- Integrative taxonomy reveals multiple lineages of the spider genus Cybaeus 1 2endemic to the Ryukyu Islands, Japan (Arachnida : Araneae : Cybaeidae) 3 Yoh Ihara^{A,D}, Naoki Koike^{B,C} and Takafumi Nakano^{B,D} 4 5 ^AHiroshima Environment & Health Association, 9-1 Hirose-kita-machi, Naka-ku, 6 7 Hiroshima 730-8631, Japan. 8 ^BDepartment of Zoology, Graduate School of Science, Kyoto University, Kyoto 606-9 8502, Japan.
- 10 ^C982 Minamichitose-machi, Nagano 380-0822, Japan.
- ${}^{D}Corresponding\ authors.\ Email:\ yoh.ihara@kanhokyo.or.jp;\ nakano@zoo.zool.kyoto-property authors.$
- 12 u.ac.jp

14

- ZooBank: urn:lsid:zoobank.org:pub:640D15AA-17F4-48EE-88B4-485CFF8FCD60
- Running title: Systematics of Ryukyu Islands Cybaeus

18	Abstract. The epigean spiders of the genus Cybaeus L. Roch, 1808 are known to have
19	diversified in western North America and the Japanese Archipelago. To date, ca. 80
20	species of Cybaeus are known from Japan, but they have not previously been recorded
21	from the Ryukyu Islands that harbour a diversity of endemic species. Here we describe
22	eight new species of Cybaeus from the Ryukyu Islands, extending the range of Cybaeus
23	southward to the central Ryukyus. Both sexes of each of the new species are described,
24	and their phylogenetic relationships are estimated using nuclear and mitochondrial gene
25	markers. Although Cybaeus okumurai, sp. nov. and C. kumadori, sp. nov. possess
26	genital features that are common in the other Japanese congeners, the other six species
27	(C. yakushimensis, sp. nov., C. kodama, sp. nov., C. amamiensis, sp. nov., C. aikana,
28	sp. nov., C. tokunoshimensis, sp. nov., and C. hikidai, sp. nov.) are characterised by an
29	elongated embolus and tubular spermathecae. These unique genital characteristics and
30	the phylogeny recovered here suggest that these features evolved independently among
31	the Japanese and Ryukyu Cybaeus species. Phylogenetic analyses highlight an unusual
32	biogeographical pattern in which C. yakushimensis and C. kodama endemic to
33	Yakushima Island in the northern Ryukyus are related to species distributed in the
34	central Ryukyus. In contrast, our phylogeny suggests that C. okumurai from
35	Tanegashima Island in the northern Ryukyus is sister to C. ashikitaensis (Komatsu,
36	1968) distributed in Kyushu of the Japanese Archipelago. The retreat constructs and
37	sympatric distribution of Cybaeus found among the Ryukyus are also briefly discussed.

Additional keywords: island fauna, morphology, phylogenetics

Introduction

4	1
4	2

Spiders belonging to the genus Cybaeus L. Koch, 1868 are epigean species inhabiting 43 moist woodlands in the Holarctic region (Bennett 2017). Cybaeus currently consists of 44 164 species with disjunct distributions from western Europe to the Caucasus, the 45 northern Far East, and the eastern and western Nearctic, and is highly diverse in western 46 47 North America and the Japanese Archipelago (World Spider Catalog, ver. 21.5, see https://wsc.nmbe.ch/, accessed 10 September 2020). Molecular phylogenetic analyses 48 49 have revealed that Cybaeus spiders endemic to western North America comprise two distinctive lineages, the 'Holarctic' and 'Californian' clades (Copley et al. 2009). The 50 Holarctic clade contains species widely distributed in North America and includes the 51type species of Cybaeus, C. tetricus (C.L. Koch, 1839), which is endemic to Europe 52 (Bennett et al. 2016). By contrast, the species belonging to the Californian clade all 53 have restricted ranges within western North America (Bennett et al. 2019). To date, 46 54 species of Cybaeus are known from North America (World Spider Catalog, ver. 21.5). 55 Japanese Cybaeus currently comprises 83 species (World Spider Catalog, ver. 56 57 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 58 Russian Far East and Kuril Islands (Marusik and Logunov 1991; Marusik and Kovblyuk 59 60 2011; Seo 2017). Although their phylogenetic relationships remain uncertain, the Japanese Cybaeus have been classified by characteristics of the palp and female 61 genitalia (Ihara 2009a). Morphology of the patellar apophysis, the retrolateral tibial 62 63 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 64 generally consists of three distinct parts: the head, stalk and base. The spermathecal 65 heads of Cybaeus are distinguished by the presence of primary pores on their surface 66 67 (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 68 69 Cybaeus daimonji Matsuda, Ihara & Nakano, 2020, primary pores and Bennett's gland have not been documented in Japanese Cybaeus (Matsuda et al. 2020). 70 71 An interesting evolutionary phenomenon known in Japanese Cybaeus is the 72 sympatry between species of different-sized classes (see Ihara 2008). To help

73 understand their species-richness and sympatric distributions, Japanese Cybaeus have 74been 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-75 sized', ranging from 5 to 10 mm; and 'large-sized', greater than 10 mm (Ihara 2004). 76 In addition to the genital and size-related features, ca. 42 of 83 of the Japanese 77 78 species of Cybaeus are known to construct tube-like silken retreats on undersides of 79 stones and woods (Y. Ihara, unpubl. data; see Ihara 2009b). The most common form of retreat is 'V-shaped' with two openings, one at each end (Ihara 2006). A similar V-80 shaped retreat is built by the Appalachian hahniid Cicurina bryantae Exline, 1936 81 (Bennett 1985). However, retreats of Cybaeus feature silk signal threads radiating from 82 the openings; no such signal threads are present in the retreats of Cicurina bryantae (see 83 Matsuda et al. 2020). In addition to the V-shaped form, three less common types of 84 retreats are constructed by the Japanese Cybaeus: V-shaped with three openings, 'Y-85 shaped' with three openings, and hexagonal with three openings (Komatsu 1961, 1968; 86 Ihara 2003, 2009b). Retreats with three openings were known previously only from 87 troglobitic species inhabiting northern Honshu Island and Shikoku Island in the 88 89 Japanese Archipelago (Komatsu 1961, 1968), but recent studies have shown that epigean species distributed in western Honshu and northern Kyushu Island also 90 construct retreats with three openings (Ihara 2003, 2009b). 91 92 Prior to our work, the southern distributional limit of Japanese Cybaeus was documented as Kyushu in the Japanese Archipelago (Ihara 2009a). To our knowledge 93 Cybaeus spiders have not previously been recorded from the Ryukyu Islands, which 94 95 form a continental island arc south of Kyushu between the Japanese Archipelago and 96 Taiwan. The Ryukyu Islands are known to harbour a unique biota with a wide variety of 97 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 98 99 Ryukyu Islands are comprised of three major biogeographic divisions: Northern 100 Ryukyus (Tanegashima Island and Yakushima Island, and adjacent islets), Central 101 Ryukyus (Amamioshima Island, Tokunoshima Island, and Okinawa Islands, and 102 adjacent islets), and Southern Ryukyus (Miyako Islands and Yaeyama Islands). The 103 divisions are separated by two tectonic depressions, the Tokara and Kerama Gaps (e.g. 104 Ota 1998; Motokawa 2000). In the present study, Cybaeus spiders were collected from

103	several islands in the Northern and Central Rydkyds. Here we present their systematic
106	accounts including an assessment of their phylogenetic relationships based on nuclear
107	and mitochondrial gene markers.
108	
109	Materials and methods
110	Samples and morphological observation
111	Previously undescribed species of Cybaeus spiders were collected from six islands in
112	the Ryukyu Islands, Japan. For comparative purposes for the molecular phylogenetic
113	analyses, specimens of a further nine Japanese species, including C. ashikitaensis
114	(Komatsu, 1968), C. daimonji, C. fuujinensis (Komatsu, 1968), C. gotoensis
115	(Yamaguchi & Yaginuma, 1971), C. itsukiensis Irie, 1998, C. kompiraensis (Komatsu,
116	1968), C. kunisakiensis Ihara, 2003, C. striatipes Bösenberg & Strand, 1906, and C.
117	ishikawai (Kishida in Komatsu, 1940), were also collected from or near their type
118	localities (Table 1). In addition, one male and two female specimens of C. ashikitaensis
119	were examined for morphological comparison: 1 #, 1 @ from the type locality (KUZ
120	Z3675, Z3677); 1 @ from Ebino, Miyazaki, Kyushu Island (KUZ Z3676). Where
121	possible, geographical coordinates for the collection sites were obtained using a GPS
122	unit (eTrex®, Garmin, Olathe, KS, USA). Specimens were preserved in 70% ethanol;
123	legs of some specimens were removed and preserved in 99% ethanol for DNA
124	extraction.
125	Epigynes were dissected from various female specimens and cleared with
126	proteinase K (100 µg/mL) (see Matsuda et al. 2020), or with hot 10% KOH + 3% H ₂ O ₂
127	(see Komatsu and Yaginuma 1968) to observe the internal structure. When more than
128	one female could be examined per species, several specimens were dissected.
129	Morphological examination of the specimens was conducted using a stereoscopic
130	microscope (models MZ-7.5 and M125C, Leica, Wetzlar, Germany). Images of
131	specimens and their dissected parts were captured with the aid of a digital microscope
132	(VHX-5000, KEYENCE, Osaka, Japan). Measurements were taken to the nearest 0.01
133	mm. Specimens examined in this study have been deposited in the Zoological
134	Collection of Kyoto University (KUZ).
135	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

137 referred to as the 'tegular apophysis' by these studies, but is referred to herein as a 138 'conductor' (Matsuda et al. 2020). The chaetotaxy of leg macrosetae follows Komatsu (1968); abbreviations for macrosetae are: p, prolateral; r, retrolateral; v, ventral. The 139 140 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 141 142 length; CP, copulatory pore; CW, carapace width; EM, embolus; FD, fertilization duct; PA, patellar apophysis; PCO, proximal arm of conductor; PER, posterior eye row; 143 144 PME, posterior margin of epigynal plate; PP, primary pore; RTA, retrolateral tibial apophysis; SB, spermathecal base; SH, spermathecal head; SP, simple pore; SS, 145 146 spermathecal stalk; TibIL, length of leg I tibia. 147 PCR and DNA sequencing 148 The procedure for extraction of genomic DNA from leg muscle was modified from 149 150 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 151 1 (ITS-1), mitochondrial cytochrome c oxidase subunit I (COI), and 16S ribosomal 152 153 RNA (16S) followed Nakano et al. (2017), and those for nuclear 28S ribosomal RNA 154 (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, 155 156 COIARAF (5'-ACAAATCATAAAGATATTGC-3') and COIARAR (5'-157 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). 158 159 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 160 161 System 9700 (Thermo Fisher Scientific, Waltham, MA, USA), or a GeneAtlas (ASTEC, 162 Shime, Fukuoka, Japan) using an Ex Taq Polymerase Kit (Takara Bio Inc., Kusatsu, 163 Shiga, Japan) The PCR mixtures were heated to 94°C for 6 min, followed by 35 cycles 164 at 94°C (10 s), 40°C for COI and 16S or 50°C for the other markers (20 s), and then 165 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. 166 167 All samples were sequenced in both directions. The CS reactions were performed using a BigDye Terminator ver. 3.1 Cycle Sequencing Kit (Thermo Fisher 168

- 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 3130xl Genetic Analyzer (Thermo
- 172 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).

- 176 Molecular phylogenetic analyses
- 177 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
- 181 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-
- 184 INS-i. The lengths of the H3, ITS-1, 28S, COI, 12S, and 16S were 328, 761, 793, 763,
- 185 335, 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
- 192 follows: for H3 1st position, TRN+G (ML), or GTR+I (BI); for H3 2nd position, JC+I;
- 193 for H3 3rd position, HKY+G; for ITS-1, GTR+I+G; for 28S, K81UF+I (ML), or GTR+I
- 194 (BI); for COI 1st position, TVM+I+G (ML), or GTR+I+G (BI); for COI 2nd position,
- 195 GTR+I; for COI 3rd position, TIM+I+G (ML), or GTR+I+G (BI); and for 12S and 16S,
- 196 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
- 199 estimated using MrBayes (ver. 3.2.7a, see
- 200 https://nbisweden.github.io/MrBayes/download.html; Ronquist et al. 2012). Two

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

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

217218

Results

- 219 Phylogenetic relationships
- 220 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
- 223 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
- 226 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).
- 229 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.

233	nov., and C. kodama, sp. nov.) constitute the monophyletic lineage D (BS = 85% , PP =
234	0.99) (Fig. 1, 2): two of these (C. yakushimensis, sp. nov. and C. kodama, sp. nov.)
235	appear to be endemic to Yakushima Island but did not form a clade while the
236	monophyly of the species from Amamioshima Island (C. amamiensis, sp. nov.) with the
237	one from Tokunoshima Island (<i>C. tokunoshimensis</i> , sp. nov.) was fully supported (BS =
238	100%, PP = 1.0); the species from Yakushima Island (C. yakushimensis, sp. nov.) forms
239	a monophyletic lineage with the Amamioshima-Tokunoshima clade, although this
240	relationship was not fully supported (BS = 65% , PP < 0.70). The remaining lineage E
241	only contains the species from Okinawa Island (C. hikidai, sp. nov.) in the Central
242	Ryukyus (Fig. 1, 2).
243	
244	Systematics
245	
246	Family Cybaeidae Banks, 1892
247	Genus Cybaeus L. Koch, 1868
248	
249	Cybaeus L. Koch, 1868: 46. Type species: Amaurobius tetricus C.L. Koch, 1839.
250	
251	Diagnosis
252	As stated in Copley et al. (2009), a differential diagnosis of the genus Cybaeus remains
253	unclarified, but species of this genus can be distinguished from other genera of Cybaeidae
254	by the following combination of characters (see Copley et al. 2009; Bennett 2017;
255	Bennett et al. 2020): two or three complete pairs of linearly arranged ventral macrosetae
256	on tibia I (sometimes four or five pairs are present, but not arranged in a linear pattern),
257	the presence of a retrolateral PA with peg setae in the male palp (Japanese species rarely
258	lack a PA), the well-developed conductor on the male bulb but never with a flat and plate-
259	like proximal arm, and, in the female, each spermatheca with a large SB and Bennett's
260	gland.
261	
262	Cybaeus okumurai, sp. nov.
263	http://zoobank.org/NomenclaturalActs/1676AFDB-F79C-490F-B8CE-4F1554855B78
264	(Fig. 3, 4A–C, F, G, 5B, C)

```
265
      Material examined
266
      Holotype. Japan: Ryukyu Islands: Tanegashima Island: #, Kunigami, 30°47′56.8″N,
267
268
       130°02′58.6″E, 9.xii.2019, Y. Ihara (KUZ Z3019).
              Paratypes. Japan: Ryukyu Islands: Tanegashima Island: 3 #, 4 @, collected
269
270
      with holotype (KUZ Z2719, Z3021–Z3026); ditto, 1 #, T. Nakano (KUZ Z3020).
             Additional specimens. Japan: Ryukyu Islands: Tanegashima Island: 2 #, 5 @,
271
      collected with holotype (KUZ Z2720-Z2722, Z3027, Z3028); 1 #, 4 @, Kunigami,
272
273
      Kishigazaki, 30°50′06.1″N, 131°03′32.1″E, 9.xii.2019 (KUZ Z3691, Z3692); 8 #, 17 @,
274
      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
275
      Z3697–Z3699; 6 #, 11 @, Furuta, 30°39′16.5″N, 131°00′50.0″E, 8.xii.2019 (KUZ
276
      Z2725, Z2727, Z2729, Z2730, Z3700–Z3702); 1 @, Nokan, 30°35′01.7″N,
277
       130°59′07.2″E, 8.xii.2019 (KUZ Z3703); 8 #, 3 @, Nakanokami, 30°26′01.3″N,
278
       130°55′23.6″E, 8.xii.2019 (KUZ Z2728, Z3704–Z3706); 4 #, 7 @, Nakanoshimo,
279
280
      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,
281
282
      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).
283
284
285
      Diagnosis
      Small to medium-sized Japanese Cybaeus. Both sexes of C. okumurai most closely
286
287
      resembles males and females of C. ashikitaensis. However, males of C. okumurai can
288
      be distinguished by their relatively wider palpal patella and tibia, and slightly prolonged
289
      PA > 0.25 \times as long as the patella (Fig. 4B, C); males of C. ashikitaensis have a
290
      relatively slender patella and tibia, and slightly small PA ca. 0.2× as long as the patella
291
      (Fig. 4D, 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

plate, and spermathecae ca. $2 \times$ wider than long in the latter; Fig. 5C, D).

295

293

296 Description

as wide (Fig. 5A, B) (loosely and compoundly curved posterior margin of epigynal

- 297 *Male (holotype, KUZ Z3019)* 298 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 299 300 formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg 301 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 + 1.60)302 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 + 1.47)2.88 + 1.49). 303 304 Carapace (Fig. 3A). Head narrow, 0.60× as wide as thoracic region; thoracic region slightly higher than head. AER slightly procurved in frontal view; PER slightly 305 306 recurved in dorsal view; AME smallest, slightly > 1/2 diameter of other eyes; ocular 307 area relatively wide, ca. 2.4× wider than long. Clypeus shorter than median ocular area. 308 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 309 310 condyle. Labium wider than long. Leg macrosetae. Leg I: tibia p2, r2, v2-2-2; metatarsus p3 (left) or 4 (right), r2, 311 v2-2-2. Leg II: tibia p4 (left) or 3 (right), r3 (left) or 2 (right), v2-2-1(r)-2; metatarsus 312 313 p4, r3, v2-2-3. 314 Abdomen (Fig. 3B). Oval; mid-posterior part widest (Fig. 3B). Colulus two groups of 3 or 5 setae. 315 316 Palp (Fig. 4A–C, F, G). PA digitiform, extended anteriorly, slightly bent 317 dorsally, dorsolateral surface with 14 peg setae. Tibia shorter than patella; RTA platelike, occupying most of length of tibia. Cymbium slender, > 2.5× longer than wide, 318 319 expanded prolaterally. Genital bulb circular in ventral view. Conductor: distal part long, 320 curved; proximal arm short, expanded. Embolus simple, originating and terminating, 321 respectively, at ca. 10 o'clock and ca. 4 o'clock in ventral view. 322 Colour (Fig. 3A, B). Carapace: head yellowish brown, with reticulate olive black 323 markings; thoracic region bright yellowish-brown, with radiating olive black bands. Chelicerae reddish brown, maxillary lobe and labium bright brown. Sternum bright 324 325 yellowish-brown, darker toward margins. Legs bright yellowish-brown, darker distally, with olive black annulations. Abdomen: dorsally olive black with pale yellow chevron 326 327 pattern; ventrally pale yellow.
 - Female (paratype, KUZ Z3023)

329 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 330 formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg 331 332 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 + 0.92)333 334 1.15). Carapace (Fig. 3C). Head 0.66× as wide as thoracic region; thoracic region 335 336 almost as high as head. AER straight in frontal view; PER slightly recurved in dorsal 337 view; AME smallest, slightly < 1/2 diameter of other eyes; ocular area relatively wide, 338 ca. 2.5× wider than long. Clypeus shorter than median ocular area. 339 Mouthparts. Chelicera geniculate, promargin of fang furrow with 3 teeth (median one largest), retromargin with 5 teeth and 5 denticles, and basally with lateral 340 condyle. Labium wider than long. 341 342 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. 343 Abdomen (Fig. 3D). Oval; mid-posterior part widest. Colulus two groups of 4 or 344 5 setae. 345 346 Genitalia (Fig. 5A, B). Posterior margin of epigynal plate curved. Atrium slightly concave, located posteromedially on epigynum. Copulatory pores separated on 347 348 either sid of atrium; CD long, thick, widened laterally. Each of SH, SS, and SB distinct, 349 bulbous; SH with at least 1 detectable primary pore posteromedially; distal end of SS 350 with Bennett's gland medially; SB large, extended anterolaterally. 351 Colour (Fig. 3C, D). Carapace: head brown, with faint olive-black markings; thoracic region bright yellowish-brown, with faint radiating black bands. Chelicerae 352 353 bright brown, maxillary lobe and labium yellowish brown, sternum bright yellowish-354 brown. Legs bright yellowish-brown, with olive black annulations. Abdomen: dorsally 355 olive black with light yellow chevron pattern; ventrally pale yellow. 356 357

Variation

Males (n = 12). Measurements (mean, followed by ranges in parentheses): CL 358 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– 359 360 2.58); TibIL/CL 0.85 (0.82–0.87). Legs longer than those of females. Palp: dorsolateral

361	surface of PA with 10–14 peg setae.
362	Females $(n = 27)$. Measurements (mean, followed by ranges in parentheses): CL
363	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–
364	2.28); TibIL/CL 0.71 (0.63–0.78).
365	
366	Distribution
367	This species is endemic to forest habitats on Tanegashima Island (Fig. 2).
368	
369	Remarks
370	Cybaeus okumurai constructs a V-shaped retreat (Fig. 22A).
371	The genital characters are consistent among the female specimens of <i>C</i> .
372	okumurai, but nonetheless, their body sizes could be grouped into two variants, small
373	(ca. 3.5–4 mm) and medium (ca. 6–7 mm) types. Both body-size types occur
374	syntopically at all collecting sites. The ITS-1 sequences, which yielded 697 bp pf
375	aligned positions, obtained from the six males (KUZ Z2719, Z2721, Z2724, Z2727-
376	Z2729; INSDC accession numbers: LC552282, LC574069–LC574073), three small
377	(KUZ Z2720, Z2726, Z2730; LC574074–LC574076) and three medium (KUZ Z2722,
378	Z2723, Z2725; LC552285, LC574077, LC574078) females were almost consistent with
379	each other; but 1 identical deletion was detected in six sequences of KUZ Z2721,
380	Z2722, Z2724, Z2725, Z2727, Z2728. These results corroborate that the males and the
381	variety-sized females all belong to the same species.
382	
383	Etymology
384	The specific name is dedicated to Dr. Ken-ichi Okumura for providing valuable
385	specimens of this new species.
386	
387	Cybaeus kumadori, sp. nov.
388	http://zoobank.org/NomenclaturalActs/E220EE51-716C-410A-B733-3675BBBAC7FC
389	(Fig. 6, 7)
390	
391	Material examined
392	Holotype. Japan: Ryukyu Islands: Mishima Islands: #, Kuroshima Island, Mt.

- 393 Yaguradake, 30°49′52.8″N, 129°56′02.1″E, 13.xii.2012, N. Koike (KUZ Z3004).
- 394 Paratypes. Japan: Ryukyu Islands: 3 #, 4 @, collected with holotype (KUZ
- 395 Z2143, Z2144, Z3005–Z3009).
- 396 Additional specimens. **Japan**: Ryukyu Islands: 3 @, collected with holotype
- 397 (KUZ Z3010).

- 399 Diagnosis
- 400 Medium-sized Japanese Cybaeus. Males of C. kumadori most closely resemble males of
- 401 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. 7E) (cymbium relatively
- broad and bulb wider than long in the latter; Fig. 19H). 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. 7G) (SB posterior to SH and SB in C. okumurai;
- 407 Fig. 5*B*).

- 409 Description
- 410 *Male* (*holotype*, *KUZ Z3004*)
- 411 *Measurements (mm).* CL 3.32, CW 2.27; head 1.38 wide; abdomen 2.94 long,
- 412 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
- 414 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 + 1.20)
- $416 \quad 3.18 + 1.46$).
- 417 Carapace (Fig. 6A). 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.
- 421 *Mouthparts*. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth
- 422 (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.
- 426 Abdomen (Fig. 6B). Oval; mid-posterior part widest. Colulus two groups of 3 or
- 427 4 setae.
- 428 Palp (Fig. 7A–E). PA lacking. Tibia almost as long as patella; RTA plate-like,
- occupying 1/2 of length of tibia. Cymbium slender, $> 2 \times$ 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
- 432 terminating, respectively, at ca. 10 o'clock and ca. 5 o'clock in ventral view.
- Colour (Fig. 6A, 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.
- 440 Female (paratype, KUZ Z3007)
- 441 *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
- 19.68 (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)
- 446 + 1.31).
- 447 Carapace (Fig. 6C). 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.
- 451 *Mouthparts.* Chelicera geniculate, promargin of fang furrow with 3 teeth
- 452 (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
- 455 p4, v2-2-1(r)-2; metatarsus p4, r1, v2-2-3.
- 456 Abdomen (Fig. 6D). Oval; mid-posterior part widest. Colulus 2 groups of 3

457 setae. *Genitalia* (Fig. 7*F*, *G*). Posterior margin of epigynal plate slightly curved. 458 Atrium slightly concave, posteromedially located on epigynum. Copulatory pores 459 460 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 461 anteromedially; SB developed, extended anterolaterally; Bennett's gland undetectable in 462 463 dorsal and medial views. 464 Colour (Fig. 6C, D). Carapace: head reddish brown, brownish black anteriorly and laterally, with brownish black marking anterior to cervical groove; thoracic region 465 466 bright yellowish-brown, with brownish black lateral sub-marginal bands. Chelicerae, 467 maxillary lobe and labium reddish brown, chelicerae darker than others. Sternum bright yellowish-brown, darker toward margins. Legs yellowish brown with brownish black 468 annulations. Abdomen: dorsally dark greyish-yellow with greyish yellow chevron 469 470 pattern; laterally with mottled pattern of dark greyish-yellow and greyish-yellow; 471 ventrally light yellow ventrally. 472 473 Variation 474 Males (n = 4). Measurements (mean, followed by ranges in parentheses): CL 475 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– 476 2.82); TibIL/CL 0.74 (0.73–0.75). Legs longer than those of females. 477Females (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– 478 479 2.63); TibIL/CL 0.66 (0.65–0.68). 480 481 Distribution 482 This species is endemic to forest habitats on Kuroshima Island in the Mishima Islands 483 (Fig. 2). 484 485 Remarks The retreat of this species is V-shaped with two openings. 486

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

487

489	in the examined specimen. The part of the spermathecae is difficult to observe because
490	it is masked by the epigynal plate ventrally and by the spermathecal stalk and head
491	medio-dorsally.
492	
493	Etymology
494	The specific name is from a Japanese word kumadori (= kabuki make-up) referring to
495	the carapace colouration of this species.
496	
497	Cybaeus yakushimensis, sp. nov.
498	http://zoobank.org/NomenclaturalActs/E4EF5027-C1DD-411E-ADF3-15037170EFB7
499	(Figs. 8, 9, 10A, D, G, 11E)
500	
501	Material examined
502	Holotype. Japan: Ryukyu Islands: Yakushima Island: #, Shirataniunsuikyo Valley,
503	30°22′38.7″N, 130°34′21.1″E, 8.xii.2012, N. Koike (KUZ Z2998).
504	Paratypes. Japan: Ryukyu Islands: Yakushima Island: 2 #, 2 @, collected with
505	holotype (KUZ Z2138, Z2999–Z3001); 1 @, along Hanayama Trail, 30°19′13.2″N,
506	130°26′45.1″E, 9.xii.2012, N. Koike (KUZ Z2140).
507	Additional specimens. Japan: Ryukyu Islands: Yakushima Island: 1 @,
508	Shirataniunsuikyo Valley, 28.x.2011 (KUZ Z2163); 1 #, 4 @, along Hanayama Trail,
509	9.xii.2012 (KUZ Z3002, Z3003, Z3678).
510	
511	Diagnosis
512	Medium-sized Japanese Cybaeus. Cybaeus yakushimensis most closely resembles C.
513	amamiensis. Males of C. yakushimensis can be differentiated from those of the latter by
514	the small and slender palp (Fig. 9A, 10A) (robust in <i>C. amamiensis</i> ; Fig. 14A, 10B).
515	Additionally, the PA of <i>C. yakushimensis</i> (Fig. 10 <i>D</i>) is shorter and less distally
516	extended than that of C. amamiensis (Fig. 10E). Females of C. yakushimensis are
517	distinguishable from those of <i>C. amamiensis</i> by the relatively short atrium and
518	ellipsoidal SB (Fig. 9D, E) (slightly longer atrium and globular SB in C. amamiensis;
519	Fig. 14D, E). The connection between the SH and SS of C. yakushimensis (Fig. 9E) is
520	less robust than the connection in C amamiensis (Fig. 14F)

```
521
522
       Description
523
524
525
526
527
528
529
       2.78 + 1.45).
```

- 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 + 1.76)
- 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 + 1.20)
- 530 Carapace (Fig. 8A). 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 531
- dorsal view; AME smallest, ca. 1/2 diameter of other eyes; ocular area ca. 2.0× wider 532
- than long. Clypeus shorter than median ocular area. 533
- 534 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 535
- condyle. Labium wider than long. 536
- Leg macrosetae. Leg I: tibia I p2, r2, v2-2-2; metatarsus p3 (left) or 4 (right), 537
- 538 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. 539
- 540 Abdomen (Fig. 8B). Oval; mid-posterior part widest. Colulus two groups of 3
- 541 setae.
- Palp (Fig. 9A–C, 10A, D, G). PA digitiform, directed anterolaterally, 542
- 543 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 544
- 545 expanded, $> 2 \times$ longer than wide. Genital bulb slightly wider than long, oval in ventral
- 546 view. Conductor extended retrolaterally; distal part expanded, curved; proximal arm
- 547 sickle-shaped. Embolus simple, long, originating and terminating respectively, at ca. 9
- o'clock and ca. 5 o'clock in ventral view. 548
- 549 Colour (Fig. 8A, B). Carapace: head brown, with reticulate brownish black
- markings; thoracic region yellowish brown, with radiating brownish black bands. 550
- 551 Chelicerae reddish brown, maxillary lobe and labium bright brown. Sternum bright
- yellowish-brown, darker toward margins. Legs yellowish brown to bright yellowish-552

- brown, with brownish black annulations. Abdomen: dorsally brownish black with light
- yellowish brown chevron pattern; ventrally light yellow.
- 555 Female (paratype, KUZ Z3001)
- *Measurements (mm)*. CL 3.20, CW 2.09; head 1.43 wide; abdomen 3.60 long,
- 2.68 wide. Ocular area 0.39 long, 0.88 wide. Sternum 1.47 long, 1.22 wide. Leg formula
- 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
- 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. 8C, 11E). Head 0.68× as wide as thoracic region; thoracic region
- height slightly shorter than head. AER almost straight in frontal view; PER almost
- straight in dorsal view; AME smallest, ca. 1/2 diameter of other eyes; ocular area $> 2.0 \times$
- as wide as length. Clypeus shorter than median ocular area.
- 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
- lateral condyle. Labium wider than long.
- 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. 8D, 11E). Oval; mid-posterior part widest. Colulus two groups of
- 572 6 setae.
- 573 *Genitalia* (Fig. 9D, E). Posterior margin of epigynal plate slightly curved.
- Atrium slightly concave, located posteromedially on epigynum. Copulatory pores
- separated on both sides of atrium; CD long, widened laterally. Each spermatheca
- forming S-shaped; SH almost tubular, located medially on vulva, with few primary
- pores posteriorly; connection between SH and SS expanded laterally; SS tubular; SB
- ellipsoid, extended and bent anterolaterally; Bennett's gland well-developed, located
- anteriorly at proximal end of SB.
- *Colour* (Fig. 8*C*, *D*, 11*E*). Carapace: head dull reddish-brown, with reticulate
- brownish black markings; thoracic region yellowish brown, with radiating brownish
- black bands. Chelicerae dark reddish-brown, maxillary lobe and labium brown. Sternum
- 583 bright brown, darker toward margins. Legs yellowish brown, with brownish black
- annulations. Abdomen: dorsally olive black with light yellow chevron pattern; ventrally

585	light yellow.
586	
587	Variation
588	Males $(n = 4)$. Measurements (mean, followed by ranges in parentheses): CL
589	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–
590	2.53); TibIL/CL 0.76 (0.74–0.78). Legs longer than those of females. Palp: dorsolateral
591	surface of PA with 7–8 peg setae.
592	Females $(n = 8)$. Measurements (mean, followed by ranges in parentheses): CL
593	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–
594	2.60); TibIL/CL 0.66 (0.63–0.68).
595	
596	Distribution
597	This species is endemic to the montane forest on Yakushima Island (Fig. 2).
598	
599	Remarks
600	No retreat has been observed for C. yakushimensis. This species co-occurs with the
601	small-sized C. kodama on Yakushima Island (Fig. 11E, F).
602	
603	Etymology
604	The specific name is an adjective derived from Yakushima Island.
605	
606	Cybaeus kodama, sp. nov.
607	http://zoobank.org/NomenclaturalActs/D629626F-0C4B-43B0-A372-54FB6CF29374
608	(Figs. 11A–D, F, 12)
609	
610	Material examined
611	Holotype. Japan: Ryukyu Islands: Yakushima Island: #, along Hanayama Trail,
612	30°19′13.2″N, 130°26′45.1″E, 9.xii.2012, N. Koike (KUZ Z3011).
613	Paratypes. Japan: Ryukyu Islands: Yakushima Island: 2 #, 4 @, collected with
614	holotype (KUZ Z2141, Z2142, Z3012–Z3015).
615	Additional specimens. Japan: Ryukyu Islands: Yakushima Island: 1 @,
616	Shirataniunsuikyo Valley, 30°22′30.2″N, 130°34′07.8″E, 8.xii.2012 (KUZ Z2139); 6

- 617 @, collected with holotype (KUZ Z3016).
- 618
- 619 Diagnosis
- 620 Small-sized Japanese Cybaeus. Males of Cybaeus kodama are only likely to be
- 621 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. 12B, C) (lacking PA in C. aikana; Fig. 16B). In addition, the
- 624 elliptically shaped bulb of *C. kodama* (Fig. 12*E*) is also unique among Japanese
- 625 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. 12G).
- 627
- 628 Description
- 629 *Male* (holotype, KUZ Z3011)
- 630 *Measurements (mm)*. CL 1.68, CW 1.15; head 0.73 wide; abdomen 1.92 long,
- 631 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
- 633 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);
- 634 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 + 0.43 + 0.43 + 0.43 + 0.43 + 0.43 + 0.43 + 0.43 + 0.44 + 0.
- 635 0.62).
- 636 Carapace (Fig. 11A). 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. $2 \times$ wider than
- long. Clypeus shorter than median ocular area.
- 640 *Mouthparts*. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth
- 641 (median one largest), retromargin with 3 (left) or 2 (right) teeth and 4 denticles, and
- basally with lateral condyle. Labium wider than long.
- 643 Leg macrosetae. Leg I: tibia p2, r0 (left) or 2 (right), v2-2-2-0; metatarsus p1,
- 644 v2-2-2. Leg II: tibia p2, v2-1(r)-1(r)-0; metatarsus p2, v2-2-3.
- 645 Abdomen (Fig. 11B). Oval; mid-posterior part widest. Colulus two groups of 3
- or 4 setae.
- 647 Palp (Fig. 12A–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.
- 650 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.
- 654 Colour (Fig. 11A, 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.
- 659 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
- 663 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);
- $664 \qquad leg III \ 3.00 \ (0.84 + 0.40 + 0.57 + 0.70 + 0.49); \ leg IV \ 3.82 \ (1.06 + 0.41 + 0.85 + 0.92 + 0.41 + 0.85 + 0.41 + 0.41 + 0.85 + 0.41 +$
- 665 0.58).
- 666 Carapace (Fig. 11C). 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.
- 669 Clypeus shorter than median ocular area.
- 670 *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.
- 673 Leg macrosetae. Leg I: tibia I p2, v2-2-2-0; metatarsus p1, v2-2-2. Leg II: tibia
- 674 p1, v2-1(r)-1(r)-0; metatarsus p2, v2-2-3.
- 675 Abdomen (Fig. 11D). Oval; mid-posterior part widest. Colulus 2 groups of 3 or 4
- setae.
- 677 Genitalia (Fig. 12F, G). Posterior margin of epigynal plate loosely curved.
- 678 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,

681 extending anterolaterally; Bennett's gland located anteriorly at basal part of SB. Colour (Fig. 11C, D, F). Carapace: head brown, with reticulate dull brownish-682 black markings; thoracic region bright yellowish-brown, with radiating dark olive-683 684 brown. Chelicerae bright brown, maxillary lobe and labium orange, sternum bright yellowish-brown. Legs yellowish brown without annulations. Abdomen: dorsally dark 685 686 olive-brown with dull yellow chevron pattern; ventrally pale yellow. 687 688 Variation Males (n = 2). Measurements (ranges): CL 1.46–1.68, CW 1.00–1.15; CW/CL 689 690 0.68; TibIL 0.97–1.09; TibIL/CL 0.65–0.66. Legs slightly longer than those of females. 691 Females (n = 9). Measurements (mean, followed by ranges in parentheses): CL 692 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). 693 694 Distribution 695 696 This species is endemic to the montane forests on Yakushima Island (Fig. 2). 697 698 Remarks No retreat has been observed for this species. This species is found sympatrically with 699 700 the medium-sized species C. yakushimensis (Fig. 11E, F). 701 702 Etymology 703 The specific name is from a Japanese word kodama (= the name of a tree-inhabiting spirit), and thus treated as indeclinable. 704 705 706 Cybaeus amamiensis, sp. nov. 707 http://zoobank.org/NomenclaturalActs/FB195659-51B4-4C27-9B4D-DF3EA707C7D3 708 (Figs. 10*B*, *E*, *H*, 13, 14) 709 Material examined 710 711 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). 712

- 713 Paratypes. Japan: Ryukyu Islands: Amamioshima Island: 2 #, 4 @, collected
- vith holotype (KUZ Z2120, Z2121, Z2988, Z2990–Z2992).
- 715 Additional specimens. **Japan**: Ryukyu Islands: Amamioshima Island: 6 #, 22 @,
- 716 collected with holotype (KUZ Z2989, Z2993); 7 @, Mt. Yuwandake, 28°17′46.5″N,
- 717 129°19′15.9″E, 12.iii.2009 (KUZ Z2133); 4 #, 28 @, ditto, 28°17′21.5″N,
- 718 129°18′52.5″E, 16.xii.2012 (KUZ Z2117, Z2118); 1 @, near Sumiyo Dam [28°17′N,
- 719 129°22′E], 12.iii.2009 (KUZ Z2130); 4 @, ditto, 14.iii.2009 (KUZ Z2131); 1 @, ditto,
- 720 26.iv.2010 (KUZ Z2125); 3 @, Kinsakubaru Forest, 28°20′49″N, 129°26′26″E,
- 721 14.iii.2009 (KUZ Z2135, Z2136); 4 @, ditto, 28°20′12.4″N, 129°26′55.0″E, 15.xii.2012
- 722 (KUZ Z2119); 6 @, near Kinsakubaru Forest, 28°21′39.5″N, 129°28′45.8″E, 19.i.2011
- 723 (KUZ Z2129); 4 @, Mt. Takinohanayama, 28°16′04.8″N, 129°26′54.2″E, 19.i.2011
- 724 (KUZ Z2126–Z2128); 1 #, 8 @, Naze-koshuku, 28°21′46.8″N, 129°28′49.9″E,
- 725 15.xii.2012 (KUZ Z2116, Z2124); 1 #, Sumiyocho-yakugachi, 28°14′47.3″N,
- 726 129°23'02.2"E, 16.xii.2012 (KUZ Z2122); 1 #, 3 @, Setouchicho-agina, 28°11'15.1"N,
- 727 129°19′35.2″E, 16.xii.2012 (KUZ Z2123).
- 729 Diagnosis

- 730 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
- 732 differentiating these two species.
- 734 Description
- 735 *Male* (holotype, KUZ Z2987)
- 736 *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
- 739 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 + 1.86)
- 740 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)
- 741 + 3.48 + 1.67).
- 742 Carapace (Fig. 13A). 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

- 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
- 148 lateral condyle. Labium wider than long.
- 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. 13B). Oval; mid-posterior part widest. Colulus two groups of 5
- 752 or 6 setae.
- 753 Palp (Fig. 10B, E, H, 14A–C). PA digitiform, directed distally, dorsolateral
- surface with 7 (left) or 8 (right) peg setae. Tibia convex in lateral view, almost as long
- as patella; RTA plate-like, occupying most of length of tibia. Cymbium expanded
- prolaterally, $> 2 \times$ longer than wide; distal part slender, long. Genital bulb slightly wider
- than long, oval in ventral view. Conductor extended retrolaterally; distal part expanded,
- slightly 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.
- 760 Colour (Fig. 13A, B). Carapace: head dark reddish-brown, with reticulate black
- markings; thoracic region brownish black, with yellowish brown marginal bands;
- yellowish brown markings mid-dorsally. Chelicerae, maxillary lobe and labium dark
- reddish-brown, chelicera darker than other parts. Sternum bright brown, darker toward
- margins. Legs yellowish brown, with olive black annulations. Abdomen: dorsally olive
- 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,
- 2.90 wide. Ocular area 0.46 long, 1.10 wide. Sternum 1.82 long, 1.64 wide. Leg
- 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); $\log III 9.35 (2.70 + 1.18 + 1.92 + 2.36 + 1.19)$; $\log IV 11.58 (3.20 + 1.14 + 2.70 + 1.40)$
- $772 \quad 3.11 + 1.43$).
- 773 Carapace (Fig. 13C). Head narrow, 0.69× 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 ca. 1/2 diameter of other eyes; ocular area
- relatively wide, 2.4× wider than long. Clypeus slightly shorter than median ocular area.

777 Mouthparts. Chelicera geniculate, promargin of fang furrow with 3 teeth 778 (median one largest), retromargin with 4 teeth and 4 denticles, and basally with lateral condyle. Labium wider than long. 779 Leg macrosetae. Leg I: tibia p2, v2-2-2-2; metatarsus p1, r1, v2-2-2. Leg II: tibia 780 p2 (left) or 3 (right), v2-2-1(r)-2; metatarsus p4, r3, v2-2-3. 781 782 Abdomen (Fig. 13D). Oval; mid-posterior part widest. Colulus two groups of 4 or 5 setae. 783 Genitalia (Fig. 14D, E). Posterior margin of epigynal plate slightly curved. 784 Atrium slightly concave, located posteromedially on epigynum. Copulatory pores 785 786 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 787 for presence of a few primary pores anteromedially; connection between SH and SS 788 expanded laterally; SS tubular; SB large, globular; Bennett's gland well-developed, 789 790 located anteriorly at basal part of SB. Colour (Fig. 13C, D). Carapace: head deeply-dark reddish-brown, with 791 792 reticulate black markings; thoracic region orange along margins, with radiating black 793 bands; yellowish brown markings mid-dorsally. Chelicerae dark reddish-brown, 794 maxillary lobe and labium reddish brown. Sternum reddish brown, darker toward 795 margins. Legs bright brown, with brownish black annulations. Abdomen: dorsally olive 796 black with bright yellowish-brown chevron pattern; laterally with mottled pattern of 797 dark brown and yellowish brown laterally; ventrally bright yellowish-brown. 798 799 Variation Males (n = 9). Measurements (mean, followed by ranges in parentheses): CL 800 801 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– 802 2.94); TibIL/CL 0.75 (0.74–0.76). Legs longer than those of females. Palp: dorsolateral 803 surface of PA with 6–10 peg setae. 804 Females (n = 26). Measurements (mean, followed by ranges in parentheses): CL 805 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). 806 807

Distribution

809	This species is endemic to the montane forests on Amamioshima Island (Fig. 2).
810	
811	Remarks
812	No retreat has been observed for this species.
813	Females of C. amamiensis share well-developed Bennett's glands in their
814	spermathecae with those of C. yakushimensis, C. tokunoshimensis, and C. hikidai.
815	
816	Etymology
817	The specific name is an adjective from Amamioshima Island.
818	
819	Cybaeus aikana, sp. nov.
820	http://zoobank.org/NomenclaturalActs/F378CB1A-AFF8-4944-90BB-7D2863522BCC
821	(Figs. 15–17)
822	
823	Material examined
824	Holotype. Japan: Ryukyu Islands: Amamioshima Island: #, Mt. Yuwandake,
825	28°17′21.5″N, 129°18′52.5″E, 15.xii.2012, N. Koike (KUZ Z3017).
826	Paratypes. Japan: Ryukyu Islands: Amamioshima Island: 2 @, collected with
827	holotype (KUZ Z2137, Z3018).
828	
829	Diagnosis
830	Small-sized Japanese Cybaeus. Males of C. aikana, C. kumadori and C. hikidai all lack
831	a PA in the palp (Fig. 7B, 16B, 19F). However, males of C. aikana can be
832	unquestionably distinguished from those of the other two congeners by its small size,
833	short and robust palp (Fig. 16B), and arcuate proximal arm of conductor (Fig. 16A, D,
834	E). Females of C. aikana, C. hikidai, and C. ishikawai are characterised by their CDs,
835	SHs and SSs all being of similar diameter. However, females of C. aikana clearly differ
836	from those of the other two species in their SBs which are located medially on the vulva
837	and are contiguous with each other (Fig. 17B) (SBs are well separated in C. hikidai and
838	C. ishikawai; Fig. 19J for C. hikidai and see fig. 2-2-30-217 in Ihara 2009a for C.
839	ishikawai).

- Description 841 842 Male (holotype, KUZ Z3017) Measurements (mm). CL 1.78, CW 1.13; head 0.76 wide; abdomen 1.50 long, 843 1.36 wide. Ocular area 0.23 long, 0.45 wide. Sternum 0.84 long, 0.76 wide. Leg 844 formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg 845 846 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 + 0.08)847 848 0.73). Carapace (Fig. 15A). Head narrow, 0.67× as wide as thoracic region; thoracic 849 region as high as head. AER slightly procurved in frontal view; PER almost straight in 850 dorsal view; AME smallest, ca. 1/2 diameter of other eyes; ocular area ca. 2× wider than 851 long. Clypeus shorter than median ocular area. 852 Mouthparts. Chelicera slightly geniculate, promargin of fang furrow with 3 teeth 853 (median one largest), retromargin with 3 teeth and 4 or 5 denticles, and basally with 854 lateral condyle. Labium wider than long. 855 Leg macrosetae. Leg I: tibia p2, v2-2-2-0; metatarsus p1, v2-2-2. Leg II: tibia 856 857 p2, v1(r)-1(r)-1(r)-0; metatarsus p2, v2-2-3. Abdomen (Fig. 15B). Oval; mid-posterior part widest. Colulus two groups of 3 858 or 4 setae. 859 860 Palp (Fig. 16). PA lacking. Tibia almost as long as patella; RTA plate-like, 861 occupying 2/3 of length of tibia. Cymbium relatively short, slightly expanded prolaterally. Genital bulb wider than long, oval in ventral view. Conductor strongly 862 863 undulating in lateral view; distal part well developed, extended distally; tip of proximal 864 arm undulating, arcuate. Embolus simple, long, originating and terminating, 865 respectively, at ca. 9 o'clock and ca. 7 o'clock in ventral view. 866 Colour (Fig. 15A, B). Carapace: head yellowish brown, with reticulate brownish 867 black markings; thoracic region light yellow, with radiating brownish black bands. Chelicerae bright brown, maxillary lobe and labium bright brown to yellowish brown. 868 869 Sternum light yellow, darker toward margins. Legs bright yellowish-brown to light yellow with slight olive black annulations. Abdomen: dorsally olive black with light 870
- 872 Female (paratype, KUZ Z3018)

yellow chevron pattern; ventrally light yellow.

- 873 Measurements (mm). CL 1.64, CW 1.05; head 0.80 wide; abdomen 1.88 long, 874 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 875 876 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); 877 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 + 0.88 +878 0.43). Carapace (Fig. 15C). Head 0.76× as wide as thoracic region; thoracic region 879 880 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 881 882 slightly $> 2 \times$ wider than long. Clypeus shorter than median ocular area. *Mouthparts*. Chelicera moderate geniculate, promargin of fang furrow with 3 883 teeth (median one largest), retromargin with 4 teeth and 4 denticles, and basally with 884 lateral condyle. Labium wider than long. 885 886 Leg macrosetae. Leg I: tibia p2, v 2-2-2-0; metatarsus p1, r1 (left) or 0 (right),
- 886 *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)-0; metatarsus p2, v2-2-3.
- 888 Abdomen (Fig. 15C). Oval; mid-posterior part widest. Colulus two groups of 4
 889 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
- 896 Colour (Fig. 15C). Carapace: head brown, with reticulate brownish black
 897 markings; thoracic region bright yellowish-brown, with radiating brownish black bands.
 898 Chelicerae, maxillary lobe and labium bright brown. Sternum bright yellowish brown,
 899 darker toward margins. Legs yellowish brown, with slight olive black annulations.
 900 Abdomen: dorsally brownish black with light yellow chevron pattern; ventrally light

with each other; Bennett's gland not detected.

- Abdomen: dorsally brownish black with light yellow chevron pattern; ventrally lightyellow.
- 903 Distribution

890

891

892

893

894

895

902

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

905	Island (Fig. 2).
906	
907	Remarks
908	This species constructs a Y-shaped retreat (Fig. 22B). Cybaeus aikana is found
909	sympatrically with C. amamiensis at Mt. Yuwandake.
910	
911	Etymology
912	The specific name is dedicated to the name of a historical figure, a woman who lived in
913	Amamioshima Island. The specific name is derived directly from her name, and thus
914	treated as indeclinable.
915	
916	Cybaeus tokunoshimensis, sp. nov.
917	http://zoobank.org/NomenclaturalActs/F0CEA7EC-D32E-4BE9-A51C-
918	ED7357991B3A
919	(Figs. 10 <i>C</i> , <i>F</i> , 18)
920	
921	Material examined
922	Holotype. Japan: Ryukyu Islands: Tokunoshima Island: #, Mt. Inokawadake,
923	27°45′53.1″N, 128°58′43.1″E, 17.xii.2012, N. Koike (KUZ Z2113).
924	Paratypes. Japan: Ryukyu Islands: Tokunoshima Island: 4 @, collected with
925	holotype (KUZ Z2112, Z2994–Z2996).
926	Additional specimens. Japan: Ryukyu Islands: Tokunoshima Island: 2 @, Mt.
927	Inokawadake, 27°46′07.6″N, 128°59′38.4″E, 27.i.2011 (KUZ Z2111); 6 @, ditto,
928	27°45′51.9″N, 128°58′37.8″E, 27.i.2011 (KUZ Z2114, Z2115); 4 @, collected with
929	holotype (KUZ Z2997).
930	
931	Diagnosis
932	Medium-sized Japanese Cybaeus. Cybaeus tokunoshimensis most closely resembles C.
933	yakushimensis and C. amamiensis. However, males of C. tokunoshimensis can be
934	distinguished from those of the other two species by the laterally extended palpal PA,
935	the relatively short, broad cymbium, and the broad, wider than long genital bulb (Fig.
936	10C, F, 18H) (directed anterolaterally PAs, relatively slender cymbia, and as long as

- 937 wide genital bulbs in C. yakushimensis and C. amamiensis; Fig. 10A, 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
- double coil around each CD (Fig. 181, J) (short epigyna and each SS not a double coiled
- around each CD in C. yakushimensis and C. amamiensis; Fig. 9D, E, 14D, E).
- 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
- located basally on each SB; Fig. 9E, 14E).

- 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
- 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 $\log III 8.09 (2.20 + 0.91 + 1.72 + 2.08 + 1.18); \log IV 9.85 (2.63 + 0.91 + 2.28 + 2.59 + 2.59 + 1.18); \log IV 9.85 (2.63 + 0.91 + 2.28 + 2.59 + 2.5$
- 953 1.44).
- 954 Carapace (Fig. 18A, 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
- 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; 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. 18B). Oval; mid-posterior part widest. Colulus two groups of 4
- 964 or 5 setae.
- 965 Palp (Fig. 10C, F, 18E–H). PA digitiform, extended anterolaterally, dorsal
- surface with 9 (left) or 8 (right) peg setae. Tibia convex in lateral view, almost as long
- as patella; RTA plate-like, occupying most of length of tibia. Cymbium relatively wide,
- 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
- 970 undulating, sickle-shaped. Embolus long, undulating along conductor, originating and
- 971 terminating respectively, at ca. 9 o'clock and ca. 7 o'clock in ventral view.
- 972 *Colour* (Fig. 18A, B). Carapace: head smoky black; thoracic region bright
- 973 yellowish-brown, with radiating black bands; bright yellowish-brown markings mid-
- dorsally. Chelicerae deep dark reddish-brown, maxillary lobe and labium brown.
- 975 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.
- 978 Female (paratype, KUZ Z2994)
- 979 *Measurements (mm)*. CL 3.23, CW 2.15; head 1.48 wide; abdomen 3.35 long,
- 980 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
- 982 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);
- 983 $\log III 7.18 (2.05 + 0.90 + 1.48 + 1.83 + 0.92); \log IV 9.01 (2.42 + 0.91 + 2.08 + 2.44 + 1.83 + 2.44 + 1.83 + 2.44 + 1.83 + 2.44 + 1.83 + 2.44 + 1.83 + 2.44 + 1.83 + 2.44 + 1.84 + 2.44 + 1.84$
- 984 1.16).
- 985 Carapace (Fig. 18C). 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
- 987 dorsal view; AME smallest, > 1/2 diameter of other eyes. Ocular area relatively wide,
- 988 2.4× wider than long. Clypeus shorter than median ocular area.
- 989 *Mouthparts*. Chelicera geniculate, promargin of fang furrow with 3 teeth
- 990 (median one largest), retromargin with 4 teeth and 4 denticles, and basally with lateral
- 991 condyle. Labium wider than long.
- 992 Leg macrosetae. Leg I: tibia p2, v2-2-2-2; metatarsus p1, r1, v2-2-3. Leg II: tibia
- 993 p3, v2-2-1(r)-2; metatarsus p4, r1, v2-2-3.
- 994 Abdomen (Fig. 18D). Oval; mid-posterior part widest. Colulus two groups of 4
- 995 or 5 setae.
- 996 Genitalia (Fig. 181, J). Posterior margin of epigynal plate loosely curved.
- 997 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
- ontinuously tubular; SH with a few primary pores medially; SS forming double coil
- around CD; SB globular, extended anterolaterally; Bennett's gland well-developed,

1001	located medially at connection between SS and SB.
1002	Colour (Fig. 18C, D). Carapace: head dark reddish-brown, with reticulate black
1003	markings; thoracic region bright yellowish-brown, with radiating black bands.
1004	Chelicerae dark reddish-brown, maxillary lobe and labium reddish brown. Sternum
1005	bright yellowish-brown, darker toward margins. Legs bright yellowish-brown, with
1006	olive black annulations. Abdomen: dorsally olive black with bright yellowish-brown
1007	chevron pattern; laterally with mottled pattern of olive black and bright yellowish-
1008	brown; ventrally light yellow.
1009	
1010	Variation
1011	Females $(n = 8)$. Measurements (mean, followed by ranges in parentheses): CL 3.04
1012	(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);
1013	TibIL/CL 0.63 (0.62–0.66).
1014	
1015	Distribution
1016	This species is endemic to the montane forest around Mt. Inokawadake on
1017	Tokunoshima Island (Fig. 2).
1018	
1019	Remarks
1020	Not retreat has been observed for C. tokunoshimensis.
1021	
1022	Etymology
1023	The specific name is an adjective from Tokunoshima Island.
1024	
1025	Cybaeus hikidai, sp. nov.
1026	http://zoobank.org/NomenclaturalActs/ECA1F9A2-61E8-4383-8E63-49EC9C3513F9
1027	(Figs. 19–21)
1028	
1029	Material examined
1030	Holotype. Japan: Ryukyu Islands: Okinawa Island: #, near Hiji Waterfall,
1031	26°42'44.1"N, 128°11'06.3"E, 22.xii.2012, N. Koike (KUZ Z2982).
1032	Paratypes. Japan: Ryukyu Islands: Okinawa Island: 2 @, collected with

```
1033
        holotype (KUZ Z2107, Z2983); 1 #, 1 @, Mt. Nagodake, 26°35′12.2″N, 128°00′22.2″E,
1034
        21.xii.2012, N. Koike (KUZ Z2106, Z2984).
               Additional specimens. Japan: Ryukyu Islands: Okinawa Island: 1 #, 8 @, Mt.
1035
        Nishimedake, 26°48′27.4″N, 128°16′08.6″E, 22.i.2011 (KUZ Z2100–Z2102); 2 @,
1036
        ditto, 25.i.2011 (KUZ Z2104); 7 @, Mt. Yonahadake, 26°43′50.5″N, 128°12′36.2″E,
1037
1038
        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,
1039
1040
        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,
1041
1042
        22.xii.2012 (KUZ Z2110); 1 @, near Taiho Dam, 26°39′04.3″N, 128°09′34.7″E,
        24.xii.2012 (KUZ Z2103).
1043
1044
1045
        Diagnosis
        Medium-sized Japanese Cybaeus. Males of C. hikidai differ from those of the other six
1046
        Ryukyu-endemic congeners (C. okumurai, C. yakushimensis, C. kodama, C.
1047
        amamiensis and C. tokunoshimensis) by the combination of lacking a PA and having an
1048
1049
        egg-shaped large genital bulb that is wider than long (Fig. 19F, H). Males of C.
1050
        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
1051
1052
        the small-sized C. aikana venry long tubular CD, SH and SS of similar diameter
1053
        throughout. But, the former can be distinguished from the latter by its well separated
        SBs located laterally on the vulva (Fig. 19J) (contiguous and medially located in the
1054
1055
        vulva of C. aikana; Fig. 17B). 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
1056
1057
        antero-laterally (Fig. 19J) (SBs directed laterally in C. ishikawai; fig. 2-2-30-217 in
1058
        Ihara 2009a).
1059
        Description
1060
1061
               Male (holotype, KUZ Z2982)
               Measurements (mm). CL 3.20, CW 2.33; head 1.40 wide; abdomen 3.10 long,
1062
```

formula, 4 > 1 > 2 > 3; length of legs (femur + patella + tibia + metatarsus + tarsus): leg

2.43 wide. Ocular area 0.37 long, 0.80 wide. Sternum 1.52 long, 1.38 wide. Leg

1063

- 1065 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 +
- 1066 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 + 2.79 + 2.48 + 1.43); leg IV 11.85 (3.05 + 0.99 + 2.79 + 2.79 + 2.48 + 1.43); leg IV 11.85 (3.05 + 0.99 + 2.79 + 2.79 + 2.48 + 1.43); leg IV 11.85 (3.05 + 0.99 + 2.79 + 2.79 + 2.48
- $1067 \quad 3.28 + 1.74$).
- 1068 Carapace (Fig. 19A, 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
- 1073 (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:
- 1076 tibia p3, r2 (left) or 3 (right), v2-2-1(r)-2; metatarsus p4, r3, v2-2-3.
- 1077 Abdomen (Fig. 19B). Oval; mid-posterior part widest. Colulus two groups of 5
- 1078 setae.
- 1079 Palp (Fig. 19E–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.
- 1082 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.
- 1085 Colour (Fig. 19A, 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.
- 1092 Female (paratype, KUZ Z2985)
- 1093 *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
- $1096 \quad I 6.95 (1.96 + 0.78 + 1.70 + 1.56 + 0.95); leg II 6.70 (1.92 + 0.81 + 1.57 + 1.49 + 0.91);$

- $\log \text{ III } 5.93 \ (1.70 + 0.74 + 1.25 + 1.44 + 0.80); \\ \log \text{ IV } 7.50 \ (2.04 + 0.70 + 1.78 + 1.9$
- 1098 1.00).
- 1099 Carapace (Fig. 19C). 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. $2.2 \times$ 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.
- 1106 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.
- 1108 Genitalia (Fig. 19I, 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.
- 1114 Colour (Fig. 19C, 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.
- 1117 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.
- 1121
- 1122 Variation
- 1123 Male (n = 3). Measurements (mean, followed by ranges in parentheses). CL 3.05
- 1124 (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);
- 1125 TibIL/CL 0.80 (0.78–0.82).
- 1126 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–
- 1128 2.45); TibIL/CL 0.64 (0.62-0.66).

1129	
1130	Distribution
1131	This species is endemic to the montane region in the northern part of Okinawa Island
1132	(Fig. 2).
1133	
1134	Remarks
1135	This species constructs a Y-shaped retreat with three openings (Fig. 22C).
1136	
1137	Etymology
1138	The specific name is dedicated to herpetologist Professor Emeritus Tsutomu Hikida at
1139	Kyoto University who has encouraged our arachnological research.
1140	
1141	Discussion
1142	
1143	Phylogenetic relationships and genital morphology of the Ryukyu Cybaeus
1144	
1145	Our study extends the distribution of the genus Cybaeus south to Okinawa Island in the
1146	Central Ryukyus and, moreover, reveals that the eight species of the Ryukyu Cybaeus
1147	are composed of five lineages. However, we failed to resolve the basal nodes and
1148	phylogenetic relationships among these species, especially among lineages $C-E$ and C .
1149	gotoensis (Fig. 1). The use of a broader taxonomic sample and additional genetic
1150	markers should help resolve phylogenetic relationships among the Japanese Cybaeus
1151	spiders, including the Ryukyu species.
1152	The eight species of the Ryukyu Cybaeus can be grouped into two types based
1153	on characteristics of the embolus and spermathecae. The first (type 1) includes two
1154	species, C. okumurai (lineage A) and C. kumadori (lineage B), which possess an
1155	embolus that is not elongated and spermathecae consisting of distinct relatively bulbous
1156	SH, SS and SB. The other six species (lineages C-E) share an elongated embolus in
1157	their males, and a pair of elongate tubular spermathecal ducts composed of SH and SS
1158	as well as a bulbous SB in their females (type 2). The type 1 genital characters seem to
1159	be most common in the Japanese Cybaeus species, while the type 2 characters have only
1160	been documented in a few species known from Honshu and Shikoku in Japan

(Kobayashi 2006; Ihara 2009a). To our knowledge, the type 2 spermatheca has never 1162 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 1163 their CDs (Seo 2016; Bennett et al. 2016); tubular SSs of the North American C. 1164 somesbar Bennett in Copley et al., 2009 are continuous with its respective CD, but its 1165 1166 SHs are lobate and diverge from the respective duct (Copley et al. 2009). 1167 The genital characteristics and phylogenetic position unquestionably show that C. okumurai, endemic to Tanegashima Island, is a close congener of C. ashikitaensis; 1168 both species belong to lineage A, with the other two species in this lineage known from 1169 1170 Kyushu. Cybaeus ashikitaensis is known from western Honshu, and northern to central regions of Kyushu in Japan, exhibiting a disjunct distribution (Ihara 2003, 2009a); 1171 spiders identified as C. ashikitaensis also occur on the southern tip of Kyushu (Y. Ihara, 1172 unpubl. data). The present phylogeny revealed that C. okumurai is sister to C. 1173 ashikitaensis from central Kyushu (near the type locality of the latter), but, nonetheless, 1174 it is possible that the southern population of "C. ashikitaensis" is the closest congener 1175 of, or conspecific with C. okumurai. 1176 The phylogenetic position of the other type 1 species, C. kumadori, remains 1177 uncertain, because this species forms a unique clade (lineage B) among the species 1178 included in the phylogenetic analyses. The characteristics of the male palp and female 1179 1180 spermathecae do not suggest any candidates for close congeners of *C. kumadori*. 1181 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 1182 1183 Island. However, the other characteristics of the palp and the female spermathecae are 1184 completely different between C. kumadori and the other two species. The precise 1185 phylogenetic position and close congeners of C. kumadori should be elucidated by a future study. 1186 1187 The four species categorized as type 2, C. yakushimensis, C. kodama, C. amamiensis, and C. tokunoshimensis, formed a well-supported clade (lineage D) among 1188 1189 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. 1190 yakushimensis, C. amamiensis and C. tokunoshimensis formed a monophyletic lineage 1191

1161

1192

within this clade. Although this relationship was not fully supported, these three species

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

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

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

1225 Japan and adjacent regions. 1226 *Implications for biogeography, distribution and natural history* 1227 1228 This study demonstrated that the Northern Ryukyus include distinctive biogeographical 1229 1230 elements of the genus Cybaeus. Cybaeus okumurai from Tanegashima Island is unquestionably related to the species endemic to Kyushu, while the two species, C. 1231 1232 yakushimensis and C. kodama, inhabiting Yakushima Island belong to the clade that 1233 includes the species endemic to Amamioshima Island and Tokunoshima Island in the 1234 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 1235 biogeographic pattern of the Ryukyu Cybaeus is incongruent with that of other 1236 epigean/ground-dwelling spiders inhabiting the Ryukyu Islands. It was shown that a 1237 species of the liphistiid *Heptathela* Kishida, 1923 in Yakushima Island is 1238 phylogenetically close to the species endemic to Kyushu, and that *Heptathela* species 1239 endemic to the Central Ryukyus do not occur north of the Tokara Gap (Xu et al. 2016, 1240 1241 2019). Because the present study did not estimate the divergence time of the Ryukyu 1242 Cybaeus, their biogeographical history should be further elucidated using a robust, timecalibrated phylogeny in a future study. It is evident from the deep divergences among 1243 1244 the four species of lineage D that the wide distribution of these species has not been 1245 formed by recent range expansion across the Tokara Gap. Sympatric distributions of different-sized species of *Cybaeus* (see Ihara 2008) 1246 1247 were also documented in the Ryukyu Cybaeus. Our study revealed that the medium-1248 sized C. yakushimensis and small-sized C. kodama were distributed sympatrically in 1249 Yakushima Island, and that the medium-sized C. amamiensis and small-sized C. aikana 1250 occurred together in Amamioshima Island. Given the deep divergence between C. 1251 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 1252 1253 Amamioshima Island may have been formed by secondary contact between these two species, or their ancestors. Although our phylogenetic analyses failed to determine the 1254 precise relationships between C. yakushimensis and C. kodama, these two species were 12551256 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.

1270

1271

1272

1257

1258

1259

1260

1261

1262

1263

1264

1265

1266

1267

1268

1269

Conflicts of interest

The authors declare no conflicts of interest.

1273

1274

Declaration of funding

- 1275 This study was supported by the Japan Society for the Promotion of Science KAKENHI
- grant no. JP18K14780, and by the Tokyo Metropolitan University Fund for TMU
- 1277 Strategic Research (Leader: Noriaki Murakami; FY2020–FY2022).

1278

1279

Acknowledgements

- We are grateful to Dr. Ken-ichi Okumura (National Museum of Nature and Science,
- 1281 Tsukuba) for providing the specimens examined in this study, and to one anonymous
- reviewer, Dr. Robert G. Bennett (Royal BC Museum) and Dr. Mark S. Harvey (Western
- 1283 Australian Museum) for their constructive comments and suggestions on this
- manuscript. We also thank Dr. Harry Taylor (Edanz Group) for editing a draft of this
- manuscript.

1286

1287

References

Bennett, R. G. (1985). The natural history and taxonomy of *Cicurina bryantae* Exline

- 1289 (Araneae, Agelenidae). *Journal of Arachnology* **13**, 87–96.
- Bennett, R. G. (1992). The spermathecal pores of spiders with special reference to
- dictynoids and amaurobioids (Araneae, Araneomorphae, Araneoclada). *Proceedings*
- of the Entomological Society of Ontario 123, 1–21.
- Bennett, R. G. (2005). Cybaeidae. In 'Spiders of North America: An Identification
- Manual.' (Eds D. Ubick, P. Paquin, P. E. Cushing, and V. Roth.) pp. 85–90.
- 1295 (American Arachnological Society: Greenville, SC, USA.)
- Bennett, R. G. (2006). Ontogeny, variation, and synonymy in North American Cybaeus
- spiders (Araneae: Cybaeidae). *The Canadian Entomologist* **138**, 473–492.
- 1298 doi:10.4039/n06-804
- Bennett, R. G. (2017). Cybaeidae. In 'Spiders of North America: An Identification
- Manual, '2nd edn. (Eds D. Ubick, P. Paquin, P. E. Cushing, and V. Roth.) pp. 96–
- 1301 101. (American Arachnological Society: Keene, NH, USA.)
- Bennett, R. [G.], Copley, C., and Copley, D. (2016). Cybaeus (Araneae: Cybaeidae): the
- Nearctic species of the Holarctic clade. *Zootaxa* **4164**, 1–67.
- 1304 doi:10.11646/zootaxa.4164.1.1
- Bennett, R. [G.], Copley, C., and Copley, D. (2019). Cybaeus (Araneae: Cybaeidae): the
- adenes species group of the Californian clade. Zootaxa **4711**, 245–274.
- 1307 doi:10.11646/zootaxa.4711.2.2
- Bennett, R. [G.], Copley, C., and Copley, D. (2020). Allocybaeina littlewalteri
- 1309 (Araneae: Cybaeidae): a new genus and species endemic to northwestern California.
- 1310 Zootaxa **4845**, 436–446. doi:10.11646/zootaxa.4845.3.8
- 1311 Copley, C. R., Bennett, R., and Perlman, S. J. (2009). Systematics of Nearctic Cybaeus
- (Araneae: Cybaeidae). *Invertebrate Systematics* **23**, 367–401. doi:10.1071/IS09001
- 1313 Ihara, Y. (2003). Cybaeus akiensis n. sp. (Araneae: Cybaeidae) from western Honshu,
- Japan, with some notes on its biology. *Acta Arachnologica* **52**, 51–57.
- 1315 doi:10.2476/asjaa.52.51
- 1316 Ihara, Y. (2004). Descriptions of large- and medium-sized species of the genus Cybaeus
- 1317 (Araneae: Cybaeidae) from the Tohoku district, northern Honshu, Japan. *Acta*
- 1318 *Arachnologica* **53**, 35–51. doi:10.2476/asjaa.53.35
- 1319 Ihara, Y. (2006). Cybaeus jinsekiensis n. sp., a spider species with protogynous
- maturation and mating plugs (Araneae: Cybaeidae). *Acta Arachnologica* **55**, 5–13.

- 1321 doi:10.2476/asjaa.55.5
- 1322 Ihara, Y. (2008). Species diversity and geographic differentiations of reproductive
- organs and body size in the genus *Cybaeus* (Araneae: Cybaeidae) in Japan. *Acta*
- 1324 *Arachnologica* **57**, 87–109. [In Japanese]. doi:10.2476/asjaa.57.87
- 1325 Ihara, Y. (2009a). Cybaeidae. In 'The Spiders of Japan: with Keys to the Families and
- Genera and Illustrations of the Species'. (Ed. H. Ono.) pp. 152–168. (Tokai
- University Press: Hadano, Japan.) [In Japanese].
- 1328 Ihara, Y. (2009b). Revision of the *Cybaeus hiroshimaensis*-group (Araneae:Cybaeidae)
- in western Japan. *Acta Arachnologica* **58**, 69–85. doi:10.2476/asjaa.58.69
- Katoh, K., and Standley, D. M. (2013). MAFFT multiple sequence alignment software
- version 7: improvements in performance and usability. *Molecular Biology and*
- 1332 Evolution **30**, 772–780. doi:10.1093/molbev/mst010
- Kobayashi, T. (2006). Ten new species of the genus *Cybaeus* (Araneae: Cybaeidae)
- from central Honshu, Japan. *Acta Arachnologica* **55**, 29–44. doi:10.2476/asjaa.55.29
- Koch, L. (1868). Die Arachnidengattungen Amaurobius, *Caelotes* and *Cybaeus*.
- 1336 Abhandlungen der Naturhistorischen Gesellschaft zu Nürnberg **4**, 1–52.
- Komatsu, T. (1940). [On five species of spiders found in the Ryugado Cave, Tosa
- 1338 Province]. *Acta Arachnologica* **5**, 186–195. [In Japanese]. doi:10.2476/asjaa.5.186
- 1339 Komatsu, T. (1961). 'Cave Spiders of Japan, Their Taxonomy, Chorology and
- Ecology.' (Arachnological Society of East Asia: Osaka, Japan.)
- Komatsu, T. (1968). 'Cave Spiders of Japan. II. Cybaeus, Dolichocybaeus and
- 1342 Heterocybaeus (Cybaeinae).' (Arachnological Society of East Asia: Osaka, Japan.)
- Komatsu, T., and Yaginuma, T. (1968). A new method for the observation of the spider
- genitalia. *Acta Arachnologica* **21**, 34. doi:10.2476/asjaa.21.34
- Koressaar, T., and Remm, M. (2007). Enhancements and modifications of primer design
- program Primer3. *Bioinformatics* **23**, 1289–1291.
- doi:10.1093/bioinformatics/btm091
- Lanfear, R., Calcott, B., Ho, S. Y. W., and Guindon, S. (2012). PartitionFinder:
- 1349 Combined selection of partitioning schemes and substitution models for phylogenetic
- analyses. *Molecular Biology and Evolution* **29**, 1695–1701.
- 1351 doi:10.1093/molbev/mss020
- Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., and Calcott, B. (2017).

- PartitionFinder 2: New methods for selecting partitioned models of evolution for
- molecular and morphological phylogenetic analyses. *Molecular Biology and*
- 1355 Evolution **34**, 772–773. doi:10.1093/molbev/msw260
- 1356 Marusik, Y. M., and Kovblyuk, M. M. (2011). 'Spiders (Arachnida, Aranei) of Siberia
- and Russian Far East.' (KMK Scientific Press Ltd.: Moscow, Russia) [In Russian].
- 1358 Marusik, Y. M., and Logunov, D. V. (1991). Spiders of the superfamily Amaurobioidea
- 1359 (Aranei) from Sakhalin and Kurily Islands. Zoologicheskii Zhurnal 70, 87–94. [In
- 1360 Russian].
- 1361 Matsuda, K., Ihara, Y., and Nakano, T. (2020). Description of a new species of Cybaeus
- 1362 (Araneae: Cybaeidae) from central Honshu, Japan. *Species Diversity* **25**, 145–152.
- 1363 doi:10.12782/specdiv.25.145
- 1364 Minh, B. Q., Schmidt, H. A., Chernomor, O., Schrempf, D., Woodhams, M. D., von
- Haeseler, A., and Lanfear, R. (2020). IQ-TREE 2: New models and efficient methods
- for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* **37**,
- 1367 1530–1534. doi:10.1093/molbev/msaa015
- 1368 Motokawa, M. (2000). Biogeography of living mammals in the Ryukyu Islands. *Tropics*
- 1369 **10**, 63–71. doi:10.3759/tropics.10.63
- Nakano, T. (2012). A new species of *Orobdella* (Hirudinida, Arhynchobdellida,
- Gastrostomobdellidae) and redescription of *O. kawakatsuorum* from Hokkaido,
- Japan with the phylogenetic position of the new species. *ZooKeys* **169**, 9–30.
- 1373 doi:10.3897/zookeys.169.2425
- Nakano, T., Ihara, Y., Kumasaki, Y., Baba, Y. G., and Tomikawa, K. (2017).
- Evaluation of the systematic status of geographical variations in *Arcuphantes*
- 1376 *hibanus* (Arachnida: Araneae: Linyphiidae), with descriptions of two new species.
- 1377 Zoological Science **34**, 331–344. doi:10.2108/zs160168
- Ota, H. (1998). Geographic patterns of endemism and speciation in amphibians and
- reptiles of the Ryukyu Archipelago, Japan, with special reference to their
- paleogeographical implications. *Population Ecology* **40**, 189–204.
- 1381 doi:10.1007/bf02763404
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G., and Suchard, M. A. (2018).
- 1383 Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic
- 1384 *Biology* **67**, 901–904. doi:10.1093/sysbio/syy032

- Ramírez, M. J. (2014). The morphology and phylogeny of dionychan spiders (Araneae:
- 1386 Araneomorphae). Bulletin of the American Museum of Natural History **390**, 1–374.
- 1387 doi:10.1206/821.1
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S.,
- Larget, B., Liu, L., Suchard, M. A., and Huelsenbeck, J. P. (2012). MrBayes 3.2:
- Efficient Bayesian phylogenetic inference and model choice across a large model
- space. Systematic Biology **61**, 539–542. doi:10.1093/sysbio/sys029
- Roth, V. D. (1993). 'Spider Genera of North America with Keys to Families and
- Genera, and a Guide to Literature,' 3rd edn. (American Arachnological Society:
- Gainesville, SC, USA.)
- Seo, B. K. (2016). Seven new species of the genus *Cybaeus* (Araneae, Cybaeidae) from
- 1396 Korea. Journal of Species Research 5, 571–583. doi:10.12651/jsr.2016.5.3.571
- Seo, B. K. (2017). Three new species and four new records of the families Cybaeidae
- and Gnaphosidae (Araneae) from Korea. *Journal of Species Research* **6**, 114–124.
- 1399 doi:10.12651/JSR.2017.6(S).114
- Shimojana, M. (2000). Description of eleven new species of the genus *Coelotes*
- (Araneae: Amaurobiidae) from the Ryukyu Islands, Japan. *Acta Arachnologica* **49**,
- 1402 165–189. doi:10.2476/asjaa.49.165
- Shimojana, M., and Haupt, J. (1998). Taxonomy and natural history of the funnel-web
- spider genus *Macrothele* (Araneae: Hexathelidae: Macrothelinae) in the Ryukyu
- Islands (Japan) and Taiwan. Species Diversity 3, 1–15. doi:10.12782/specdiv.3.1
- Tanikawa, A., and Miyashita, T. (2008). A revision of Japanese spiders of the genus
- 1407 Dolomedes (Araneae: Pisauridae) with its phylogeny based on mt-DNA. Acta
- 1408 *Arachnologica* **57**, 19–35. doi:10.2476/asjaa.57.19
- 1409 Untergasser, A., Cutcutache, I., Koressaar, T., Ye, J., Faircloth, B. C., Remm, M., and
- Rozen, S. G. (2012). Primer3—new capabilities and interfaces. *Nucleic Acids*
- 1411 *Research* **40**, e115. doi:10.1093/nar/gks596
- 1412 Wessel, P., and Smith, W.H.F. (1996). A global, self-consistent, hierarchical, high-
- resolution shoreline database. *Journal of Geophysical Research: Solid Earth* **101**,
- 1414 8741–8743. doi:10.1029/96jb00104
- 1415 Xu, X., Liu, F., Chen, J., Ono, H., Agnarsson, I., Li, D., and Kuntner, M. (2016). Pre-
- Pleistocene geological events shaping diversification and distribution of primitively

segmented spiders on East Asian margins. *Journal of Biogeography* **43**, 1004–1019.

doi:10.1111/jbi.12687

Xu, X., Ono, H., Kuntner, M., Liu, F., and Li, D. (2019). A taxonomic monograph of the liphistiid spider genus *Heptathela*, endemic to Japanese islands. *ZooKeys* **888**, 1–50. doi:10.3897/zookeys.888.34494

1423	FIGURE LEGENDS AND TABLE CAPTIONS
1424	
1425	Fig. 1. Bayesian inference tree (mean $\ln L = -10554.32$) for 3421 bp of nuclear histone
1426	H3, internal transcribed spacer 1, 28S rRNA, mitochondrial COI, 12S rRNA, and 16S
1427	rRNA markers. Numbers on nodes represent bootstrap values for maximum likelihood
1428	and Bayesian posterior probabilities.
1429	
1430	Fig. 2. Map showing the distributions of the lineages that contain Cybaeus species in
1431	the Ryukyu Islands. Inset phylogeny is identical with that in Fig. 1. The map and
1432	lineages are colour-shaded to indicate the species collection localities. The map is based
1433	on Wessel and Smith (1996).
1434	
1435	Fig. 3. Cybaeus okumurai, sp. nov., male holotype (KUZ Z3019: A, B) and female
1436	paratype (KUZ Z3024: C, D). (A, C) prosoma, dorsal; (B, D) abdomen, dorsal. Scale
1437	bars: 1 mm.
1438	
1439	Fig. 4. Cybaeus okumurai, sp. nov., male holotype (KUZ Z3019: A-C, F, G); Cybaeus
1440	ashikitaensis (Komatsu), male from Ashikita, Kyushu Island (KUZ Z3675: D, E). (A)
1441	left palp, retrolateral; (B, D) tibia and patella (left palp), retrolateral; (C, E) tibia and
1442	patella (left palp), retro-dorsolateral; (F) cymbium (left palp), dorsal; (G) cymbium (left
1443	palp), ventral. Scale bars: (A) 500 μ m; (B-G) 200 μ m.
1444	
1445	Fig. 5. Cybaeus okumurai, sp. nov., female paratypes (KUZ Z3023: A; KUZ Z3025: B);
1446	Cybaeus ashikitaensis (Komatsu), females from Ebino (KUZ Z3676: C) and Ashikita
1447	(KUZ Z3677: D), Kyushu Island. (A , C) epigyne, ventral; (B , D) spermathecae, dorsal.
1448	Scale bars: 200 μm.
1449	
1450	Fig. 6. Cybaeus kumadori, sp. nov., male holotype (KUZ Z3004: A, B) and female
1451	paratype (KUZ Z3007: C, D). (A, C) prosoma, dorsal; (B, D) abdomen, dorsal. Scale
1452	bars: 1 mm.
1/53	

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,
- 1458 dorsal. Scale bars: (*A*) 500 μm; (*B*) 250 μm; (*C*–*G*) 200 μm.

- 1460 **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
- 1462 bars: 1 mm.

1463

- **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.

1468

- Fig. 10. Cybaeus yakushimensis, sp. nov., male holotype (KUZ Z2998: A, D, G);
- 1470 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 μ m;
- $1473 \quad (D-H) 200 \, \mu \text{m}.$

1474

- 1475 **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 μ m; (E, F) 1 mm.

1479

- 1480 **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.

1485

1486 **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
- 1488 bars: 1 mm.

- 1490 **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.

1494

- **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,
- 1497 dorsal. Scale bars: (*A*, *B*) 500 μm; (*C*) 1 mm.

1498

- 1499 **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.

1503

- Fig. 17. Cybaeus aikana, sp. nov., female paratypes (KUZ Z2137: B; KUZ Z3018: A).
- 1505 (A) epigyne, ventral; (B) spermathecae, dorsal. Scale bars: 200 μm.

1506

- 1507 **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
- 1512 μm ; (*F–J*) 200 μm .

- 1514 **Fig. 19.** Cybaeus hikidai, sp. nov., male holotype (KUZ Z2982: A, B, E–H) and female
- 1515 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)
- 1517 cymbium (left palp), dorsal; (H) bulb (left palp), ventral; (I) epigyne, ventral; (J)
- 1518 spermathecae, dorsal. Scale bars: (A–D) 1 mm; (E) 500 μm; (F, H–J) 200 μm; (G) 250

1519 μm. 1520 Fig. 20. Cybaeus hikidai, sp. nov., schematic drawing of epigyne and spermathecae. 15211522ventral (left) and dorsal (right), based on female paratype (KUZ Z2107). 1523 1524 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). 1525 1526 Scale bars: 200 µm. 1527 1528 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 1529Mt. Yuwandake, Amamioshima Island; (C) Cybaeus hikidai, sp. nov. from Mt. 1530 Yonahadake, Okinawa Island. 1531 1532 Table 1. Samples with voucher numbers, collection locality and DDBJ accession 1533 numbers used for molecular analyses 1534 Sequences marked with an asterisk (*) were obtained for the first time in the present 1535 1536 study; KUZ, Zoological Collection of Kyoto University 1537

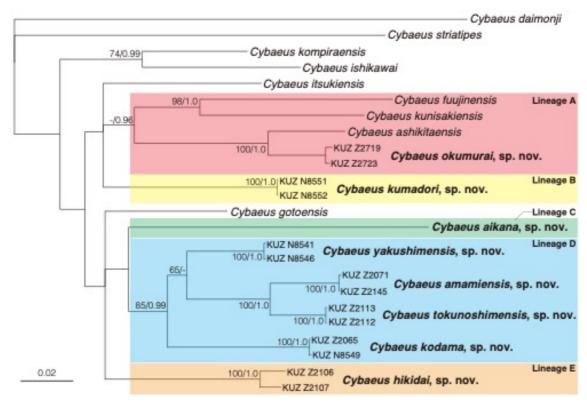


Fig. 1. Bayesian inference tree (mean $\ln L = -10554.32$) for 3421 bp of nuclear histone H3, internal transcribed spacer 1, 28S rRNA, mitochondrial COI, 12S rRNA, and 16S rRNA markers. Numbers on nodes represent bootstrap values for maximum likelihood and Bayesian posterior probabilities.

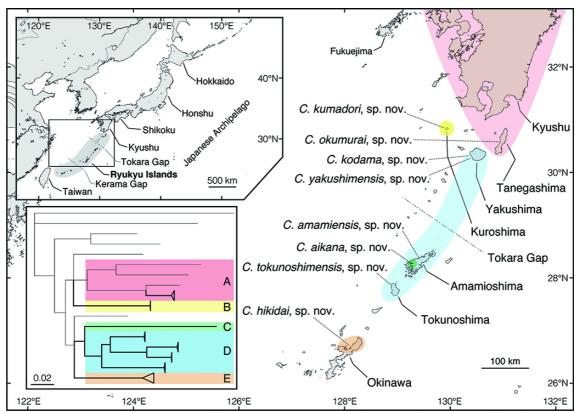
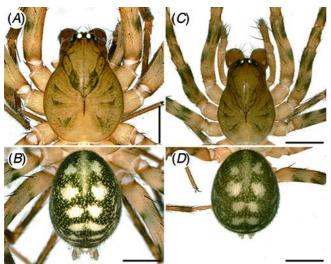


Fig. 2. Map showing the distributions of the lineages that contain *Cybaeus* species in the Ryukyu Islands. Inset phylogeny is identical with that in Fig. 1. The map and lineages are colour-shaded to indicate the species collection localities. The map is based on Wessel and Smith (1996).

1548



1552

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.

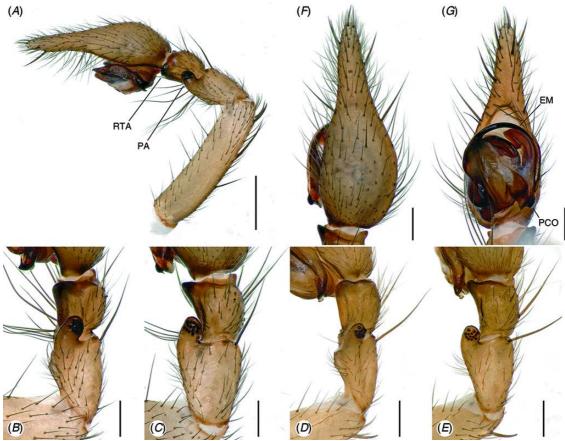


Fig. 4. Cybaeus okumurai, sp. nov., male holotype (KUZ Z3019: A–C, F, G); Cybaeus ashikitaensis (Komatsu), male from Ashikita, Kyushu Island (KUZ Z3675: D, E). (A) left palp, retrolateral; (B, D) tibia and patella (left palp), retrolateral; (C, E) tibia and patella (left palp), retro-dorsolateral; (F)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

 $1560 \\ 1561$

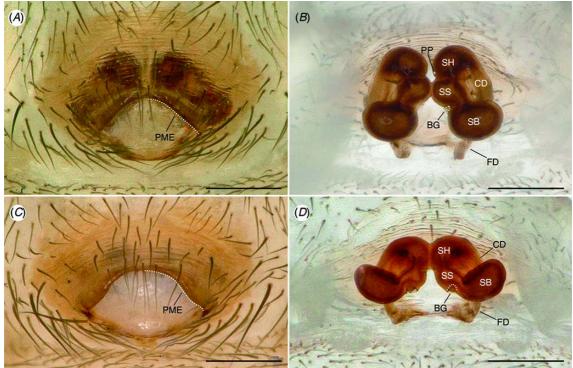
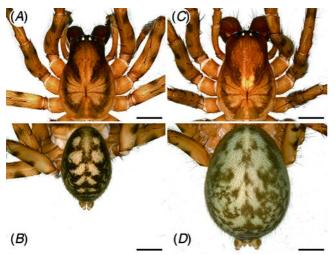


Fig. 5. *Cybaeus okumurai*, sp. nov., female paratypes (KUZ Z3023: *A*; KUZ Z3025: *B*); *Cybaeus ashikitaensis* (Komatsu), females from Ebino (KUZ Z3676: *C*) and Ashikita (KUZ Z3677: *D*), Kyushu Island. (*A*, *C*) epigyne, ventral; (*B*, *D*) spermathecae, dorsal. Scale bars: 200 μm.



 $\begin{array}{c} 1568 \\ 1569 \end{array}$

1570

 $1571 \\ 1572$

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.

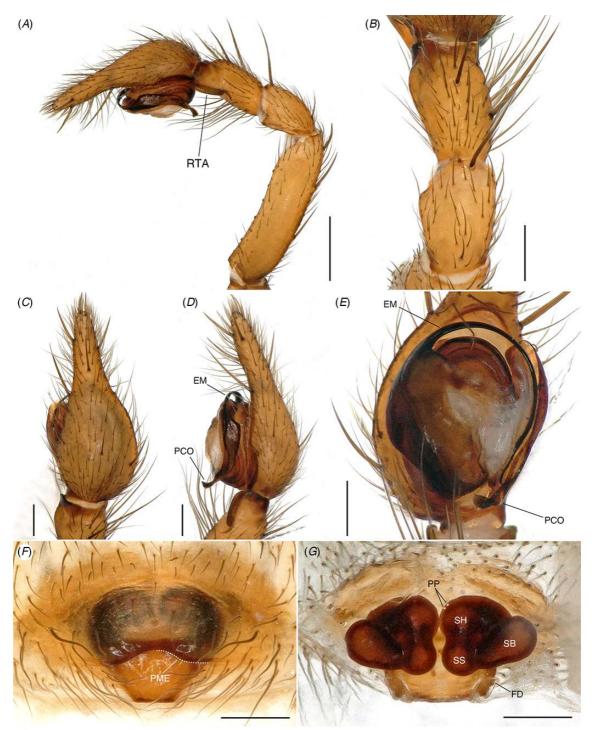
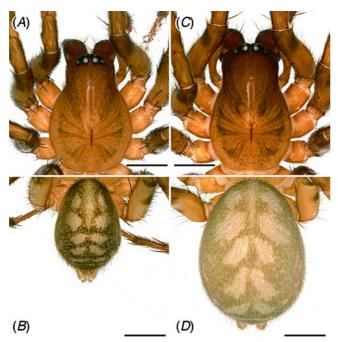


Fig. 7. *Cybaeus kumadori*, sp. nov., male holotype (KUZ Z3004: *A–E*) and female paratypes (KUZ Z2144: *G*; KUZ Z3007: *F*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) cymbium (left palp), dorsal; (*D*) cymbium and bulb (left palp), retrolateral; (*D*) bulb (left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

 $\begin{array}{c} 1573 \\ 1574 \end{array}$



 $\begin{array}{c} 1580 \\ 1581 \end{array}$

1582

 $1583 \\ 1584$

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.

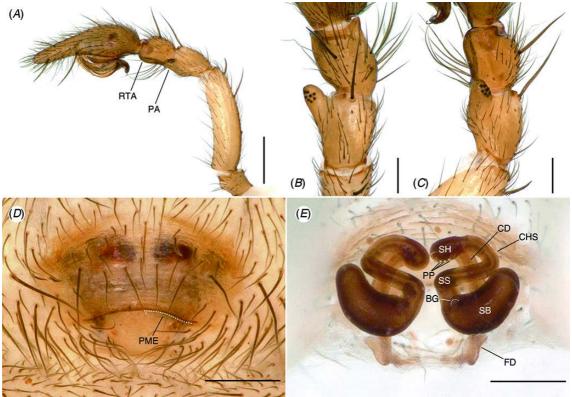


Fig. 9. *Cybaeus yakushimensis*, sp. nov., male holotype (KUZ Z2998: *A–C*) and female paratypes (KUZ Z2138: *E*; KUZ Z3001: *D*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) epigyne, ventral; (*E*) spermathecae,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

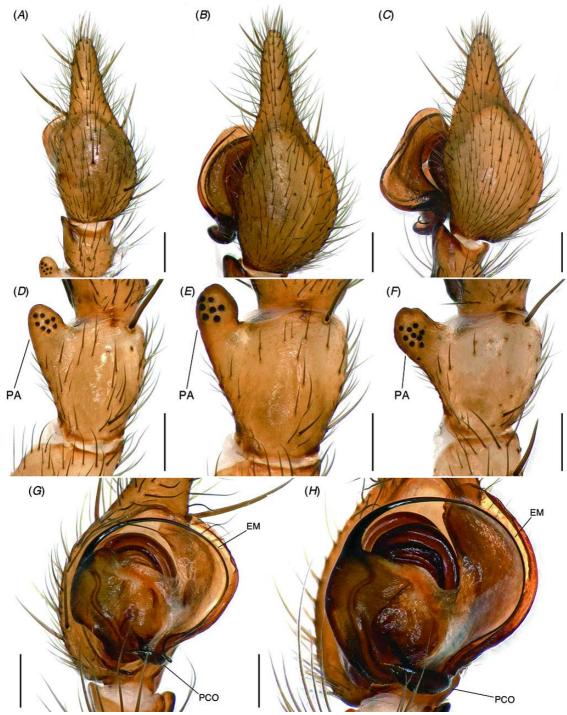
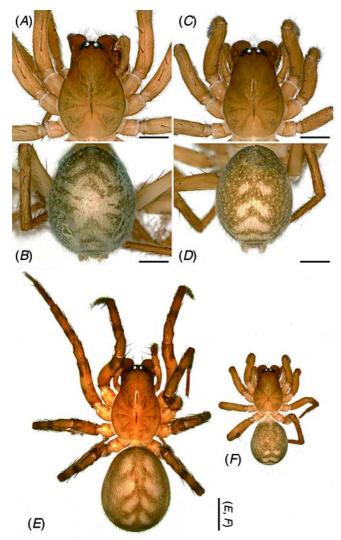


Fig. 10. *Cybaeus yakushimensis*, sp. nov., male holotype (KUZ Z2998: A, D, G); *Cybaeus amamiensis*, sp. nov., male holotype (KUZ Z2987: B, E, H); *Cybaeus tokunoshimensis* (KUZ Z2113: C, F). (A–C) cymbium (left palp), dorsal; (D–F) tibia (left palp), retro-dorsolateral; (G, H) bulb (left palp), ventral.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

 $1596 \\ 1597$



 $1601 \\ 1602$

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 μ m; (E, F) 1 mm.

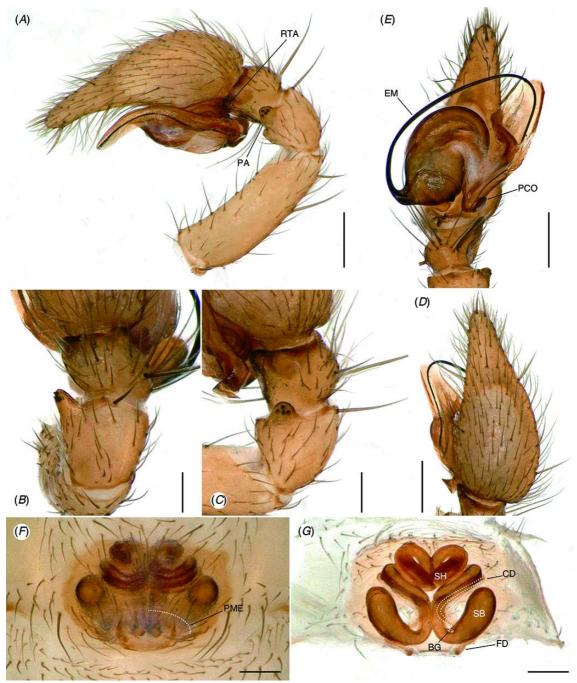


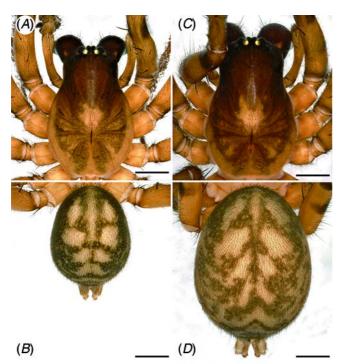
Fig. 12. *Cybaeus kodama*, sp. nov., male holotype (KUZ Z3011: *A–E*) and female paratypes (KUZ Z2142: *G*; KUZ Z3014: *F*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) cymbium (left palp), dorsal; (*E*) bulb (left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

 $1604 \\ 1605$

1606 1607

1608

 $1609 \\ 1610$



 $\begin{array}{c} 1611 \\ 1612 \end{array}$

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.

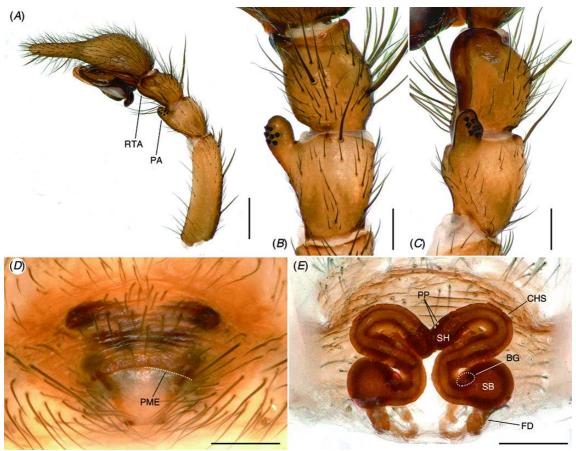
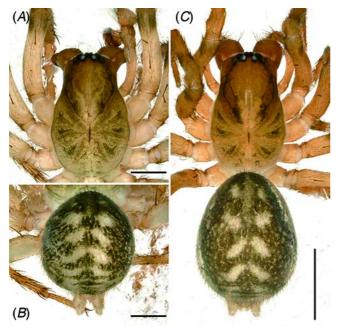


Fig. 14. *Cybaeus amamiensis*, sp. nov., male holotype (KUZ Z2987: *A–C*) and female paratypes (KUZ Z2121: *E*; KUZ Z2991: *D*). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) tibia and patella (left palp), retrolateral; (*D*) epigyne, ventral; (*E*) spermathecae, dorsal.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



 $\begin{array}{c} 1622 \\ 1623 \end{array}$

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 μ m; (C) 1 mm.

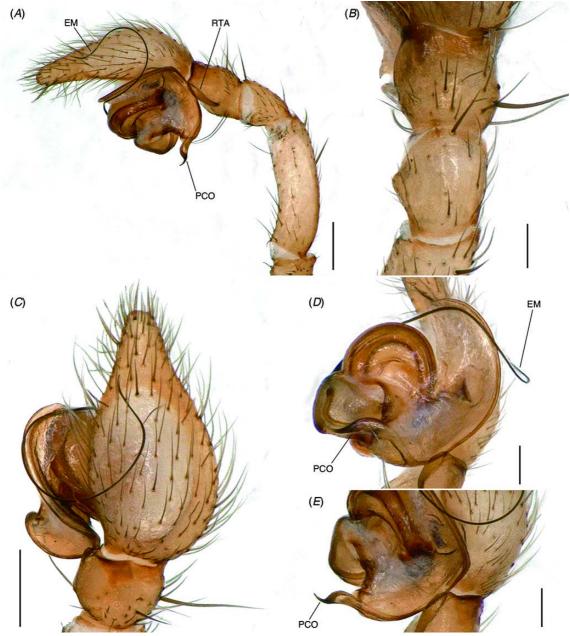


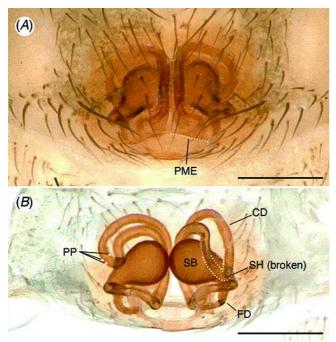
Fig. 16. *Cybaeus aikana*, sp. nov., male holotype (KUZ Z3017). (*A*) left palp, retrolateral; (*B*) tibia and patella (left palp), dorsal; (*C*) cymbium (left palp), dorsal; (*D*) bulb (left palp), ventral; (*E*) conductor (left palp), proximal end, posteroventral. Scale bars: (*A*, *C*) 200 μm; (*B*,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

 $\begin{array}{c} 1627 \\ 1628 \end{array}$

1629

1630

 $1631 \\ 1632$



 $\begin{array}{c} 1633 \\ 1634 \end{array}$

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

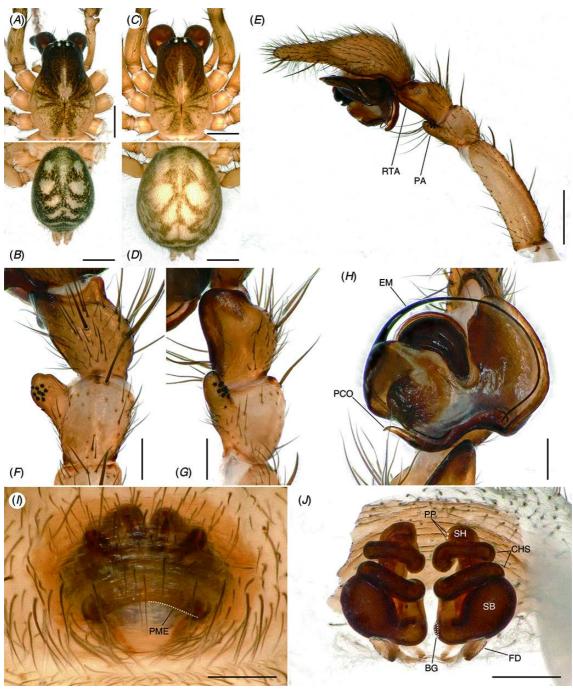


Fig. 18. *Cybaeus tokunoshimensis*, sp. nov., male holotype (KUZ Z2113: A, B, E–H) and female paratypes (KUZ Z2112: J; KUZ Z2994: C, D;KUZ Z2995: I). (A, C) prosoma, dorsal; (B, D) abdomen, dorsal; (E) left palp, retrolateral; (E) tibia and patella (left palp), dorsal; (E) tibia and patella (left palp),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

 $1637 \\ 1638$

 $1639 \\ 1640$

 $1641 \\ 1642$

 $1643 \\ 1644$

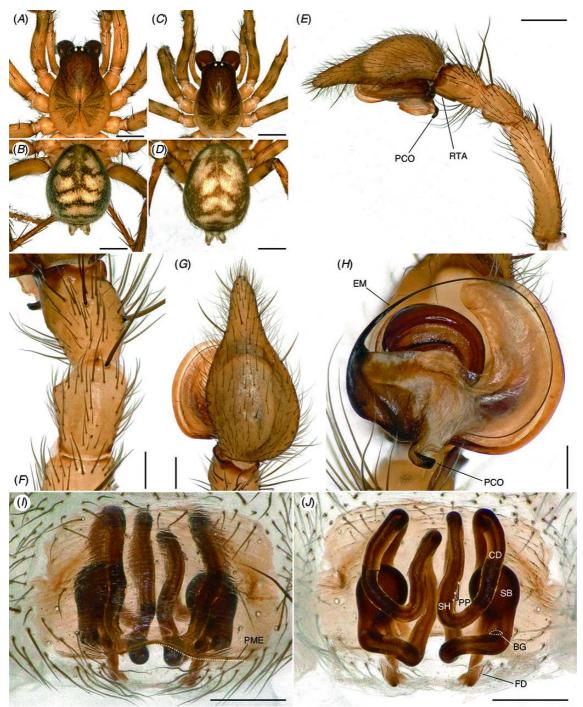


Fig. 19. *Cybaeus hikidai*, sp. nov., male holotype (KUZ Z2982: *A, B, E–H*) and female paratypes (KUZ Z2107: *I, J*; KUZ Z2984: *C, D*). (*A, C*) prosoma, dorsal; (*B, D*) abdomen, dorsal; (*E*) left palp, retrolateral; (*F*) tibia and patella (left palp), dorsal; (*G*) cymbium (left palp), dorsal; (*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.

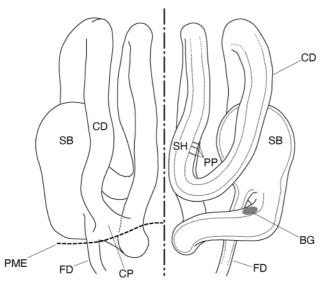


 Fig. 20. *Cybaeus hikidai*, sp. nov., schematic drawing of epigyne and spermathecae. ventral (left) and dorsal (right), based on female paratype (KUZ Z2107).

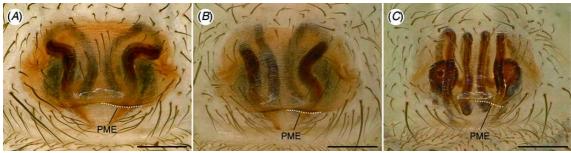


Fig. 21. *Cybaeus hikidai*, sp. nov., epigyne, ventral. (*A*) paratype (KUZ Z2984); (*B*) female from Mt. Nagodake, Okinawa Island (KUZ Z2985); (*C*) paratype (KUZ Z2983). Scale bars: 200 μm.

 $\begin{array}{c} 1657 \\ 1658 \end{array}$



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,	LC552280*	LC552282*	LC552281*		LC552279*	
Cybaeus okumurai, sp. nov.	KUZ Z2723	Tanegashima Island 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.	KUZ Z2112	Mt. Inokawadake, Tokunoshima Island	LC552258*	LC552261*	LC552260*	LC552259*	LC552257*	
Cybaeus tokunoshimensis, sp.	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,	LC552182*	LC552185*	LC552184*	LC552183*	
Cybaeus kompiraensis	KUZ Z2317	Kyushu Kompirado Cave, Kochi, Shikoku	LC552179*	LC552181*	LC552180*	LC552178*	
Cybaeus kunisakiensis Cybaeus striatipes	KUZ Z2303 KUZ Z2718	Mt. Futagosan, Oita, Kyushu Mt. Rausudake, Shari, Hokkaido	LC552197* LC552174*	LC552200* LC552177*	LC552199* LC552176*	LC552198* LC552175*	LC552196*