDye Terminator ver. 3.1 Cycle Sequencing Kit (Thermo Fisher

Scientific). Each CS reaction mixture was incubated at 96°C for 2 min, followed by 40 cycles of 96°C (10 s), 50°C (5 s), and 60°C (42 s). The products were collected by ethanol precipitation and sequenced on an ABI 3130*xl* Genetic Analyzer (Thermo Fisher Scientific). The obtained sequences were edited using DNA BASER (Heracle Biosoft S.R.L., Piteşti, Argeş, Romania). The DNA sequences obtained in this study were deposited with the DNA Databank of Japan (DDBJ).

Molecular phylogenetic analyses

Phylogenetic relationships of the Ryukyu *Cybaeus* spiders were estimated based on the dataset consisting of H3, ITS-1, 28S, COI, 12S and 16S sequences obtained from 24 samples (Table 1); *C. daimonji* and *C. striatipes* were treated *a priori* as the outgroup. The alignments of H3 and COI were trivial, as no indels were observed. The 12S and 16S sequences were aligned using MAFFT L-INS-i (ver. 7.453, see https://mafft.cbrc.jp/alignment/software/; Katoh and Standley 2013), ITS-1 sequences were aligned using MAFFT FFT-NS-i, and 28S sequences were aligned by MAFFT G-INS-i. The lengths of the H3, ITS-1, 28S, COI, 12S, and 16S were 328, 761, 793, 763, 335, and 441 bp, respectively. The concatenated sequences thus yielded 3421 bp of aligned positions.

Phylogenetic trees were reconstructed using maximum likelihood (ML) and Bayesian inference (BI). The best-fit partition scheme and models were identified based on the corrected Akaike information criterion (AICc) using PartitionFinder (ver. 2.1.1, see http://www.robertlanfear.com/partitionfinder/; Lanfear *et al.* 2017) with the 'greedy' algorithm (Lanfear *et al.* 2012). The selected partition scheme and models were as follows: for H3 1st position, TRN+G (ML), or GTR+I (BI); for H3 2nd position, JC+I; for H3 3rd position, HKY+G; for ITS-1, GTR+I+G; for 28S, K81UF+I (ML), or GTR+I (BI); for COI 1st position, TVM+I+G (ML), or GTR+I+G (BI); for COI 2nd position, GTR+I; for COI 3rd position, TIM+I+G (ML), or GTR+I+G (BI); and for 12S and 16S, GTR+G. The ML phylogenetic tree was calculated using IQ-TREE (ver. 2.0-rc1, see http://www.iqtree.org/; Minh *et al.* 2020) with non-parametric bootstrapping (BS) conducted with 1000 replicates. BI tree and Bayesian posterior probabilities (PP) were estimated using MrBayes (ver. 3.2.7a, see https://nbisweden.github.io/MrBayes/download.html; Ronquist *et al.* 2012). Two

independent runs for four Markov chains were conducted for 15 million generations, and the tree was sampled every 100 generations. The parameter estimates and convergence were checked using Tracer (ver. 1.7.1, see http://tree.bio.ed.ac.uk/software/tracer/; Rambaut *et al.* 2018), and the first 40001 trees were discarded based on the results.

Species recognition and taxonomic arrangement

In this study, we define a full-species account for each operational taxonomic unit (OTU) by an integrative approach based on results of both morphological examination and molecular phylogenetic analyses. We preliminary recognised OTUs by morphological distinctiveness taking into account their allopatric distributions in the Ryukyu Islands. We then verified taxonomic status of each of the morphology-based OTUs by our molecular phylogeny. The morphology-based OTU, which forms a monophyletic lineage, is defined as a unique species. All new species described here are arranged according to the results of our phylogeny and their distributions in the north-south direction along the Ryukyu Islands.

Results

Phylogenetic relationships

The obtained BI (mean ln $L = -10554.32$; Fig. 1) and ML (ln $L = -10487.61$; not shown) tree had almost identical topologies. Although our analyses failed to resolve basal relationships of the in-group taxa, they demonstrated that the eight new species of *Cybaeus* spiders from the Ryukyu Islands comprise five lineages (lineages A−E in Fig. 1). Lineage A, which was not supported in the ML analysis (BS < 50%, PP = 0.96), consists of the three species distributed in Kyushu (*C. fuujinensis*, *C. kunisakiensis*, and *C. ashikitaensis*) and the new species (*C. okumurai*, sp. nov.) from Tanegashima Island in the Northern Ryukyus (Fig. 1, 2); the monophyly of a group containing *C. ashikitaensis* and *C. okumurai*, sp. nov. was fully supported (BS = 100%, PP = 1.0). Lineage B comprises only *C. kumadori*, sp. nov. from Kuroshima Island (Northern Ryukyus) (Fig. 1, 2). Lineage C consists of a single specimen (*C. aikana*, sp. nov.) from Amamioshima Island in the Central Ryukyus (Fig. 1, 2). Four species from the Ryukyu Islands (*C. yakushimensis*, sp. nov., *C. amamiensis*, sp. nov., *C. tokunoshimensis*, sp.

nov., and *C. kodama*, sp. nov.) constitute the monophyletic lineage D (BS = 85%, PP = 0.99) (Fig. 1, 2): two of these (*C. yakushimensis*, sp. nov. and *C. kodama*, sp. nov.) appear to be endemic to Yakushima Island but did not form a clade while the monophyly of the species from Amamioshima Island (*C. amamiensis*, sp. nov.) with the one from Tokunoshima Island (*C. tokunoshimensis*, sp. nov.) was fully supported (BS = 100%, PP = 1.0); the species from Yakushima Island (*C. yakushimensis*, sp. nov.) forms a monophyletic lineage with the Amamioshima-Tokunoshima clade, although this relationship was not fully supported (BS = 65%, PP < 0.70). The remaining lineage E only contains the species from Okinawa Island (*C. hikidai*, sp. nov.) in the Central Ryukyus (Fig. 1, 2).

Systematics

Family **Cybaeidae** Banks, 1892

Genus ***Cybaeus*** L. Koch, 1868

Cybaeus L. Koch, 1868: 46. Type species: *Amaurobius tetricus* C.L. Koch, 1839.

Diagnosis

As stated in Copley *et al.* (2009), a differential diagnosis of the genus *Cybaeus* remains unclarified, but species of this genus can be distinguished from other genera of Cybaeidae by the following combination of characters (see Copley *et al.* 2009; Bennett 2017; Bennett *et al.* 2020): two or three complete pairs of linearly arranged ventral macrosetae on tibia I (sometimes four or five pairs are present, but not arranged in a linear pattern), the presence of a retrolateral PA with peg setae in the male palp (Japanese species rarely lack a PA), the well-developed conductor on the male bulb but never with a flat and plate-like proximal arm, and, in the female, each spermatheca with a large SB and Bennett's gland.

Cybaeus okumurai, sp. nov.

http://zoobank.org/NomenclaturalActs/1676AFDB-F79C-490F-B8CE-4F1554855B78

(Fig. 3, 4*A*–*C*, *F*, *G*, 5*B*, *C*)

Material examined

Holotype. **Japan**: *Ryukyu Islands*: Tanegashima Island: #, Kunigami, 30°47′56.8″N, 130°02′58.6″E, 9.xii.2019, Y. Ihara (KUZ Z3019).

Paratypes. **Japan**: *Ryukyu Islands*: Tanegashima Island: 3 #, 4 @, collected with holotype (KUZ Z2719, Z3021–Z3026); ditto, 1 #, T. Nakano (KUZ Z3020).

Additional specimens. **Japan**: *Ryukyu Islands*: Tanegashima Island: 2 #, 5 @, collected with holotype (KUZ Z2720–Z2722, Z3027, Z3028); 1 #, 4 @, Kunigami, Kishigazaki, 30°50′06.1″N, 131°03′32.1″E, 9.xii.2019 (KUZ Z3691, Z3692); 8 #, 17 @, Nishino-omote, near Saikyo Dam, 30°45′55.8″N, 131°02′06.1″E, 9.xii.2019 (KUZ Z3693–Z3696); 4 #, 6 @, Anno, 30°44′05.7″N, 131°02′52.9″E, 7.xii.2019 (KUZ Z3697–Z3699; 6 #, 11 @, Furuta, 30°39′16.5″N, 131°00′50.0″E, 8.xii.2019 (KUZ Z2725, Z2727, Z2729, Z2730, Z3700–Z3702); 1 @, Nokan, 30°35′01.7″N, 130°59′07.2″E, 8.xii.2019 (KUZ Z3703); 8 #, 3 @, Nakanokami, 30°26′01.3″N, 130°55′23.6″E, 8.xii.2019 (KUZ Z2728, Z3704–Z3706); 4 #, 7 @, Nakanoshimo, 30°23′19.1″N, 130°54′23.2″E, 8.xii.2019 (KUZ Z2723, Z2724, Z2726, Z3707, Z3708); 1 #, Anjo, 4.i.2013, Ken-ichi Okumura (KUZ Z3709); 2 @, Anno, Mt. Amamegakura, 4.i.2013, K. Okumura (KUZ Z2716, Z2717); 1 #, 1 @, Furuta, 3.i.2013, K. Okumura (KUZ Z3710); 1 #, 1 @, ditto, 4.i.2013, K. Okumura (KUZ Z3711).

Diagnosis

Small to medium-sized Japanese *Cybaeus*. Both sexes of *C. okumurai* most closely resembles males and females of *C. ashikitaensis*. However, males of *C. okumurai* can be distinguished by their relatively wider palpal patella and tibia, and slightly prolonged PA > 0.25× as long as the patella (Fig. 4*B*, *C*); males of *C. ashikitaensis* have a relatively slender patella and tibia, and slightly small PA ca. 0.2× as long as the patella (Fig. 4*D*, *E*). Females of *C. okumurai* differ from those of *C. ashikitaensis* in the tightly and simply curved posterior margin of epigynal plate, and spermathecae nearly as long as wide (Fig. 5*A*, *B*) (loosely and compoundly curved posterior margin of epigynal plate, and spermathecae ca. 2× wider than long in the latter; Fig. 5*C*, *D*).

Description

Male (*holotype*, *KUZ Z3019*)

Measurements (*mm*). CL 2.96, CW 2.16; head 1.30 wide; abdomen 2.64 long, 1.94 wide. Ocular area 0.32 long, 0.76 wide. Sternum 1.34 long, 1.30 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 10.17 (2.64 + 0.96 + 2.53 + 2.44 + 1.60); leg II 9.70 (2.60 + 0.96 + 2.27 + 2.40 + 1.47); leg III 8.52 (2.34 + 0.86 + 1.81 + 2.26 + 1.25); leg IV 10.41 (2.75 + 0.89 + 2.40 + 2.88 + 1.49).

Carapace (Fig. 3*A*). Head narrow, 0.60× as wide as thoracic region; thoracic region slightly higher than head. AER slightly procurved in frontal view; PER slightly recurved in dorsal view; AME smallest, slightly > 1/2 diameter of other eyes; ocular area relatively wide, ca. 2.4× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 3 teeth and 6 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p2, r2, v2-2-2-2; metatarsus p3 (left) or 4 (right), r2, v2-2-2. Leg II: tibia p4 (left) or 3 (right), r3 (left) or 2 (right), v2-2-1(r)-2; metatarsus p4, r3, v2-2-3.

Abdomen (Fig. 3*B*). Oval; mid-posterior part widest (Fig. 3*B*). Colulus two groups of 3 or 5 setae.

Palp (Fig. 4*A–C*, *F*, *G*). PA digitiform, extended anteriorly, slightly bent dorsally, dorsolateral surface with 14 peg setae. Tibia shorter than patella; RTA plate-like, occupying most of length of tibia. Cymbium slender, > 2.5× longer than wide, expanded prolaterally. Genital bulb circular in ventral view. Conductor: distal part long, curved; proximal arm short, expanded. Embolus simple, originating and terminating, respectively, at ca. 10 o'clock and ca. 4 o'clock in ventral view.

Colour (Fig. 3*A*, *B*). Carapace: head yellowish brown, with reticulate olive black markings; thoracic region bright yellowish-brown, with radiating olive black bands. Chelicerae reddish brown, maxillary lobe and labium bright brown. Sternum bright yellowish-brown, darker toward margins. Legs bright yellowish-brown, darker distally, with olive black annulations. Abdomen: dorsally olive black with pale yellow chevron pattern; ventrally pale yellow.

Female (*paratype*, *KUZ Z3023*)

Measurements (*mm*). CL 2.71, CW 1.85; head 1.22 wide; abdomen 3.18 long, 2.34 wide. Ocular area 0.30 long, 0.74 wide. Sternum 1.26 long, 1.17 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 8.03 (2.20 + 0.86 + 2.00 + 1.88 + 1.09); leg II 7.71 (2.14 + 0.85 + 1.84 + 1.84 + 1.04); leg III 6.70 (1.91 + 0.79 + 1.36 + 1.72 + 0.92); leg IV 8.55 (2.30 + 0.78 + 1.98 + 2.34 + 1.15).

Carapace (Fig. 3*C*). Head 0.66× as wide as thoracic region; thoracic region almost as high as head. AER straight in frontal view; PER slightly recurved in dorsal view; AME smallest, slightly < 1/2 diameter of other eyes; ocular area relatively wide, ca. 2.5× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 5 teeth and 5 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p2, r0 (left) or 1 (right), v2-2-2-2; metatarsus p3, v2-2-2. Leg II: tibia p3, v2-2-1(r)-1(p); metatarsus p4, r0 (left) or 1 (right), v2-2-3.

Abdomen (Fig. 3*D*). Oval; mid-posterior part widest. Colulus two groups of 4 or 5 setae.

Genitalia (Fig. 5*A*, *B*). Posterior margin of epigynal plate curved. Atrium slightly concave, located posteromedially on epigynum. Copulatory pores separated on either sid of atrium; CD long, thick, widened laterally. Each of SH, SS, and SB distinct, bulbous; SH with at least 1 detectable primary pore posteromedially; distal end of SS with Bennett's gland medially; SB large, extended anterolaterally.

Colour (Fig. 3*C*, *D*). Carapace: head brown, with faint olive-black markings; thoracic region bright yellowish-brown, with faint radiating black bands. Chelicerae bright brown, maxillary lobe and labium yellowish brown, sternum bright yellowish-brown. Legs bright yellowish-brown, with olive black annulations. Abdomen: dorsally olive black with light yellow chevron pattern; ventrally pale yellow.

Variation

Males (*n* = 12). Measurements (mean, followed by ranges in parentheses): CL 2.82 (2.50–2.96), CW 2.03 (1.82–2.16); CW/CL 0.72 (0.69–0.74); TibIL 2.40 (2.14–2.58); TibIL/CL 0.85 (0.82–0.87). Legs longer than those of females. Palp: dorsolateral

surface of PA with 10–14 peg setae.

Females (*n* = 27). Measurements (mean, followed by ranges in parentheses): CL 2.38 (1.72–3.06), CW 1.67 (1.18–2.14); CW/CL 0.70 (0.66–0.74); TibIL 1.70 (1.09–2.28); TibIL/CL 0.71 (0.63–0.78).

Distribution

This species is endemic to forest habitats on Tanegashima Island (Fig. 2).

Remarks

Cybaeus okumurai constructs a V-shaped retreat (Fig. 22*A*).

The genital characters are consistent among the female specimens of *C. okumurai*, but nonetheless, their body sizes could be grouped into two variants, small (ca. 3.5–4 mm) and medium (ca. 6–7 mm) types. Both body-size types occur syntopically at all collecting sites. The ITS-1 sequences, which yielded 697 bp pf aligned positions, obtained from the six males (KUZ Z2719, Z2721, Z2724, Z2727–Z2729; INSDC accession numbers: LC552282, LC574069–LC574073), three small (KUZ Z2720, Z2726, Z2730; LC574074–LC574076) and three medium (KUZ Z2722, Z2723, Z2725; LC552285, LC574077, LC574078) females were almost consistent with each other; but 1 identical deletion was detected in six sequences of KUZ Z2721, Z2722, Z2724, Z2725, Z2727, Z2728. These results corroborate that the males and the variety-sized females all belong to the same species.

Etymology

The specific name is dedicated to Dr. Ken-ichi Okumura for providing valuable specimens of this new species.

Cybaeus kumadori, sp. nov.

http://zoobank.org/NomenclaturalActs/E220EE51-716C-410A-B733-3675BBBAC7FC

(Fig. 6, 7)

Material examined

Holotype. **Japan**: *Ryukyu Islands*: Mishima Islands: #, Kuroshima Island, Mt.

Yaguradake, 30°49′52.8″N, 129°56′02.1″E, 13.xii.2012, N. Koike (KUZ Z3004).

Paratypes. **Japan**: *Ryukyu Islands*: 3 #, 4 @, collected with holotype (KUZ Z2143, Z2144, Z3005–Z3009).

Additional specimens. **Japan**: *Ryukyu Islands*: 3 @, collected with holotype (KUZ Z3010).

Diagnosis

Medium-sized Japanese *Cybaeus*. Males of *C. kumadori* most closely resemble males of the medium-sized *C. hikidai* in lacking a PA, but the former differs from the latter in having a slender cymbium and a bulb longer than wide (Fig. 7*E*) (cymbium relatively broad and bulb wider than long in the latter; Fig. 19*H*). Among *Cybaeus* species inhabiting the Ryukyu Islands, only females of *C. kumadori* and *C. okumurai* possess distinctly bulbous SH and SS. The former can be distinguished from the latter by its SB located laterally to the SH and SS (Fig. 7*G*) (SB posterior to SH and SB in *C. okumurai*; Fig. 5*B*).

Description

Male (*holotype, KUZ Z3004*)

Measurements (*mm*). CL 3.32, CW 2.27; head 1.38 wide; abdomen 2.94 long, 2.00 wide. Ocular area 0.36 long, 0.87 wide. Sternum 1.50 long, 1.40 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 10.44 (2.93 + 1.01 + 2.44 + 2.48 + 1.58); leg II 9.74 (2.55 + 0.97 + 2.30 + 2.44 + 1.48); leg III 8.67 (2.32 + 0.96 + 1.81 + 2.38 + 1.20); leg IV 10.88 (2.78 + 0.97 + 2.49 + 3.18 + 1.46).

Carapace (Fig. 6*A*). Head narrow, 0.61× as wide as thoracic region; thoracic region almost as high as head. AER almost straight in frontal view; PER slightly recurved in dorsal view; AME smallest, > 1/2 diameter of other eyes; ocular area relatively wide, ca. 2.4× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 5 teeth and 4 or 5 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p3, r3 (left) or 2 (right), v2-2-2-2; metatarsus p4, r2,

v2-2-3. Leg II: tibia p4, r2 (left) or 3 (right), v2-2-1(r)-2; metatarsus p3, r3, v2-2-3.

Abdomen (Fig. 6*B*). Oval; mid-posterior part widest. Colulus two groups of 3 or 4 setae.

Palp (Fig. 7*A–E*). PA lacking. Tibia almost as long as patella; RTA plate-like, occupying 1/2 of length of tibia. Cymbium slender, > 2× longer than wide, expanded prolaterally. Genital bulb slightly longer than wide, oval in ventral view. Conductor: distal part moderately long; proximal arm hooked. Embolus simple, originating and terminating, respectively, at ca. 10 o'clock and ca. 5 o'clock in ventral view.

Colour (Fig. 6*A*, *B*). Carapace: head brown, black anteriorly and laterally, with black markings on anterior to cervical groove; thoracic region yellowish brown, with brownish black lateral sub-marginal bands. Chelicerae dark reddish-brown, maxillary lobe and labium reddish brown. Sternum yellowish brown, darker toward margins. Legs bright yellowish-brown with brownish black annulations. Abdomen: dorsally olive black with dull yellow chevron pattern; laterally with mottled pattern of dark olive-black and dull yellow; ventrally light yellow.

Female (*paratype, KUZ Z3007*)

Measurements (*mm*). CL 3.50, CW 2.35; head 1.60 wide; abdomen 4.55 long, 3.38 wide. Ocular area: 0.39 long, 0.95 wide. Sternum 1.55 long, 1.43 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 9.68 (2.68 + 1.07 + 2.38 + 2.25 + 1.30); leg II 9.16 (2.50 + 1.04 + 2.17 + 2.22 + 1.23); leg III 8.24 (2.30 + 1.03 + 1.70 + 2.12 + 1.09); leg IV 10.39 (2.78 + 1.04 + 2.36 + 2.90 + 1.31).

Carapace (Fig. 6*C*). Head 0.68× as wide as thoracic region; thoracic region height slightly shorter than head. AER slightly procurved in frontal view; PER almost straight in dorsal view. AME smallest, ca. 1/2 diameter of other eyes. Ocular area relatively wide, ca. 2.4× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 5 teeth and 5 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p3, v2-2-2-2; metatarsus p1, r1, v2-2-3. Leg II: tibia p4, v2-2-1(r)-2; metatarsus p4, r1, v2-2-3.

Abdomen (Fig. 6*D*). Oval; mid-posterior part widest. Colulus 2 groups of 3

setae.

Genitalia (Fig. 7*F*, *G*). Posterior margin of epigynal plate slightly curved. Atrium slightly concave, posteromedially located on epigynum. Copulatory pores separated on either side of atrium; CD conspicuously visible through epigynal plate in ventral view. Each of SH, SS, and SB distinct, bulbous; SH with few primary pores anteromedially; SB developed, extended anterolaterally; Bennett's gland undetectable in dorsal and medial views.

Colour (Fig. 6*C*, *D*). Carapace: head reddish brown, brownish black anteriorly and laterally, with brownish black marking anterior to cervical groove; thoracic region bright yellowish-brown, with brownish black lateral sub-marginal bands. Chelicerae, maxillary lobe and labium reddish brown, chelicerae darker than others. Sternum bright yellowish-brown, darker toward margins. Legs yellowish brown with brownish black annulations. Abdomen: dorsally dark greyish-yellow with greyish yellow chevron pattern; laterally with mottled pattern of dark greyish-yellow and greyish-yellow; ventrally light yellow ventrally.

Variation

Males (n = 4). Measurements (mean, followed by ranges in parentheses): CL 3.39 (3.16–3.78), CW 2.31 (2.14–2.60); CW/CL 0.68 (0.67–0.69); TibIL 2.52 (2.35–2.82); TibIL/CL 0.74 (0.73–0.75). Legs longer than those of females.

Females (n = 7). Measurements (mean, followed by ranges in parentheses): CL 3.40 (2.76–3.94), CW 2.26 (1.80–2.63); CW/CL 0.66 (0.65–0.67); TibIL 2.25 (1.81–2.63); TibIL/CL 0.66 (0.65–0.68).

Distribution

This species is endemic to forest habitats on Kuroshima Island in the Mishima Islands (Fig. 2).

Remarks

The retreat of this species is V-shaped with two openings.

Bennett's gland of this species may be located at the ventral surface of the connection between the spermathecal stalk and base, but the glands were not observable

in the examined specimen. The part of the spermathecae is difficult to observe because it is masked by the epigynal plate ventrally and by the spermathecal stalk and head medio-dorsally.

Etymology

The specific name is from a Japanese word kumadori (= kabuki make-up) referring to the carapace colouration of this species.

Cybaeus yakushimensis, sp. nov.

http://zoobank.org/NomenclaturalActs/E4EF5027-C1DD-411E-ADF3-15037170EFB7

(Figs. 8, 9, 10*A*, *D*, *G*, 11*E*)

Material examined

Holotype. **Japan**: *Ryukyu Islands*: Yakushima Island: #, Shirataniunsuikyo Valley, 30°22′38.7″N, 130°34′21.1″E, 8.xii.2012, N. Koike (KUZ Z2998).

Paratypes. **Japan**: *Ryukyu Islands*: Yakushima Island: 2 #, 2 @, collected with holotype (KUZ Z2138, Z2999–Z3001); 1 @, along Hanayama Trail, 30°19′13.2″N, 130°26′45.1″E, 9.xii.2012, N. Koike (KUZ Z2140).

Additional specimens. **Japan**: *Ryukyu Islands*: Yakushima Island: 1 @, Shirataniunsuikyo Valley, 28.x.2011 (KUZ Z2163); 1 #, 4 @, along Hanayama Trail, 9.xii.2012 (KUZ Z3002, Z3003, Z3678).

Diagnosis

Medium-sized Japanese *Cybaeus*. *Cybaeus yakushimensis* most closely resembles *C. amamiensis*. Males of *C. yakushimensis* can be differentiated from those of the latter by the small and slender palp (Fig. 9*A*, 10*A*) (robust in *C. amamiensis*; Fig. 14*A*, 10*B*). Additionally, the PA of *C. yakushimensis* (Fig. 10*D*) is shorter and less distally extended than that of *C. amamiensis* (Fig. 10*E*). Females of *C. yakushimensis* are distinguishable from those of *C. amamiensis* by the relatively short atrium and ellipsoidal SB (Fig. 9*D*, *E*) (slightly longer atrium and globular SB in *C. amamiensis*; Fig. 14*D*, *E*). The connection between the SH and SS of *C. yakushimensis* (Fig. 9*E*) is less robust than the connection in *C. amamiensis* (Fig. 14*E*).

Description

Male (*holotype*, *KUZ Z2998*)

Measurements (*mm*). CL 2.99, CW 2.13; head 1.25 wide; abdomen 2.25 long, 1.65 wide. Ocular area 0.37 long, 0.73 wide. Sternum 1.43 long, 1.36 wide. Leg formula, 1 > 4 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 10.02 (2.60 + 0.95 + 2.33 + 2.38 + 1.76); leg II 9.46 (2.43 + 0.91 + 2.12 + 2.22 + 1.78); leg III 7.83 (2.12 + 0.86 + 1.61 + 2.04 + 1.20); leg IV 9.87 (2.53 + 0.89 + 2.22 + 2.78 + 1.45).

Carapace (Fig. 8*A*). Head narrow, 0.59× as wide as thoracic region; thoracic region almost as high as head. AER straight in frontal view; PER almost straight in dorsal view; AME smallest, ca. 1/2 diameter of other eyes; ocular area ca. 2.0× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 5 teeth and 4 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia I p2, r2, v2-2-2-2; metatarsus p3 (left) or 4 (right), r2, v2-2-2. Leg II: tibia p3, r2 (left) or 3 (right), v2-2-1(r)-2; metatarsus p4, r2 (left) or 1 (right), v2-2-3.

Abdomen (Fig. 8*B*). Oval; mid-posterior part widest. Colulus two groups of 3 setae.

Palp (Fig. 9*A–C*, 10*A*, *D*, *G*). PA digitiform, directed anterolaterally, dorsolateral surface with 8 (left) or 7 (right) peg setae. Tibia slightly shorter than patella; RTA plate-like, occupying 3/4 of length of tibia. Cymbium prolaterally expanded, > 2× longer than wide. Genital bulb slightly wider than long, oval in ventral view. Conductor extended retrolaterally; distal part expanded, curved; proximal arm sickle-shaped. Embolus simple, long, originating and terminating respectively, at ca. 9 o'clock and ca. 5 o'clock in ventral view.

Colour (Fig. 8*A*, *B*). Carapace: head brown, with reticulate brownish black markings; thoracic region yellowish brown, with radiating brownish black bands. Chelicerae reddish brown, maxillary lobe and labium bright brown. Sternum bright yellowish-brown, darker toward margins. Legs yellowish brown to bright yellowish-

553 brown, with brownish black annulations. Abdomen: dorsally brownish black with light
554 yellowish brown chevron pattern; ventrally light yellow.
555 *Female* (*paratype, KUZ Z3001*)
556 *Measurements* (*mm*). CL 3.20, CW 2.09; head 1.43 wide; abdomen 3.60 long,
557 2.68 wide. Ocular area 0.39 long, 0.88 wide. Sternum 1.47 long, 1.22 wide. Leg formula
558 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 8.48
559 (2.30 + 0.96 + 2.04 + 1.99 + 1.19); leg II 7.99 (2.24 + 0.94 + 1.84 + 1.87 + 1.10); leg III
560 7.07 (1.90 + 0.90 + 1.43 + 1.82 + 1.02); leg IV 9.14 (2.44 + 0.91 + 2.05 + 2.48 + 1.26).
561 *Carapace* (Fig. 8*C*, 11*E*). Head 0.68× as wide as thoracic region; thoracic region
562 height slightly shorter than head. AER almost straight in frontal view; PER almost
563 straight in dorsal view; AME smallest, ca. 1/2 diameter of other eyes; ocular area > 2.0×
564 as wide as length. Clypeus shorter than median ocular area.
565 *Mouthparts*. Chelicera geniculate, promargin of fang furrow with 3 teeth
566 (median one largest), retromargin with 5 teeth and 4 or 5 denticles, and basally with
567 lateral condyle. Labium wider than long.
568 *Leg macrosetae*. Leg I: tibia with p2, v2-2-2-1(p); metatarsus p2 (left) or 1
569 (right), r1, v2-2-2. Leg II: tibia p3, v2-2-1(r)-1(p); metatarsus p3 (left) or 4 (right), r1,
570 v2-2-3.
571 *Abdomen* (Fig. 8*D*, 11*E*). Oval; mid-posterior part widest. Colulus two groups of
572 6 setae.
573 *Genitalia* (Fig. 9*D*, *E*). Posterior margin of epigynal plate slightly curved.
574 Atrium slightly concave, located posteromedially on epigynum. Copulatory pores
575 separated on both sides of atrium; CD long, widened laterally. Each spermatheca
576 forming S-shaped; SH almost tubular, located medially on vulva, with few primary
577 pores posteriorly; connection between SH and SS expanded laterally; SS tubular; SB
578 ellipsoid, extended and bent anterolaterally; Bennett's gland well-developed, located
579 anteriorly at proximal end of SB.
580 *Colour* (Fig. 8*C*, *D*, 11*E*). Carapace: head dull reddish-brown, with reticulate
581 brownish black markings; thoracic region yellowish brown, with radiating brownish
582 black bands. Chelicerae dark reddish-brown, maxillary lobe and labium brown. Sternum
583 bright brown, darker toward margins. Legs yellowish brown, with brownish black
584 annulations. Abdomen: dorsally olive black with light yellow chevron pattern; ventrally

light yellow.

Variation

Males (*n* = 4). Measurements (mean, followed by ranges in parentheses): CL 3.12 (2.92–3.32), CW 2.15 (2.00–2.26); CW/CL 0.69 (0.68–0.71); TibIL 2.38 (2.16–2.53); TibIL/CL 0.76 (0.74–0.78). Legs longer than those of females. Palp: dorsolateral surface of PA with 7–8 peg setae.

Females (*n* = 8). Measurements (mean, followed by ranges in parentheses): CL 3.32 (2.65–3.62), CW 2.19 (1.74–2.70); CW/CL 0.66 (0.64–0.71); TibIL 2.20 (1.68–2.60); TibIL/CL 0.66 (0.63–0.68).

Distribution

This species is endemic to the montane forest on Yakushima Island (Fig. 2).

Remarks

No retreat has been observed for *C. yakushimensis*. This species co-occurs with the small-sized *C. kodama* on Yakushima Island (Fig. 11*E*, *F*).

Etymology

The specific name is an adjective derived from Yakushima Island.

Cybaeus kodama, sp. nov.

http://zoobank.org/NomenclaturalActs/D629626F-0C4B-43B0-A372-54FB6CF29374

(Figs. 11*A*–*D*, *F*, 12)

Material examined

Holotype. **Japan**: *Ryukyu Islands*: Yakushima Island: #, along Hanayama Trail, 30°19′13.2″N, 130°26′45.1″E, 9.xii.2012, N. Koike (KUZ Z3011).

Paratypes. **Japan**: *Ryukyu Islands*: Yakushima Island: 2 #, 4 @, collected with holotype (KUZ Z2141, Z2142, Z3012–Z3015).

Additional specimens. **Japan**: *Ryukyu Islands*: Yakushima Island: 1 @, Shirataniunsuikyo Valley, 30°22′30.2″N, 130°34′07.8″E, 8.xii.2012 (KUZ Z2139); 6

@, collected with holotype (KUZ Z3016).

Diagnosis

Small-sized Japanese *Cybaeus*. Males of *Cybaeus kodama* are only likely to be confused with those of *C. aikana*, the only other 'small-sized' species endemic to the Ryukyu Islands. The two species are clearly distinguishable by the presence of a small PA in *C. kodama* (Fig. 12*B*, *C*) (lacking PA in *C. aikana*; Fig. 16*B*). In addition, the elliptically shaped bulb of *C. kodama* (Fig. 12*E*) is also unique among Japanese *Cybaeus* species. Females of *C. kodama* can be easily distinguished from those of all other Ryukyu *Cybaeus* species by the long CDs running adjacent to the SSs (Fig. 12*G*).

Description

Male (*holotype, KUZ Z3011*)

Measurements (*mm*). CL 1.68, CW 1.15; head 0.73 wide; abdomen 1.92 long, 1.56 wide. Ocular area 0.24 long, 0.46 wide. Sternum 0.84 long, 0.80 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 4.45 (1.24 + 0.50 + 1.09 + 0.96 + 0.66); leg II 4.16 (1.16 + 0.48 + 0.94 + 0.93 + 0.65); leg III 3.59 (1.00 + 0.43 + 0.73 + 0.86 + 0.57); leg IV 4.50 (1.23 + 0.45 + 1.06 + 1.14 + 0.62).

Carapace (Fig. 11*A*). Head narrow, 0.63× as wide as thoracic region. Thoracic region almost as high as head. AER straight in frontal view; PER almost straight in dorsal view; AME smallest, < 1/2 diameter of other eyes; ocular area ca. 2× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 3 (left) or 2 (right) teeth and 4 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p2, r0 (left) or 2 (right), v2-2-2-0; metatarsus p1, v2-2-2. Leg II: tibia p2, v2-1(r)-1(r)-0; metatarsus p2, v2-2-3.

Abdomen (Fig. 11*B*). Oval; mid-posterior part widest. Colulus two groups of 3 or 4 setae.

Palp (Fig. 12*A*–*E*). Palp relatively short. PA small, on retrolateral anterior margin of patella, semicircular in lateral view, lateral surface with 4 peg setae. Tibia

short, slightly shorter than patella; RTA plate-like, occupying most of length of tibia. Cymbium slightly expanded prolaterally. Genital bulb elliptic in ventral view, major axis ca. 2× longer than minor axis. Conductor: distal part well developed, elongate distally; proximal arm small, strongly undulating. Embolus simple, long, originating and terminating, respectively, at ca. 7 o'clock and ca. 5 o'clock in ventral view.

Colour (Fig. 11*A*, *B*). Carapace: head yellowish brown, with reticulate brownish black markings; thoracic region bright yellowish-brown, with radiating brownish black bands. Chelicerae bright brown, maxillary lobe and labium orange, sternum bright yellowish-brown. Legs bright yellowish-brown, without annulations. Abdomen: dorsally olive black with light yellow chevron pattern; ventrally light yellow.

Female (*paratype, KUZ Z3013*)

Measurements (*mm*). CL 1.54, CW 1.06; head 0.72 wide; abdomen 1.76 long, 1.32 wide. Ocular area 0.25 long, 0.49 wide. Sternum 0.76 long, 0.76 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 3.69 (1.06 + 0.47 + 0.87 + 0.76 + 0.53); leg II 3.52 (1.01 + 0.46 + 0.75 + 0.78 + 0.52); leg III 3.00 (0.84 + 0.40 + 0.57 + 0.70 + 0.49); leg IV 3.82 (1.06 + 0.41 + 0.85 + 0.92 + 0.58).

Carapace (Fig. 11*C*). Head 0.68× as wide as thoracic region. Thoracic region almost as high as head. AER straight in frontal view; PER almost straight in dorsal view; AME smallest, < 1/2 diameter of other eyes; ocular area ca. 2× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera moderate geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 4 teeth and 4 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia I p2, v2-2-2-0; metatarsus p1, v2-2-2. Leg II: tibia p1, v2-1(r)-1(r)-0; metatarsus p2, v2-2-3.

Abdomen (Fig. 11*D*). Oval; mid-posterior part widest. Colulus 2 groups of 3 or 4 setae.

Genitalia (Fig. 12*F*, *G*). Posterior margin of epigynal plate loosely curved. Atrium located posteromedially on epigynum. CD long, running along SS. SH and SS continuously tubular, forming spermathecal duct; SH located medially on vulva, SHs contiguous with each other, primary pore inconspicuous in dorsal view; SB ellipsoidal,

extending anterolaterally; Bennett's gland located anteriorly at basal part of SB.

Colour (Fig. 11*C*, *D*, *F*). Carapace: head brown, with reticulate dull brownish-black markings; thoracic region bright yellowish-brown, with radiating dark olive-brown. Chelicerae bright brown, maxillary lobe and labium orange, sternum bright yellowish-brown. Legs yellowish brown without annulations. Abdomen: dorsally dark olive-brown with dull yellow chevron pattern; ventrally pale yellow.

Variation

Males (*n* = 2). Measurements (ranges): CL 1.46–1.68, CW 1.00–1.15; CW/CL 0.68; TibIL 0.97–1.09; TibIL/CL 0.65–0.66. Legs slightly longer than those of females.

Females (*n* = 9). Measurements (mean, followed by ranges in parentheses): CL 1.49 (1.40–1.61), CW 1.03 (0.93–1.09); CW/CL 0.69 (0.66–0.73); TibIL 0.85 (0.77–0.92); TibIL/CL 0.57 (0.55–0.59).

Distribution

This species is endemic to the montane forests on Yakushima Island (Fig. 2).

Remarks

No retreat has been observed for this species. This species is found sympatrically with the medium-sized species *C. yakushimensis* (Fig. 11*E*, *F*).

Etymology

The specific name is from a Japanese word kodama (= the name of a tree-inhabiting spirit), and thus treated as indeclinable.

Cybaeus amamiensis, sp. nov.

http://zoobank.org/NomenclaturalActs/FB195659-51B4-4C27-9B4D-DF3EA707C7D3

(Figs. 10*B*, *E*, *H*, 13, 14)

Material examined

Holotype. **Japan**: *Ryukyu Islands*: Amamioshima Island: #, Mt. Yuwandake, 28°17′21.5″N, 129°18′52.5″E, 15.xii.2012, N. Koike (KUZ Z2987).

Paratypes. **Japan**: *Ryukyu Islands*: Amamioshima Island: 2 #, 4 @, collected with holotype (KUZ Z2120, Z2121, Z2988, Z2990–Z2992).

Additional specimens. **Japan**: *Ryukyu Islands*: Amamioshima Island: 6 #, 22 @, collected with holotype (KUZ Z2989, Z2993); 7 @, Mt. Yuwandake, 28°17′46.5″N, 129°19′15.9″E, 12.iii.2009 (KUZ Z2133); 4 #, 28 @, ditto, 28°17′21.5″N, 129°18′52.5″E, 16.xii.2012 (KUZ Z2117, Z2118); 1 @, near Sumiyo Dam [28°17′N, 129°22′E], 12.iii.2009 (KUZ Z2130); 4 @, ditto, 14.iii.2009 (KUZ Z2131); 1 @, ditto, 26.iv.2010 (KUZ Z2125); 3 @, Kinsakubaru Forest, 28°20′49″N, 129°26′26″E, 14.iii.2009 (KUZ Z2135, Z2136); 4 @, ditto, 28°20′12.4″N, 129°26′55.0″E, 15.xii.2012 (KUZ Z2119); 6 @, near Kinsakubaru Forest, 28°21′39.5″N, 129°28′45.8″E, 19.i.2011 (KUZ Z2129); 4 @, Mt. Takinohanayama, 28°16′04.8″N, 129°26′54.2″E, 19.i.2011 (KUZ Z2126–Z2128); 1 #, 8 @, Naze-koshuku, 28°21′46.8″N, 129°28′49.9″E, 15.xii.2012 (KUZ Z2116, Z2124); 1 #, Sumiyocho-yakugachi, 28°14′47.3″N, 129°23′02.2″E, 16.xii.2012 (KUZ Z2122); 1 #, 3 @, Setouchicho-agina, 28°11′15.1″N, 129°19′35.2″E, 16.xii.2012 (KUZ Z2123).

Diagnosis

Medium- to large-sized Japanese *Cybaeus*. *Cybaeus amamiensis* is most likely to be confused *C. yakushimensis*. See the Diagnosis of *C. yakushimensis* for details of differentiating these two species.

Description

Male (*holotype, KUZ Z2987*)

Measurements (*mm*). CL 3.85, CW 2.63; head 1.65 wide; abdomen 3.13 long, 2.43 wide. Ocular area 0.46 long, 1.00 wide. Sternum 1.70 long, 1.50 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 12.02 (3.10 + 1.18 + 2.94 + 2.94 + 1.86); leg II 11.57 (3.08 + 1.20 + 2.70 + 2.84 + 1.75); leg III 10.08 (2.78 + 1.05 + 2.14 + 2.68 + 1.43); leg IV 12.43 (3.30 + 1.14 + 2.84 + 3.48 + 1.67).

Carapace (Fig. 13*A*). Head narrow, 0.63× as wide as thoracic region; thoracic region slightly higher than head. AER slightly procurved in frontal view; PER almost straight in dorsal view; AME smallest, slightly > 1/2 diameters of other eyes; ocular

745 area 2.2× wider than long. Clypeus slightly shorter than median ocular area.
746 *Mouthparts*. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth
747 (median one largest), retromargin with 4 teeth and 4 or 5 denticles, and basally with
748 lateral condyle. Labium wider than long.
749 *Leg macrosetae*. Leg I: tibia p2, r2, v2-2-2-2; metatarsus p4 (left) or 3 (right), r1,
750 v2-2-3. Leg II: tibia p2, r2, v2-2-1(r)-2; metatarsus p4, r1, v2-2-3.
751 *Abdomen* (Fig. 13*B*). Oval; mid-posterior part widest. Colulus two groups of 5
752 or 6 setae.
753 *Palp* (Fig. 10*B*, *E*, *H*, 14*A*–*C*). PA digitiform, directed distally, dorsolateral
754 surface with 7 (left) or 8 (right) peg setae. Tibia convex in lateral view, almost as long
755 as patella; RTA plate-like, occupying most of length of tibia. Cymbium expanded
756 prolaterally, > 2× longer than wide; distal part slender, long. Genital bulb slightly wider
757 than long, oval in ventral view. Conductor extended retrolaterally; distal part expanded,
758 slightly curved; proximal arm sickle-shaped. Embolus simple, long, originating and
759 terminating, respectively, at ca. 9 o'clock and ca. 5 o'clock in ventral view.
760 *Colour* (Fig. 13*A*, *B*). Carapace: head dark reddish-brown, with reticulate black
761 markings; thoracic region brownish black, with yellowish brown marginal bands;
762 yellowish brown markings mid-dorsally. Chelicerae, maxillary lobe and labium dark
763 reddish-brown, chelicera darker than other parts. Sternum bright brown, darker toward
764 margins. Legs yellowish brown, with olive black annulations. Abdomen: dorsally olive
765 black with dull yellow chevron pattern; ventrally bright yellowish-brown.
766 *Female* (*paratype, KUZ Z2990*)
767 *Measurements* (*mm*). CL 4.23, CW 2.76; head 1.90 wide; abdomen 4.15 long,
768 2.90 wide. Ocular area 0.46 long, 1.10 wide. Sternum 1.82 long, 1.64 wide. Leg
769 formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg
770 I 11.26 (3.10 + 1.32 + 2.76 + 2.60 + 1.48); leg II 10.72 (3.05 + 1.26 + 2.50 + 2.51 +
771 1.40); leg III 9.35 (2.70 + 1.18 + 1.92 + 2.36 + 1.19); leg IV 11.58 (3.20 + 1.14 + 2.70 +
772 3.11 + 1.43).
773 *Carapace* (Fig. 13*C*). Head narrow, 0.69× as wide as thoracic region; thoracic
774 region almost as high as head. AER straight in frontal view; PER slightly recurved in
775 dorsal view; AME smallest, slightly ca. 1/2 diameter of other eyes; ocular area
776 relatively wide, 2.4× wider than long. Clypeus slightly shorter than median ocular area.

Mouthparts. Chelicera geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 4 teeth and 4 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p2, v2-2-2-2; metatarsus p1, r1, v2-2-2. Leg II: tibia p2 (left) or 3 (right), v2-2-1(r)-2; metatarsus p4, r3, v2-2-3.

Abdomen (Fig. 13*D*). Oval; mid-posterior part widest. Colulus two groups of 4 or 5 setae.

Genitalia (Fig. 14*D*, *E*). Posterior margin of epigynal plate slightly curved. Atrium slightly concave, located posteromedially on epigynum. Copulatory pores separated on either side of atrium; CD located along atrial margin to medially. Each spermatheca forming S-shaped; SH medially located on vulva, undifferentiated except for presence of a few primary pores anteromedially; connection between SH and SS expanded laterally; SS tubular; SB large, globular; Bennett's gland well-developed, located anteriorly at basal part of SB.

Colour (Fig. 13*C*, *D*). Carapace: head deeply-dark reddish-brown, with reticulate black markings; thoracic region orange along margins, with radiating black bands; yellowish brown markings mid-dorsally. Chelicerae dark reddish-brown, maxillary lobe and labium reddish brown. Sternum reddish brown, darker toward margins. Legs bright brown, with brownish black annulations. Abdomen: dorsally olive black with bright yellowish-brown chevron pattern; laterally with mottled pattern of dark brown and yellowish brown laterally; ventrally bright yellowish-brown.

Variation

Males (*n* = 9). Measurements (mean, followed by ranges in parentheses): CL 3.64 (3.06–3.94), CW 2.45 (2.10–2.74); CW/CL 0.67 (0.66–0.70); TibIL 2.73 (2.28–2.94); TibIL/CL 0.75 (0.74–0.76). Legs longer than those of females. Palp: dorsolateral surface of PA with 6–10 peg setae.

Females (*n* = 26). Measurements (mean, followed by ranges in parentheses): CL 4.00 (2.89–4.80), 2.67 (1.91–3.16); CW/CL 0.67 (0.65–0.70); TibIL 2.63 (1.88–3.28); TibIL/CL 0.66 (0.64–0.68).

Distribution

This species is endemic to the montane forests on Amamioshima Island (Fig. 2).

Remarks

No retreat has been observed for this species.

Females of *C. amamiensis* share well-developed Bennett's glands in their spermathecae with those of *C. yakushimensis*, *C. tokunoshimensis*, and *C. hikidai*.

Etymology

The specific name is an adjective from Amamioshima Island.

Cybaeus aikana, sp. nov.

http://zoobank.org/NomenclaturalActs/F378CB1A-AFF8-4944-90BB-7D2863522BCC

(Figs. 15–17)

Material examined

Holotype. **Japan**: *Ryukyu Islands*: Amamioshima Island: #, Mt. Yuwandake, 28°17′21.5″N, 129°18′52.5″E, 15.xii.2012, N. Koike (KUZ Z3017).

Paratypes. **Japan**: *Ryukyu Islands*: Amamioshima Island: 2 @, collected with holotype (KUZ Z2137, Z3018).

Diagnosis

Small-sized Japanese *Cybaeus*. Males of *C. aikana*, *C. kumadori* and *C. hikidai* all lack a PA in the palp (Fig. 7*B*, 16*B*, 19*F*). However, males of *C. aikana* can be unquestionably distinguished from those of the other two congeners by its small size, short and robust palp (Fig. 16*B*), and arcuate proximal arm of conductor (Fig. 16*A*, *D*, *E*). Females of *C. aikana*, *C. hikidai*, and *C. ishikawai* are characterised by their CDs, SHs and SSs all being of similar diameter. However, females of *C. aikana* clearly differ from those of the other two species in their SBs which are located medially on the vulva and are contiguous with each other (Fig. 17*B*) (SBs are well separated in *C. hikidai* and *C. ishikawai*; Fig. 19*J* for *C. hikidai* and see fig. 2-2-30-217 in Ihara 2009*a* for *C. ishikawai*).

Description

Male (*holotype*, *KUZ Z3017*)

Measurements (*mm*). CL 1.78, CW 1.13; head 0.76 wide; abdomen 1.50 long, 1.36 wide. Ocular area 0.23 long, 0.45 wide. Sternum 0.84 long, 0.76 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 4.49 (1.26 + 0.48 + 1.07 + 0.98 + 0.70); leg II 4.11 (1.15 + 0.48 + 0.92 + 0.93 + 0.63); leg III 3.56 (0.99 + 0.46 + 0.68 + 0.88 + 0.55); leg IV 4.68 (1.23 + 0.48 + 1.06 + 1.18 + 0.73).

Carapace (Fig. 15*A*). Head narrow, 0.67× as wide as thoracic region; thoracic region as high as head. AER slightly procurved in frontal view; PER almost straight in dorsal view; AME smallest, ca. 1/2 diameter of other eyes; ocular area ca. 2× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 3 teeth and 4 or 5 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p2, v2-2-2-0; metatarsus p1, v2-2-2. Leg II: tibia p2, v1(r)-1(r)-1(r)-0; metatarsus p2, v2-2-3.

Abdomen (Fig. 15*B*). Oval; mid-posterior part widest. Colulus two groups of 3 or 4 setae.

Palp (Fig. 16). PA lacking. Tibia almost as long as patella; RTA plate-like, occupying 2/3 of length of tibia. Cymbium relatively short, slightly expanded prolaterally. Genital bulb wider than long, oval in ventral view. Conductor strongly undulating in lateral view; distal part well developed, extended distally; tip of proximal arm undulating, arcuate. Embolus simple, long, originating and terminating, respectively, at ca. 9 o'clock and ca. 7 o'clock in ventral view.

Colour (Fig. 15*A*, *B*). Carapace: head yellowish brown, with reticulate brownish black markings; thoracic region light yellow, with radiating brownish black bands. Chelicerae bright brown, maxillary lobe and labium bright brown to yellowish brown. Sternum light yellow, darker toward margins. Legs bright yellowish-brown to light yellow with slight olive black annulations. Abdomen: dorsally olive black with light yellow chevron pattern; ventrally light yellow.

Female (*paratype*, *KUZ Z3018*)

Measurements (*mm*). CL 1.64, CW 1.05; head 0.80 wide; abdomen 1.88 long, 1.42 wide. Ocular area 0.22 long, 0.46 wide. Sternum 0.82 long, 0.74 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 3.67 (1.08 + 0.48 + 0.84 + 0.74 + 0.53); leg II 3.42 (1.03 + 0.47 + 0.72 + 0.72 + 0.48); leg III 2.96 (0.84 + 0.44 + 0.56 + 0.66 + 0.46); leg IV 3.69 (1.06 + 0.45 + 0.88 + 0.87 + 0.43).

Carapace (Fig. 15*C*). Head 0.76× as wide as thoracic region; thoracic region height slightly shorter than head. AER slightly procurved in frontal view; PER almost straight in dorsal view; AME smallest, ca. 1/2 diameter of other eyes; ocular area slightly > 2× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera moderate geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 4 teeth and 4 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p2, v 2-2-2-0; metatarsus p1, r1 (left) or 0 (right), v2-2-2. Leg II: tibia p2, v1(r)-1(r)-1(r)-0; metatarsus p2, v2-2-3.

Abdomen (Fig. 15*C*). Oval; mid-posterior part widest. Colulus two groups of 4 setae.

Genitalia (Fig. 17). Posterior margin of epigynal plate slightly concave anteriorly. Atrium located posteriorly on epigynum. Copulatory pores separated on either side of atrium; CD conspicuously visible through epigynal plate in ventral view. CD, SH and SS tubular and of similar diameter from copulatory pore to SB; SH with a few primary pores in dorsal view; SB large, pear-shaped, located medially, contiguous with each other; Bennett's gland not detected.

Colour (Fig. 15*C*). Carapace: head brown, with reticulate brownish black markings; thoracic region bright yellowish-brown, with radiating brownish black bands. Chelicerae, maxillary lobe and labium bright brown. Sternum bright yellowish brown, darker toward margins. Legs yellowish brown, with slight olive black annulations. Abdomen: dorsally brownish black with light yellow chevron pattern; ventrally light yellow.

Distribution

This species in known only from the type locality on Mt. Yuwandake on Amamioshima

Island (Fig. 2).

Remarks

This species constructs a Y-shaped retreat (Fig. 22*B*). *Cybaeus aikana* is found sympatrically with *C. amamiensis* at Mt. Yuwandake.

Etymology

The specific name is dedicated to the name of a historical figure, a woman who lived in Amamioshima Island. The specific name is derived directly from her name, and thus treated as indeclinable.

Cybaeus tokunoshimensis, sp. nov.

http://zoobank.org/NomenclaturalActs/F0CEA7EC-D32E-4BE9-A51C-ED7357991B3A

(Figs. 10*C*, *F*, 18)

Material examined

Holotype. **Japan**: *Ryukyu Islands*: Tokunoshima Island: #, Mt. Inokawadake, 27°45′53.1″N, 128°58′43.1″E, 17.xii.2012, N. Koike (KUZ Z2113).

Paratypes. **Japan**: *Ryukyu Islands*: Tokunoshima Island: 4 @, collected with holotype (KUZ Z2112, Z2994–Z2996).

Additional specimens. **Japan**: *Ryukyu Islands*: Tokunoshima Island: 2 @, Mt. Inokawadake, 27°46′07.6″N, 128°59′38.4″E, 27.i.2011 (KUZ Z2111); 6 @, ditto, 27°45′51.9″N, 128°58′37.8″E, 27.i.2011 (KUZ Z2114, Z2115); 4 @, collected with holotype (KUZ Z2997).

Diagnosis

Medium-sized Japanese *Cybaeus*. *Cybaeus tokunoshimensis* most closely resembles *C. yakushimensis* and *C. amamiensis*. However, males of *C. tokunoshimensis* can be distinguished from those of the other two species by the laterally extended palpal PA, the relatively short, broad cymbium, and the broad, wider than long genital bulb (Fig. 10*C*, *F*, 18*H*) (directed anterolaterally PAs, relatively slender cymbia, and as long as

937 wide genital bulbs in *C. yakushimensis* and *C. amamiensis*; Fig. 10*A*, *B*, *D*, *E*, *G*, *H*).
938 Females of *C. tokunoshimensis* are distinguishable from those of *C. yakushimensis* and
939 *C. amamiensis* by the slightly longer epigynum and, especially, by each SS forming a
940 double coil around each CD (Fig. 18*I*, *J*) (short epigyna and each SS not a double coiled
941 around each CD in *C. yakushimensis* and *C. amamiensis*; Fig. 9*D*, *E*, 14*D*, *E*).
942 Additionally, Bennett's gland in *C. tokunoshimensis* is set apart from the bulbous SB on
943 the posterior portion of the SH (the glands in *C. yakushimensis* and *C. amamiensis* are
944 located basally on each SB; Fig. 9*E*, 14*E*).
945
946 *Description*
947 *Male* (*holotype*, *KUZ Z2113*)
948 *Measurements* (*mm*). CL 3.12, CW 2.18; head 1.35 wide; abdomen 2.68 long,
949 2.04 wide. Ocular area 0.34 long, 0.81 wide. Sternum 1.44 long, 1.32 wide. Leg
950 formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg
951 I 9.60 (2.53 + 0.95 + 2.30 + 2.36 + 1.46); leg II 9.21 (2.44 + 0.96 + 2.13 + 2.28 + 1.40);
952 leg III 8.09 (2.20 + 0.91 + 1.72 + 2.08 + 1.18); leg IV 9.85 (2.63 + 0.91 + 2.28 + 2.59 +
953 1.44).
954 *Carapace* (Fig. 18*A*, *B*). Head narrow, 0.62× as wide as thoracic region; thoracic
955 region higher than head. AER almost straight in frontal view; PER almost straight in
956 dorsal view; AME smallest, slightly > 1/2 diameter of other eyes. Ocular area relatively
957 wide, 2.4× wider than long. Clypeus shorter than median ocular area.
958 *Mouthparts*. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth
959 (median one largest), retromargin with 5 teeth and 6 denticles, and basally with lateral
960 condyle. Labium wider than long.
961 *Leg macrosetae*. Leg I: tibia p2, r2, v2-2-2-2; metatarsus p4, r1, v2-2-3. Leg II:
962 tibia p3, r2, v2-2-1(r)-2; metatarsus p4, r2, v2-2-3.
963 *Abdomen* (Fig. 18*B*). Oval; mid-posterior part widest. Colulus two groups of 4
964 or 5 setae.
965 *Palp* (Fig. 10*C*, *F*, 18*E*–*H*). PA digitiform, extended anterolaterally, dorsal
966 surface with 9 (left) or 8 (right) peg setae. Tibia convex in lateral view, almost as long
967 as patella; RTA plate-like, occupying most of length of tibia. Cymbium relatively wide,
968 ca. 2× longer than wide, expanded prolaterally. Genital bulb wider than long, oval in

ventral view. Conductor: distal part large, well developed; proximal arm strongly undulating, sickle-shaped. Embolus long, undulating along conductor, originating and terminating respectively, at ca. 9 o'clock and ca. 7 o'clock in ventral view.

Colour (Fig. 18*A*, *B*). Carapace: head smoky black; thoracic region bright yellowish-brown, with radiating black bands; bright yellowish-brown markings mid-dorsally. Chelicerae deep dark reddish-brown, maxillary lobe and labium brown. Sternum yellowish brown, darker toward margins. Legs light yellowish-brown with brownish black annulations. Abdomen: dorsally olive black with light yellow chevron pattern; ventrally bright yellowish-brown.

Female (paratype, KUZ Z2994)

Measurements (*mm*). CL 3.23, CW 2.15; head 1.48 wide; abdomen 3.35 long, 2.50 wide. Ocular area 0.37 long, 0.90 wide. Sternum 1.45 long, 1.30 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 8.54 (2.38 + 0.96 + 2.06 + 1.96 + 1.18); leg II 8.13 (2.28 + 0.94 + 1.89 + 1.88 + 1.14); leg III 7.18 (2.05 + 0.90 + 1.48 + 1.83 + 0.92); leg IV 9.01 (2.42 + 0.91 + 2.08 + 2.44 + 1.16).

Carapace (Fig. 18*C*). Head 0.69× as wide as thoracic region; thoracic region almost as high as head. AER almost straight in frontal view; PER almost straight in dorsal view; AME smallest, > 1/2 diameter of other eyes. Ocular area relatively wide, 2.4× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 4 teeth and 4 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p2, v2-2-2-2; metatarsus p1, r1, v2-2-3. Leg II: tibia p3, v2-2-1(r)-2; metatarsus p4, r1, v2-2-3.

Abdomen (Fig. 18*D*). Oval; mid-posterior part widest. Colulus two groups of 4 or 5 setae.

Genitalia (Fig. 18*I*, *J*). Posterior margin of epigynal plate loosely curved. Atrium concave, located posteromedially on epigynum. Copulatory pores separated on either side of atrium; CD not visible beneath epigynal plate in ventral view. SH and SS continuously tubular; SH with a few primary pores medially; SS forming double coil around CD; SB globular, extended anterolaterally; Bennett's gland well-developed,

located medially at connection between SS and SB.

Colour (Fig. 18*C*, *D*). Carapace: head dark reddish-brown, with reticulate black markings; thoracic region bright yellowish-brown, with radiating black bands. Chelicerae dark reddish-brown, maxillary lobe and labium reddish brown. Sternum bright yellowish-brown, darker toward margins. Legs bright yellowish-brown, with olive black annulations. Abdomen: dorsally olive black with bright yellowish-brown chevron pattern; laterally with mottled pattern of olive black and bright yellowish-brown; ventrally light yellow.

Variation

Females (*n* = 8). Measurements (mean, followed by ranges in parentheses): CL 3.04 (2.34–3.28); CW 2.00 (1.55–2.15); CW/CL 0.66 (0.65–0.67); TibIL 1.93 (1.45–2.10); TibIL/CL 0.63 (0.62–0.66).

Distribution

This species is endemic to the montane forest around Mt. Inokawadake on Tokunoshima Island (Fig. 2).

Remarks

Not retreat has been observed for *C. tokunoshimensis*.

Etymology

The specific name is an adjective from Tokunoshima Island.

Cybaeus hikidai, sp. nov.

http://zoobank.org/NomenclaturalActs/ECA1F9A2-61E8-4383-8E63-49EC9C3513F9

(Figs. 19–21)

Material examined

Holotype. **Japan**: *Ryukyu Islands*: Okinawa Island: #, near Hiji Waterfall, 26°42′44.1″N, 128°11′06.3″E, 22.xii.2012, N. Koike (KUZ Z2982).

Paratypes. **Japan**: *Ryukyu Islands*: Okinawa Island: 2 @, collected with

holotype (KUZ Z2107, Z2983); 1 #, 1 @, Mt. Nagodake, 26°35′12.2″N, 128°00′22.2″E, 21.xii.2012, N. Koike (KUZ Z2106, Z2984).

Additional specimens. **Japan**: *Ryukyu Islands*: Okinawa Island: 1 #, 8 @, Mt. Nishimedake, 26°48′27.4″N, 128°16′08.6″E, 22.i.2011 (KUZ Z2100–Z2102); 2 @, ditto, 25.i.2011 (KUZ Z2104); 7 @, Mt. Yonahadake, 26°43′50.5″N, 128°12′36.2″E, 20.xii.2012 (KUZ Z2105); 3 @, 1 juvenile, Mt. Nagodake, 21.xii.2012 (KUZ Z2985, Z2986, Z3679); 3 @, 1 juvenile, Mt. Fuenjichidake, 26°45′17.0″N, 128°14′31.1″E, 22.xii.2012 (KUZ Z2108); 1 #, Mt. Onishidake, 26°49′02.8″N, 128°17′52.7″E, 22.xii.2012 (KUZ Z2109); 2 @, Mt. Nishimedake, 26°48′27.1″N, 128°16′04.7″E, 22.xii.2012 (KUZ Z2110); 1 @, near Taiho Dam, 26°39′04.3″N, 128°09′34.7″E, 24.xii.2012 (KUZ Z2103).

Diagnosis

Medium-sized Japanese *Cybaeus*. Males of *C. hikidai* differ from those of the other six Ryukyu-endemic congeners (*C. okumurai*, *C. yakushimensis*, *C. kodama*, *C. amamiensis* and *C. tokunoshimensis*) by the combination of lacking a PA and having an egg-shaped large genital bulb that is wider than long (Fig. 19*F*, *H*). Males of *C. kumadori* and *C. aikana* also lack a PA; differentiating them from the male *C. hikidai* is discussed in the Diagnoses of those species. Females of *C. hikidai* share with those of the small-sized *C. aikana* venry long tubular CD, SH and SS of similar diameter throughout. But, the former can be distinguished from the latter by its well separated SBs located laterally on the vulva (Fig. 19*J*) (contiguous and medially located in the vulva of *C. aikana*; Fig. 17*B*). Females of *C. hikidai* are also similar to those of *C. ishikawai* the former can be distinguished from the latter by the SBs that are directed antero-laterally (Fig. 19*J*) (SBs directed laterally in *C. ishikawai*; fig. 2-2-30-217 in Ihara 2009*a*).

Description

Male (*holotype, KUZ Z2982*)

Measurements (*mm*). CL 3.20, CW 2.33; head 1.40 wide; abdomen 3.10 long, 2.43 wide. Ocular area 0.37 long, 0.80 wide. Sternum 1.52 long, 1.38 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg

I 10.90 (2.89 + 1.03 + 2.62 + 2.60 + 1.76); leg II 10.47 (2.83 + 1.01 + 2.50 + 2.52 + 1.61); leg III 9.49 (2.58 + 0.94 + 2.06 + 2.48 + 1.43); leg IV 11.85 (3.05 + 0.99 + 2.79 + 3.28 + 1.74).

Carapace (Fig. 19*A*, *B*). Head narrow, 0.60× as wide as thoracic region; thoracic region slightly higher than head. AER almost straight in frontal view; PER straight in dorsal view; AME smallest, > 1/2 diameter of other eyes; ocular area ca. 2.2× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 4 teeth and 6 or 7 denticles, and basally with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p3, r2, v2-2-2-2; metatarsus p4, r2, v2-2-3. Leg II: tibia p3, r2 (left) or 3 (right), v2-2-1(r)-2; metatarsus p4, r3, v2-2-3.

Abdomen (Fig. 19*B*). Oval; mid-posterior part widest. Colulus two groups of 5 setae.

Palp (Fig. 19*E–H*). PA lacking. Tibia almost as long as patella; RTA plate-like, occupying half of length of tibia. Cymbium relatively wide, ca. 2× longer than wide, expanded prolaterally. Genital bulb wider than long, egg-shaped in ventral view. Conductor: distal part large, expanded antero-medially; proximal arm small, undulating, tip twisted. Embolus simple, long, originating and terminating, respectively, at ca. 9 o'clock and ca. 6 o'clock in ventral view.

Colour (Fig. 19*A*, *B*). Carapace: head dark brown with reticulate brownish black markings; thoracic region bright yellowish-brown along lateral and posterior margins, with radiating brownish black bands; yellowish brown spot on middle part. Chelicerae dark reddish-brown, maxillary lobe and labium brown. Sternum yellowish brown, darker toward margins. Legs: femur bright yellowish-brown; other segments yellowish brown with slight olive black annulations. Abdomen: dorsally olive black with bright yellowish brown chevron pattern; ventrally bright yellowish brown.

Female (*paratype, KUZ Z2985*)

Measurements (*mm*). CL 2.63, CW 1.82; head 1.24 wide; abdomen 3.15 long, 2.40 wide. Ocular area 0.34 long, 0.76 wide. Sternum 1.18 long, 1.14 wide. Leg formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg I 6.95 (1.96 + 0.78 + 1.70 + 1.56 + 0.95); leg II 6.70 (1.92 + 0.81 + 1.57 + 1.49 + 0.91);

leg III 5.93 (1.70 + 0.74 + 1.25 + 1.44 + 0.80); leg IV 7.50 (2.04 + 0.70 + 1.78 + 1.98 + 1.00).

Carapace (Fig. 19*C*). Head narrow, 0.68× as wide as thoracic region; thoracic region slightly higher than head. AER almost straight in frontal view; PER straight in dorsal view; AME smallest, > 1/2 diameter of other eyes; ocular area ca. 2.2× wider than long. Clypeus shorter than median ocular area.

Mouthparts. Chelicera more geniculate than that of male, promargin of fang furrow with 3 teeth (median one largest), retromargin with 4 teeth and 5 or 6 denticles, and basal with lateral condyle. Labium wider than long.

Leg macrosetae. Leg I: tibia p2, v2-2-2-1(p); metatarsus r1, v2-2-2. Leg II: tibia p4 (left) or 3 (right), v2-2-1(r)-0; metatarsus p4, r1, v2-2-3.

Genitalia (Fig. 19*I, J*, 20, 21). Posterior margin of epigynal plate slightly curved. Atrium located posteriorly on epigynum. Copulatory pores separated on both sides of atrium; CD long, conspicuous through epigynal plate. CD, SH and SS continuously tubular, of similar diameter throughout; SH with a few primary pores laterally; SB large, globular, directed antero-laterally; Bennett's gland well-developed, located anteriorly at connection between SS and SB.

Colour (Fig. 19*C, D*). Carapace: head dark brown, with reticulate black markings; thoracic region yellowish brown along lateral to posterior margins, with radiating brownish black bands; bright yellowish-brown marking mid-dorsally. Chelicerae, maxillary lobe and labium brown, chelicerae darker than other parts. Sternum bright yellowish-brown. Legs: femur bright yellowish-brown; other segments yellowish brown with slight olive black annulations. Abdomen: dorsally olive black with light yellow chevron pattern; ventrally light yellow.

Variation

Male (*n* = 3). Measurements (mean, followed by ranges in parentheses). CL 3.05 (2.82–3.20), CW 2.19 (2.00–2.33); CW/CL 0.72 (0.71–0.73); TibIL 2.45 (2.21–2.62); TibIL/CL 0.80 (0.78–0.82).

Female (*n* = 12). Measurements (mean, followed by ranges in parentheses). CL 2.88 (2.31–3.76), CW 1.91 (1.54–2.50); CW/CL 0.66 (0.64–0.69); TibIL 1.86 (1.47–2.45); TibIL/CL 0.64 (0.62-0.66).

Distribution

This species is endemic to the montane region in the northern part of Okinawa Island (Fig. 2).

Remarks

This species constructs a Y-shaped retreat with three openings (Fig. 22*C*).

Etymology

The specific name is dedicated to herpetologist Professor Emeritus Tsutomu Hikida at Kyoto University who has encouraged our arachnological research.

Discussion

Phylogenetic relationships and genital morphology of the Ryukyu Cybaeus

Our study extends the distribution of the genus *Cybaeus* south to Okinawa Island in the Central Ryukyus and, moreover, reveals that the eight species of the Ryukyu *Cybaeus* are composed of five lineages. However, we failed to resolve the basal nodes and phylogenetic relationships among these species, especially among lineages C–E and *C. gotoensis* (Fig. 1). The use of a broader taxonomic sample and additional genetic markers should help resolve phylogenetic relationships among the Japanese *Cybaeus* spiders, including the Ryukyu species.

The eight species of the Ryukyu *Cybaeus* can be grouped into two types based on characteristics of the embolus and spermathecae. The first (type 1) includes two species, *C. okumurai* (lineage A) and *C. kumadori* (lineage B), which possess an embolus that is not elongated and spermathecae consisting of distinct relatively bulbous SH, SS and SB. The other six species (lineages C–E) share an elongated embolus in their males, and a pair of elongate tubular spermathecal ducts composed of SH and SS as well as a bulbous SB in their females (type 2). The type 1 genital characters seem to be most common in the Japanese *Cybaeus* species, while the type 2 characters have only been documented in a few species known from Honshu and Shikoku in Japan

(Kobayashi 2006; Ihara 2009*a*). To our knowledge, the type 2 spermatheca has never been reported from other Far Eastern regions or North America. The elongated CD has been described in several Korean and American species, but their SHs are distinct from their CDs (Seo 2016; Bennett *et al*. 2016); tubular SSs of the North American *C. somesbar* Bennett in Copley *et al*., 2009 are continuous with its respective CD, but its SHs are lobate and diverge from the respective duct (Copley *et al*. 2009).

The genital characteristics and phylogenetic position unquestionably show that *C. okumurai*, endemic to Tanegashima Island, is a close congener of *C. ashikitaensis*; both species belong to lineage A, with the other two species in this lineage known from Kyushu. *Cybaeus ashikitaensis* is known from western Honshu, and northern to central regions of Kyushu in Japan, exhibiting a disjunct distribution (Ihara 2003, 2009*a*); spiders identified as *C. ashikitaensis* also occur on the southern tip of Kyushu (Y. Ihara, unpubl. data). The present phylogeny revealed that *C. okumurai* is sister to *C. ashikitaensis* from central Kyushu (near the type locality of the latter), but, nonetheless, it is possible that the southern population of "*C. ashikitaensis*" is the closest congener of, or conspecific with *C. okumurai*.

The phylogenetic position of the other type 1 species, *C. kumadori*, remains uncertain, because this species forms a unique clade (lineage B) among the species included in the phylogenetic analyses. The characteristics of the male palp and female spermathecae do not suggest any candidates for close congeners of *C. kumadori*. Among the Ryukyu *Cybaeus* species, *C. kumadori* lacks a PA in the male palp, a feature which it shares with *C. aikana* in Amamioshima Island and *C. hikidai* on Okinawa Island. However, the other characteristics of the palp and the female spermathecae are completely different between *C. kumadori* and the other two species. The precise phylogenetic position and close congeners of *C. kumadori* should be elucidated by a future study.

The four species categorized as type 2, *C. yakushimensis*, *C. kodama*, *C. amamiensis*, and *C. tokunoshimensis*, formed a well-supported clade (lineage D) among the Ryukyu *Cybaeus*. It is noteworthy that the two species endemic to Yakushima Island, *C. yakushimensis* and *C. kodama*, were not monophyletic in our analyses, but *C. yakushimensis*, *C. amamiensis* and *C. tokunoshimensis* formed a monophyletic lineage within this clade. Although this relationship was not fully supported, these three species

1193 share the following genital characters: digitiform PA, elongated embolus originating at
1194 the ca. 9 o'clock position in ventral view, a pair of laterally expanded SS, and a well-
1195 developed Bennett's gland. By contrast, males of *C. kodama* have a small PA, an
1196 embolus originating at the ca. 7 o'clock position in ventral view, and its females possess
1197 spermathecal ducts that are coiled at the anterior part of vulva. The morphological
1198 features of these four species therefore corroborate their phylogenetic relationships as
1199 suggested by the analyses of the present study.

1200 Our analyses were unable to determine the phylogenetic positions of *C. aikana*
1201 and *C. hikidai*. Although both species possess the type 2 genital characters, these two
1202 species differ from the other four type 2 species, *C. yakushimensis*, *C. kodama*, *C.*
1203 *amamiensis* and *C. tokunoshimensis*, in lacking the PA in the male palp. In addition, *C.*
1204 *aikana* and *C. hikidai* are distinguished from those four species by the tubular SH that is
1205 continuous with the tubular CD and is indistinguishable from the latter except for the
1206 presence of primary pores that indicate the position of the SH in the four species. Our
1207 field observations of *C. aikana* and *C. hikidai* clarified that these two species both
1208 construct Y-shaped retreats. *Cybaeus ishikawai* and *C. kompiraensis*, which are
1209 endemic to Shikoku, are also known to construct Y-shaped retreats (Komatsu 1940,
1210 1968), and *C. ishikawai* also possesses an elongated embolus in the male palp without a
1211 PA, and tubular spermathecal ducts in females (Ihara 2009*a*, fig. 2-2-30-216–219; as
1212 *Cybaeus* sp.). However, the present phylogeny did not reveal a close relationship among
1213 *C. aikana*, *C. hikidai*, and *C. ishikawai* as well as *C. kompiraensis* suggesting that both
1214 the genital characteristics and the Y-shaped retreat are not synapomorphies of a clade
1215 containing these species, but probably homoplastic.

1216 It remains uncertain whether the type 2 genital features (the elongated embolus
1217 and tubular formation of the spermathecae) have evolved multiple times in lineages C–
1218 E, because the present phylogenies failed to estimate a robust relationship in these
1219 lineages. However, the phylogenetic position of *C. ishikawai* suggests that these genital
1220 characteristics have arisen independently at least between *C. ishikawai* and the six
1221 species endemic to the Ryukyu Islands. *Cybaeus melanoparvus* Kobayashi, 2006, which
1222 was described from central Honshu, also possesses the type 2 embolus and
1223 spermathecae (Kobayashi 2006). Further systematic studies should be carried out to
1224 clarify the evolutionary history of the genital characters of *Cybaeus* spiders inhabiting

Japan and adjacent regions.

Implications for biogeography, distribution and natural history

This study demonstrated that the Northern Ryukyus include distinctive biogeographical elements of the genus *Cybaeus*. *Cybaeus okumurai* from Tanegashima Island is unquestionably related to the species endemic to Kyushu, while the two species, *C. yakushimensis* and *C. kodama*, inhabiting Yakushima Island belong to the clade that includes the species endemic to Amamioshima Island and Tokunoshima Island in the Central Ryukyus. Therefore, the range of the members of the monophyletic lineage D encompasses both the Northern and Central Ryukyus across the Tokara Gap. This biogeographic pattern of the Ryukyu *Cybaeus* is incongruent with that of other epigean/ground-dwelling spiders inhabiting the Ryukyu Islands. It was shown that a species of the liphistiid *Heptathela* Kishida, 1923 in Yakushima Island is phylogenetically close to the species endemic to Kyushu, and that *Heptathela* species endemic to the Central Ryukyus do not occur north of the Tokara Gap (Xu *et al*. 2016, 2019). Because the present study did not estimate the divergence time of the Ryukyu *Cybaeus*, their biogeographical history should be further elucidated using a robust, time-calibrated phylogeny in a future study. It is evident from the deep divergences among the four species of lineage D that the wide distribution of these species has not been formed by recent range expansion across the Tokara Gap.

Sympatric distributions of different-sized species of *Cybaeus* (see Ihara 2008) were also documented in the Ryukyu *Cybaeus*. Our study revealed that the medium-sized *C. yakushimensis* and small-sized *C. kodama* were distributed sympatrically in Yakushima Island, and that the medium-sized *C. amamiensis* and small-sized *C. aikana* occurred together in Amamioshima Island. Given the deep divergence between *C. amamiensis* and *C. aikana* and the fact that *C. amamiensis* is sister to *C. tokunoshimensis*, the sympatric distribution of *C. amamiensis* and *C. aikana* in Amamioshima Island may have been formed by secondary contact between these two species, or their ancestors. Although our phylogenetic analyses failed to determine the precise relationships between *C. yakushimensis* and *C. kodama*, these two species were also genetically highly divergent from each other, indicating that the sympatric

occurrence of *C. yakushimensis* and *C. kodama* may also be explained by secondary contact between these two species in Yakushima Island.

Our study also revealed the occurrence of the different-sized mature individuals within a single Ryukyu *Cybaeus* species. Our finding of size dimorphism in females of *C. okumurai* suggests that females of *C. okumurai* undergo at least two types of life cycle. *Cybaeus* species distributed in western Japan appear to exhibit a life cycle of two or more years (Ihara 2006, 2009*a*); spiders may overwinter as juveniles and then mature in the following autumn. Given the occurrence of small-sized mature females in *C. okumurai*, a number of its females may mature in the autumn and winter immediately after hatching. Additional field surveys and systematic studies are essential to understand the sympatric distribution of the different-sized species, and of different-sized individuals of the same species, and the broader natural histories in the Ryukyu *Cybaeus* species.

Conflicts of interest

The authors declare no conflicts of interest.

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FIGURE LEGENDS AND TABLE CAPTIONS

Fig. 1. Bayesian inference tree (mean ln $L = -10554.32$) for 3421 bp of nuclear histone H3, internal transcribed spacer 1, 28S rRNA, mitochondrial COI, 12S rRNA, and 16S rRNA markers. Numbers on nodes represent bootstrap values for maximum likelihood and Bayesian posterior probabilities.

Fig. 2. Map showing the distributions of the lineages that contain *Cybaeus* species in the Ryukyu Islands. Inset phylogeny is identical with that in Fig. 1. The map and lineages are colour-shaded to indicate the species collection localities. The map is based on Wessel and Smith (1996).

Fig. 3. *Cybaeus okumurai*, sp. nov., male holotype (KUZ Z3019: *A*, *B*) and female paratype (KUZ Z3024: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal. Scale bars: 1 mm.

Fig. 4. *Cybaeus okumurai*, sp. nov., male holotype (KUZ Z3019: *A*–C, *F*, *G*); *Cybaeus ashikitaensis* (Komatsu), male from Ashikita, Kyushu Island (KUZ Z3675: *D*, *E*). (*A*) left palp, retrolateral; (*B*, *D*) tibia and patella (left palp), retrolateral; (*C*, *E*) tibia and patella (left palp), retro-dorsolateral; (*F*) cymbium (left palp), dorsal; (*G*) cymbium (left palp), ventral. Scale bars: (*A*) 500 μm; (*B*–*G*) 200 μm.

Fig. 5. *Cybaeus okumurai*, sp. nov., female paratypes (KUZ Z3023: *A*; KUZ Z3025: *B*); *Cybaeus ashikitaensis* (Komatsu), females from Ebino (KUZ Z3676: *C*) and Ashikita (KUZ Z3677: *D*), Kyushu Island. (*A*, *C*) epigyne, ventral; (*B*, *D*) spermathecae, dorsal. Scale bars: 200 μm.

Fig. 6. *Cybaeus kumadori*, sp. nov., male holotype (KUZ Z3004: *A*, *B*) and female paratype (KUZ Z3007: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal. Scale bars: 1 mm.

Fig. 7. *Cybaeus kumadori*, sp. nov., male holotype (KUZ Z3004: *A*–*E*) and female

paratypes (KUZ Z2144: *G*; KUZ Z3007: *F*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) cymbium (left palp), dorsal; (*D*) cymbium and bulb (left palp), retrolateral; (*D*) bulb (left palp), ventral; (*H*) epigyne, ventral; (*I*) spermathecae, dorsal. Scale bars: (*A*) 500 μm; (*B*) 250 μm; (*C*–*G*) 200 μm.

Fig. 8. *Cybaeus yakushimensis*, sp. nov., male holotype (KUZ Z2998: *A*, *B*) and female paratype (KUZ Z3001: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal. Scale bars: 1 mm.

Fig. 9. *Cybaeus yakushimensis*, sp. nov., male holotype (KUZ Z2998: *A*–*C*) and female paratypes (KUZ Z2138: *E*; KUZ Z3001: *D*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) epigyne, ventral; (*E*) spermathecae, dorsal. Scale bars: (*A*) 500 μm; (*B*–*E*) 200 μm.

Fig. 10. *Cybaeus yakushimensis*, sp. nov., male holotype (KUZ Z2998: *A*, *D*, *G*); *Cybaeus amamiensis*, sp. nov., male holotype (KUZ Z2987: *B*, *E*, *H*); *Cybaeus tokunoshimensis* (KUZ Z2113: *C*, *F*). (*A*–*C*) cymbium (left palp), dorsal; (*D*–*F*) tibia (left palp), retro-dorsolateral; (*G*, *H*) bulb (left palp), ventral. Scale bars: (*A*–*C*) 250 μm; (*D*–*H*) 200 μm.

Fig. 11. *Cybaeus kodama*, sp. nov., male holotype (KUZ Z3011: *A*, *B*) and female paratype (KUZ Z3013: *C*, *D*, *F*); *Cybaeus yakushimensis*, sp. nov., female from Hanayama Trail, Yakushima Island (KUZ Z3003; *E*) (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal; (*E*, *F*) habitus, dorsal. Scale bars: (*A*–*D*) 500 μm; (*E*, *F*) 1 mm.

Fig. 12. *Cybaeus kodama*, sp. nov., male holotype (KUZ Z3011: *A*–*E*) and female paratypes (KUZ Z2142: *G*; KUZ Z3014: *F*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) cymbium (left palp), dorsal; (*E*) bulb (left palp), ventral; (*F*) epigyne, ventral; (*G*) spermathecae, dorsal. Scale bars: (*A*, *D*, *E*) 200 μm; (*B*, *C*, *F*, *G*) 100 μm.

Fig. 13. *Cybaeus amamiensis*, sp. nov., male holotype (KUZ Z2987: *A*, *B*) and female

paratype (KUZ Z2991: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal. Scale bars: 1 mm.

Fig. 14. *Cybaeus amamiensis*, sp. nov., male holotype (KUZ Z2987: *A*–*C*) and female paratypes (KUZ Z2121: *E*; KUZ Z2991: *D*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) epigyne, ventral; (*E*) spermathecae, dorsal. Scale bars: (*A*) 500 μm; (*B*–*E*) 200 μm.

Fig. 15. *Cybaeus aikana*, sp. nov., male holotype (KUZ Z3017: *A*, *B*) and female paratype (KUZ Z3018: *C*). (*A*) prosoma, dorsal; (*B*) abdomen, dorsal; (*C*) habitus, dorsal. Scale bars: (*A*, *B*) 500 μm; (*C*) 1 mm.

Fig. 16. *Cybaeus aikana*, sp. nov., male holotype (KUZ Z3017). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) cymbium (left palp), dorsal; (*D*) bulb (left palp), ventral; (*E*) conductor (left palp), proximal end, posteroventral. Scale bars: (*A*, *C*) 200 μm; (*B*, *D*, *E*) 100 μm.

Fig. 17. *Cybaeus aikana*, sp. nov., female paratypes (KUZ Z2137: *B*; KUZ Z3018: *A*). (*A*) epigyne, ventral; (*B*) spermathecae, dorsal. Scale bars: 200 μm.

Fig. 18. *Cybaeus tokunoshimensis*, sp. nov., male holotype (KUZ Z2113: *A*, *B*, *E*–*H*) and female paratypes (KUZ Z2112: *J*; KUZ Z2994: *C*, *D*;KUZ Z2995: *I*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal; (*E*) left palp, retrolateral; (*F*) tibia and patella (left palp), dorsal; (*G*) tibia and patella (left palp), retrolateral; (*H*) bulb (left palp), ventral; (*I*) epigyne, ventral; (*J*) spermathecae, dorsal. Scale bars: (*A*–*D*) 1 mm; (*E*) 500 μm; (*F*–*J*) 200 μm.

Fig. 19. *Cybaeus hikidai*, sp. nov., male holotype (KUZ Z2982: *A*, *B*, *E*–*H*) and female paratypes (KUZ Z2107: *I*, *J*; KUZ Z2984: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal; (*E*) left palp, retrolateral; (*F*) tibia and patella (left palp), dorsal; (*G*) cymbium (left palp), dorsal; (*H*) bulb (left palp), ventral; (*I*) epigyne, ventral; (*J*) spermathecae, dorsal. Scale bars: (*A*–D) 1 mm; (*E*) 500 μm; (*F*, *H*–*J*) 200 μm; (*G*) 250

μm.

Fig. 20. *Cybaeus hikidai*, sp. nov., schematic drawing of epigyne and spermathecae. ventral (left) and dorsal (right), based on female paratype (KUZ Z2107).

Fig. 21. *Cybaeus hikidai*, sp. nov., epigyne, ventral. (*A*) paratype (KUZ Z2984); (*B*) female from Mt. Nagodake, Okinawa Island (KUZ Z2985); (*C*) paratype (KUZ Z2983). Scale bars: 200 μm.

Fig. 22. Retreats of *Cybaeus* spiders from the Ryukyu Islands. (*A*) *Cybaeus okumurai*, sp. nov., from Nishino-omote, Tanegashima Island; (*B*) *Cybaeus aikana*, sp. nov. from Mt. Yuwandake, Amamioshima Island; (*C*) *Cybaeus hikidai*, sp. nov. from Mt. Yonahadake, Okinawa Island.

Table 1. Samples with voucher numbers, collection locality and DDBJ accession numbers used for molecular analyses

Sequences marked with an asterisk (*) were obtained for the first time in the present study; KUZ, Zoological Collection of Kyoto University

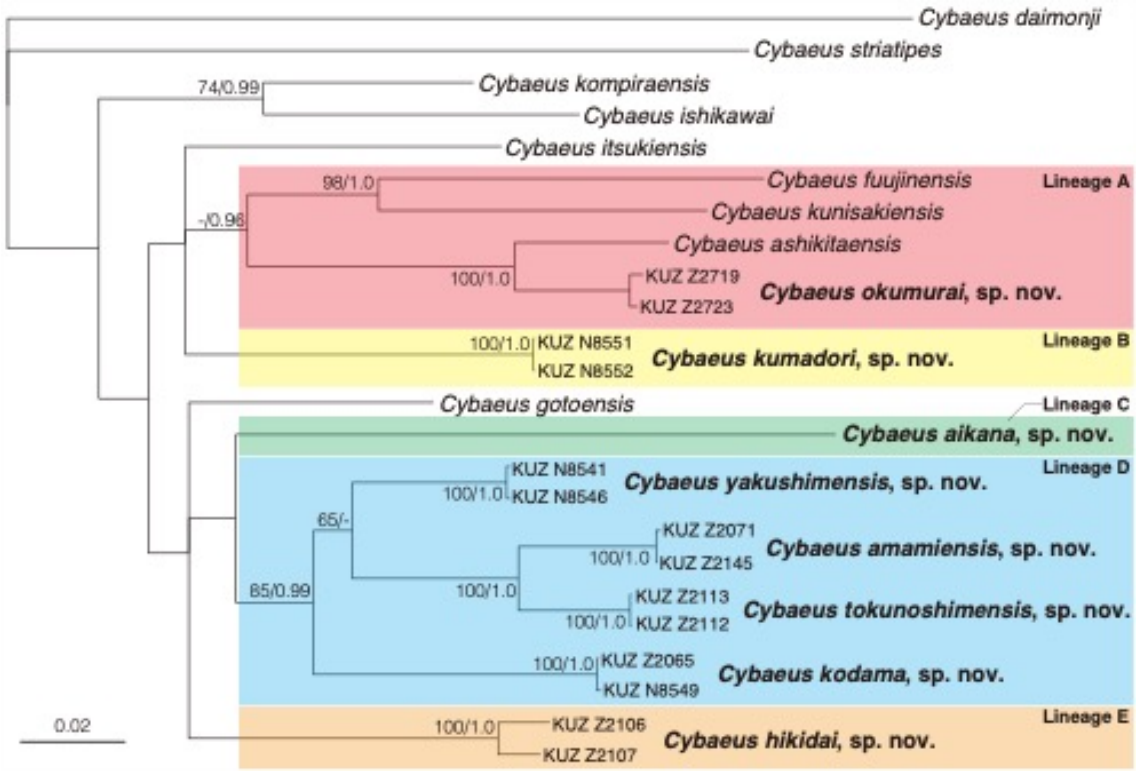

Fig. 1. Bayesian inference tree (mean ln $L = -10554.32$) for 3421 bp of nuclear histone H3, internal transcribed spacer 1, 28S rRNA, mitochondrial COI, 12S rRNA, and 16S rRNA markers. Numbers on nodes represent bootstrap values for maximum likelihood and Bayesian posterior probabilities.

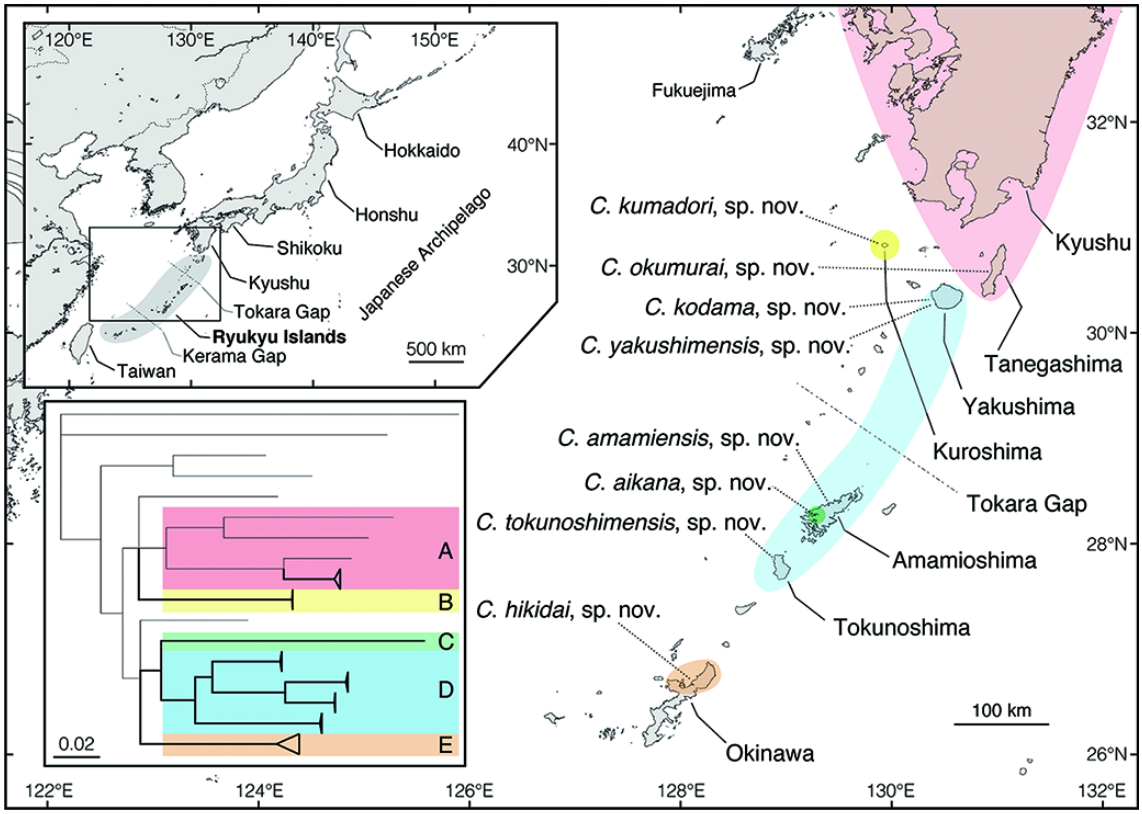

Fig. 2. Map showing the distributions of the lineages that contain *Cybaeus* species in the Ryukyu Islands. Inset phylogeny is identical with that in Fig. 1. The map and lineages are colour-shaded to indicate the species collection localities. The map is based on Wessel and Smith (1996).

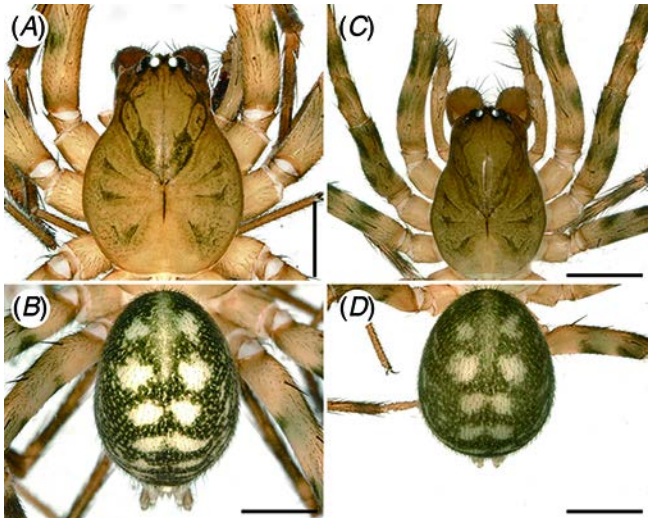

Fig. 3. *Cybaeus okumurai*, sp. nov., male holotype (KUZ Z3019: *A*, *B*) and female paratype (KUZ Z3024: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal. Scale bars: 1 mm.

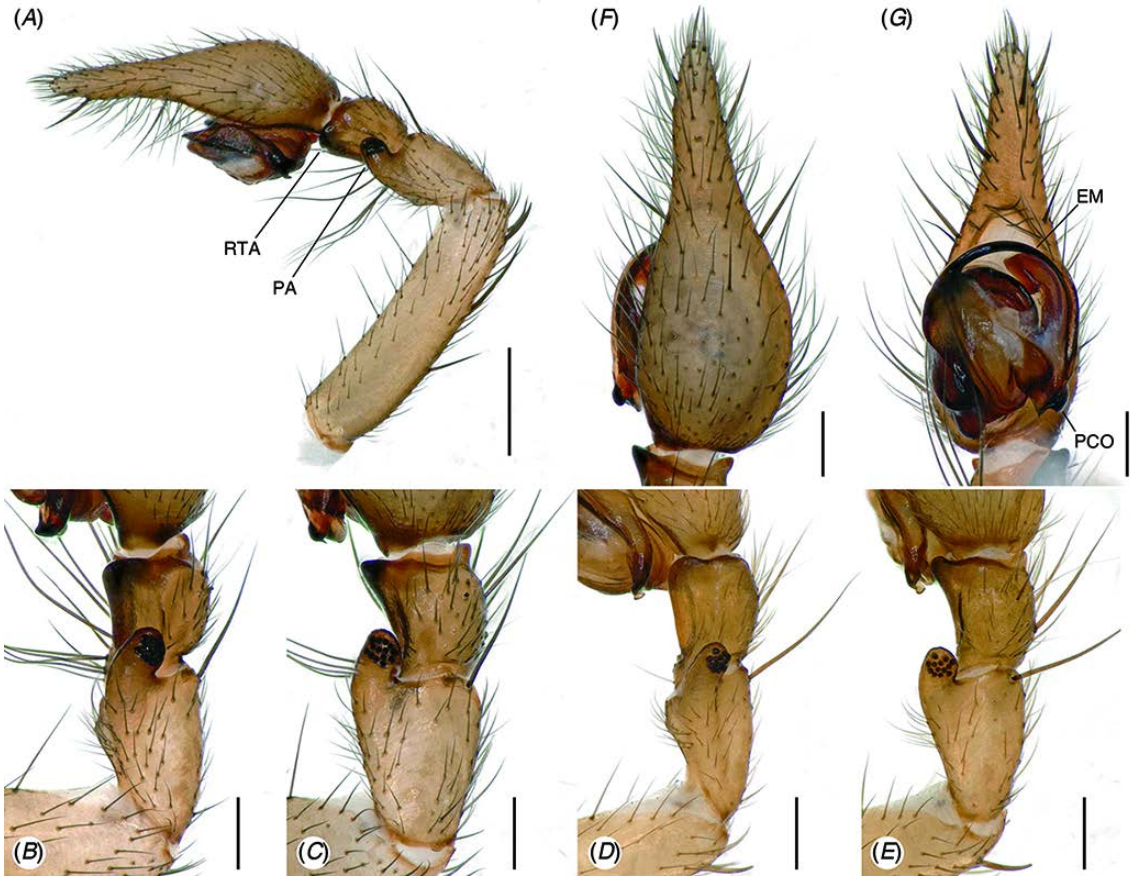

Fig. 4. *Cybaeus okumurai*, sp. nov., male holotype (KUZ Z3019: *A*–C, *F*, *G*); *Cybaeus ashikitaensis* (Komatsu), male from Ashikita, Kyushu Island (KUZ Z3675: *D*, *E*). (*A*) left palp, retrolateral; (*B, D*) tibia and patella (left palp), retrolateral; (*C*, *E*) tibia and patella (left palp), retro-dorsolateral; (*F*) cymbium (left palp), dorsal; (*G*) cymbium (left palp), ventral. Scale bars: (*A*) 500 μm; (*B*–*G*) 200 μm.

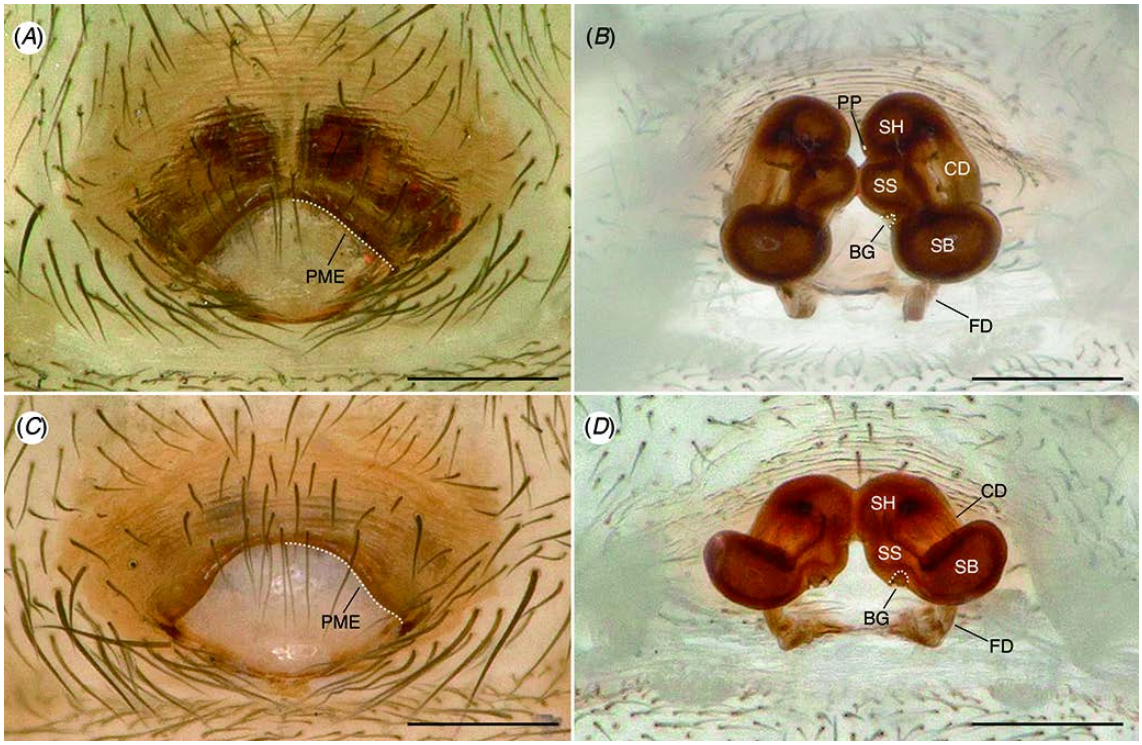

Fig. 5. *Cybaeus okumurai*, sp. nov., female paratypes (KUZ Z3023: *A*; KUZ Z3025: *B*); *Cybaeus ashikitaensis* (Komatsu), females from Ebino (KUZ Z3676: *C*) and Ashikita (KUZ Z3677: *D*), Kyushu Island. (*A*, *C*) epigyne, ventral; (*B*, *D*) spermathecae, dorsal. Scale bars: 200 μm.

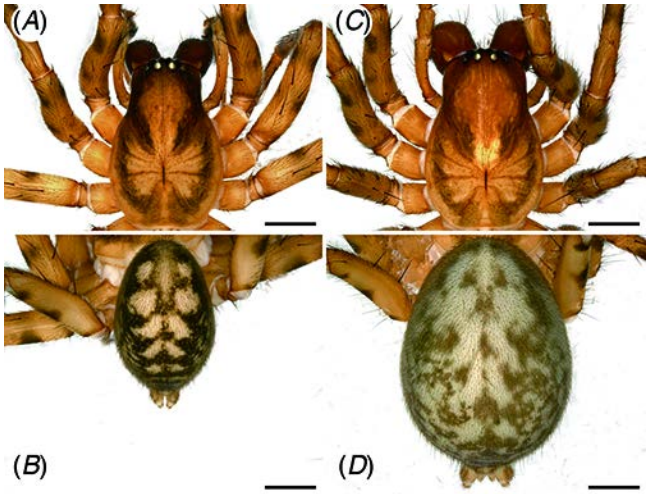

Fig. 6. *Cybaeus kumadori*, sp. nov., male holotype (KUZ Z3004: *A*, *B*) and female paratype (KUZ Z3007: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal. Scale bars: 1 mm.

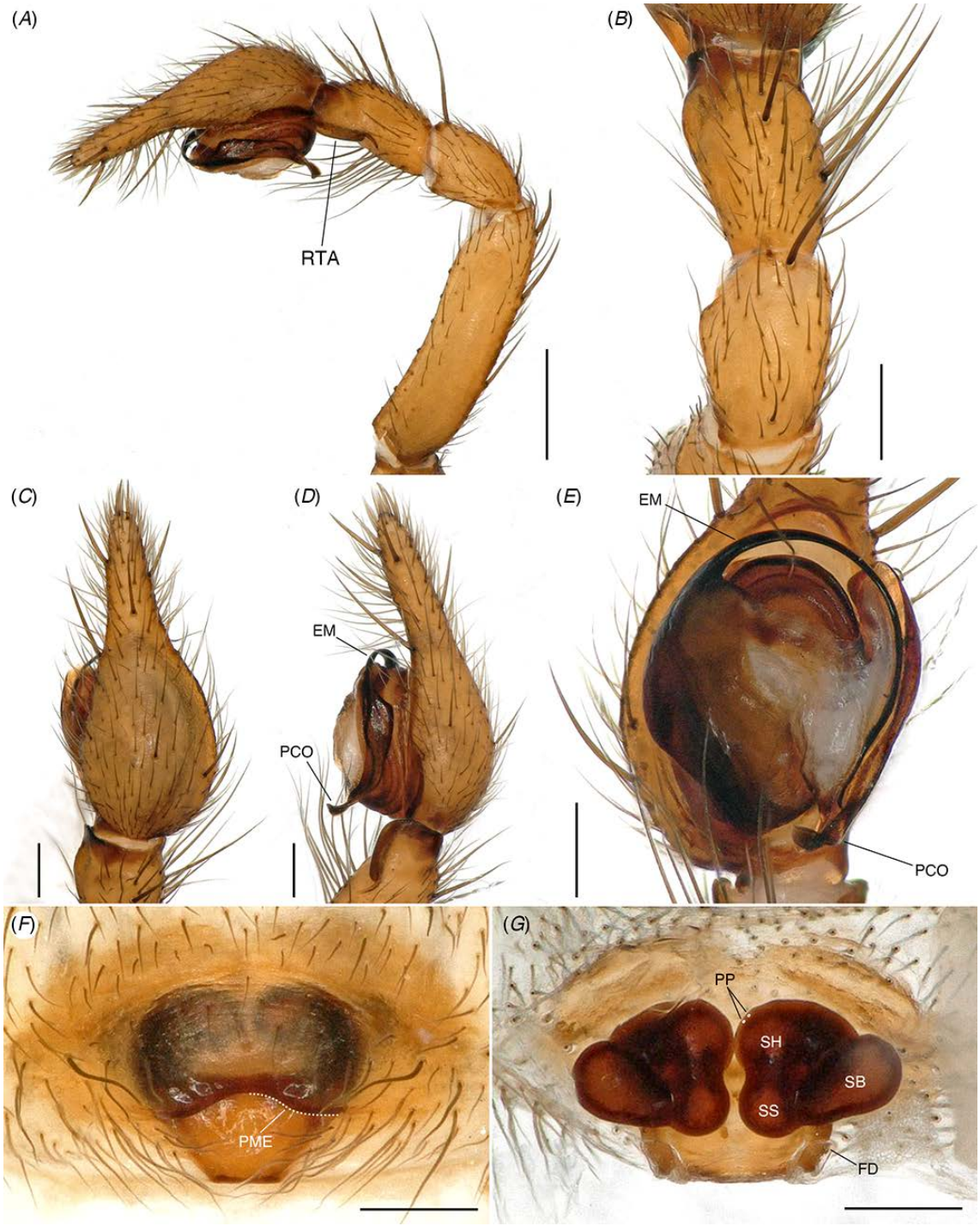

Fig. 7. *Cybaeus kumadori*, sp. nov., male holotype (KUZ Z3004: *A*–*E*) and female paratypes (KUZ Z2144: *G*; KUZ Z3007: *F*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) cymbium (left palp), dorsal; (*D*) cymbium and bulb (left palp), retrolateral; (*D*) bulb (left palp), ventral; (*H*) epigyne, ventral; (*I*) spermathecae, dorsal. Scale bars: (*A*) 500 μm; (*B*) 250 μm; (*C*–*G*) 200 μm.

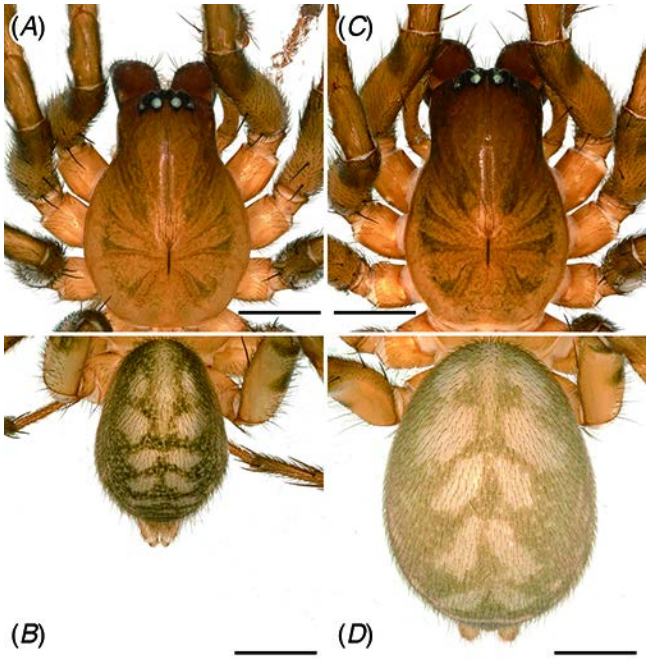

Fig. 8. *Cybaeus yakushimensis*, sp. nov., male holotype (KUZ Z2998: *A*, *B*) and female paratype (KUZ Z3001: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal. Scale bars: 1 mm.

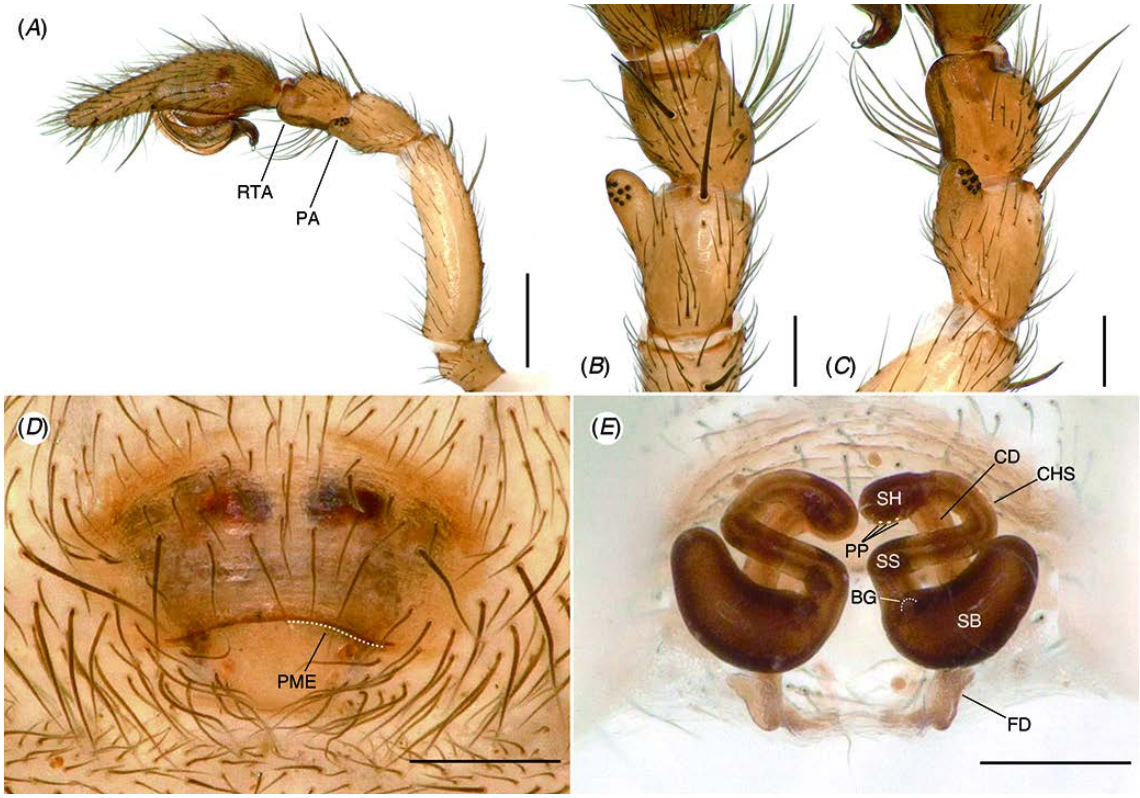

Fig. 9. *Cybaeus yakushimensis*, sp. nov., male holotype (KUZ Z2998: *A*–*C*) and female paratypes (KUZ Z2138: *E*; KUZ Z3001: *D*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) epigyne, ventral; (*E*) spermathecae, dorsal. Scale bars: (*A*) 500 μm; (*B*–*E*) 200 μm.

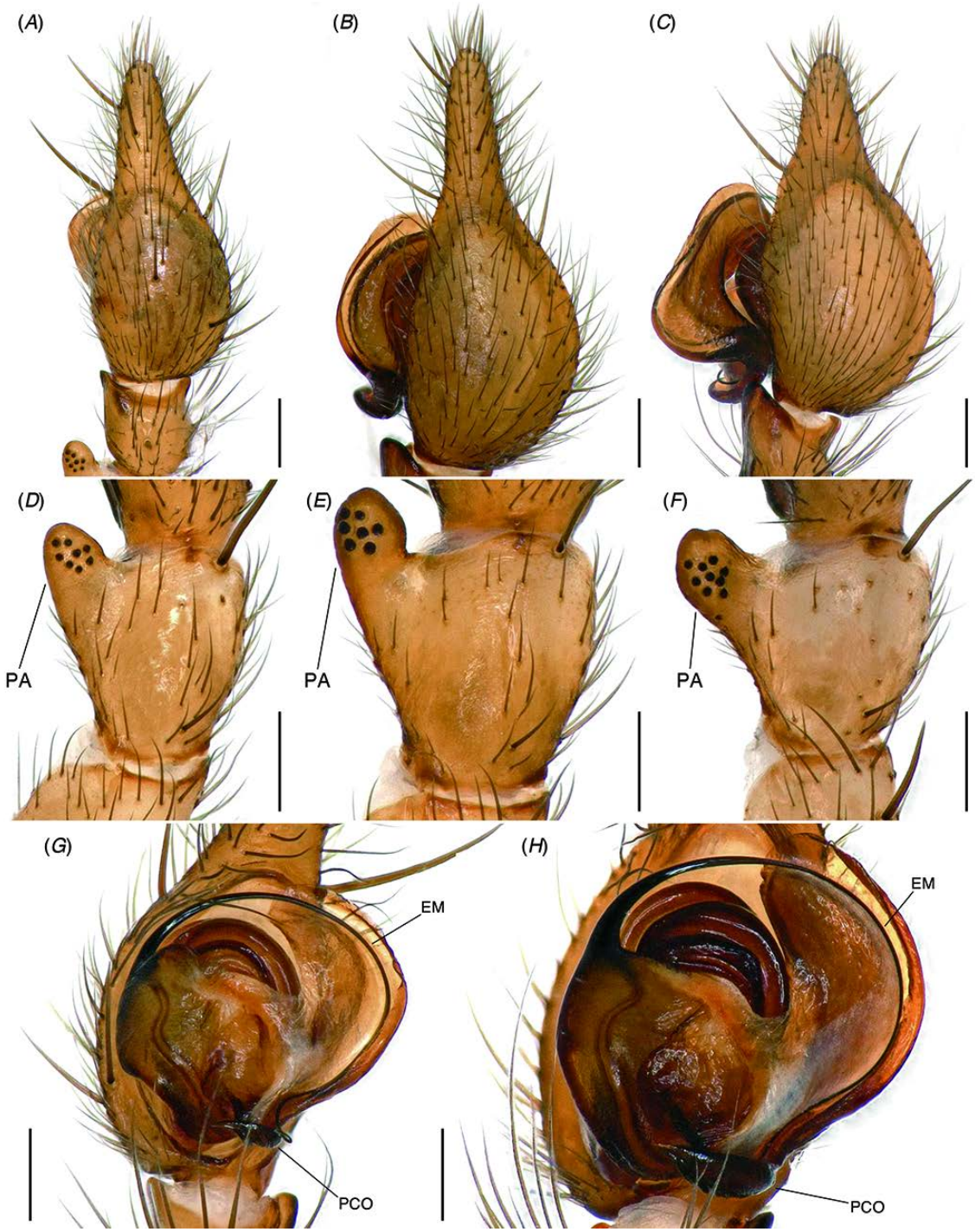

Fig. 10. *Cybaeus yakushimensis*, sp. nov., male holotype (KUZ Z2998: *A*, *D*, *G*); *Cybaeus amamiensis*, sp. nov., male holotype (KUZ Z2987: *B*, *E*, *H*); *Cybaeus tokunoshimensis* (KUZ Z2113: *C*, *F*). (*A–C*) cymbium (left palp), dorsal; (*D–F*) tibia (left palp), retro-dorsolateral; (*G*, *H*) bulb (left palp), ventral. Scale bars: (*A–C*) 250 μm; (*D–H*) 200 μm.

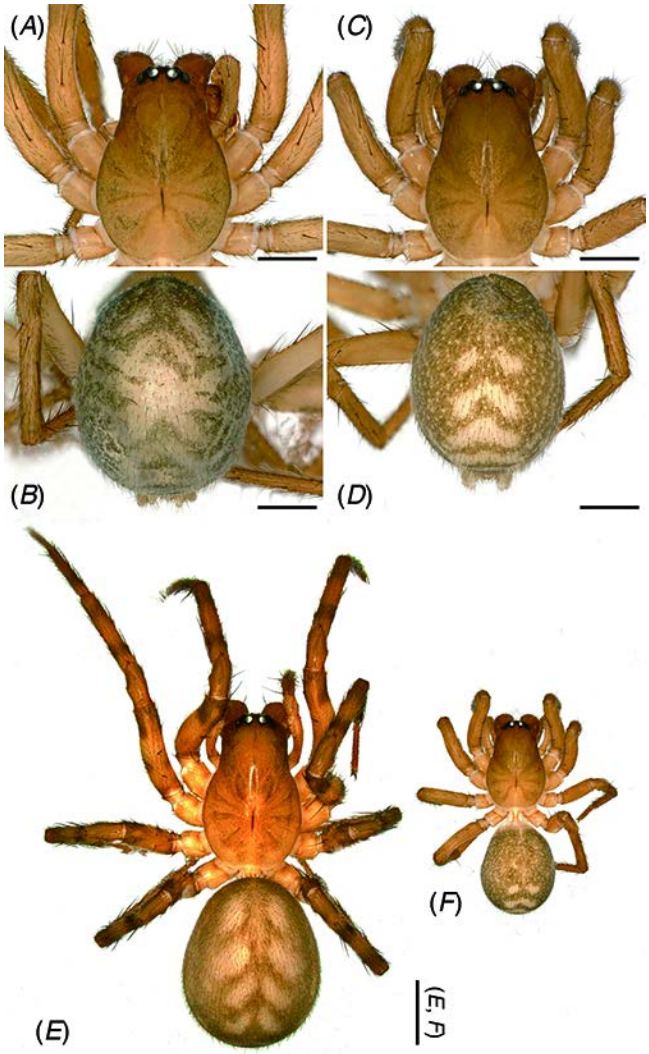

Fig. 11. *Cybaeus kodama*, sp. nov., male holotype (KUZ Z3011: *A*, *B*) and female paratype (KUZ Z3013: *C*, *D*, *F*); *Cybaeus yakushimensis*, sp. nov., female from Hanayama Trail, Yakushima Island (KUZ Z3003; *E*) (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal; (*E*, *F*) habitus, dorsal. Scale bars: (*A*–*D*) 500 μm; (*E*, *F*) 1 mm.

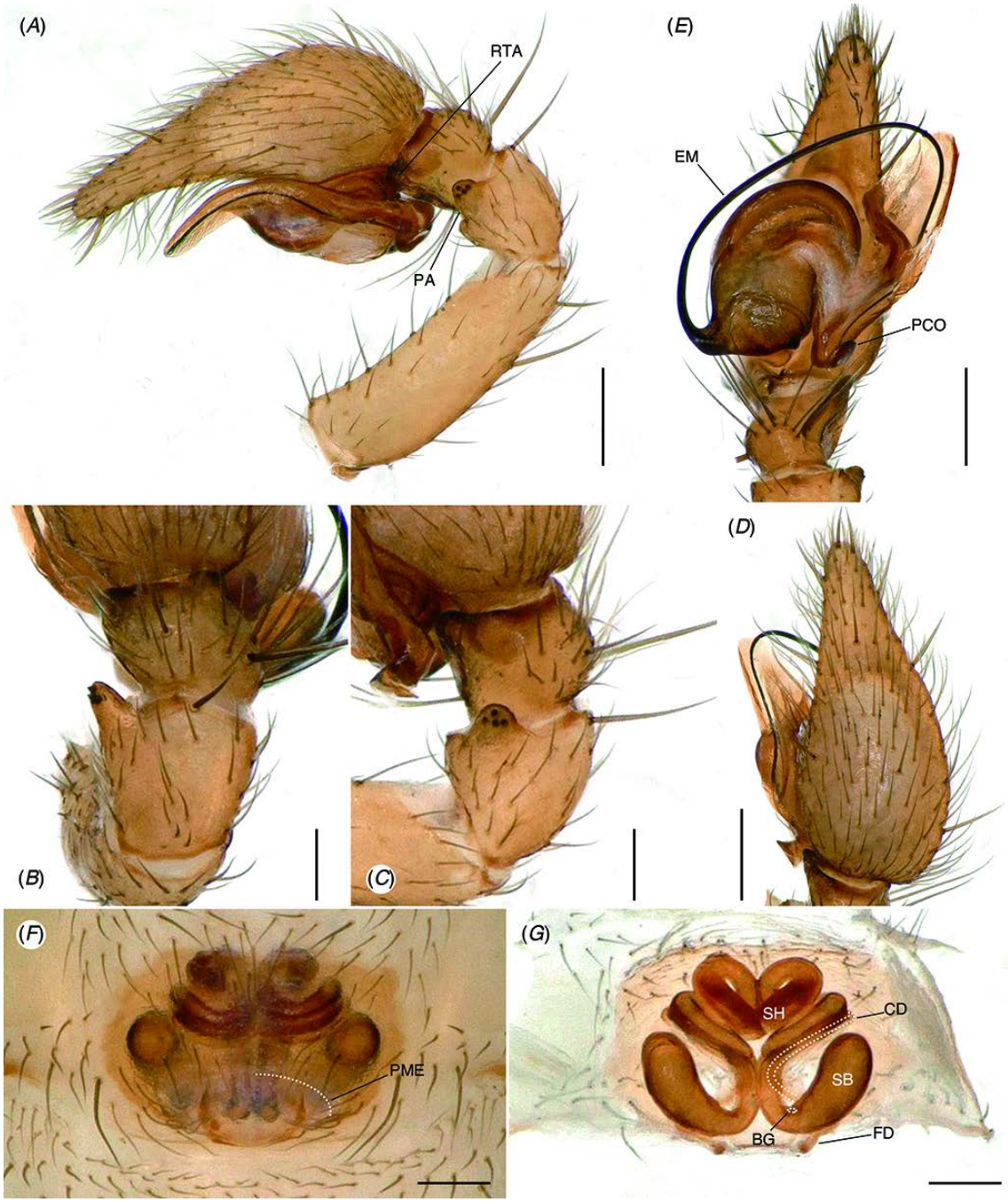

Fig. 12. *Cybaeus kodama*, sp. nov., male holotype (KUZ Z3011: *A*–*E*) and female paratypes (KUZ Z2142: *G*; KUZ Z3014: *F*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) cymbium (left palp), dorsal; (*E*) bulb (left palp), ventral; (*F*) epigyne, ventral; (*G*) spermathecae, dorsal. Scale bars: (*A*, *D*, *E*) 200 μm; (*B*, *C*, *F*, *G*) 100 μm.

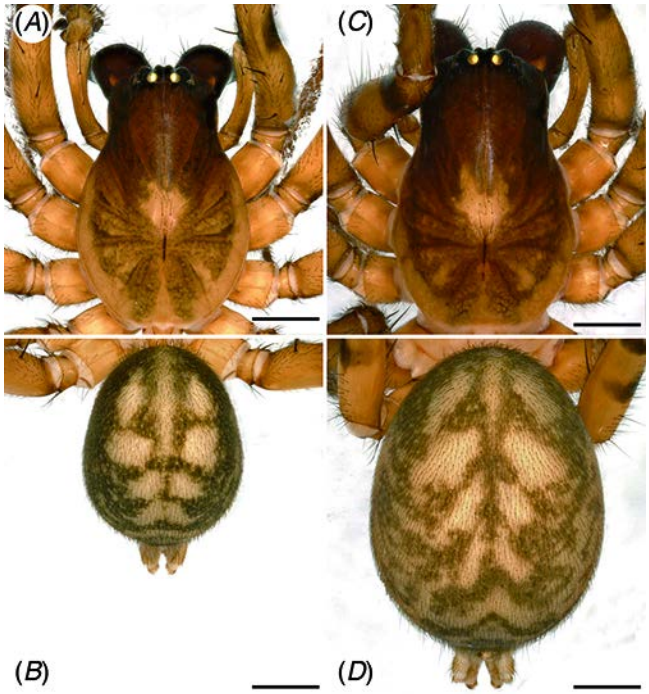

Fig. 13. *Cybaeus amamiensis*, sp. nov., male holotype (KUZ Z2987: *A*, *B*) and female paratype (KUZ Z2991: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal. Scale bars: 1 mm.

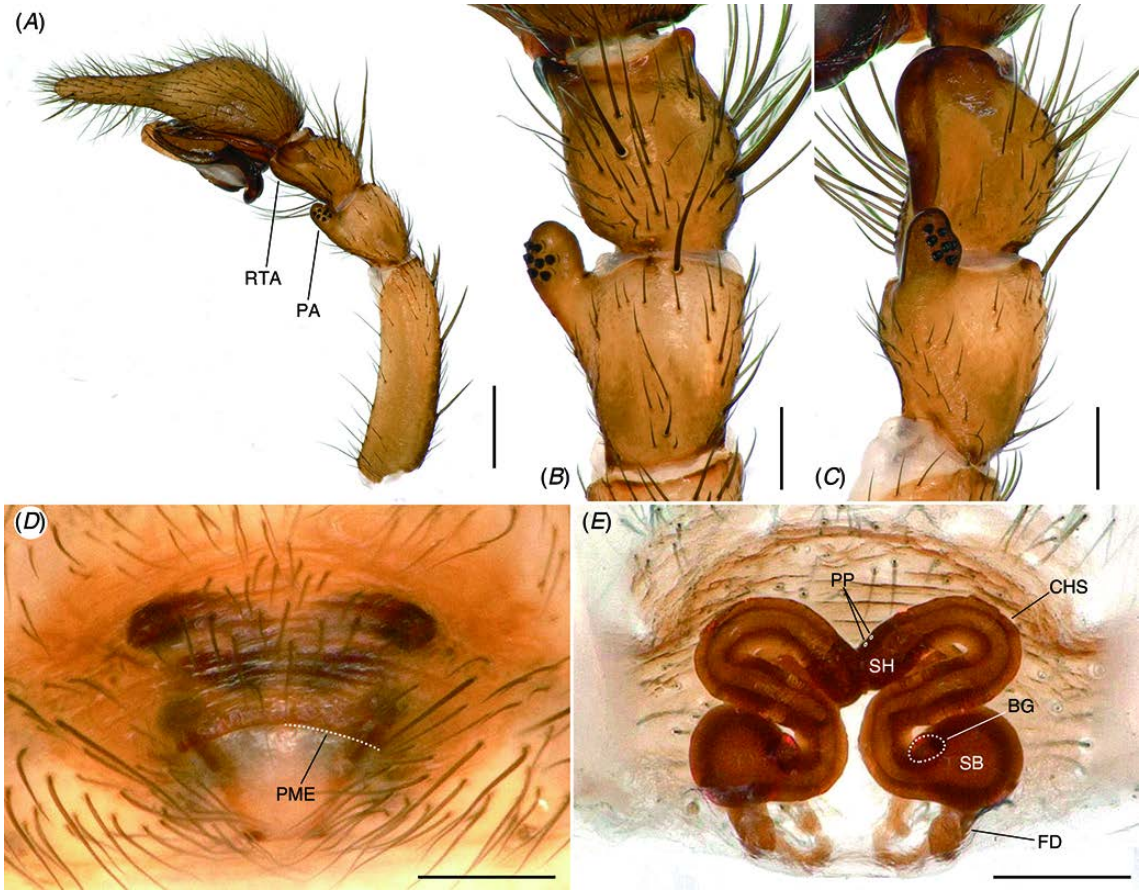

Fig. 14. *Cybaeus amamiensis*, sp. nov., male holotype (KUZ Z2987: *A*–*C*) and female paratypes (KUZ Z2121: *E*; KUZ Z2991: *D*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) epigyne, ventral; (*E*) spermathecae, dorsal. Scale bars: (*A*) 500 μm; (*B*–*E*) 200 μm.

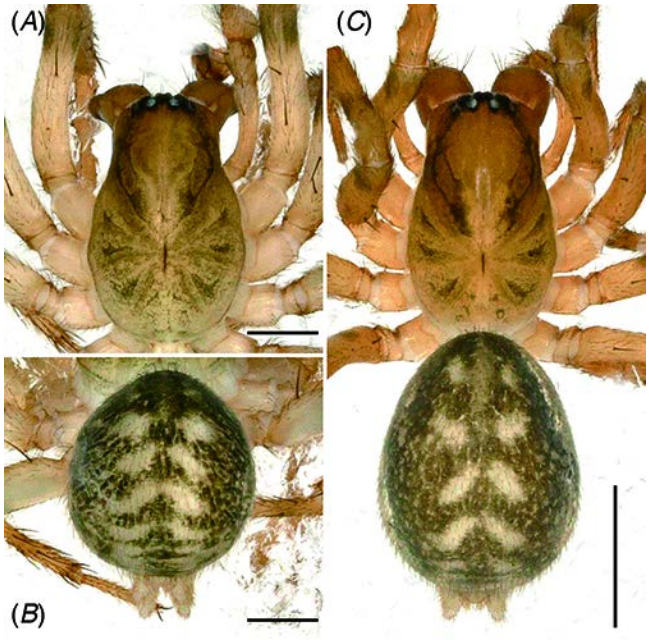

Fig. 15. *Cybaeus aikana*, sp. nov., male holotype (KUZ Z3017: *A*, *B*) and female paratype (KUZ Z3018: *C*). (*A*) prosoma, dorsal; (*B*) abdomen, dorsal; (*C*) habitus, dorsal. Scale bars: (*A*, *B*) 500 μm; (*C*) 1 mm.

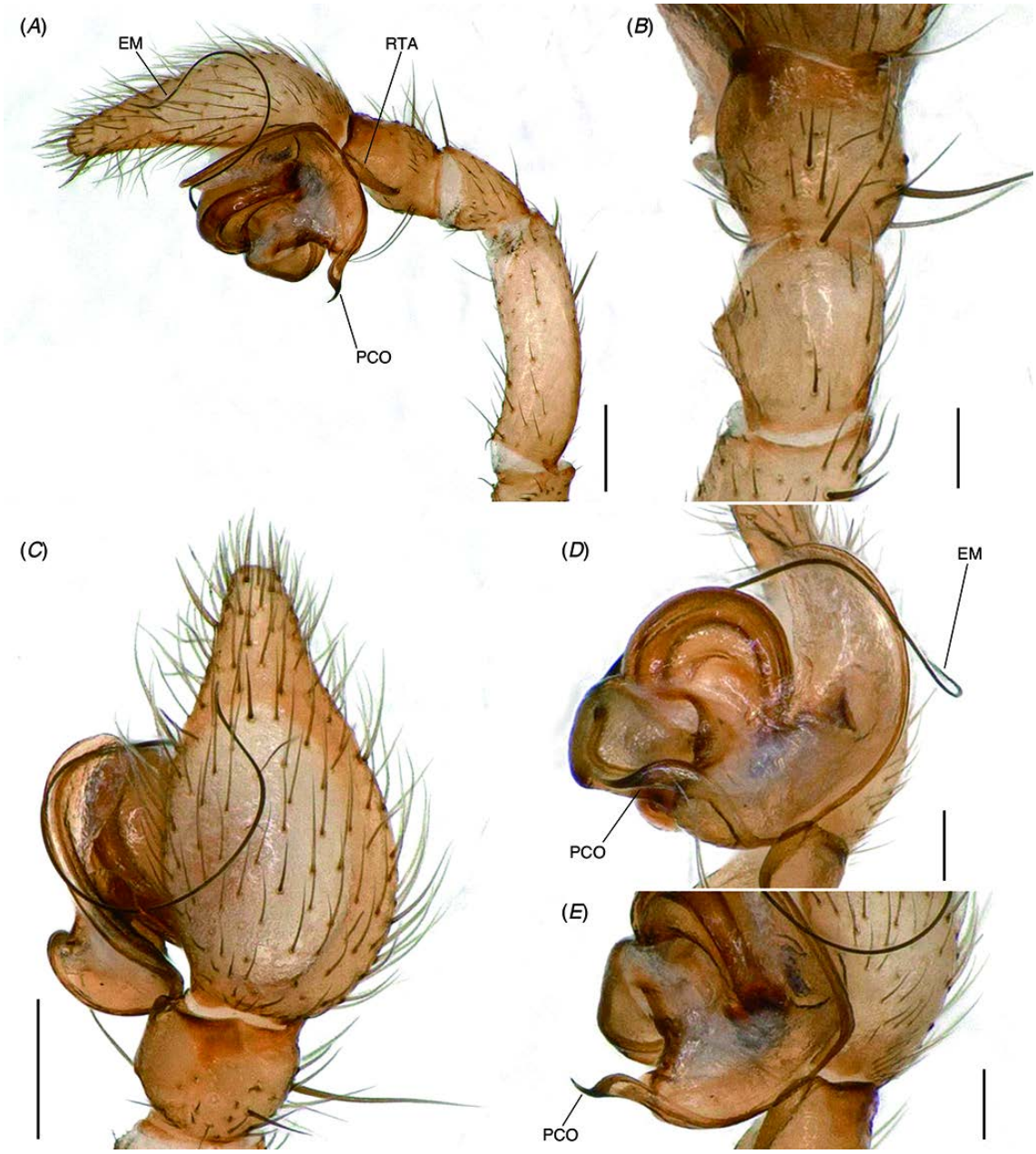

Fig. 16. *Cybaeus aikana*, sp. nov., male holotype (KUZ Z3017). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) cymbium (left palp), dorsal; (*D*) bulb (left palp), ventral; (*E*) conductor (left palp), proximal end, posteroventral. Scale bars: (*A*, *C*) 200 μm; (*B*, *D*, *E*) 100 μm.

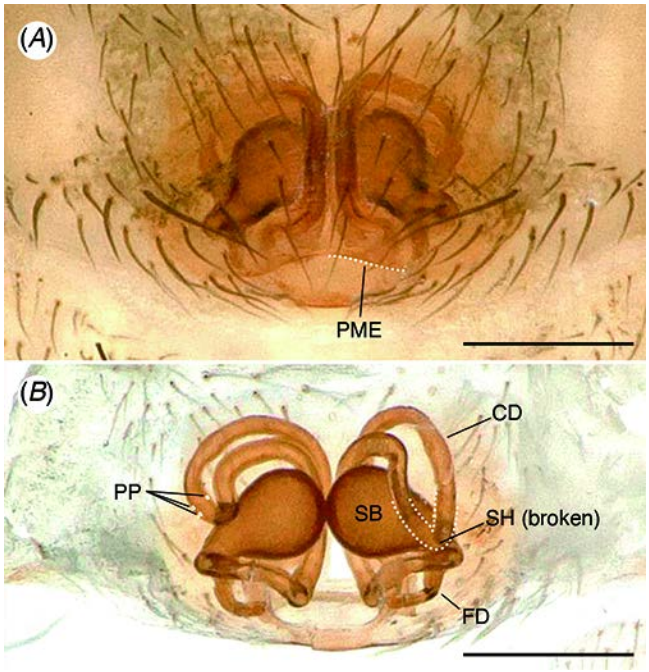

Fig. 17. *Cybaeus aikana*, sp. nov., female paratypes (KUZ Z2137: *B*; KUZ Z3018: *A*). (*A*) epigyne, ventral; (*B*) spermathecae, dorsal. Scale bars: 200 μm.

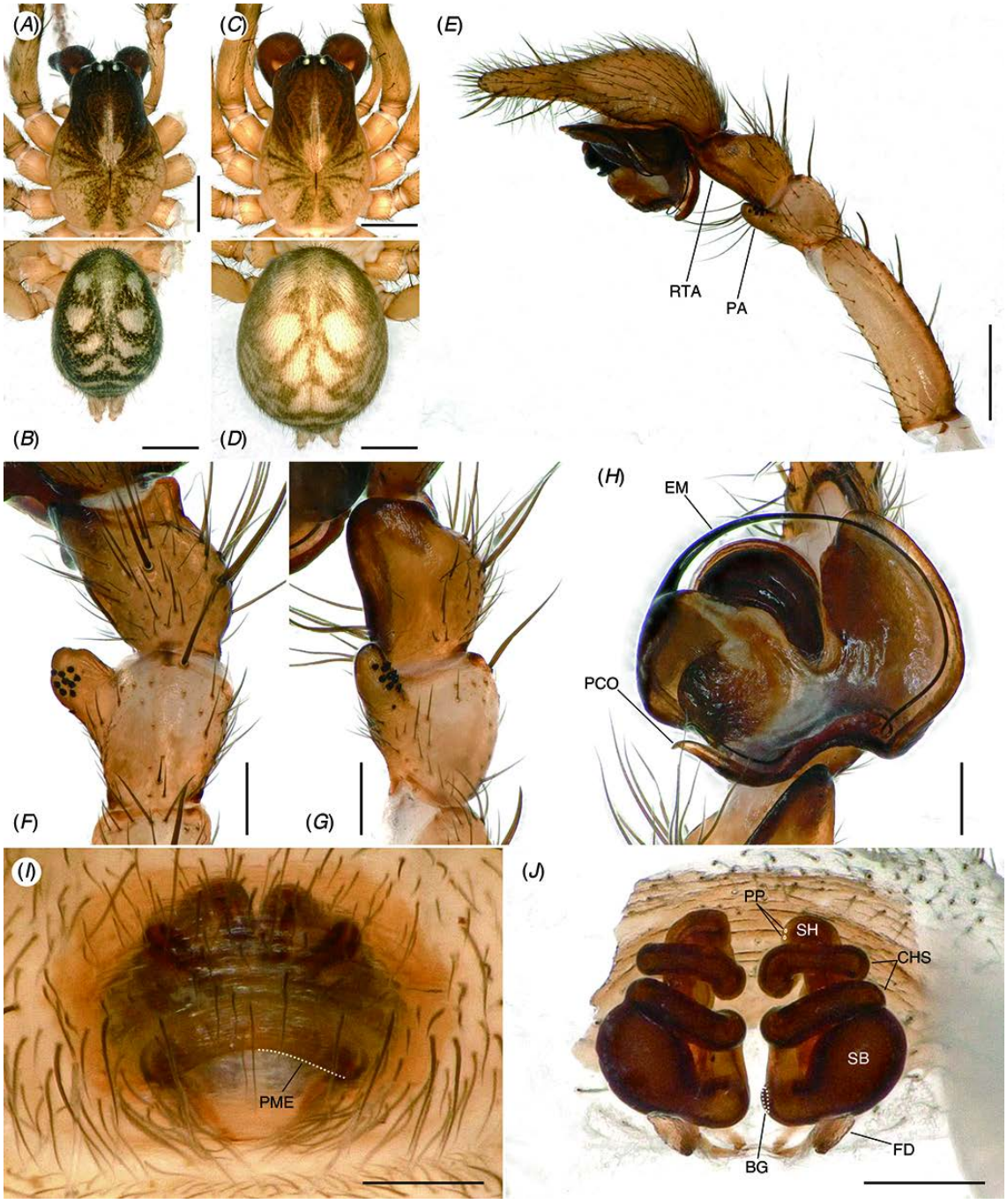

Fig. 18. *Cybaeus tokunoshimensis*, sp. nov., male holotype (KUZ Z2113: *A*, *B*, *E–H*) and female paratypes (KUZ Z2112: *J*; KUZ Z2994: *C*, *D*;KUZ Z2995: *I*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal; (*E*) left palp, retrolateral; (*F*) tibia and patella (left palp), dorsal; (*G*) tibia and patella (left palp), retrolateral; (*H*) bulb (left palp), ventral; (*I*) epigyne, ventral; (*J*) spermathecae, dorsal. Scale bars: (*A–D*) 1 mm; (*E*) 500 μm; (*F–J*) 200 μm.

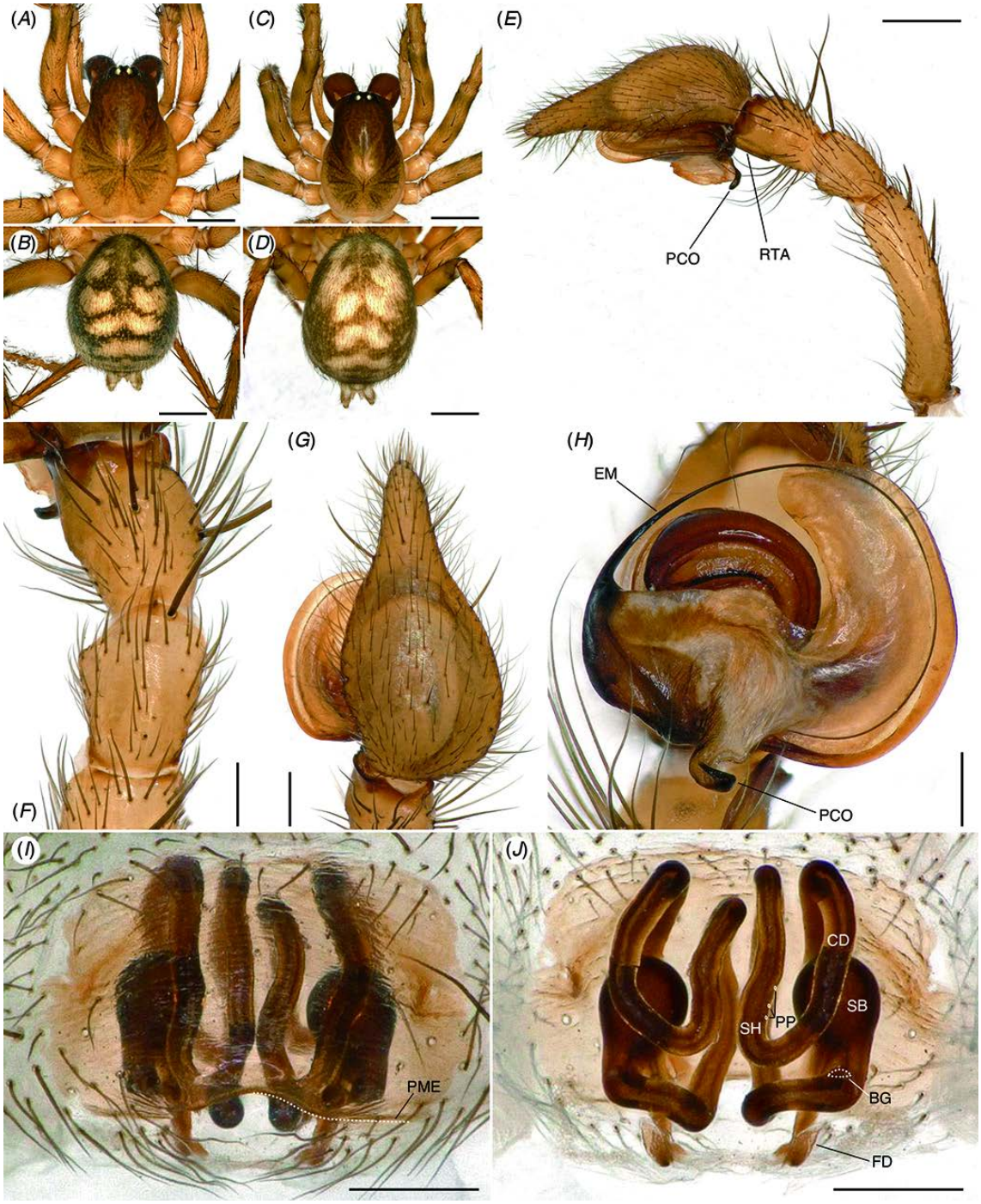

Fig. 19. *Cybaeus hikidai*, sp. nov., male holotype (KUZ Z2982: *A*, *B*, *E*–*H*) and female paratypes (KUZ Z2107: *I*, *J*; KUZ Z2984: *C*, *D*). (*A*, *C*) prosoma, dorsal; (*B*, *D*) abdomen, dorsal; (*E*) left palp, retrolateral; (*F*) tibia and patella (left palp), dorsal; (*G*) cymbium (left palp), dorsal; (*H*) bulb (left palp), ventral; (*I*) epigyne, ventral; (*J*) spermathecae, dorsal. Scale bars: (*A*–D) 1 mm; (*E*) 500 μm; (*F*, *H*–*J*) 200 μm; (*G*) 250 μm.

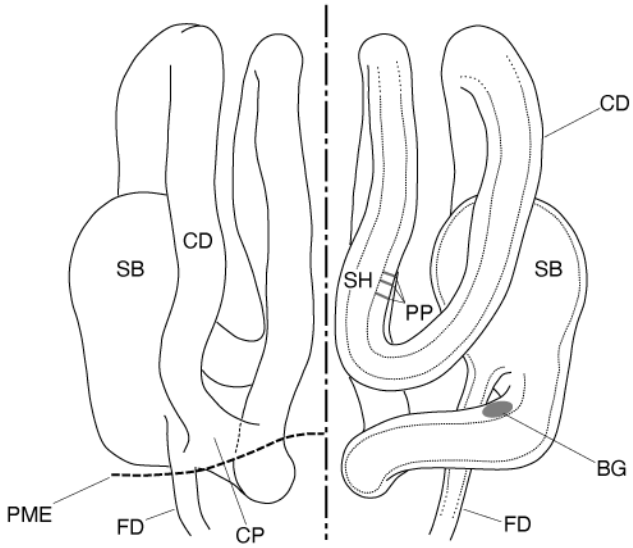

Fig. 20. *Cybaeus hikidai*, sp. nov., schematic drawing of epigyne and spermathecae. ventral (left) and dorsal (right), based on female paratype (KUZ Z2107).

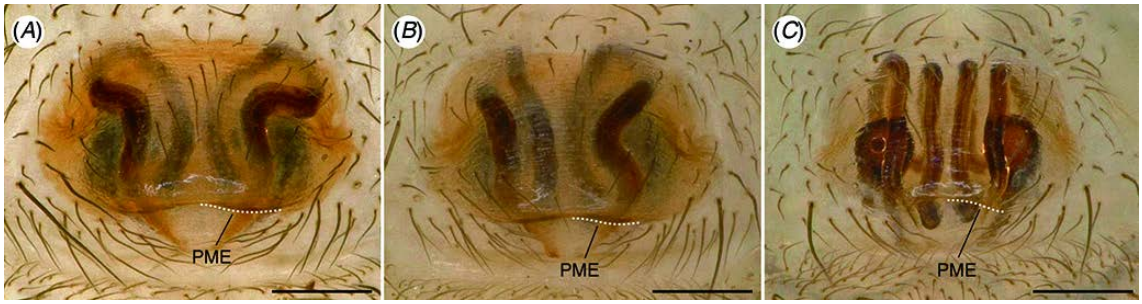

Fig. 21. *Cybaeus hikidai*, sp. nov., epigyne, ventral. (*A*) paratype (KUZ Z2984); (*B*) female from Mt. Nagodake, Okinawa Island (KUZ Z2985); (*C*) paratype (KUZ Z2983). Scale bars: 200 μm.

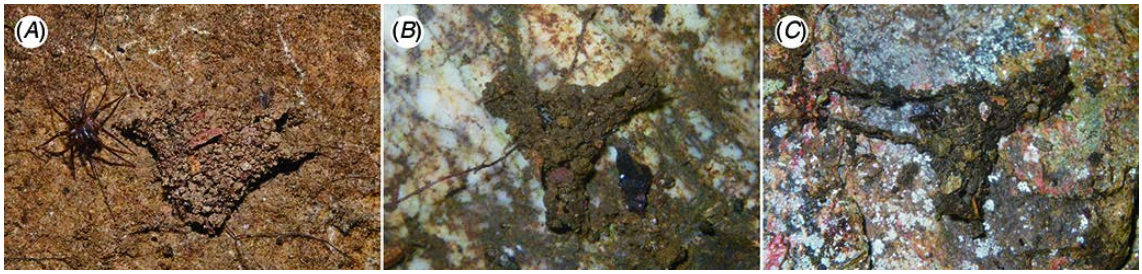

Fig. 22. Retreats of *Cybaeus* spiders from the Ryukyu Islands. (*A*) *Cybaeus okumurai*, sp. nov., from Nishino-omote, Tanegashima Island; (*B*) *Cybaeus aikana*, sp. nov. from Mt. Yuwandake, Amamioshima Island; (*C*) *Cybaeus hikidai*, sp. nov. from Mt. Yonahadake, Okinawa Island.

Table 1. Samples with voucher numbers, collection locality and DDBJ accession numbers used for molecular analyses

Sequences marked with an asterisk (*) were obtained for the first time in the present study; KUZ, Zoological Collection of Kyoto University

Taxa	Voucher #	Locality	28S rRNA	ITS1	Histone H3	COI	12S rRNA	16S rRNA
Cybaeus okumurai, sp. nov.	KUZ Z2719	Kunigami, Nishinoomote, Tanegashima Island	LC552280*	LC552282*	LC552281*		LC552279*	
Cybaeus okumurai, sp. nov.	KUZ Z2723	Nakanoshimo, Minamitane, Tanegashima Island	LC552283*	LC552285*	LC552284*			
Cybaeus yakushimensis, sp. nov.	KUZ Z2138	Shiratani-unsuikyo Valley, Yakushima Island	LC552207*	LC552209*	LC552208*		LC552205*	LC552206*
Cybaeus yakushimensis, sp. nov.	KUZ Z2140	Hanayama Trail, Kurio, Yakushima Island	LC552212*	LC552214*	LC552213*		LC552210*	LC552211*
Cybaeus kodama, sp. nov.	KUZ Z2141	Hanayama Trail, Kurio, Yakushima Island	LC552215*	LC552218*	LC552217*	LC552216*		
Cybaeus kodama, sp. nov.	KUZ Z2142	Hanayama Trail, Kurio, Yakushima Island	LC552219*	LC552222*	LC552221*	LC552220*		
Cybaeus kumadori, sp. nov.	KUZ Z2143	Mt. Yaguradake, Kuroshima Island, Mishima Islands	LC552225*	LC552228*	LC552227*	LC552226*	LC552223*	LC552224*
Cybaeus kumadori, sp. nov.	KUZ Z2144	Mt. Yaguradake, Kuroshima Island, Mishima Islands	LC552230*	LC552233*	LC552232*	LC552231*	LC552229*	
Cybaeus amamiensis, sp. nov.	KUZ Z2120	Mt. Yuwandake, Amamioshima Island	LC552236*	LC552239*	LC552238*	LC552237*	LC552234*	LC552235*
Cybaeus amamiensis, sp. nov.	KUZ Z2121	Mt. Yuwandake, Amamioshima Island	LC552242*	LC552245*	LC552244*	LC552243*	LC552240*	LC552241*
Cybaeus aikana, sp. nov.	KUZ Z2137	Mt. Yuwandake, Amamioshima Island	LC552248*		LC552250*	LC552249*	LC552246*	LC552247*
Cybaeus tokunoshimensis, sp. nov.	KUZ Z2112	Mt. Inokawadake, Tokunoshima Island	LC552258*	LC552261*	LC552260*	LC552259*	LC552257*	
Cybaeus tokunoshimensis, sp. nov.	KUZ Z2113	Mt. Inokawadake, Tokunoshima Island	LC552253*	LC552256*	LC552255*	LC552254*	LC552251*	LC552252*
Cybaeus hikidai, sp. nov.	KUZ Z2106	Mt. Nagodake, Nago, Okinawajima Island	LC552264*	LC552267*	LC552266*	LC552265*	LC552262*	LC552263*
Cybaeus hikidai, sp. nov.	KUZ Z2107	Hiji-otaki Fall, Kunigami, Okinawajima Island	LC552270*	LC552273*	LC552272*	LC552271*	LC552268*	LC552269*
Cybaeus ashikitaensis	KUZ Z2213	Itsuki, Kumamoto, Kyushu	LC552192*	LC552195*	LC552194*	LC552193*	LC552191*	
Cybaeus daimonji	KUZ Z2755	Mt. Daimonjiyama, Kyoto, Honshu	LC529207	LC529208	LC529206	LC529209	LC529211	LC529210
Cybaeus fuujinensis	KUZ Z2199	Fujindo Cave, Kumamoto, Kyushu	LC552187*	LC552190*	LC552189*	LC552188*	LC552186*	
Cybaeus gotoensis	KUZ Z2251	Iana Cave, Fukuejima Island, Goto Islands	LC552201*	LC552204*	LC552203*	LC552202*		
Cybaeus ishikawai	KUZ Z2715	near Ryugado Cave, Kochi, Shikoku	LC552276*	LC552278*	LC552277*		LC552274*	LC552275*

Cybaeus itsukiensis	KUZ Z2184	Tsuzurasedo Cave, Kumamoto, Kyushu	LC552182*	LC552185*	LC552184*	LC552183*	
Cybaeus kompiraensis	KUZ Z2317	Kompirado Cave, Kochi, Shikoku	LC552179*	LC552181*	LC552180*	LC552178*	
Cybaeus kunisakiensis	KUZ Z2303	Mt. Futagosan, Oita, Kyushu	LC552197*	LC552200*	LC552199*	LC552198*	LC552196*
Cybaeus striatipes	KUZ Z2718	Mt. Rausudake, Shari, Hokkaido	LC552174*	LC552177*	LC552176*	LC552175*	

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