

Multiple origins and complex evolutionary history of *Cryptops* centipedes (Chilopoda: Scolopendromorpha: Cryptopidae) inhabiting East Asian islands, with systematics of Japanese species

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ABSTRACT

Cryptops Leach, 1814 is a genus of generally small, blind centipedes that mostly inhabit epigeal habitats. With more than 150 species described worldwide, *Cryptops* is one of the most widespread and speciose genera within the class Chilopoda. Although previous studies have indicated a complex evolutionary history, the biogeography of *Cryptops* species largely remains unclear owing to a lack of molecular data from some regions such as the easternmost part of Asia. Moreover, the taxonomic status of several species from this region also remains uncertain. In this study, we addressed systematics and phylogeography of *Cryptops* species from East Asian islands, mainly the Japanese Archipelago and the Ryukyu Islands. Here, based on molecular phylogeny of nuclear and mitochondrial loci as well as morphology, we reexamined the taxonomic accounts of *C. japonicus* Takakuwa, 1934, *C. navis* Chamberlin, 1930, and *C. striatus* Takakuwa, 1936, and describe a new species, *Cryptops dupliporus* sp. nov. Molecular phylogenetic and dating analyses showed that the East Asian species are non-monophyletic, originating from at least three independent lineages. The analyses also showed significant differences in the degree of intraspecific divergence among species, presumably reflecting different dispersal abilities and colonization histories to the East Asian islands. Our results indicate that the species richness of *Cryptops* on East Asian islands is an outcome of ancient relics of continental origin as well as recent radiation, possibly through colonization from southwestern Pacific islands by oceanic currents.

Keywords: cryptic diversity, endemic species, Japanese Archipelago, nomenclature, phylogeography, relict species, Ryukyu Islands, Taiwan, widespread species

Online summary

Cryptops is one of the most widespread and speciose genera of centipedes, but its evolutionary history remains unclear owing to insufficient biogeographic and systematic studies. This study clarifies the systematic status of four East Asian species of *Cryptops*, including a new species. Molecular analyses show that these species originated from at least three divergences, revealing both continental relict and recently colonized lineages. This study demonstrates complex spatial and temporal processes shaping species diversity and distributions, which may be common in centipedes.

Introduction

The class Chilopoda is an ancient arthropod lineage with fossil records dating back to the Silurian, and comprises more than 3000 described extant species worldwide (Shear and Bonamo 1988; Edgecombe and Bonato 2011; Bonato et al. 2016). Based on their ancient origins and generally limited dispersal abilities, some of the taxa have been utilized as suitable subjects for historical biogeographic studies. In particular, the effects of continental vicariance have been studied in the context of Gondwanan biogeography (Edgecombe et al. 2002; Edgecombe and Giribet 2004; Hollington and Edgecombe 2004; Giribet and Edgecombe 2006, 2013; Joshi and Edgecombe 2019; Joshi et al. 2020; Manivannan et al. 2024). Spatial patterns of biodiversity, including the determinants of regional species richness and intraspecific diversity, have also been intensively studied in some regions (e.g., Pereira et al. 1997; Kettle and Arthur 2000; Arthur and Kettle 2001; Arthur et al. 2001; Simaiakis and Mylonas 2006, 2008; Simaiakis et al. 2011, 2012; Joshi and Karanth 2012, 2013; Velez et al. 2012; Oeyen et al. 2014; Simaiakis and Strona 2015; Bharti et al. 2021, 2023). Accordingly, a high degree of endemism has been revealed in several taxa (e.g., Edgecombe et al. 2015; Voigtländer et al. 2017; Bharti et al. 2021; Bonato et al. 2023), and a previous study indicated that the current species and genetic diversity of centipedes may be associated with their low dispersal ability (Bharti et al. 2023). By contrast, several species show evidence of oversea dispersal (Lewis 1981) and implications on ancient trans-oceanic dispersal (Manivannan et al. 2024). A striking example of evolutionary history is revealed in *Strigamia* Gray, 1843, a geophilomorph genus with most members inhabiting Holarctic forest soils. Bonato et al. (2017) showed that the European littoral species *S. maritima* (Leach, 1817) is more closely related to East Asian species than to its European congeners. This result suggests a historical connection between European and East Asian fauna of small soil-dwelling species, highlighting the importance of

extensive taxon sampling across continents. Overall, the current centipede fauna is composed of both local endemic and widespread species, and thus their biogeography is presumed to be shaped by complex spatial and temporal processes.

Cryptops Leach, 1814 is a scolopendromorph genus consisting of more than 150 species that are usually small and blind, and primarily inhabit epigeal or trogloditic habitats; it is one of the most widespread and diverse genera of Chilopoda, found on most continents as well as major continental islands and some oceanic islands (Bonato and Zapparoli 2011; Edgecombe et al. 2020; Schileyko et al. 2020). Despite their small body size and cryptic habits, several *Cryptops* species have been recorded from extremely wide geographical ranges (e.g., Verhoeff 1940; Lewis 2011, 2013; Schileyko and Stoev 2016; Popovici and Edgecombe 2025), implying that they can disperse over long distances (Verhoeff 1940; Lewis 2011). However, understanding of their dispersal and diversification is limited by insufficient ecological and molecular phylogenetic studies.

The phylogeography of *Cryptops* has been studied in a few works, such as by Muriene et al. (2011) who discussed the origin and diversification of South Pacific species, and by Wesener et al. (2016) and Vahtera et al. (2020) who revealed genetic divergence within species that are widespread across Europe. Overviews of phylogeny within the genus were provided by Vahtera et al. (2013) and Edgecombe et al. (2020), who revealed that the primarily Mediterranean *C. trisulcatus* Brölemann, 1902 is more closely related to Asian species than to other European species, suggesting a faunal connection across the continent. Nonetheless, the biogeographic history of *Cryptops* species is still unclear, with DNA sequences of only 20 species available from quite limited areas, such as Europe, Africa, the New World and Australasian regions.

Previous records indicate that *Cryptops* centipedes are particularly diverse and rich in South America, the Mediterranean region, central and southern Africa, Madagascar, and Australia (Bonato and Zapparoli 2011). By contrast, *Cryptops* species are relatively scarce in some regions, such as the easternmost part of Asia (including the Japanese Archipelago, the Korean Peninsula, the Ryukyu Islands and Taiwan), even though taxonomic works have been conducted in this region since the 1930s. To date, four species of *Cryptops* have been recorded from this region: *Cryptops navis* Chamberlin, 1930, *Cryptops japonicus* Takakuwa, 1934, *Cryptops nigropictus* Takakuwa, 1936, and *Cryptops striatus* Takakuwa, 1936 (Chao and Chang 2003, 2008; Shinohara et al. 2015; Jonishi and Nakano 2020), aside from an uncertain record of *Cryptops haasei* Attems, 1903 (Chamberlin and Wang 1952). However, the phylogenetic positions of the East Asian species, which is essential to reveal the

evolutionary history of *Cryptops* (see above), are yet to be determined. Furthermore, the morphological features of *C. japonicus* have not been revised based on topotypic materials since the brief descriptions by the original author (Takakuwa 1934, 1936, 1940), except for descriptions of Taiwanese specimens (Chao 2008; Lewis 2013). Likewise, the taxonomic account of *C. striatus* has not been revised since its original description (Takakuwa 1936) and is still insufficient.

In this study, members of the genus *Cryptops* were extensively sampled from the Japanese Archipelago and the Ryukyu Islands. The evolutionary relationships and divergence times of *Cryptops* species are inferred using the sequence data newly obtained in this study along with those from previous studies. Their biogeographic history, especially the origin and diversification of the species in East Asian islands, is discussed based on phylogenetic and divergence dating analyses. Based on both molecular phylogeny and morphological features, three of the previously known East Asian *Cryptops* species are taxonomically re-evaluated, and a new species is described.

Materials and methods

Taxon sampling and morphological examination

Most of the specimens studied by Yoshioki Takakuwa, including the type series of *C. japonicus*, are thought to be lost (Takashima 1954; Chao and Chang 2008; Jonishi and Nakano 2022a). In addition, we were unable to find the original material of *C. striatus* in the remnants of Takakuwa's collection (see Jonishi and Nakano 2022a), and therefore assume that they are also lost. Thus, this study was conducted using only newly collected specimens.

A total of 45 specimens of *C. japonicus* were collected from 12 localities across Honshu, Shikoku, Kyushu, and the Ryukyu Islands. Seven specimens of *C. striatus* were obtained from 4 localities in eastern Honshu, near the type locality of this species. Our specimens of *C. navis* consisted of 11 individuals obtained from the Ryukyu Islands, including Amami (Oshima) and Okinawa islands, along with the 8 specimens examined in Jonishi and Nakano (2020). In addition, a total of 4 unidentified specimens were collected from eastern Honshu (Tokyo) and from Amami, Ishigaki, and Iriomote islands in the Ryukyu Islands (Fig. 1).

The specimens were fixed and preserved in 99% or 80% ethanol and then observed under a Leica M125C stereoscopic microscope (Leica Microsystems, Wetzlar, Germany). Several specimens were photographed using a Sony a6500 digital camera combined with a Laowa 65-mm macro lens, the Leica M125C equipped with a Leica

MC170 HD digital camera, and an Olympus DP23 digital camera mounted on an Olympus BX53 phase contrast microscope (Olympus, Tokyo, Japan). Photographs taken with the MC170 camera were processed using Leica Application Suite v. 4.1.2. All specimens examined are deposited in the Zoological Collection of Kyoto University (KUZ). The terminology for external features follows Lewis et al. (2005) and Bonato et al. (2010a).

DNA extraction, amplification and sequencing

Genomic DNA was extracted from leg samples using the DNA Blood and Tissue Kit (Qiagen, Hilden, Germany), or the NucleoSpin Tissue kit (Macherey-Nagel, Duren, Germany), or following a method modified from Okamoto et al. (2006) using Protein Precipitation Solution (Promega Corporation, Madison, USA). Two nuclear and two mitochondrial markers, namely 18S rRNA (18S), 28S rRNA (28S), 16S rRNA (16S), and cytochrome *c* oxidase subunit I (COI), were selected for molecular analyses following previous studies (e.g., Edgecombe et al. 2012, 2020; Vahtera et al. 2013, 2020). The target regions were amplified using the following primer sets: 18S1F/18S5R (Giribet et al. 1996), 18S3F/18Sbi (Giribet et al. 1996, 1999), and 18Sa2.0/18S9R (Giribet et al. 1996, 1999) for 18S; 28Sa/28Srd5b (Whiting et al. 1997; Schwendinger and Giribet 2005) for 28S; 16Sar/16Sb (Xiong and Kocher 1991; Edgecombe et al. 2002) for 16S; and LCO1490/HCO2198 (Folmer et al. 1994) or the reverse primer HCOoutout (Schwendinger and Giribet 2005) for COI. 18S fragments were amplified by TaKaRa Ex Taq DNA polymerase or TaKaRa Ex Premier DNA Polymerase (Takara Bio Inc., Shiga, Japan), using a LifeECO Thermal Cycler (Bioer Technology, Hangzhou, China) or a GeneAmp PCR System 9700 (Thermo Fisher Scientific, Waltham, USA). The PCR mixtures were heated to 94 °C for 5 min, followed by 35 cycles at 94 °C for 10 s, 60 °C for 20 s, and 72 °C for 30–60 s, with a final extension at 72 °C for 6 min. Methods for PCR amplification of other regions and the DNA sequencing process mostly followed Jonishi and Nakano (2022b, 2024). A total of 113 sequences obtained in the present study were deposited in the International Nucleotide Sequence Databases (INSD) through the DNA Data Bank of Japan (Supplementary Table S1).

Sequence alignment

In addition to the sequences newly obtained in this study, 104 sequences of *Cryptops* species and 64 sequences of outgroup taxa retrieved from INSD were included in the dataset (Supplementary Table S1). Unreliable terminal parts of several 28S sequences

obtained from INSD were excluded from the analyses. The nuclear 18S, 28S, and the mitochondrial 16S sequences were aligned using MAFFT with the Q-INS-i algorithm (Kuraku et al. 2013; Katoh et al. 2019) considering the RNA secondary structure information. To remove ambiguity (e.g., base shifts between identical sequences), the alignments were manually adjusted and then subsampled using Gblocks v. 0.91b (Castresana 2000). The alignment of COI sequences was straightforward because no indels were observed. The concatenated sequences yielded 3189 bp of aligned positions composed of 658 bp of COI, 300 bp of 16S, 1761 bp of 18S, and 470 bp of 28S.

Phylogenetic reconstruction

Bayesian inference (BI) was used to infer phylogenetic relationships using two separate datasets. The first was composed of all the sequences of ingroup taxa shown in Supplementary Table S1 (“total dataset”), including eight sequences of which only the COI region is available on the INSD. The best-fit partition schemes and substitution models were chosen based on the Bayesian Information Criterion using the “greedy” algorithm in PartitionFinder v. 2.1.1 (Lanfear et al. 2012, 2016). The selected partition schemes and models are as follows: SYM + I + G for COI 1st position and 18S; GTR + I + G for COI 2nd position and 16S; GTR + G for COI 3rd position; and K80 + I + G for 28S. The BI trees and Bayesian posterior probabilities (BPP) were estimated in MrBayes v. 3.2.7 (Ronquist et al. 2012). Two independent runs of four Markov chain Monte Carlo (MCMC) simulations were conducted for 10 million generations, with a sampling frequency of 100 generations. After checking the parameter estimates and convergence using Tracer v. 1.7.2 (Rambaut et al. 2018), the first 25% of the trees were discarded as burn-in.

A preliminary analysis using the “total dataset” failed to reconstruct robust phylogenetic relationships among several *Cryptops* species. Therefore, eight sequences that contained only the COI region were removed (“selected dataset”). The BI trees and BPP were then estimated in MrBayes, as described above, with MCMC conducted for 8 million generations, with a sampling frequency of 100 generations, and the first 35% of the trees discarded as burn-in.

Distance analysis

Uncorrected pairwise distances were calculated using the 658-bp COI region in MEGA 11 (Tamura et al. 2021), with the setting “pairwise deletion” of missing data.

Divergence dating

To date, four fossil records can be used to calibrate the phylogeny of blind scolopendromorph centipedes (see Benavides et al. 2023; Edgecombe et al. 2023): *Cratoraricrus oberlii* Wilson, 2003 from the Lower Cretaceous Crato Formation for divergence of the crown group Taktikospina Benavides et al., 2023; *Cryptops* sp. from Eocene Baltic amber (Bachofen-Echt 1942) for the crown group Tykhepoda Benavides et al., 2023; *Theatops groehni* Edgecombe et al., 2023, also from Baltic amber, for Plutoniumidae Bollman, 1893 + Scolopocryptopidae Pocock, 1896; and *Scolopocryptops simojovelensis* Edgecombe et al., 2012 from Miocene Chiapas amber for the crown group *Scolopocryptops* Newport, 1844. To obtain robust divergence date estimates in which these calibrations can be used, a dataset larger than the focus taxa but including fewer sequences per species was compiled (Supplementary Table S1).

A time-calibrated BI tree was reconstructed using BEAST v. 2.6.6 (Bouckaert et al. 2019) under an uncorrelated relaxed clock with a lognormal distribution and a Yule speciation prior. The four genes and three codon positions of COI were partitioned; the tree and clock model were linked across all four loci, but substitution rates were separately estimated for each partition. The best-fit substitution models estimated by PartitionFinder were as follows: SYM + I + G for COI 1st position, GTR + I + G + X for COI 2nd position and 16S, HKY + I + G + X for COI 3rd position, and TRNEF + I + G for 18S and 28S. For divergence date calibration, four constraints based on the fossil records and preceding studies were employed (Supplementary Table S2); the monophyly of the family Scolopocryptopidae was also fixed, in accordance with Benavides et al. (2023). Within *Cryptops*, the monophyly of several nodes were constrained based on strong support from the results in MrBayes. The MCMC was run for 1 billion generations, sampling one tree every 1000 generations. After examining the effective sample sizes of parameters and convergence using Tracer v. 1.7.2, the program LogCombiner (part of the BEAST package) was used to resample the trees at a lower frequency (every 5000 generations), discarding the initial 10% of the trees as burn-in. The maximum clade credibility tree, with median node ages and 95% highest posterior density (HPD), was produced by the TreeAnnotator program in the BEAST package.

Results

Molecular phylogeny and pairwise distances

The overall topology obtained using the “selected dataset” (mean $\ln L = -23863.3$; Fig. 2) was concordant with the results of Vahtera et al. (2013) and Edgecombe et al. (2020). Within the genus, several European species, such as *C. hortensis* (Donovan, 1810) and

the Japanese *C. striatus*, formed a fully supported clade (hereinafter, the “Holarctic” lineage) that is a sister group of all other species; the monophyly of the latter group was also strongly supported (BPP = 0.99). The latter group comprises two clades: a clade composed of Neotropical, Afrotropical, and Australasian species (BPP = 0.98; the “Gondwanan” lineage) and the other clade composed of species from Palearctic (Europe and Japan), Oriental (Vietnam, Thailand and Indonesia), and Australasian (Fiji) regions (BPP = 1.0; the “Laurasian” lineage). In this clade, an unidentified specimen from Amami Island in Japan (hereinafter *Cryptops* sp. 2) was resolved as a sister taxon of the remainders. Specimens of *C. japonicus* and *C. navis*, respectively, were recovered with full support. Two unidentified specimens from the southern Ryukyu Islands formed a monophyletic group (BPP = 0.99; hereinafter *Cryptops* sp. 1) that is a sister taxon of *C. navis*. The other unidentified specimen from Tokyo, which is described as *C. dupliporus* sp. nov. herein, formed a fully supported clade with *C. japonicus* and *C. doriae*.

Within *C. japonicus*, three clades were recovered with strong support: specimens from eastern Honshu, Kyushu, and Tanegashima Island (hereinafter clade 1; locality numbers J1, J8 and J10 in Fig. 1, 2); specimens from central Honshu and Shikoku (clade 2; J2–J5); and specimens from Okinawa Island (clade 3; J11 and J12). However, the phylogenetic positions of the other specimens were not resolved. The uncorrected COI pairwise distances within each clade was in the range of 6.4%–15.6%; the distances between clades were in the range of 14.8%–19.3%.

In the preliminary analysis using the “total dataset” (Supplementary Fig. S1), COI sequences of the European *C. croaticus* Verhoeff, 1931 and the North American *C. leucopodus* (Rafinesque, 1820) were nested within the “Holarctic” lineage.

Among the COI sequences submitted as “*C. japonicus*” from Taiwan, four sequences were nested within the Japanese *C. japonicus* (AB610780), *C. navis* (AB610777), *Cryptops* sp. 1 (AB610778), and *C. dupliporus* sp. nov. (AB675008), respectively. Sequences from southern Taiwan (AB610779) and Itu Aba Island (AB672645) formed a monophyletic group (BPP = 0.97) with *C. indicus* (Silvestri, 1924) from Vietnam and *C. weberi* (Pocock, 1891) from Indonesia.

Divergence time estimates

The crown *Cryptops* was estimated to have diverged since the Cretaceous (95% HPD interval: 64.28–112.88 Mya) (Fig. 3; Supplementary Fig. S2). Within the genus, the 95% HPD intervals for the time to the most recent common ancestor (TMRCA) were 31.61–65.18 Mya for the “Holarctic” lineage, 50.99–92.65 Mya for the “Gondwanan”

lineage, and 47.65–86.3 Mya for the “Laurasian” lineage.

Systematics

Order **Scolopendromorpha** Pocock, 1895

Family **Cryptopidae** Kohlrausch, 1881

Genus ***Cryptops*** Leach, 1814

Type species: *Scolopendra hortensis* Donovan, 1810, by monotypy.

***Cryptops japonicus* Takakuwa, 1934**

Fig. 4–8

Japanese name. Nihon-menashimukade

Cryptops japonicus Takakuwa, 1934a: 389–390, fig. 14 (available name). — Takakuwa 1934b: 404–405, fig. 12, 13 (invalidly described as new). — Takakuwa 1936: 236–237. — Takakuwa 1940: 63–65, fig. 66–68. — Takakuwa in Kishida and Takakuwa 1949: 940: fig. 2689. — Takakuwa and Miyosi 1971: 733. — Song et al. 2010: 378, table 1. — Shinohara et al. 2015: 879, 893, 905, fig. 5. *Cryptops japonicus* (in part) — Chao and Chang 2003: 4, 9, 10, fig. 16, table 1. — Chao 2008: 68–71, Fig 71, 73, 74. — Chao and Chang 2008: 5, 14, fig. 9E, F. — Lewis 2013: 15, fig. 37, 38. *Cryptops* cf. *japonicus* — Popovici and Edgecombe 2025: 230–232, fig. 2.

Type specimens. *Cryptops japonicus* was described based on five specimens (one male and four females) from Kokura (in Kitakyushu City, Fukuoka Prefecture), Kyushu, Japan, although Takakuwa (1934a) did not designate any types. These syntypes are presumed to be lost (see Materials and methods), but there is no doubt about the identity of *C. japonicus* because no other *Cryptops* species has been known from the type locality. Because the current situation does not meet the conditions of Article 75.1 of the International Code of Zoological Nomenclature (hereinafter, the Code) (International Commission on Zoological Nomenclature 1999), a neotype for *C. japonicus* is not designated here.

Material examined. JAPAN – **Kanagawa Prefecture** • 1 ♀, 14.3 mm (KUZ Z6440); Manazuru-machi, Ashigarashimo-gun; 35°8.61'N, 139°9.14'E, approx. 40 m alt.; 30 Jan.

2023 – **Mie Prefecture** • 1 ♂, 9.5 mm (KUZ Z6445), 4 ♀, 6.7–11.2 mm (KUZ Z6441, Z6443, Z6446, and Z6447), and 2 specimens, 5.2 mm (KUZ Z6442) and 9.0 mm (KUZ Z6444); Aso, Taiki-cho, Watarai County; 34°19.47'N, 136°24.27'E; approx. 160 m alt.; 23 Apr. 2021 – **Osaka Prefecture** • 2 ♂, 7.9 mm (KUZ Z6448) and 10.7 mm (KUZ Z6449); Kagata, Kawachinagano City; 34°22.85'N, 135°33.54'E; approx. 460 m alt.; 9 Nov. 2021 – **Tokushima Prefecture** • 1 ♂, 11.7 mm (KUZ Z6450) and 1 ♀, 12.2 mm (KUZ Z6451); Nagayasu, Naka County; 33°48.48'N, 134°20.64'E; approx. 240 m alt.; 28 May 2021 – **Ehime Prefecture** • 1 ♂, 9.2 mm (KUZ Z6453), 1 ♀, 9.8 mm (KUZ Z6456), and 3 specimens, 8.3–11.9 mm (KUZ Z6452, Z6454, and Z6455); Mt. Keyama, Nogawa, Uwajima; 33°12.05'N, 132°36.41'E; approx. 1040 m alt.; 17 Oct. 2019 – **Fukuoka Prefecture** • 1 ♂, 10.4 mm (KUZ Z6457); Hakata, Fukuoka City; 33°34.97'N, 130°25.92'E; approx. 10 m alt.; 11 Nov. 2022 – **Miyazaki Prefecture** • 1 ♀, 15.1 mm (KUZ Z6458); Mitate, Hinokage-cho Town, Nishiusuki County; 32°48.32'N, 131°28.08'E; approx. 750 m alt.; 30 May 2021 – **Saga Prefecture** • 2 ♂, 8.6 mm (KUZ Z6459) and 12.1 mm (KUZ Z6460); Otonari, Kashima; 33°0.7'N, 130°5.56'E; approx. 420 m alt.; 27 Jul. 2023 – Kagoshima Prefecture – **Tanegashima Island** • 1 ♀, 11.4 mm (KUZ Z6461); Kakinaga, Minamitane Town; 30°25.03'N, 130°56.54'E; approx. 70 m alt.; 8 Dec. 2019 • 2 ♂, 7.7 mm (KUZ Z6469) and 7.8 mm (KUZ Z6464), 2 ♀, 7.2 mm (KUZ Z6467) and 8.3 mm (KUZ Z6470), and 3 specimens, 7.9–8.4 mm (KUZ Z6465, Z6466, and Z6468); same locality as for preceding; 30°24.95'N, 130°56.65'E; approx. 90 m alt.; 11 Nov. 2020 • 1 ♂, 9.0 mm (KUZ Z6471); Nakanokami, Minamitane-cho; 30°26.02'N, 130°55.32'E; approx. 170 m alt.; 11 Nov. 2020 • 1 ♂, 7.5 mm (KUZ Z6463) and 1 ♀, 8.2 mm (KUZ Z6462); Annnou, Nishinoomote; 30°44.68'N, 131°3.14'E; approx. 210 m alt.; 10 Nov. 2020 – Okinawa Prefecture – **Okinawa Island** • 1 ♀, 9 mm (KUZ Z6474) and 1 specimen, 10.7 mm (KUZ Z6473); near Mt. Katsuu-dake, Motobu-cho, Kunigami County; 26°37.88'N, 127°56.27'E; approx. 310 m alt.; 14 Jun. 2022; • 2 ♀, 8.5 mm (KUZ Z6476) and 9.0 mm (KUZ Z6475), 1 specimen, 10.3 mm (KUZ Z6477), and 8 eggs (KUZ Z6480); Mt. Fuenchiji, Yona, Kunigami-son, Kunigami County; 26°45.17'N, 128°14.57'E, approx. 380 m alt.; 16 Jun. 2022.

Diagnosis. Cephalic plate with anterolateral sutures almost reduced, posterior margin overlapped by tergite 1. Clypeus with 2 + 1 + 2 + 2 and 5–7 prelabral setae. Forcipular coxosternite with anterior margin slightly bilobed or almost straight, with 2 + 2 large submarginal setae. Tergite 1 lacking transverse suture. Sternites 2–19 with cruciform sulci. Legs 1–19 with undivided tarsus, all legs with single accessory spine up to

approx. 1/2 length of pretarsus. Coxopleural pore field elongate oval, composed of up to 40 pores occupying up to approx. 35% of surface of coxopleuron, with wide pore-free area posteriorly. Saw teeth on ultimate leg 0–1 + 3–9 + 2–4.

Description (variations given in parentheses). Body length up to approx. 15 mm in 80% ethanol. Color in life and in ethanol brownish orange on head, brownish yellow on other segments, legs and ultimate legs (uniformly brownish yellow in ethanol) (Fig. 4a, b).

Antenna 1.0–2.2 mm in length, approx. $2.3\text{--}3.1 \times$ as long as cephalic plate, composed of 17 articles (Fig. 4b). Basalmost article scattered with long setae and short setae; articles 2–3 with sparse long setae and short setae, short setae denser on distal half on ventral surface; subsequent articles with long setae in a whorl around basal part, and short setae denser than those on articles 1–3 (Fig. 5a).

Cephalic plate as long as wide or longer than wide (slightly wider than long in KUZ Z6440 and Z6457), with sparse fine setae; anterolateral sutures almost reduced or absent, paramedian sutures not visible (short, almost reduced paramedian sutures visible on posterior margin in KUZ Z6473, Z6475 and Z6477); posterior margin overlapped by tergite 1 (overlapping tergite 1 in KUZ Z6448) (Fig. 4b, c). Clypeus with 2 + 1 + 2 + 2 (and a few minute setae between rows) and 5–7 prelabral setae (Fig. 5b, c). Labrum with rounded side-pieces and single mid-piece tooth.

Second maxillae with semi-transparent, dense dorsal brush shorter than pretarsus; pretarsus apically hooked, accompanied by ventral projection.

Forcipular coxosternite covered with sparse short setae; anterior margin slightly bilobed or almost straight, with 2 large (and 1–3 small) submarginal setae on each side (Fig. 4d, 5d, e). Tarsungulum as long as (slightly longer or shorter than) forcipular trochanteroprefemur (Fig. 4d). Calyx of venom gland ovoid, located in anterolateral part of trochanteroprefemur.

Tergites covered with sparse fine setae; tergite 1 lacking sutures (or with short paramedian sutures on anterior margin); tergite 2 with short paramedian sutures near posterior margin (sutures also present near anterior margin, or sutures absent); paramedian sutures complete on tergites 3 (4)–20 (19), lateral crescentic sulci present on tergites 3 (2)–20; weak median keel delimited by paired shallow sulci present on mid body tergites (not visible in some specimens) (Fig. 4b). Tergite of ultimate leg-bearing segment with posterior margin subtriangular; median depression present on posterior half.

Sternites sparsely or moderately setose; sternites 2–19 (20) with cruciform

sulci (sternites 1 and/or 20 with slight depression in some specimens), of which transverse sulci curved (median longitudinal sulcus slightly shallower than transverse one) (Fig. 6a). Sternite of ultimate leg-bearing segment with lateral margins weakly rounded, posterior margin almost straight or slightly convex (slightly concave in KUZ Z6474) (Fig. 6b).

Spiracles ovoid or almost circular, largest on leg-bearing segment 3 (Fig. 6c).

Legs finely setose on all articles; leg 20 of male with dense short setae on prefemur, femur and tibia (or prefemur and femur only) ventrally (Fig. 6g, h). Legs 1–19 with undivided tarsus; tarsus of leg 20 clearly divided and flexed (faintly divided and not flexed in KUZ Z6473 and Z6477) (Fig. 6g–i); all legs with single accessory spine approx. 1/4–1/2 length of pretarsus (Fig. 6e, f).

Coxopleural pore field elongate oval, occupying approx. 15%–35% of surface of coxopleuron, composed of up to 31 pores of approximately uniform or gradationally variable size; wide pore-free area present posteriorly and posteroventrally. Coxopleural pore field with a few setae of various length; dorsal region and posterior margin, respectively, with a few minute setae and enlarged ones; 1 enlarged seta and a few minute setae present between pore field and posterior margin (Fig. 6d).

Ultimate leg approx. 2.0–4.0 mm (prefemur, 0.44–0.94 mm; femur, 0.44–1.03 mm; tibia, 0.33–0.66 mm; tarsus 1, 0.26–0.49 mm; tarsus 2, 0.38–0.76 mm; pretarsus, 0.06–0.13 mm). All articles with fine setae; enlarged setae present on prefemur (medially, ventrally, and/or laterally) and femur (medially and/or ventrally). Tibia and tarsus 1, respectively, with a pair of short, “tubercle-like” (sensu Lewis 2009) spinous processes dorsodistally (Fig. 5f). Femur, tibia and tarsus 1 with 1 (0), 3–9 and 2–4 saw teeth, respectively (Fig. 5f).

Variation. Pretarsal accessory spine approx. 1/4–1/3 length of pretarsus in specimens from Okinawa Island (locality numbers J11 and J12; KUZ Z6473–Z6477), approx. 1/3–1/2 length of pretarsus in specimens from other localities (Fig. 6e, f). Saw tooth on ultimate femur absent in specimens from Okinawa Island (KUZ Z6473–Z6477).

Distribution. Known from Honshu, Shikoku, Kyushu in the Japanese Archipelago, the Ryukyu Islands, and the Izu Islands (Takakuwa 1934a, b, 1940; Shinohara 1949; Takano 1978a, b, 1980; Kuwabara 1984; Ishii 1999; Hagino 2016). Also recorded from the Korean Peninsula (Yun 1997), northeast China (formerly Manchuria) (Takakuwa 1936, 1940), and Taiwan (Chao and Chang 2003, 2008; Chao 2008; Lewis 2013). However, our phylogenetic tree (Supplementary Fig. S1) implies that “*C. japonicus*” sensu Chao

and Chang comprises at least five species, including misidentified specimens of *C. navis* and *C. dupliporus* sp. nov. (see Results). The specimens identified as “*C. japonicus*” by Chao and Chang (2003, 2008) and by Chao (2008) thus need to be reexamined.

Remarks. This species was established in Takakuwa (1934a, in Japanese), based on specimens from Kyushu in Japan. Takakuwa (1934b, in German) introduced “*Cryptops* [sic] *japonicus* n. sp.” again, providing almost the same contents (see Jonishi and Nakano 2022) but with less detailed description. Based on specimens from the Korean Peninsula and northeast China (formerly Manchuria), Takakuwa (1936) added the following features to the description of this species: 1) triangular prominence with robust setae between antennae; 2) cephalic plate often with short incomplete “median” sutures (vs. sutures absent in Takakuwa 1934a); 3) tergites 1 and 2 often with indistinct longitudinal sulci (vs. sulci absent in Takakuwa 1934a, b); 4) coxopleural pore field composed of approx. 30 pores, occupying anterior 2/3 of coxopleuron (vs. about 40 pores occupying anterior 3/4 in Takakuwa 1934a, b) (summarized in Lewis 2013). Takakuwa (1936, 1940) also mentioned the presence of one or two saw teeth on the ultimate femur of *C. japonicus*, whereas in Takakuwa (1934a, b) he had stated that the saw tooth is occasionally present.

The examined specimens agree with Takakuwa’s descriptions except for the following aspects. 1) The triangular prominence between antennae was not observed. Such a “prominence” has not been described in other *Cryptops* species (e.g., Lewis 2013) and possibly refers to the anterior apex of the cephalic plate. 2) The “median” sutures on the cephalic plate, which presumably refers to paramedian sutures, were not visible in the present specimens except for KUZ Z6473, Z6475, and Z6477. 3) Tergites 1 and 2 mostly lack sutures or sulci, although anterior short paramedian sutures on tergites 1 and 2 are present in KUZ Z6473 and tergite 2 occasionally bears short paramedian sutures on the posterior half. 4) The longitudinal and transverse sulci on sternites are equally developed, or the transverse sulcus is slightly deeper and more apparent than the longitudinal one (vs. longitudinal sulcus longer and more apparent in Takakuwa [1934a, b]). The appearance of cruciform sulci is dependent on the angle of illumination (Lewis 1999, 2009, 2013) and may have been mistakenly described in Takakuwa (1934a, b). 5) Tibia and tarsus 1 of the ultimate leg bear small spinous processes. The processes are insignificant and may have been overlooked by Takakuwa (1934a, b, 1936, 1940), who mentioned that the processes (“Zähnchen” in Takakuwa [1934b] or “Endzähne” in Takakuwa [1936]) are absent.

In the present specimens, the maximum body length is smaller (< 20 mm) and the number of coxal pores is less (up to approx. 30) than what is described in Takakuwa (1934a, b, 1936, 1940) (up to 25 mm, approx. 40 pores; Fig. 7). However, even relatively small individuals (approx. 10 mm) are sexually mature, as confirmed by the presence of spermatophores or egg-laying behavior (Fig. 8).

As summarized by Lewis (2013), Takakuwa (1934a, b) distinguished *C. japonicus* from *C. doriae* based on the number of coxal pores, the absence of a glabrous area on the ultimate prefemur, and the number of saw teeth on the ultimate leg. Takakuwa (1936) later stated that *C. japonicus* differs from *C. doriae* in the absence of spinous processes on all articles of the ultimate leg. The characters of the numbers of coxal pores, and saw teeth and spinous processes of the ultimate leg, cannot conclusively distinguish between these species (Lewis 2013). Nonetheless, *C. japonicus* clearly differs from *C. doriae* in the undivided tarsus of legs 1–19 (vs. tarsi mostly divided in *C. doriae*) and a single accessory spine (vs. two spines) (Schileyko 2007; Lewis 2013). The distinctness of *C. japonicus* is also supported by the molecular phylogeny (Fig. 2). Takakuwa (1936) also compared *C. japonicus* with *C. tahitianus* Chamberlin, 1920, stating that *C. japonicus* differs from the latter in the number of antennal articles, the presence of saw tooth/teeth of the ultimate femur, and the number of saw teeth on subsequent articles. Although *C. tahitianus* actually bears a minute saw tooth on the ultimate femur (Lewis 2011, 2013), *C. japonicus* can be distinguished by the undivided tarsus (vs. tarsi divided in *C. tahitianus*) and a single, well-developed accessory spine on the leg (vs. two minute accessory spines) (Lewis 2013).

Popovici and Edgecombe (2025) recorded small, immature individuals (3–10 mm) of “*Cryptops* cf. *japonicus*” from the Aldabra Atoll in the Seychelles. The characters of the Aldabra specimens are consistent with the present materials except for “traits characteristic of juvenile specimens”, such as a reduced number of coxal pores (< 10) and indistinct paramedian sutures on the tergites. In the Japanese populations, even relatively small individuals (approx. 10 mm) are sexually mature (see above); the number of coxal pores is generally greater (8–31), and the tergal paramedian sutures are distinct. It is possible that the Aldabra population was artificially introduced from East Asia, and that the different environments caused differences in growth rates between the Japanese and Aldabra specimens, as speculated for an introduced population of *C. doriae* in England (Lewis 2007; Popovici and Edgecombe 2025). As mentioned by Popovici and Edgecombe (2025), however, taxonomic treatment of the Aldabra population needs to be determined based on the morphology of mature specimens as well as molecular data.

Cryptops navis Chamberlin, 1930

Fig. 9–11

Japanese name. Futamata-menashimukade

Cryptops navis Chamberlin, 1930: 65. — Lewis 2013: 19, fig. 50–54. — Jonishi and Nakano 2020: 865–869, fig. 3–4.

Cryptops sinensis Chamberlin, 1940: 49. — Lewis 2013: 25–26, fig. 67–69.

Type specimen. A holotype, collected at Honolulu, Hawaii, on 3 Oct. 1930, in soil from Singapore by R. V. Chamberlin, is preserved at the National Museum of Natural History, Washington D.C.

Material examined. JAPAN – Kagoshima Prefecture – **Amami Island** • 1 specimen, 8.0 mm (KUZ Z6485); Miyakozaki, Yamato-son; 28°22.62'N, 129°24.31'E; approx. 10 m alt.; 27 Mar. 2022 • 1 specimen, 6.8 mm (KUZ Z6489); same locality as for preceding; 28°22.68'N; 129°24.32'E; approx. 40 m alt. 22 Jun. 2022 • 1 ♀, 7.3 mm (KUZ Z6486); Yuwangama, Yamato-son; 28°21.08'N; 129°25.16'E; approx. 150 m alt.; 27 Mar. 2022 • 1 ♀, 8.5 mm (KUZ Z6487); Sumiyo-cho; 28°16.82'N, 129°24.3'N; approx. 50 m alt.; 19 Jun. 2022 • 1 specimen, 7.6 mm (KUZ Z6488); same locality as for preceding; 28°16.93'N, 129°24.31'E; approx. 90 m alt.; 19 Jun. 2022 • 1 ♂, 7.2 mm (KUZ Z6490); Gamôzaki park, Kasari-cho; 28°29.88'N, 129°39.07'E; approx. 140 m alt.; 23 Jun. 2022 – Okinawa prefecture – **Okinawa Island** • 1 specimen, 8.7 mm (KUZ Z6491); Hentona, Kunigami-son, Kunigami County; 26°44.33'N, 128°10.5'E; approx. 20 m alt.; 7 Apr. 2022 • 1 ♂, 7.2 mm (KUZ Z6493); near Mt. Nekumachiji, Ogimi-son, Kunigami County; 26°41.09'N, 128°8.06'E; approx. 240 m alt.; 16 Jun. 2022 • 1 ♀, 9.6 mm (KUZ Z6492); Mt. Nago-dake, Nago City; 26°35.45'N, 128°0.25'E; approx. 200 m alt.; 14 Jun. 2022 • 1 specimen, 6.4 mm (KUZ Z6494), Gushichan, Yaese-cho, Shimajiri County; 26°7.16'N 127°44.78'E; approx. 40 m alt.; 27 Sept. 2022 – **Tokashiki Island** • 1 specimen, 14.9 mm (KUZ Z2974); Tokashiki; 26°11.77'N, 127°21.66'E; approx. 10 m alt.; 13 Mar. 2019 • 5 specimens, 5.9–12.6 mm (KUZ Z2975–Z2979); same locality as for preceding; 14 May 2019 – **Minamidaito Island** • 1 specimen, 10.6 mm (KUZ Z2980) and 1 damaged specimen (body length not measured; KUZ Z2981); Shioya Beach; 25°49.64'N, 131°12.98'E; approx. 20 m alt.; 29 Oct. 2019 – **Kurima Island** • 1 specimen, 4.4 mm (KUZ Z6495); Shimoji; 24°43.2'N, 125°15.38'E; approx. 20 m alt.;

25 May 2022.

Diagnosis. Cephalic plate with short anterolateral sutures, posterior margin overlapped by tergite 1. Clypeus with 2 + 1 + 2 and 5–6 prelabral setae. Forcipular coxosternite with anterior margin weakly bilobed, with 3 + 3 or 2 + 2 submarginal setae. Tergite 1 lacking transverse suture. Sternites 2–19 with cruciform sulci. Legs 1–19 with undivided tarsus, all legs with single accessory spine approx. 1/2 length of pretarsus; leg 20 with dense short setae ventrally. Coxopleural pore field subtriangular, occupying approx. 15%–30% of surface of coxopleuron, composed of up to 60 pores, leaving wide pore-free area posteriorly. Saw teeth on ultimate leg 1 + 4–7 + 2, of which distal one on tibia bifid.

Description. Body length up to approx. 15 mm in 80% ethanol. Color in life and in ethanol brownish orange on head, brownish yellow on leg-bearing segments, legs and ultimate legs (Fig. 9a, b).

Antenna 1.2–2.4 mm in length, approx. 2.1–3.1 × as long as cephalic plate, composed of 17 articles (Fig. 9b). Basalmost article scattered with long setae and short setae (an irregular whorl of long setae present on distal part in KUZ Z2974); articles 2 and 3 with sparse long setae and short setae; 4th and subsequent articles with long setae forming an irregular whorl around basal part, and dense short setae (Fig. 10a).

Cephalic plate longer than wide (0.54–0.78 mm × 0.45–0.74 mm), with sparse fine setae; short anterolateral sutures present, short paramedian sutures present near posterior margin in KUZ Z2974 (unapparent or not visible in smaller specimens); posterior margin overlapped by tergite 1 (Fig. 9b, c). Clypeus with 2 + 1 + 2 and 5–6 prelabral setae (Fig. 10b, c). Labrum with rounded side-pieces and single mid-piece tooth.

Second maxillae with semi-transparent, dense dorsal brush approx. as long as or shorter than pretarsus; pretarsus apically hooked, accompanied by ventral projection.

Forcipular coxosternite covered with sparse fine setae; anterior margin weakly bilobed, with 3 + 3 submarginal setae of which lateral ones smallest (absent in smaller specimens) (Fig. 9d, 10c). Tarsungulum almost as long as (slightly longer or shorter than) forcipular trochanteroprefemur (Fig. 9d). Calyx of venom gland ovoid, located in anterolateral part of trochanteroprefemur.

Tergites covered with sparse fine setae; tergites 1 and 2 lacking sutures (short paramedian sutures present on anterior margin of tergite 1 and posterior margin of tergite 2); paramedian sutures complete on tergites 3 (4 or 5)–20 (19); lateral crescentic sulci

present on tergites 3–20; weak median keel with shallow longitudinal sulci on each side present on mid body tergites (Fig. 9b). Tergite of ultimate leg-bearing segment with posterior margin subtriangular, median depression present on posterior half.

Sternites moderately setose; sternites 2–19 with cruciform sulci, of which transverse ones curved and longer than median longitudinal ones (transverse suture also present on sternite 20; sternites 1 and/or 20 with shallow depression in some specimens) (Fig. 11a). Sternite of ultimate leg-bearing segment with sides slightly converging posteriorly, posterior margin weakly rounded (Fig. 11b).

Spiracles ovoid or almost circular (Fig. 11c).

Legs finely setose; leg 20 with dense short setae on prefemur, femur and tibia ventrally (or prefemur and femur only) (Fig. 11e). Legs 1–19 with undivided tarsus; tarsus of leg 20 clearly divided; all legs with single accessory spine approx. 1/2 length of pretarsus (Fig. 11e, f).

Coxopleural pore field subtriangular, occupying approx. 15%–30% of surface of coxopleuron, composed of up to 24 pores of approximately uniform or gradationally variable size; wide pore-free areas are present posteriorly and posteroventrally (Fig. 11d). Coxopleural pore field with a few minute setae and enlarged ones; dorsal area and posterior margin, respectively, with a few minute setae and enlarged ones; 0–3 enlarged or minute setae present between pore field and posterior margin (Fig. 11d).

Ultimate leg approx. 2.1–3.1 mm (prefemur, 0.51–0.76 mm; femur, 0.46–0.74 mm; tibia, 0.34–0.54 mm; tarsus 1, 0.25–0.4 mm; tarsus 2, 0.42–0.63 mm; pretarsus, 0.07–0.1 mm). All articles with fine setae; enlarged setae present on lateral, ventral and medial surface of prefemur, and ventral and medial surface of femur; prefemur with longitudinal glabrous area medially (sparsely setose in KUZ Z2980, single enlarged seta present in KUZ Z6490). Tibia and tarsus 1, respectively, with a pair of short, “tubercle-like” (sensu Lewis 2009) spinous processes dorsodistally (Fig. 10d). Femur, tibia and tarsus 1 with 1, 4–7 and 2 saw teeth, respectively, distal saw tooth on tibia bifid (Fig. 10d).

Distribution. Known from the Ryukyu Islands, Japan (Amami, Okinawa, Tokashiki, and Minamidaito islands, and Kurima Island near Miyako Island), northern Taiwan (submitted to INSD as “*C. japonicus*”; AB610777), an unknown locality in China (Chamberlin 1940), and Singapore (Chamberlin 1930).

Remarks. Jonishi and Nakano’s (2020) statement that this species lacks sutures on the cephalic plate was incorrect and is corrected in the description above.

The shape of the saw teeth on the ultimate leg is variable in some species, such as *C. doriae* (see Lewis 2007); however, in *C. navis* the distal saw tooth on the tibia is invariably bifid (Fig. 10d) and is regarded as a diagnostic character of this species.

Only two individuals of this species have previously been recorded from Singapore and China (Chamberlin 1930, 1940; Lewis 2013) aside from our specimens from the Ryukyu Islands (see Jonishi and Nakano 2020). In the Ryukyu specimens, the number of coxal pores is smaller (up to 24) than those of Chamberlin's (1930, 1940) specimens (up to more than 50 pores) (Lewis 2013). The intraspecific variation in this character, as well as the actual geographic range of *C. navis*, need to be assessed based on extensive taxon sampling and molecular analyses (see Discussion).

***Cryptops striatus* Takakuwa, 1936**

Fig. 12–14

Japanese name. Suji-menashimukade

Cryptops striatus Takakuwa, 1936: 237–238, 241, fig. 1–3. — Takakuwa 1940: 65–66, fig. 69–71. — Shinohara et al. 2015: 879, 905.

Type specimens. No types were designated in the original description. The introduction in Takakuwa (1936) stated that he obtained multiple specimens at Enoshima (a small island near the coast of eastern Honshu) and at “Ôsima-Insel” (presumably Izu Oshima Island in the Izu Islands), Japan. In the description of *C. striatus*, however, he mentioned only Enoshima as the locality of this species. Takashima (1954) also mentioned that six syntypes from Enoshima were preserved by Dr. Yasunori Miyosi after Takakuwa passed away, indicating that the description of *C. striatus* was based on specimens from Enoshima. Therefore, the type locality of this species is restricted to Enoshima in accordance with Article 73.2.3 of the Code.

The syntypes preserved by Miyosi are presumed to be lost because no such specimens were found in the remnants of his collection (see Jonishi and Nakano 2022). However, there is no doubt about the identity of this species because *C. striatus* is the only *Cryptops* species with a transverse suture on tergite 1, known in specimens from the type locality. Since the nomenclatural status of this species does not meet the conditions of Article 75.1 of the Code, a neotype is not designated for *C. striatus* in this study.

Material examined. JAPAN – **Shizuoka Prefecture** • 1 ♂, 9.4 mm (KUZ Z6496); Izu City; 34°50.13'N, 138°55.78'E; approx. 590 m alt.; 2 May 2022 • 2 ♂, 9.3 mm (KUZ Z6497) and 9.7 mm (KUZ Z6498), and 1 ♀, 10.7 mm (KUZ Z6499); Susono City, Suyama, near Jurigihyoketsu Cave; 35°15.92'N, 138°47.95'E; approx. 910 m alt.; 2 Jun. 2022 – **Chiba Prefecture** • 1 ♀, 9.3 mm (KUZ Z6500) and 1 ♂, 7.8 mm (KUZ Z6501); Kamogawa City, Kiyosumi; 35°9.72'N, 140°9.6'E; approx. 180 m alt.; 1 Feb. 2023 – **Tokyo** • 1 specimen, 6 mm (KUZ Z6502); Izu-Oshima Island, Senzu; 34°44.46'N, 139°26.44'E; approx. 200 m alt.; 11 Feb. 2023.

Diagnosis. Cephalic plate with short anterolateral and paramedian sutures, posterior margin overlapping tergite 1. Clypeus with a few setae in irregular row and 6–7 prelabral setae. Forcipular coxosternite with anterior margin slightly bilobed or almost straight with shallow median diastema, with single seta behind anterior margin on each side. Tergite 1 with V-shaped anterior transverse suture and inverted Y-shaped posterior suture with pointed corners. Sternites 2–19 with cruciform sulci, of which transverse ones sclerotized. Legs 1–19 with undivided tarsus; legs with single accessory spine longer than 1/2 length of pretarsus. Coxopleural pore field occupying approx. 20%–30% of surface of coxopleuron, composed of 13–24 pores, with narrow pore-free area posteriorly. Saw teeth on ultimate leg 0 + 4–6 + 3–4.

Description of adults (variations given in parentheses). Body length 9.3–10.7 mm in 80% ethanol. Color in life and in ethanol brownish orange on head, ochre or brownish yellow on other segments, legs and ultimate legs (Fig. 12a, b).

Antenna 1.5–1.8 mm, approx. 2.2–2.4× as long as cephalic plate, composed of 17 articles (Fig. 12b). Three basal articles scattered with robust setae of various length and minute setae; 4th and subsequent articles with sparse long setae forming a ring around basal part, and short setae; short setae denser on 5th or 6th and subsequent articles (Fig. 13a, b).

Cephalic plate longer than wide (0.65–0.75 mm × 0.6–0.7 mm), with sparse fine setae and minute setae; short anterolateral and paramedian sutures present near anterior and posterior margins, respectively; posterior margin overlapping tergite 1 (Fig. 12b, c). Clypeus with a few large and minute setae in irregular row, and 6–7 prelabral setae (Fig. 13c, d). Labrum with rounded side-pieces and single mid-piece tooth.

Second maxillae with semi-transparent dorsal brush approx. as long as pretarsus; pretarsus apically hooked, ventral projection present.

Forcipular coxosternite with sparse short setae; anterior margin slightly

rounded or almost straight, divided by shallow median diastema, with single seta behind anterior margin on each side (one or a few minute marginal setae present in KUZ Z6497 and Z6500) (Fig. 12d, 13d). Tarsungulum slightly shorter than forcipular trochanteroprefemur (Fig. 12d). Calyx of venom gland ovoid, located between tibia and tarsungulum.

Tergites covered with sparse fine setae and minute setae (Fig. 12b). Tergite 1 with V-shaped anterior transverse suture and inverted Y-shaped posterior suture with pointed corners, lateral diagonal sutures sometimes diverging anteriorly from corners of posterior suture (Fig. 12b, c); tergite 2 with short paramedian sutures on posterior half; paramedian sutures complete on tergites 3–20; lateral crescentic sulci present on tergites 3–19 or 20; oblique sutures present on anterior tergites; median keel delimited by paired shallow longitudinal sulci present on mid body tergites (Fig. 12b). Tergite of ultimate leg-bearing segment with posterior margin subtriangular; slight median depression present near posterior margin.

Sternites with sparse setae near anterior and posterior margins; median longitudinal sulcus present on sternites 1 (2)–19 (20), sclerotized transverse sulcus present on sternites 2–19 (Fig. 14a). Sternite of ultimate leg-bearing segment with sides converging posteriorly, posterior margin almost straight or weakly convex (Fig. 14b).

Spiracles ovoid, largest on leg-bearing segment 3 (Fig. 14c).

Legs finely setose on all articles; leg 20 of male with dense short setae on ventral surface of prefemur, femur and tibia (Fig. 14e, f). Legs 1–19 with undivided tarsus; tarsus of leg 20 flexed; all legs with single accessory spine longer than 1/2 length of pretarsus (approx. 1/2 length of pretarsus on some legs) (Fig. 14e–g).

Coxopleural pore field occupying approx. 20%–30% of surface of coxopleuron, composed of 13–24 pores of various size; narrow pore-free area present posteriorly and posteroventrally (Fig. 14d). Coxopleural pore field with a few short setae; dorsal area with 3–4 enlarged setae (and 1–2 short setae present in KUZ Z6497 and Z6498), posterior margin with a few enlarged setae and minute ones; 1 enlarged seta present between pore field and posterior margin (Fig. 14d).

Ultimate leg approx. 2.47–2.85 mm (prefemur, 0.69–0.77 mm; femur, 0.55–0.7 mm; tibia, 0.37–0.46 mm; tarsus 1, 0.25–0.31 mm; tarsus 2, 0.43–0.48 mm; pretarsus, 0.1–0.13 mm). Fine setae present on all articles; robust, “lanceolate” (sensu Lewis et al. 2005) setae present on lateral, ventral and medial surfaces of prefemur, and ventral and medial surfaces of femur (prefemur with longitudinal glabrous area in KUZ Z6500) (Fig. 13e, f). Tibia and tarsus 1, respectively, with a pair of short, “tubercle-like” (sensu Lewis 2009) spinous processes dorsodistally (Fig. 13e, f). Femur lacking saw tooth;

tibia and tarsus 1 with 4–8 and 3–4 saw teeth, respectively.

Variation. Setae on anterior surface of basal antennal articles longer in females (KUZ Z6499 and Z6500; Fig. 13b) than in males (KUZ Z6496–Z6498; Fig. 13a), which may represent sexual dimorphism.

Distribution. Eastern Honshu and the Izu Islands, Japan (Takakuwa 1936, 1940; Shinohara 1949; Takano 1978b, 1980; Kuwabara 1984; Ishii 1999; Hagino 2016).

Remarks. Takakuwa (1936, 1940) provided the same description for *C. striatus* in German and Japanese, respectively. The present specimens agree with Takakuwa's descriptions except for the following features. 1) Takakuwa (1936) stated that the cephalic plate lacks sutures or sulci, while fig. 1 in Takakuwa (1936) shows a semicircular suture near the anterior margin. In our specimens, a pair of short anterolateral (not semicircular) sutures are present. Takakuwa also mentioned that “a very indistinct median longitudinal furrow” is usually present. Such a median furrow is not observed in our specimens, although a pair of short paramedian sutures are present near the posterior margin. 2) Tergal paramedian sutures are incomplete on tergite 2 and complete on tergites 3–20, whereas Takakuwa (1936, 1940) stated that the sutures are complete on tergites 2–19. Although this character is consistent in all examined specimens, the distinctness of the paramedian sutures may be variable in *C. striatus*. 3) The tibia and tarsus 1 of the ultimate leg bear minute spinous processes, although Takakuwa (1936, 1940) mentioned that the spinous process (“lateralen Endzahn” in Takakuwa [1936]) is absent. However, the processes are small and insignificant, and may have been overlooked by Takakuwa (1936, 1940). 4) Calyx of the venom gland is located between the tibia and tarsungulum, whereas Takakuwa's (1936) fig. 2 indicates that the calyx is present between the femur and tibia.

In the examined specimens, the body length is relatively small (9–10 mm in KUZ Z6496–Z6500) and the number of coxal pores (13–24) is reduced compared with those features described by Takakuwa (1936, 1940) (17 mm, with approx. 30 pores). However, the presence of spermatophores in KUZ Z6497 (body length 9.3 mm) indicates that the specimen is mature. KUZ Z6502, which is much smaller (6 mm), presumably is a juvenile.

Takakuwa (1936) compared this species with *C. micrus* Chamberlin, 1922 and stated that *C. striatus* differs in the absence of paramedian sutures on the cephalic plate, an almost straight anterior margin of the coxosternite (vs. anterior margin weakly

bilobed in *C. micrus*), the number of coxal pores (4 in *C. micrus*), and saw teeth on the tibia and tarsus of the ultimate leg. The characters of the cephalic plate (see above) and saw teeth on the ultimate leg cannot distinguish between these two species. Nonetheless, *C. striatus* is clearly distinct from *C. micrus* in the presence of an inverted Y-shaped suture on tergite 1 (vs. “paired longitudinal sulci” in *C. micrus*), absence of a saw tooth on ultimate femur, and absence of a dorsal groove on the ultimate leg (Chamberlin 1922; Attems 1930).

The inverted Y-shaped suture on tergite 1, which is characteristic of *C. striatus*, is shared by several *Cryptops* species, including *C. trisulcatus* Brölemann, 1902 and *C. legagus* Edgecombe et al., 2020. Among them, *C. heathi* Chamberlin, 1914 and *C. floridanus* Chamberlin, 1925 are similar to *C. striatus* in the presence of diagonal sutures diverging from the corners of the Y-shaped suture. However, *C. striatus* can be distinguished from *C. heathi* by the absence of large marginal setae on the coxosternite (vs. 3 + 3 marginal setae present in *C. heathi*), coxopleuron with more than 10 pores and a narrow pore-free area (vs. a few pores and wide pore-free strip), and absence of a longitudinal groove on the ultimate leg (vs. dorsal longitudinal groove present) (Chamberlin 1914; Attems 1930). *Cryptops striatus* also differs from *C. floridanus* in the long accessory spine on the legs (vs. minute accessory spines in *C. floridanus*), the ultimate leg with the prefemur longer than femur (vs. prefemur significantly shorter than femur), and absence of femoral saw teeth (vs. 1 or 2 saw tooth/teeth present) (Chamberlin 1925; Crabill 1969; Shelley 2002).

***Cryptops dupliporus* sp. nov.**

urn:lsid:zoobank.org:act:3AC882D4-F6FF-4E9E-8203-0C6BAF28A8CA

Fig. 7, 15–17

Suggested Japanese name. Yasoana-menashimukade

Material examined. Holotype: ♀, 17.8 mm (KUZ Z6484); JAPAN: Tokyo, Minato District, Shiba Park; 35°39.53'N, 139°44.81'E; approx. 20 m alt.; 27 Nov. 2024; Taiga Kato leg.

Diagnosis. Cephalic plate with anterolateral and paramedian sutures almost reduced, posterior margin overlapped by tergite 1. Clypeus with 2 + 1 + 2 + 2 and 10 prelabral setae. Forcipular coxosternite with anterior margin almost straight, with 2 or 3 large submarginal setae on each side. Tergite 1 lacking sutures. Sternites 2–19 with equally

developed cruciform sulci. Legs 1–19 with undivided tarsus, all legs with single accessory spine approx. 1/2 length of pretarsus. Coxopleural pore field elongate oval, composed of approx. 80 pores occupying approx. 35% of surface of coxopleuron, with wide pore-free area posteriorly. Saw teeth on ultimate leg 0 + 7 + 4, of which distal one on tibia bifid.

Description. Body length approx. 17.8 mm in 80% ethanol. Color in ethanol brownish orange on head and ultimate leg-bearing segments, brownish yellow on other segments, legs, and ultimate legs (Fig. 15a).

Antenna 3.4 mm in length, approx. $3.8 \times$ as long as cephalic plate, composed of 17 articles. Basalmost article with a ring of long setae around distal part of article, and a few long setae and short setae scattered near basal part; article 2 with two rings of long setae around basal and distal parts, respectively, and sparse long setae and short setae; article 3 with long setae forming a ring around basal part and scattered on distal part, and dense short setae near distal part; articles 4–17 with long setae in a whorl around basal part and dense short setae; short setae denser on 4th and subsequent articles (Fig. 15c, d, 16a).

Cephalic plate slightly longer than wide (approx. $0.9 \text{ mm} \times 0.85 \text{ mm}$), its surface sparsely covered with fine setae, anterolateral and paramedian sutures almost reduced; posterior margin overlapped by tergite 1 (Fig. 15c). Clypeus with $2 + 1 + 2 + 2$ and several minute setae in irregular row, and 10 prelabral setae (Fig. 16b). Labrum with rounded side-pieces and single mid-piece tooth.

Second maxillae with semi-transparent, dense dorsal brush shorter than pretarsus; pretarsus apically hooked, accompanied by ventral projection.

Forcipular coxosternite covered with short setae and minute setae; anterior margin almost straight with weak median diastema, with 2 or 3 long and 2 short submarginal setae on each side (Fig. 15d, 16b). Tarsungulum almost as long as forcipular trochanteroprefemur (Fig. 15d). Calyx of venom gland ovoid, located in anterolateral part of trochanteroprefemur.

Tergites covered with sparse fine setae; tergite 1 with short, almost reduced paramedian sutures on posterior margin; tergite 2 with paramedian sutures on posterior half; tergites 3–20 with complete paramedian sutures and lateral crescentic sulci, and weak median keel delimited by paired shallow sulci (Fig. 15b). Tergite of ultimate leg-bearing segment with posterior margin subtriangular; median depression present on posterior half.

Sternites moderately setose; sternite 1 with longitudinal sulcus and shallow

transverse sulcus; sternites 2–20 with cruciform sulci, of which longitudinal and transverse ones equally developed (Fig. 17a). Sternite of ultimate leg-bearing segment with lateral margins broadly rounded, posterior margin almost straight (Fig. 17b).

Spiracles ovoid or almost circular, largest on leg-bearing segment 3 (Fig. 17c, d).

Legs finely setose on all articles; legs 1–19 with undivided tarsus; tarsus of leg 20 faintly divided but not flexed; all legs with single accessory spine approx. 1/2 length of pretarsus (Fig. 17f, g).

Coxopleural pore filed on left coxopleuron elongate oval, occupying approx. 35% of surface of coxopleuron, composed of 78 pores of various size; wide pore-free area present posteriorly and posteroventrally (Fig. 17e). Coxopleural pore filed with a few short robust setae and minute setae; dorsal region and posterior margin, respectively, with a few enlarged setae and minute ones; 3 enlarged setae and minute seta present between pore field and posterior margin (Fig. 17e).

Ultimate leg approx. 3.75 mm (prefemur, 0.98 mm; femur, 0.9 mm; tibia, 0.59 mm; tarsus 1, 0.46 mm; tarsus 2, 0.71 mm; pretarsus, 0.16 mm). All articles with fine setae; enlarged setae present on prefemur (laterally, ventrally and medially) and femur (ventrally and medially), thicker on medial surfaces of both articles (“lanceolate” sensu Lewis et al. 2005) (Fig. 16c). Tibia and tarsus 1, respectively, with a pair of short (“tubercle-like” sensu Lewis 2009) spinous processes dorsodistally (Fig. 16c). Femur lacking saw tooth, tibia with 7 and tarsus 1 with 4 saw teeth; distal saw tooth on tibia bifid (Fig. 16c).

Etymology. The specific name is derived from the Latin compound noun “duplic-” (duplex; double) and “porus” (pores), referring to the high number of coxal pores, which is approximately twice the number typically found on its closest relatives.

Distribution. Known from the type locality and from Keelung (Jilóng) in northern Taiwan (submitted to INSD as “*C. japonicus*”; AB675008). *Cryptops dupliporus* sp. nov. is recorded only from anthropogenic habitats and seems to have been artificially introduced to these localities; its natural habitats and distribution are unknown.

Remarks. This species is closely related to *C. doriae* and *C. japonicus* (see Results). However, *C. dupliporus* sp. nov. can be distinguished from these species by the following features: the presence of 78 coxal pores (vs. up to approx. 40 pores in *C. japonicus* and *C. doriae* when comparing individuals of the same body length) (see

Discussion), undivided tarsi (vs. tarsi mostly divided in *C. doriae*) and single long accessory spine on the pretarsus (vs. two short spines in *C. doriae*) of the leg, and absence of a femoral saw tooth/teeth on the ultimate leg (vs. saw tooth/teeth mostly present in *C. japonicus* and *C. doriae*) (Lewis 2013). The new species further differs from *C. japonicus* in its robust, “lanceolate” setae (sensu Lewis et al. 2005) on the ultimate leg (vs. setae much thinner in *C. japonicus*).

The new species resembles *C. niuensis* Chamberlin, 1920, although the phylogenetic tree does not indicate an especially close affinity. *Cryptops dupliporus* sp. nov. differs from *C. niuensis* in the presence of a median depression on the ultimate tergite (vs. depression absent), the number of coxal pores (approx. 30 in *C. niuensis*), and the absence of a saw tooth on the ultimate femur (vs. saw tooth present) (Lewis 2013, 2016).

Cryptops dupliporus sp. nov. shares several diagnostic characters with *C. nigropictus*, but can be distinguished by the number of coxal pores (up to 31 in *C. nigropictus*) and the presence of spinous processes on the tibia and tarsus 1 of the ultimate leg (vs. process absent) (e.g., Takakuwa 1936, 1940; Chao and Chang 2008; Lewis 2011). The new species also differs from Taiwanese specimens of *C. nigropictus* in the distribution of antennal setae (basal 4 articles with sparse, long setae in *C. nigropictus*) (Takakuwa 1936, 1940; Chao and Chang 2008) and the absence of dense setae on the ventral surface of leg 20 (vs. setae present) (Takakuwa 1936, 1940). However, the former character may be variable in *C. nigropictus* (see description of the synonymous *C. basilewskyi* Matic & Darabantu, 1977 in Lewis [2011]), and the latter character was described in the original description based on just two individuals (Takakuwa 1936) and is subject to sexual dimorphism in some species (Lewis 2013) (see descriptions of *C. japonicus* and *C. striatus*, above).

Discussion

Taxonomic assessment of Japanese *Cryptops*

The distinctness of three previously known species, namely *C. japonicus*, *C. navis*, and *C. striatus*, is strongly supported by both morphological features and molecular phylogeny. The phylogenetic analyses detected three additional species, one of which is described as *C. dupliporus* sp. nov. in this study. *Cryptops* spp. 1 and 2, both collected from the Ryukyu Islands, are distinct from their congeners and presumably represent undescribed species. However, since we have only a small number of juveniles and a damaged specimen, we refrain from formally describing them as new species.

Aside from the species recognized in this study, Chamberlin and Wang (1952) recorded *C. haasei* Attems, 1903 from “Japan, without more detailed locality”. As this record lacks detailed taxonomic accounts, and *C. haasei* has not been recorded since Chamberlin and Wang (1952), the occurrence of this species in Japan is not considered here.

In addition, *C. nigropictus* has been recorded from Okinawa Island in the Ryukyu Islands (Ômine and Itô 1998). However, the reliability of this record cannot be evaluated because those authors did not provide a taxonomic account nor clarify the deposition of their specimens. Considering that *C. nigropictus* has not been recorded from the Ryukyu Islands since Ômine and Itô (1998), the distribution of this species should be reexamined. Ômine (1969) and Ômine and Itô (1998) also stated that *C. striatus* is found on Okinawa Island. In the current study, however, *C. striatus* was obtained only from eastern Japan and not found in the Ryukyu Islands, suggesting that the taxonomic identity of *C. striatus* sensu Ômine and Itô (1998) should also be reexamined.

The molecular phylogeny shows deep genetic divergence within *C. japonicus* (Fig. 2) and indicates that *C. japonicus* consists of at least three clades. The genetic divergence among these clades (14.8%–19.3% in COI) roughly corresponds to the interspecific distances observed in European *Cryptops* species (13.4%–21.1%: Wesener et al. 2016). Furthermore, the maximum divergence within each clade (14.6%–15.6%) exceeds the barcoding gap (up to 11.3%) observed in Wesener et al. (2016). Therefore, it is highly possible that each clade represents a species of its own or should be further split into multiple species. In this study, however, all specimens are recognized as *C. japonicus* because the analysis failed to depict a well-resolved topology. For example, the phylogenetic position of KUZ Z6457, which is nearest to the type locality of *C. japonicus* (locality number J6 in Fig. 1), is unresolved, which makes it difficult to define species boundaries within *C. japonicus*. In addition, no significant morphological difference was observed among populations, although the pretarsal accessory spine is consistently short and the ultimate femur lacks a saw tooth in specimens from Okinawa Island (see above), which correspond to clade 3. The length of pretarsal accessory spine alone has not been utilized to distinguish species (Lewis 2016), and the presence/absence of femoral saw tooth is variable in *C. japonicus* specimens from other localities in Japan. However, these characters may be useful to differentiate species in combination with a well-resolved phylogenetic tree.

Both morphology and molecular phylogeny indicate that *C. dupliporus* sp. nov. is closely related to *C. doriae* and *C. japonicus*. The new species is especially similar to

C. japonicus, from which it differs in the number of coxal pores, the thickness of setae on the ultimate prefemur and femur, and absence of a saw tooth/teeth on the ultimate femur.

The number of coxal pores is subject to large intraspecific variation in this genus (e.g., Lewis 1999, 2013; Schileyko 2008; Edgecombe et al. 2020) and is regarded as a character of “little or no value” (Lewis 2009). In some cases, however, this character can be used to differentiate closely related species (Lewis 2013; Vahtera et al. 2020). In *C. japonicus*, the number of pores increases roughly in proportion to the body length (as observed in *C. dilagus* Archey, 1921; Archey 1924, and in *C. doriae* and *C. nepalensis* Lewis, 1999; Lewis 1999), with the maximum number being approx. 40 (Fig. 7). The presence of 78 pores in *C. dupiporus* sp. nov. is obviously out of this typical range. Additionally, given the results from phylogenetic analysis, it is reasonable to consider the number of pores as a diagnostic character to differentiate these two species, not intraspecific variation within *C. japonicus*. The large number of coxal pores, as well as other characters such as the single long accessory spine of legs, also allow *C. dupliporus* sp. nov. to be distinguished from other *C. doriae*-like species, including *C. nepalensis*, *C. tahitianus*, and species of the former subgenus *Trichocryptops* Verhoeff, 1937 (see Lewis 2016) (Table S3).

Cryptops dupliporus sp. nov. also differs from *C. japonicus* in the length, density and arrangement of antennal setae (Fig. 5a, 16a). However, such differences have been rarely utilized as diagnostic characters in *Cryptops*, and it is difficult to evaluate this difference between the species. Even so, the character of antennal setae may be useful to differentiate species if it is further explored in future taxonomic practices (see Lewis 2009).

Subgenus and species group-level classifications

The genus *Cryptops* is classified into four subgenera: the nominotypical subgenus *Cryptops* Leach, 1814, and *Trigonocryptops* Verhoeff, 1906, *Haplocryptops* Verhoeff, 1934, and *Paracryptops* Pocock, 1891. The most speciose subgenus *Cryptops* comprises species with an anterior transverse suture on tergite 1 (the *anomalans* group sensu Lewis 2013) and those without the suture. Lewis (2011, 2013) divided the latter into two groups: the *hortensis* group, which lacks a saw tooth/saw teeth on the ultimate femur, and the *doriae* group, which bears at least one femoral saw tooth. The species examined in this study share the diagnostic characters of the nominotypical subgenus provided in Schileyko et al. (2020). Of these, *C. striatus* is morphologically assigned to the *anomalans* group; *C. japonicus* and *C. navis* are the *doriae* group species because

they usually bear a saw tooth/teeth on the ultimate femur; and *C. dupliporus* sp. nov., which lacks a femoral saw tooth, is assigned to the *hortensis* group.

In the phylogenetic tree, however, the subgenus *Cryptops* is non-monophyletic with respect to *Trigonocryptops* and *Paracryptops*, as already indicated in previous studies (Murienne et al. 2011; Edgecombe et al. 2012, 2020; Vahtera et al. 2012, 2013). Our results are also consistent with Vahtera et al. (2013) and Edgecombe et al. (2020) in that the members of the *anomalans*, *hortensis*, and *doriae* groups, respectively, are not monophyletic.

The “Holarctic” lineage, which includes the type species *C. hortensis* and the Japanese *C. striatus*, corresponds to *Cryptops* sensu stricto. Although several “Laurasian” species such as *C. japonicus* share the diagnostic features of *Cryptops* sensu stricto, the subgeneric classification is not employed in this study considering the polyphyletic nature of this subgenus. The concept of the nominotypical subgenus, presumably defined by shared plesiomorphic characters (Murienne et al. 2011; Vahtera et al. 2012), needs to be revised based on phylogeny and synapomorphic characters.

Historical biogeographical implications

The estimated divergence ages of the “Holarctic”, “Gondwanan”, and “Laurasian” lineages are younger than the breakup of Pangea, which had been completed by the early Cretaceous period (Matthews et al. 2016). This implies that divergence into these lineages was not related to continental vicariance. Given that Gondwana was already split into multiple landmasses by the Late Cretaceous (Matthews et al. 2016; Müller et al. 2016), the divergence between the “Gondwanan” and “Laurasian” lineages and subsequent diversification may have been associated with ancient long-distance dispersal, as speculated for other terrestrial arthropods, such as carabid beetles (Andujar et al. 2016), zalmoxid and triaenonychid harvestmen (Sharma and Giribet 2012; Derkarabetian et al. 2021), and scutigeromorph centipedes (Manivannan et al. 2024).

The “Holarctic” lineage is distributed in Europe, southeastern North America, and eastern Honshu in Japan. Given that most of the “Holarctic” species are known from Europe, one can argue that *C. striatus* was artificially introduced to Japan. However, the divergence of *C. striatus* from its sister group (31.61–65.18 Mya) and genetic diversity within *C. striatus* are sufficient to negate human-mediated dispersal. Similar distributions in the Northern Hemisphere are also known in the geophilomorph genus *Dicellogophilus* Cook, 1896 (found in central Europe, southwestern North America, and Japan) (Bonato et al. 2010b; Tsukamoto and Eguchi 2024) and the scolopendromorph family Plutonidiumidae Bollman 1893, especially *Theatops* Newport,

1844 (Mediterranean region, southern North America, and central China) (Shelley 2002; Di et al. 2010). Such highly disjunct ranges are presumed to be relics of once more-widespread distributions (Bonato et al. 2003, 2010b; Di et al. 2010; Bonato and Zapparoli 2011; Edgecombe et al. 2023). Edgecombe et al. (2023) hypothesized that the range of Plutonidium was influenced by the transition from the Eocene to the Oligocene, when the warm forest habitat, which *Theatops* species inhabit, was fragmented by climate changes and glaciation. The estimated divergence age within “Holarctic” *Cryptops* (31.61–65.18 Mya) overlaps with the Paleocene–Eocene thermal maximum, when a rapid rise in global temperatures caused major changes in flora and fauna (Huber and Caballero 2011). Thus, one hypothesis is that the ancestors of this lineage spread across the Holarctic and diversified during the early Eocene hyperthermals, and thereafter their ranges became fragmented during or after the transition to the Oligocene. However, the “Holarctic” species are not restricted to especially warm habitats (e.g., Shelley 2002; Wesener et al. 2016; Iorio and Jacquemin 2025), and hence it is uncertain whether their current distribution was shaped by global cooling.

Our analysis based on the “total dataset” failed to resolve the phylogenetic position of the North American *C. leucopodus*, for which only COI sequences were available (Supplementary Fig. S1). Thus, the dispersal process of the “Holarctic” ancestral populations remains unclear. Additional sequence data of North American species will be required to reveal the evolutionary history of this lineage. Considering that disjunct distributions across the Northern Hemisphere are observed in other centipede taxa (see above) as well as in harvestmen of the family Sironidae (Giribet 2000; Boyer et al. 2007; Giribet et al. 2017; Derkarabetian et al. 2024) and the superfamily Travunioidea (Kury and Mendes 2007; Derkarabetian et al. 2018), biogeographic studies of the “Holarctic” *Cryptops* may help us understand a common process in the formation of the Holarctic soil fauna.

The “Laurasian” lineage comprises species from former Laurasian landmasses (e.g., *C. trisulcatus* in Europe, *C. japonicus* in the Japanese Archipelago, and *C. doriae* and *C. indicus* in continental Southeast Asia), while several species from oceanic islands (e.g., *C. niuensis* from Fiji, and “*C. japonicus*” from Itu Aba Island [see above]) are nested within this lineage. Although the analyses failed to reconstruct robust basal relationships of these species, the topology implies multiple colonization from the Laurasian landmass to oceanic islands.

Among them, three insular species comprise a monophyletic group: *C. niuensis*, distributed in South Pacific oceanic islands; *C. navis*, widely distributed in

Taiwan and the Ryukyu Islands, including two oceanic islands (Minamidaito and Miyako islands; locality numbers N8 and N9); and *Cryptops* sp. 1, in Taiwan and the southern Ryukyus. Notably, all sequenced specimens of *C. navis* share almost identical haplotypes, with a few single-base substitutions in the COI and 16S regions. The low intraspecific divergence indicates rampant gene flow among populations, presumably due to dispersal by an oceanic current. Alternatively, human introduction from a single source population is also possible, but oversea dispersal is still plausible, as *C. navis* inhabits a wide range of habitats including those near the seashore (see collecting localities of *C. navis* in this study and in Jonishi and Nakano [2020]). Given that this species was originally described from Singapore (Chamberlin 1930), *C. navis* may be widespread in coastal habitats from the Ryukyu Islands to Southeast Asia. Extensive faunal surveys and future ecological (life history), physiological (tolerance to submersion in water and salinity), and population genetic studies will help reveal the dispersal abilities and population dynamics of this species.

By contrast, *Cryptops* sp. 1, which is a sister taxon of *C. navis*, shows deep genetic divergence among populations (Fig. 2; Supplementary Fig. S1), suggesting that dispersal ability of this species is much lower than that of *C. navis*. The genetic diversity within *C. niuensis* in Fiji and Vanuatu is also significant, with the estimated divergence age ca. 10 Mya (Murienne et al. 2011). A possible hypothesis to explain the modern distribution and genetic structure is that their ancestor was a rafting species widespread across the western and southern Pacific Ocean, and the ancestors of *Cryptops* sp. 1 and *C. niuensis*, respectively, lost vagility as they adapted to inland habitat, whereas *C. navis* maintained its dispersal ability. A similar situation, in which endemic species are nested within widespread seafaring superspecies, is observed in scincid lizards of the genus *Emoia* in the western Pacific islands (Richmond et al. 2021). Previous authors pointed out that an ecological shift from littoral to inland forest habitat has occurred in the endemic species, suggesting that *Emoia* species might be in the early stages of the taxon cycle (Wilson 1959, 1961). In *Cryptops*, however, no significant habitat difference was observed among species; for instance, *C. navis* was collected from a wide variety of habitats including mountain forests and coast, and *Cryptops* sp. 1 was also collected from habitats near the seashore. Therefore, the mechanism underlying the transition from widespread to local endemic species is uncertain. This group, potentially widely distributed in the western and southern Pacific islands, awaits further phylogenetic and ecological studies.

In this study, *C. japonicus* was sequenced widely from continental islands of East Asia. The analyses recovered three divergent groups within *C. japonicus* (clades 1–

3). Yet this result does not simply reflect the geographic distance among these locations, because two specimens from Tanegashima Island (J9 and J10) did not form a monophyletic group and the localities of clade 1 (J1, J8, and J10 in Fig. 1) are not geographically close to each other. A similar disjunct distribution (including eastern Honshu, Kyushu, and Tanegashima Island) is known in terrestrial slugs of the genus *Meghimatium* (Ito et al. 2023), but it is uncertain how such a distribution was formed.

Deep genetic divergence within single morphospecies has been also observed in *C. parisi*, which contains three lineages distributed across central Europe (Wesener et al. 2016). The difference in *C. japonicus*, however, is that the distribution of each population is sparse and genetic divergence within each lineage is large (up to 15.6% in COI; see above), whereas the three lineages within *C. parisi* are widely, continuously distributed and intra-lineage diversity is low (up to 1.1% in COI). These results imply that the populations of *C. japonicus* are isolated from each other and this species is much less vagile compared with *C. parisi*.

The Japanese Archipelago is estimated to have separated from the Eurasian Continent ca. 15–25 Mya (Isozaki et al. 2010; Yanai et al. 2010; Isozaki 2019). Southwest (SW) Japan, consisting of single large continental fragment, and northeast (NE) Japan, composed of multiple smaller fragments, are supposed to have separated independently from different parts of the Eurasian Continent (Otofuji et al. 1985; Otofuji 1996; Kitamura et al. 2001). This scenario is consistent with the distribution of small invertebrates, such as epigean spiders of the family Cybaeidae (Sugawara et al. 2024) and terrestrial and freshwater snails of the family Pomatiopsidae (Kameda and Kato 2011), in which two large lineages are distributed in the SW and NE regions of Japan, respectively, and the NE lineage is further split into sublineages shaped by their past geographic isolation. Our dating analysis estimated that diversification within *C. japonicus* on the Japanese mainland occurred in the Oligocene or early Miocene (95% HPD interval: 16.64–32.47 Mya). Therefore, the intraspecific divergence may be related to the formation of the Japanese Archipelago. However, the distribution of clade 1 (see above) is inconsistent with the pattern mentioned above, which makes it unclear whether the distribution of *C. japonicus* was influenced by the geotectonic events. Further taxon sampling and evolutionary analysis in a higher resolution are needed to reconstruct dispersal processes and a detailed biogeographic history of *C. japonicus*.

Our molecular phylogenetic and dating analyses showed that East Asian *Cryptops* are non-monophyletic, originating from at least three independent divergences. Different degrees of intraspecific differentiation presumably reflect the differences in their dispersal abilities and colonization histories to the East Asian

islands.

Referring to the widespread distributions of several species, Lewis (2011) speculated that *Cryptops* species can disperse over long distances by some mechanisms or that *Cryptops* is “an ancient genus with slowly evolving species”. The present results indicate that both scenarios might apply to East Asian *Cryptops*, because *C. japonicus* and *C. striatus*, respectively, are “ancient” and “relict” species of continental origins, whereas *C. navis* and related species seem to have recently radiated from Pacific islands. A similar faunal composition, including both relictual and recently colonized lineages, is also indicated in the Neotropical Geophilomorpha (Pereira et al. 1997). Overall, our analyses demonstrated an example of complex spatial and temporal processes having formed the current diversity and distribution, which may be common in members of the class Chilopoda.

Data availability. All molecular data used in this study are available from the International Nucleotide Sequence Database Collaboration (INSDC) repository (see Supplementary Table S1).

Conflicts of interest. The authors have no conflict of interest to declare.

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Figures and Tables

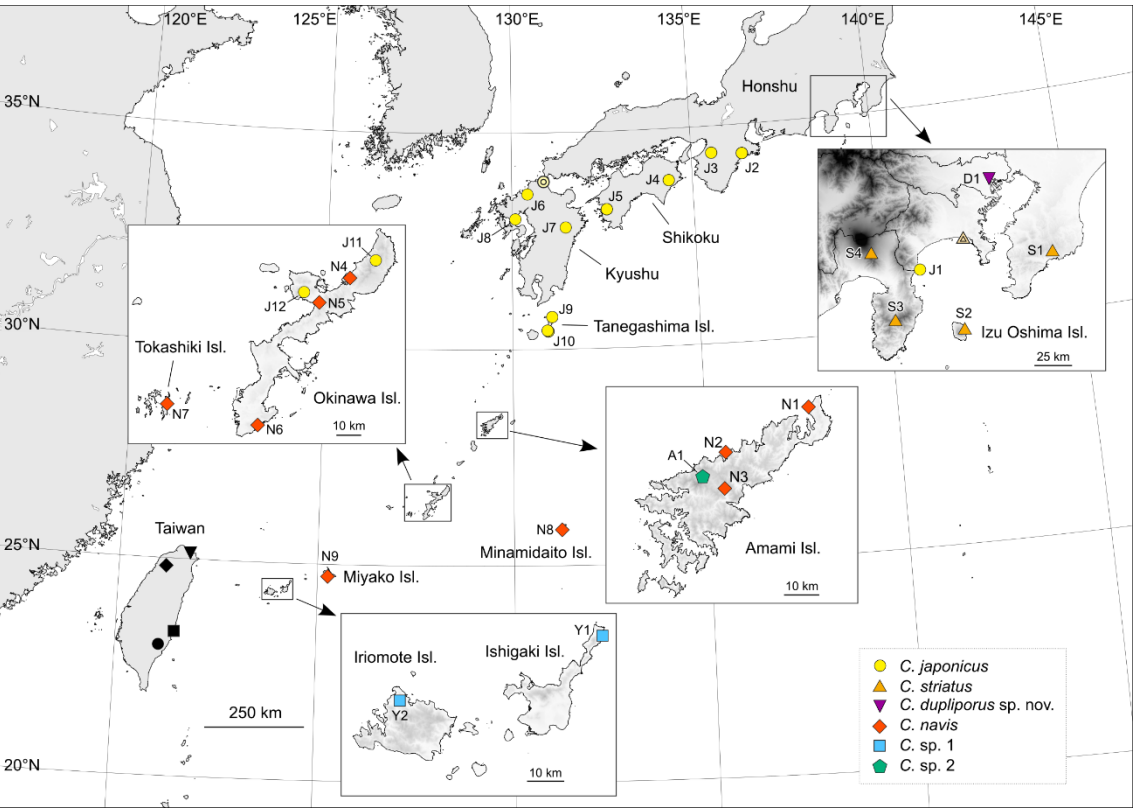


Fig. 1. Collection localities of *Cryptops* species in this study. Symbols with two lines denote the type localities of *C. japonicus* and *C. striatus*, respectively. Black symbols indicate localities of the sequence data obtained from INSD. Locality numbers (J1–J12, D1, S1–S4, N1–N9, A1 and Y1–Y2) are indicated in Fig. 2 and Supplementary Table S1.

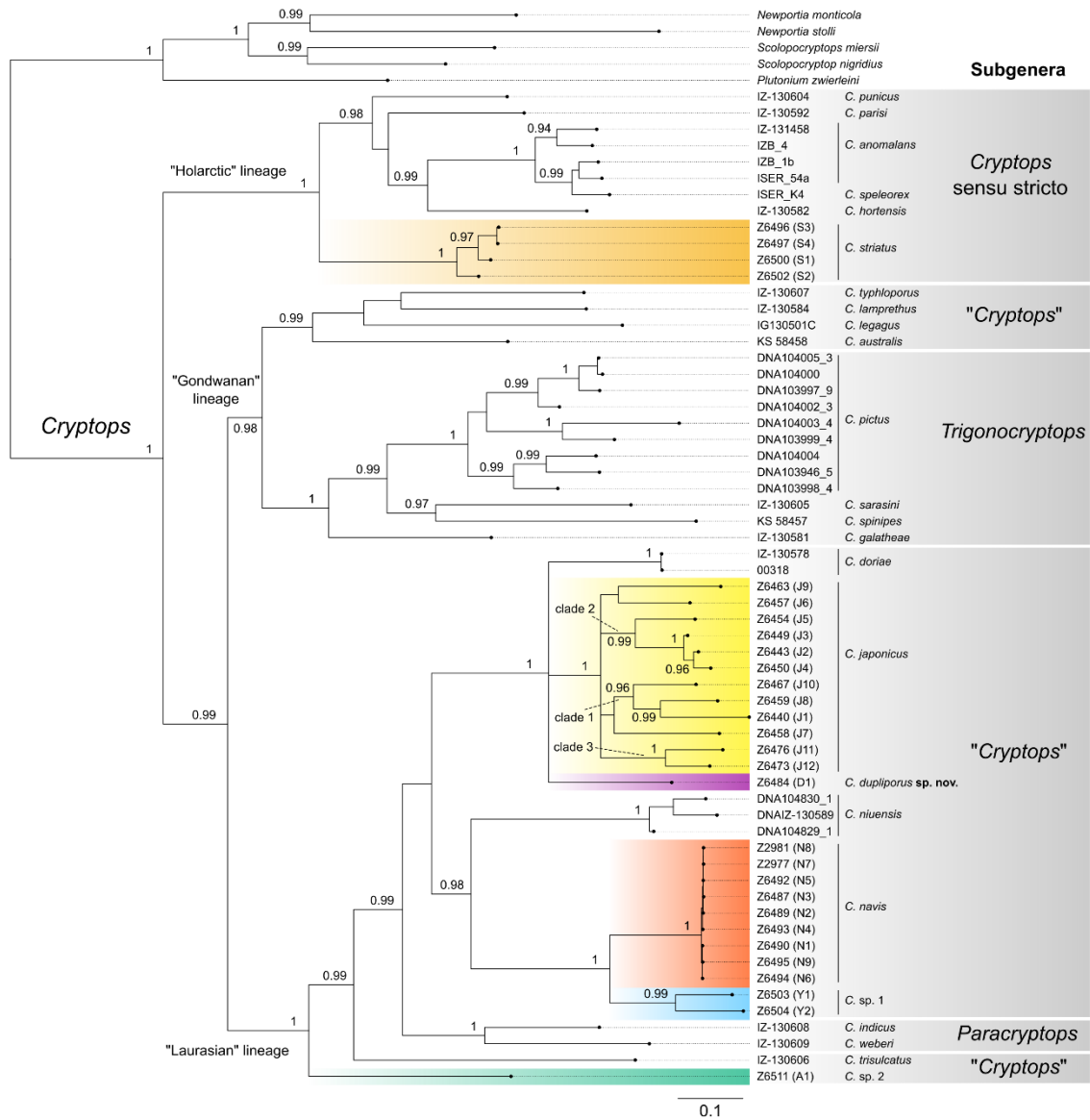


Fig. 2. Bayesian Inference tree for 3189 bp-aligned positions of the 18S, 28S, 16S and COI sequences of the “selected dataset”. Numbers on nodes indicate Bayesian posterior probabilities ≥ 0.9 . Horizontal colored bands indicate the East Asian species examined in this study. Locality numbers (J1–J12, D1, S1–S4, N1–N9, A1 and Y1–Y2) are shown in Fig. 1 and Supplementary Table S1.

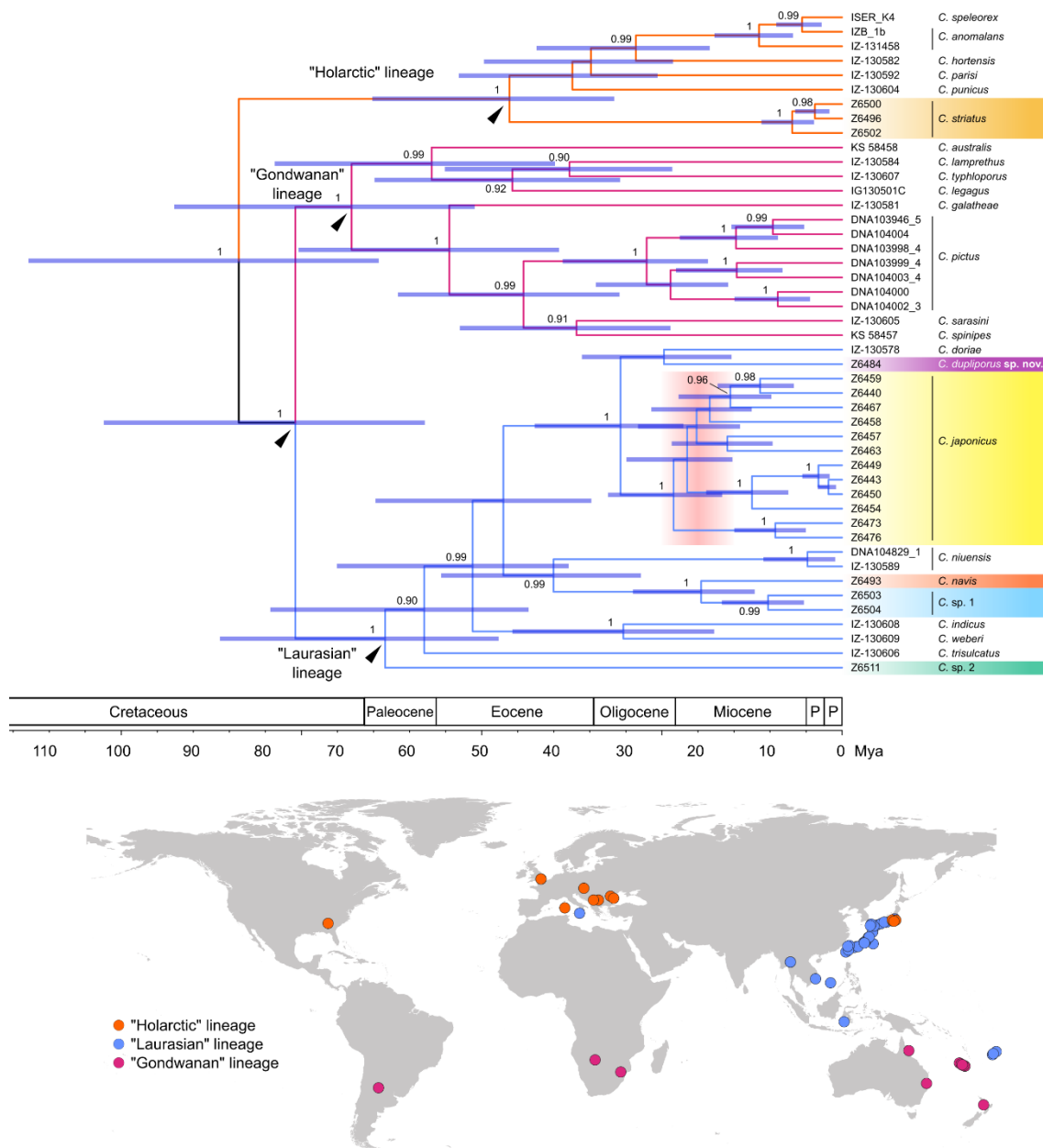


Fig. 3. Time-calibrated BI tree for 3189 bps of 18S, 28S, 16S and COI sequences (outgroups excluded) and localities of the samples. Numbers on nodes indicate Bayesian posterior probabilities ≥ 0.9 . Node bars represent 95% highest posterior density. Horizontal colored bands indicate the East Asian species examined in this study. Dates of formation of the Japanese Archipelago (15–25 Mya) are indicated by a vertical band. The monophyly of the nodes denoted by triangles was fixed during the MCMC. See Supplementary Fig. S2 for a full result.

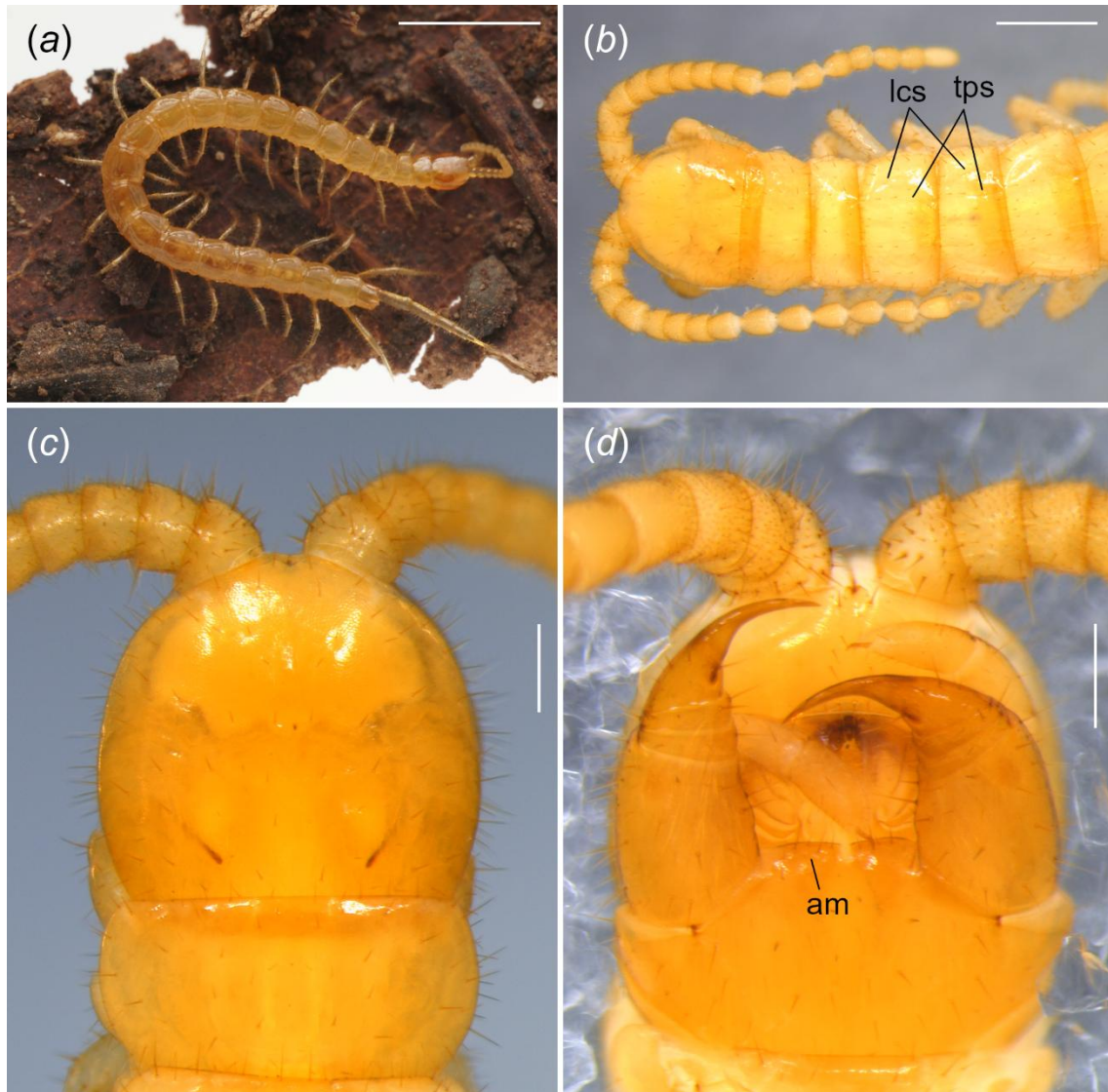


Fig. 4. *Cryptops japonicus* Takakuwa, 1934, KUZ Z6450, ♂ (a), KUZ Z6457, ♂ (b), and KUZ Z6440, ♀ (c, d). (a) Live specimen, dorsal view. (b) Head and tergites 1–5, dorsal view. (c) Cephalic plate and tergite 1, dorsal view. (d) Head, ventral view. Abbreviations: am, anterior margin of forcipular coxosternite; lcs, lateral crescentic sulcus on tergite; tps, tergal paramedian suture. Scale bars: 2.5 mm (a); 0.5 mm (b); 0.2 mm (c, d).

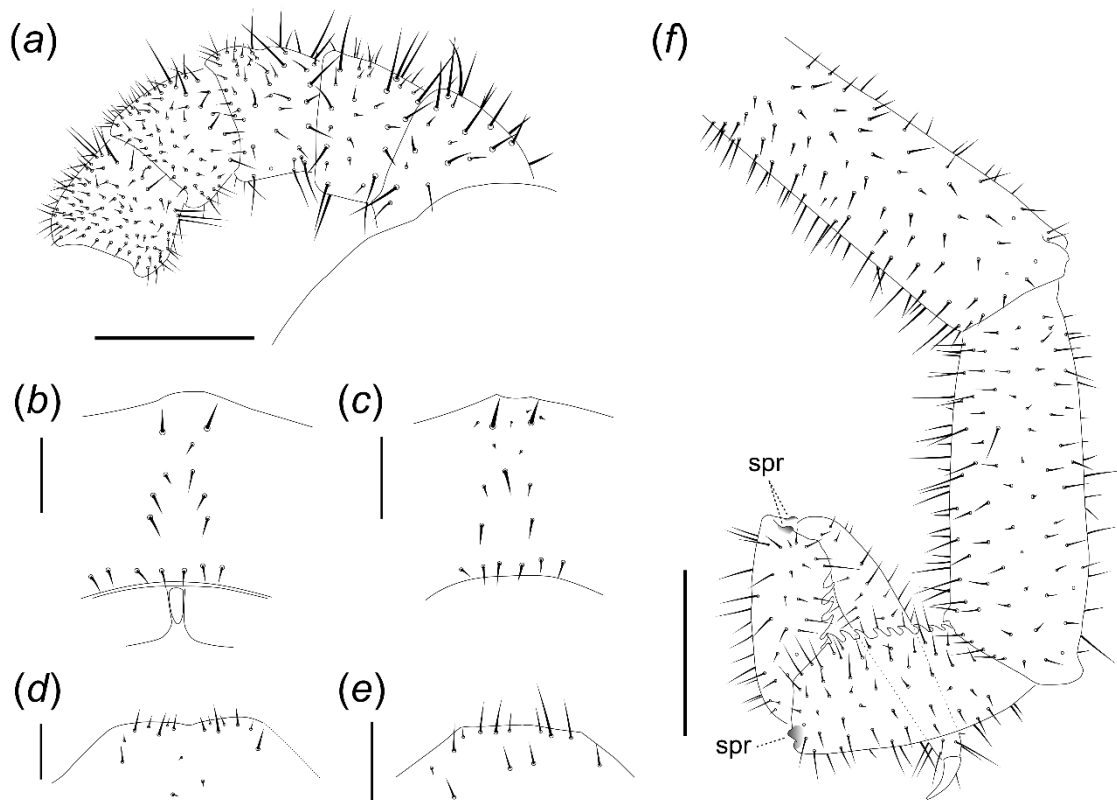


Fig. 5. *Cryptops japonicus* Takakuwa, 1934, KUZ Z6457, ♂ **(a)**, KUZ Z6440, ♀ **(b, d, f)**, KUZ Z6449, ♂ **(c)**, and KUZ Z6448, ♂ **(e)**. **(a)** Basal articles of left antenna, dorsal view. **(b, c)** Clypeal setae, ventral view. **(d, e)** Anterior margin of forcipular coxosternite, ventral view. **(f)** Left ultimate leg, lateral view. Abbreviation: spr, spinous process. Scale bars: 0.2 mm **(a)**; 0.1 mm **(b–e)**; 0.5 mm **(f)**.

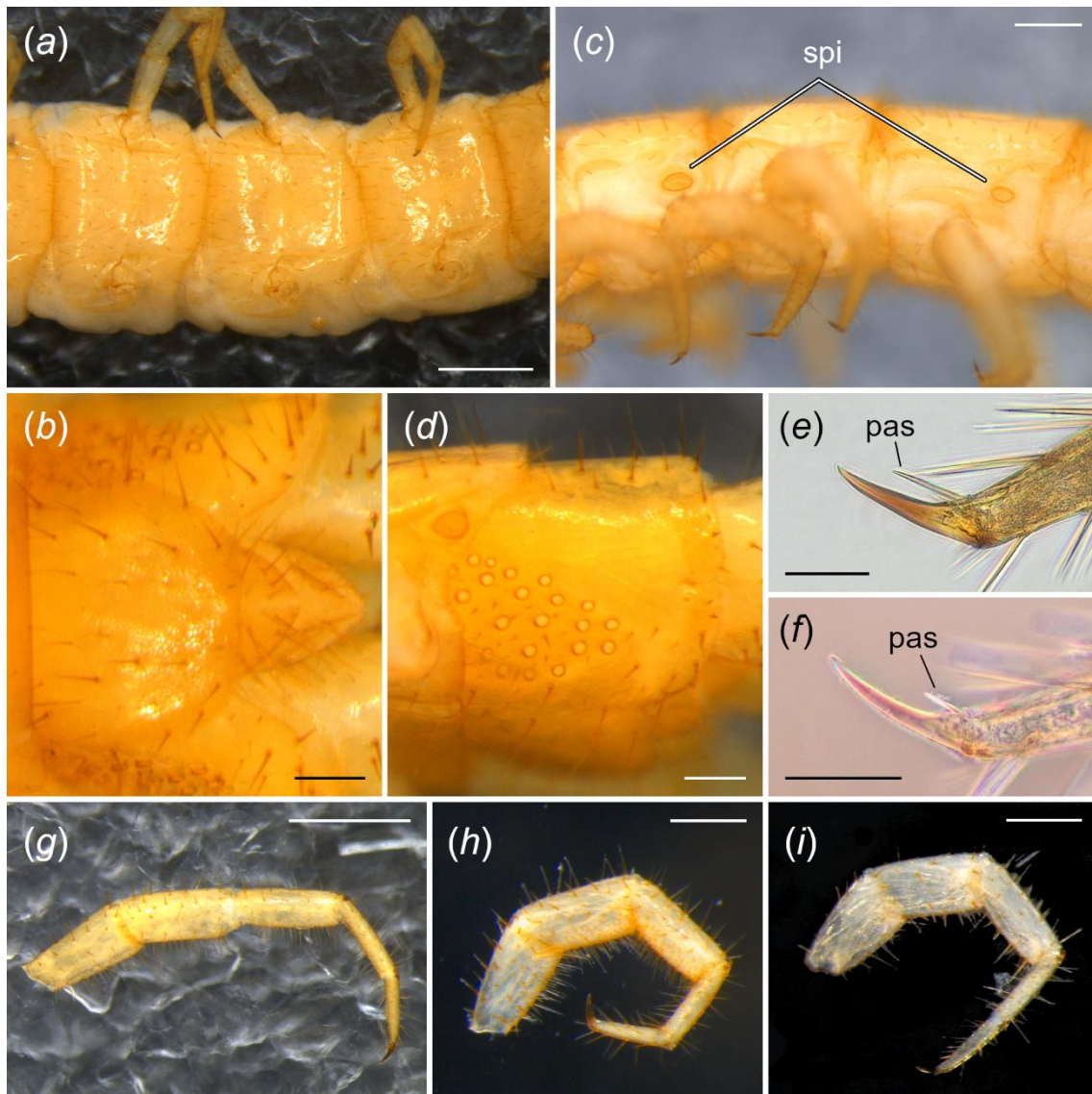


Fig. 6. *Cryptops japonicus* Takakuwa, 1934, KUZ Z6440, ♀ (**a–e, g**), KUZ Z6473 (**f, i**), and KUZ Z6448, ♂ (**h**). (**a**) Sternites 11–13, ventral view. (**b**) Sternite of ultimate leg-bearing segment, ventral view. (**c**) Left spiracles on leg-bearing segments 3 and 5, lateral view. (**d**) Left coxopleuron, lateral view. (**e**) Pretarsus and accessory spine of left leg 8, lateral view. (**f**) Pretarsus and accessory spine of left leg 11, lateral view. (**g, h**) Left leg 20, lateral view. (**i**) Right leg 20, medial view. Abbreviations: pas, pretarsal accessory spine; spi, spiracle. Scale bars: 0.5 mm (**a, g**); 0.1 mm (**b, d**); 0.2 mm (**c, h, i**); 0.05 mm (**e, f**).

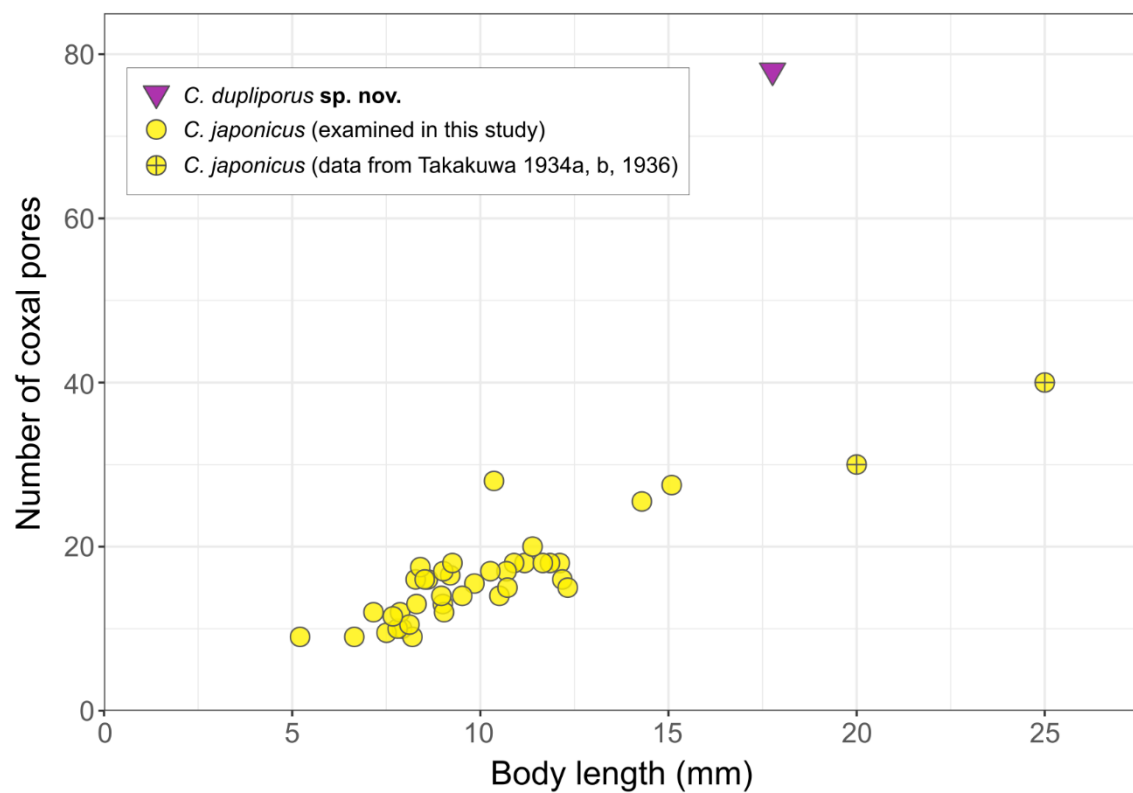


Fig. 7. Body length and the number of coxal pores in *C. japonicus* Takakuwa, 1934 and *C. dupliporus* sp. nov.

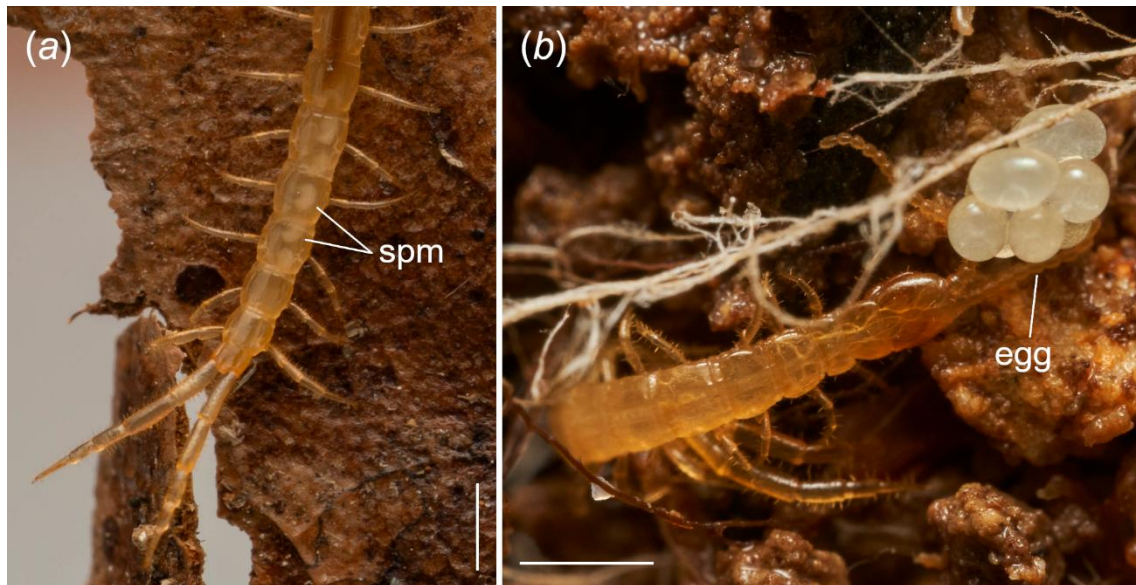


Fig. 8. *Cryptops japonicus* Takakuwa, 1934, KUZ Z6448, ♂ (a), KUZ Z6475, ♀, and Z6480, eggs (b). (a) Posterior part of male live specimen. (b) Female live specimen with eggs. Abbreviation: spm, spermatophore. Scale bars: approx. 1 mm (a, b)

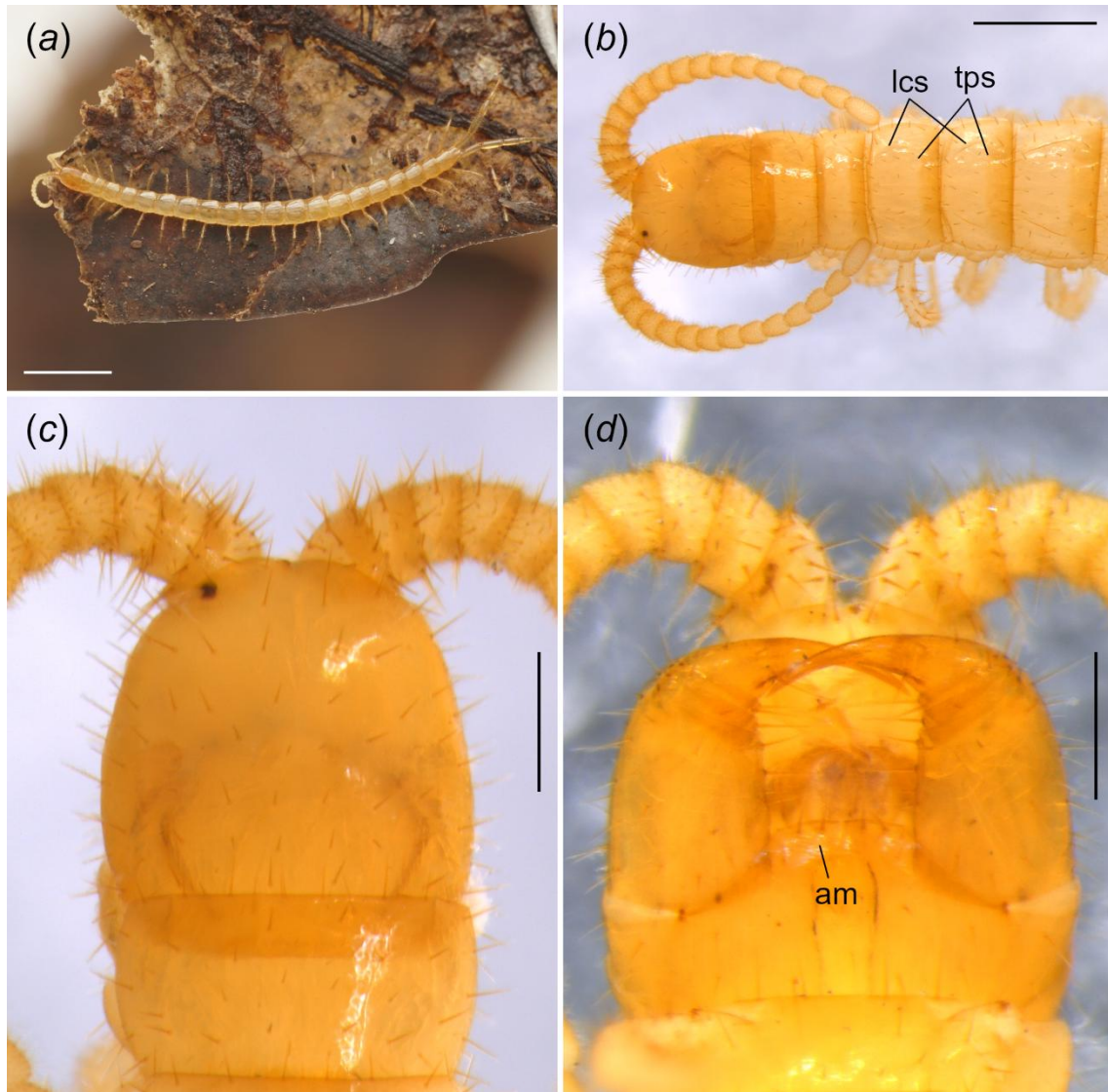


Fig. 9. *Cryptops navis* Chamberlin, 1930, KUZ Z6487, ♀ **(a)**, KUZ Z6488 **(b, c)**, and KUZ Z6492, ♀ **(d)**. **(a)** Live specimen, dorsal view. **(b)** Head and tergites 1–5, dorsal view. **(c)** Cephalic plate and tergite 1, dorsal view. **(d)** Head, ventral view. Abbreviations: am, anterior margin of forcipular coxosternite; lcs, lateral crescentic sulcus on tergite; tps, tergal paramedian suture. Scale bars: 2.5 mm **(a)**; 0.5 mm **(b)**; 0.2 mm **(c, d)**.

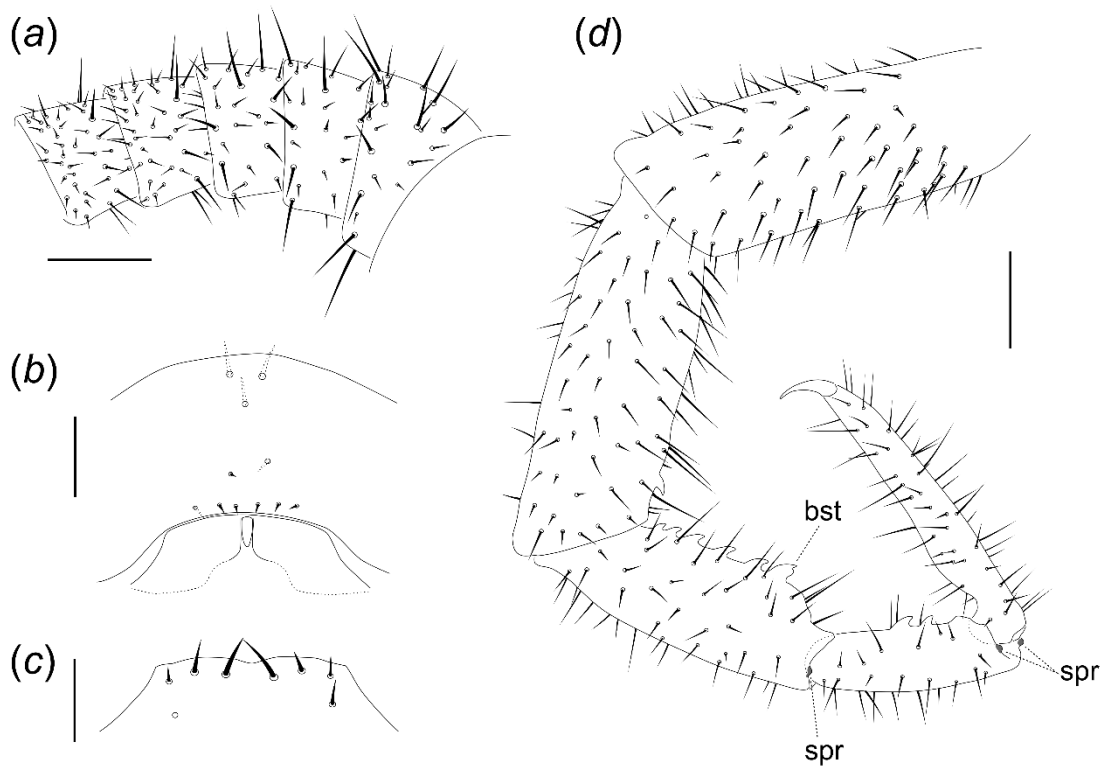


Fig. 10. *Cryptops navis* Chamberlin, 1930, KUZ Z6487, ♀ **(a)**, KUZ Z6492, ♀ **(b)**, and KUZ Z2974 **(c, d)**. **(a)** Basal articles of left antenna, dorsal view. **(b)** Clypeal setae, ventral view. **(c)** Anterior margin of forcipular coxosternite, ventral view. **(d)** Right ultimate leg, lateral view. Abbreviation: bst, bifid saw tooth; spr, spinous process. Scale bars: 0.1 mm **(a–c)**; 0.2 mm **(d)**.

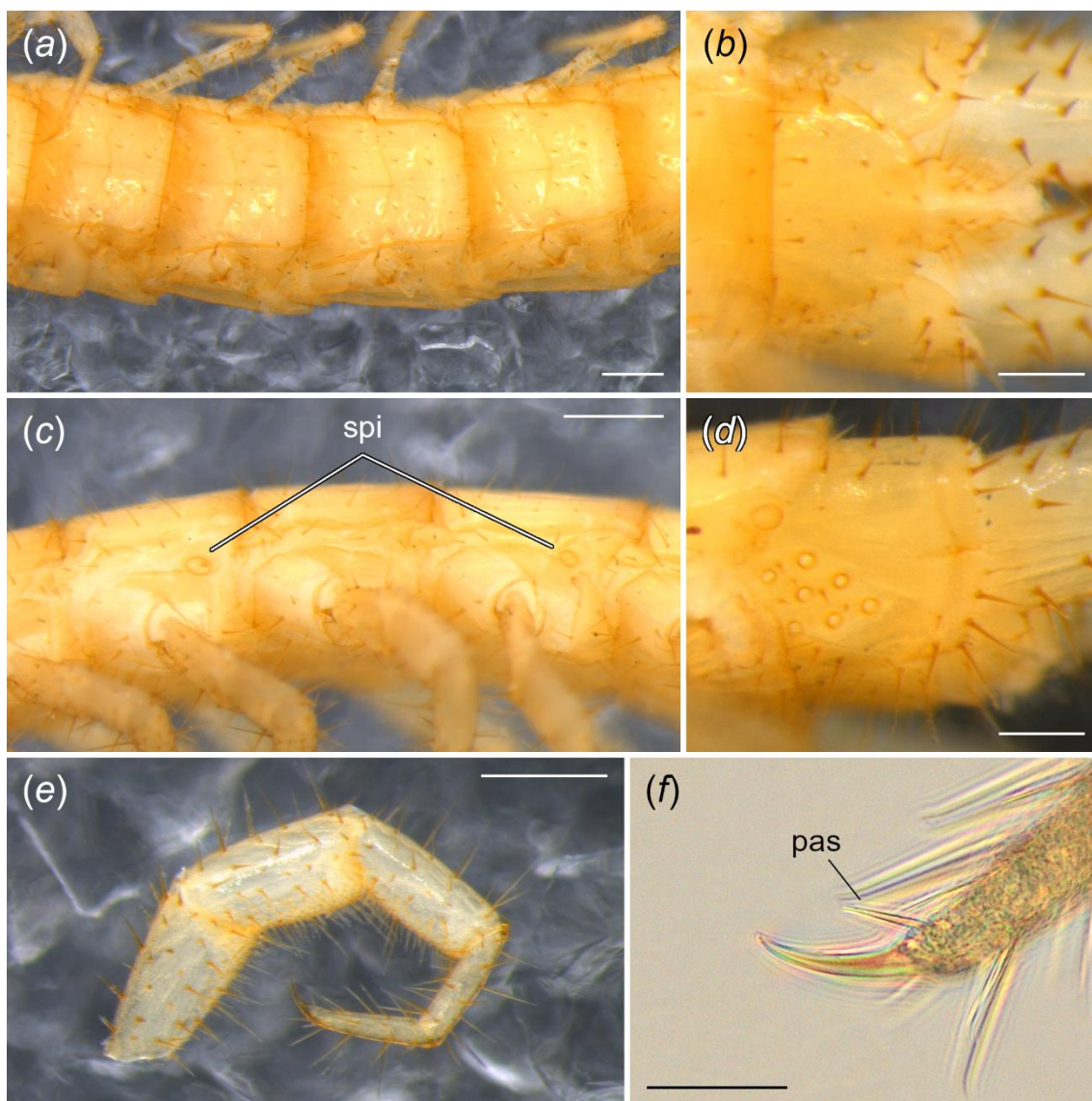


Fig. 11. *Cryptops navis* Chamberlin, 1930, KUZ Z6492, ♀ (**a**, **c**, **f**), KUZ Z6490, ♂ (**b**), and KUZ Z6488 (**d**, **e**). (**a**) Sternites 9–12, ventral view. (**b**) Sternite of ultimate leg-bearing segment, ventral view. (**c**) Left spiracles on leg-bearing segments 3 and 5, lateral view. (**d**) Left coxopleuron, lateral view. (**e**) Left leg 20, lateral view. (**f**) Pretarsus and accessory spine of right leg 7, medial view. Abbreviations: pas, pretarsal accessory spine; spi, spiracle. Scale bars: 0.2 mm (**a**, **c**, **e**), 0.1 mm (**b**, **d**), 0.05 mm (**f**).

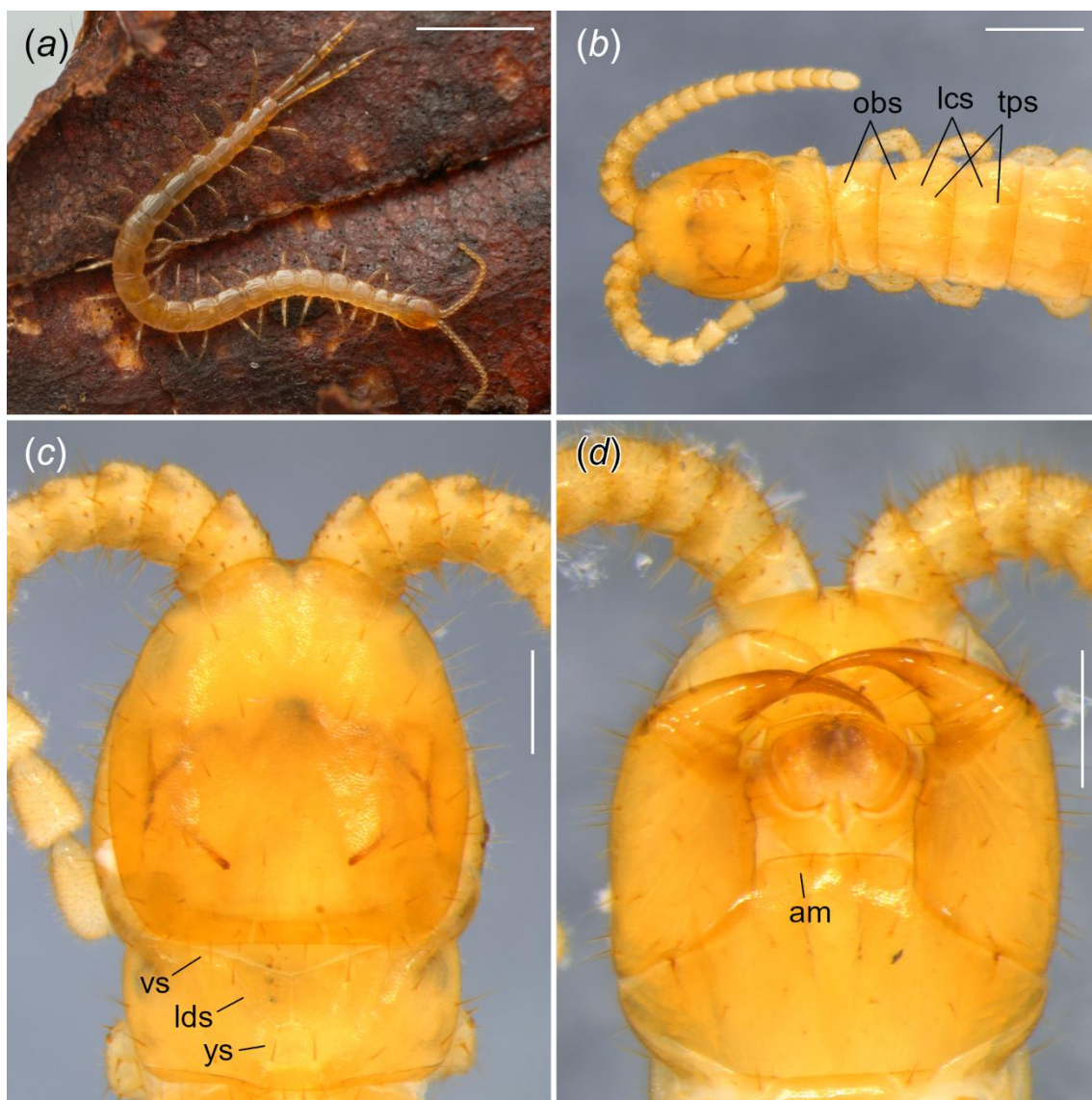


Fig. 12. *Cryptops striatus* Takakuwa, 1936, KUZ Z6499, ♀ (a), KUZ Z6497, ♂ (b, c), and KUZ Z6500, ♀ (d). (a) Live specimen, dorsal view. (b) Head and tergites 1–5, dorsal view. (c) Cephalic plate and tergite 1, dorsal view. (d) Head, ventral view. Abbreviations: am, anterior margin of forcipular coxosternite; lcs, lateral crescentic sulcus on tergite; lds, lateral diagonal suture; obs, oblique suture on tergite; tps, tergal paramedian suture; vs, V-shaped anterior transverse suture; ys, inverted Y-shaped posterior suture. Scale bars: 2.5 mm (a); 0.5 mm (b); 0.2 mm (c, d).

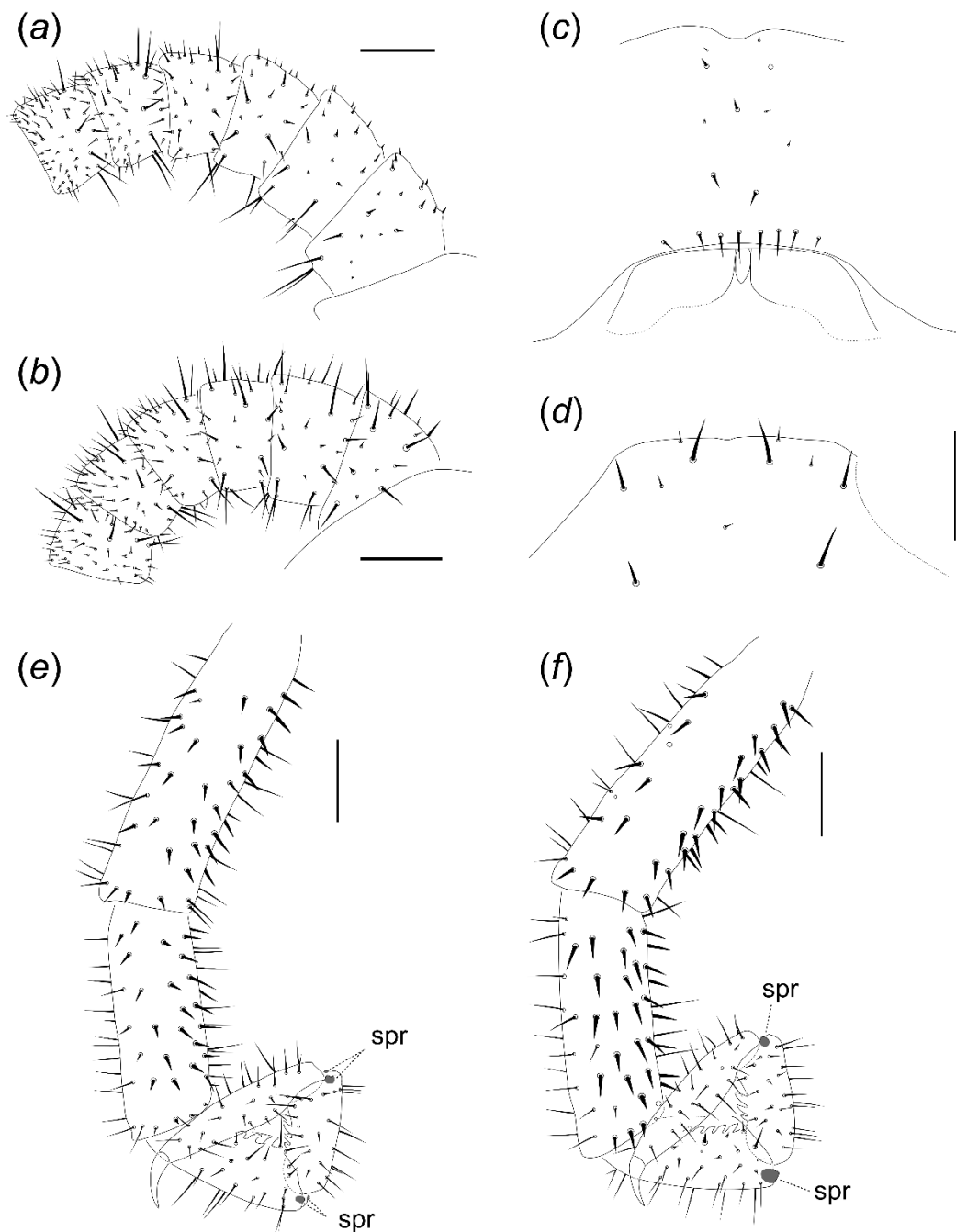


Fig. 13. *Cryptops striatus* Takakuwa, 1936, KUZ Z6498, ♂ (**a, e**), KUZ Z6499, ♀ (**b**), KUZ Z6497, ♂ (**c**), and KUZ Z6500, ♀ (**d, f**). (**a, b**) Basal articles of left antenna, dorsal view. (**c**) Clypeal setae, ventral view. (**d**) Anterior margin of forcipular coxosternite, ventral view. (**e, f**) Left ultimate leg, medial view. Abbreviation: spr, spinous process. Scale bars: 0.2 mm (**a, b, e, f**); 0.1 mm (**c, d**).

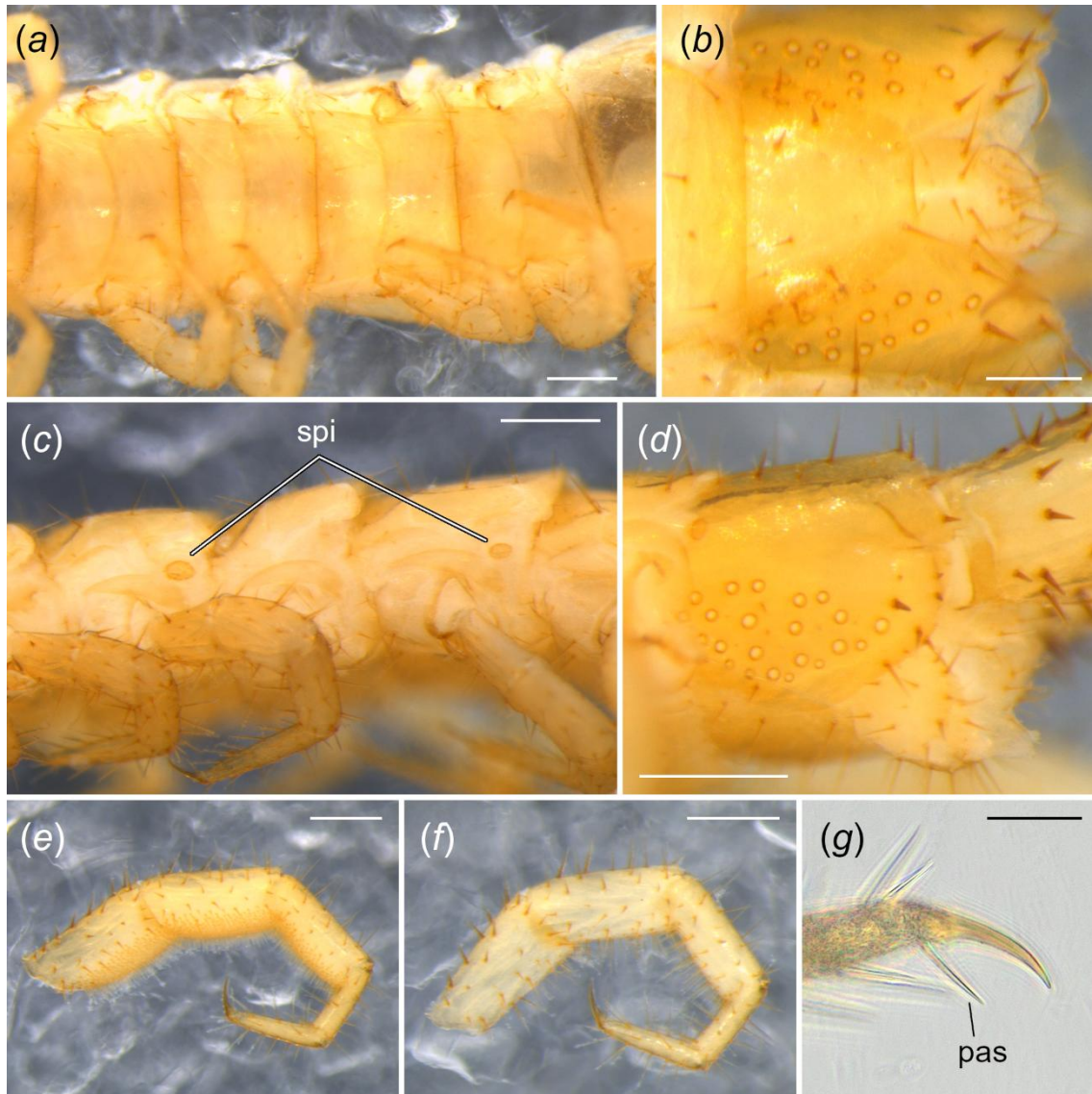


Fig. 14. *Cryptops striatus* Takakuwa, 1936. KUZ Z6497, ♂ (**a**, **c**, **e**), KUZ Z6500, ♀ (**b**, **g**), KUZ Z6498, ♂ (**d**), and KUZ Z6499, ♀ (**f**). (**a**) Sternites 11–14, ventral view. (**b**) Sternite of ultimate leg-bearing segment, ventral view. (**c**) Left spiracles on leg-bearing segments 3 and 5, lateral view. (**d**) Left coxopleuron, lateral view. (**e**, **f**) Left leg 20, lateral view. (**g**) Pretarsus and accessory spine of right leg 16, medial view. Abbreviations: pas, pretarsal accessory spine; spi, spiracle. Scale bars: 0.2 mm (**a**, **c**–**f**); 0.1 mm (**b**); 0.05 mm (**g**).

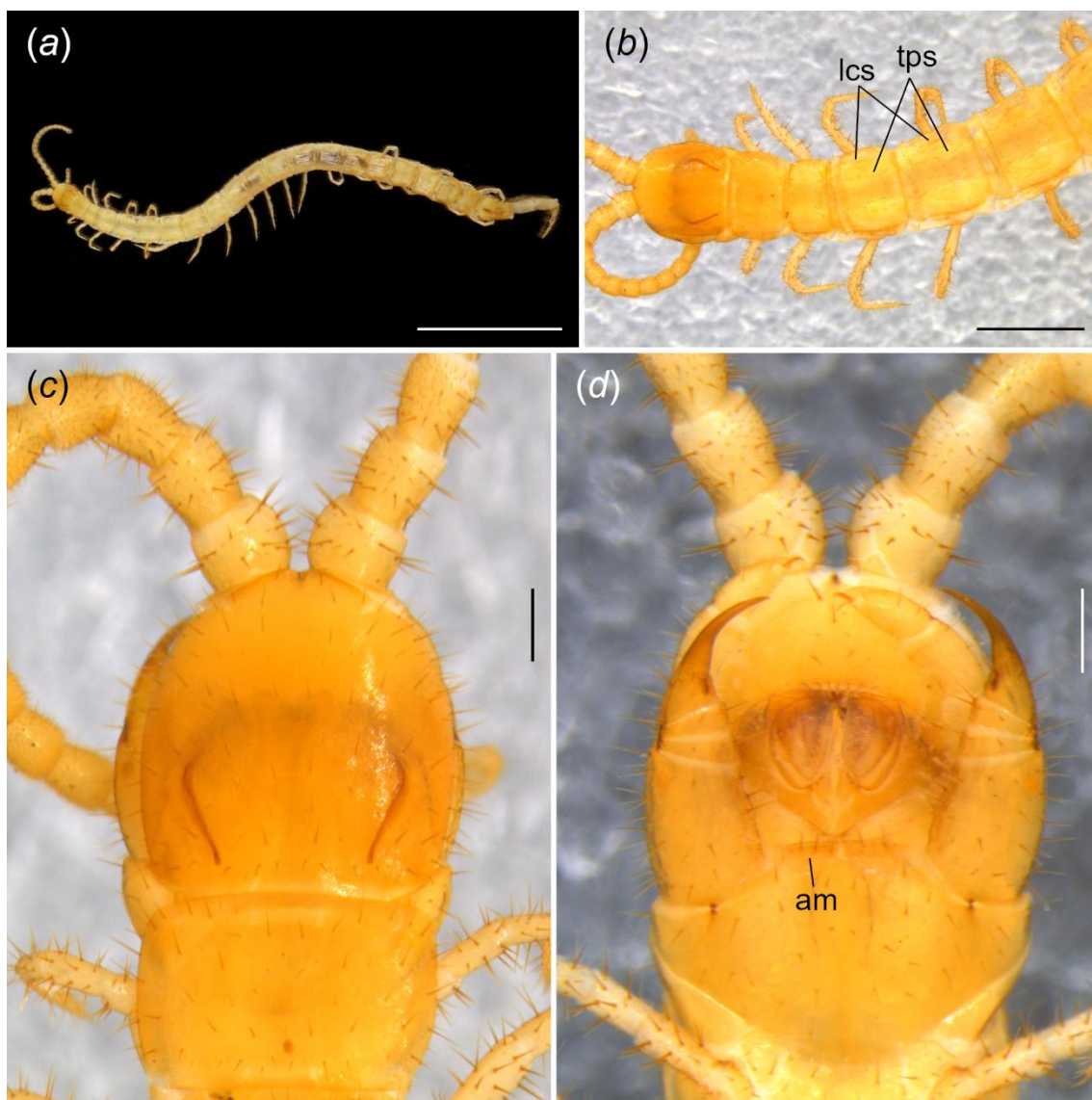


Fig. 15. *Cryptops dupliporus* sp. nov. holotype, ♀ (KUZ Z6484). **(a)** Habitus, dorsal view. **(b)** Head and tergites 1–5, dorsal view. **(c)** Cephalic plate and tergite 1, dorsal view. **(d)** Head, ventral view. Abbreviations: am, anterior margin of forcipular coxosternite; lcs, lateral crescentic sulcus on tergite; tps, tergal paramedian suture. Scale bars: 5 mm **(a)**; 1 mm **(b)**; 0.2 mm **(c, d)**.

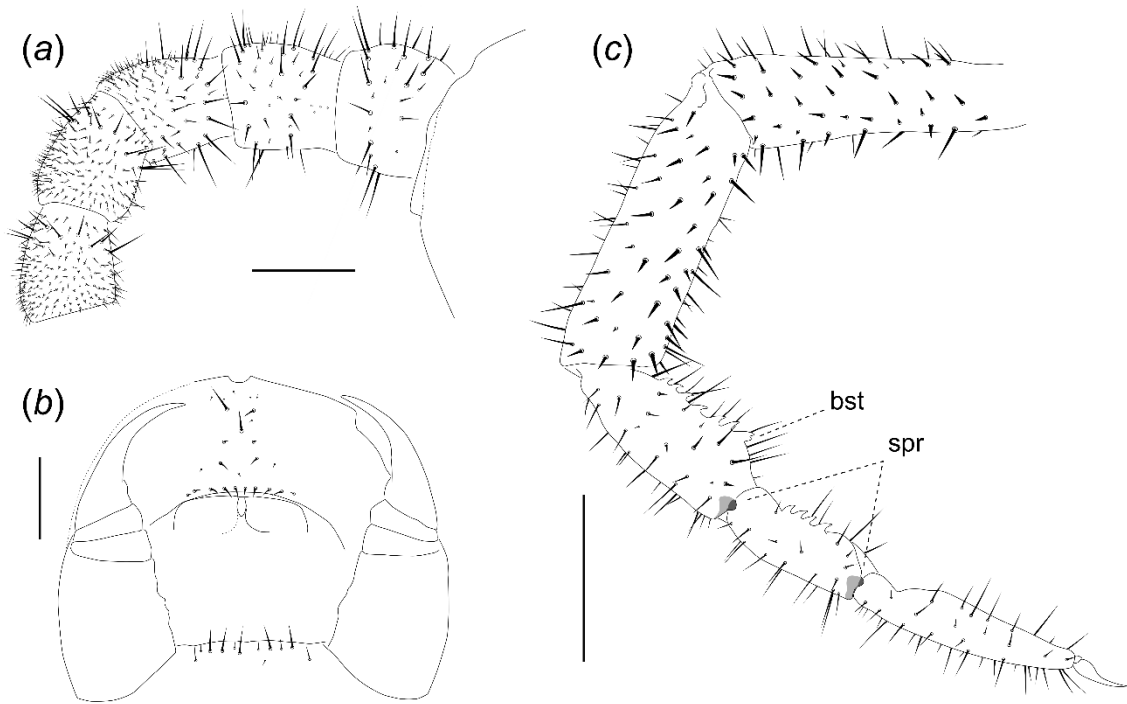


Fig. 16. *Cryptops dupliporus* sp. nov. holotype, ♀ (KUZ Z6484). **(a)** Basal articles of left antenna, dorsal view. **(b)** Clypeus and anterior margin of forcipular coxosternite, ventral view. **(c)** Left ultimate leg, medial view. Abbreviations: bst, bifid saw tooth; spr, spinous process. Scale bars: 0.2 mm **(a, b)**; 0.5 mm **(c)**.

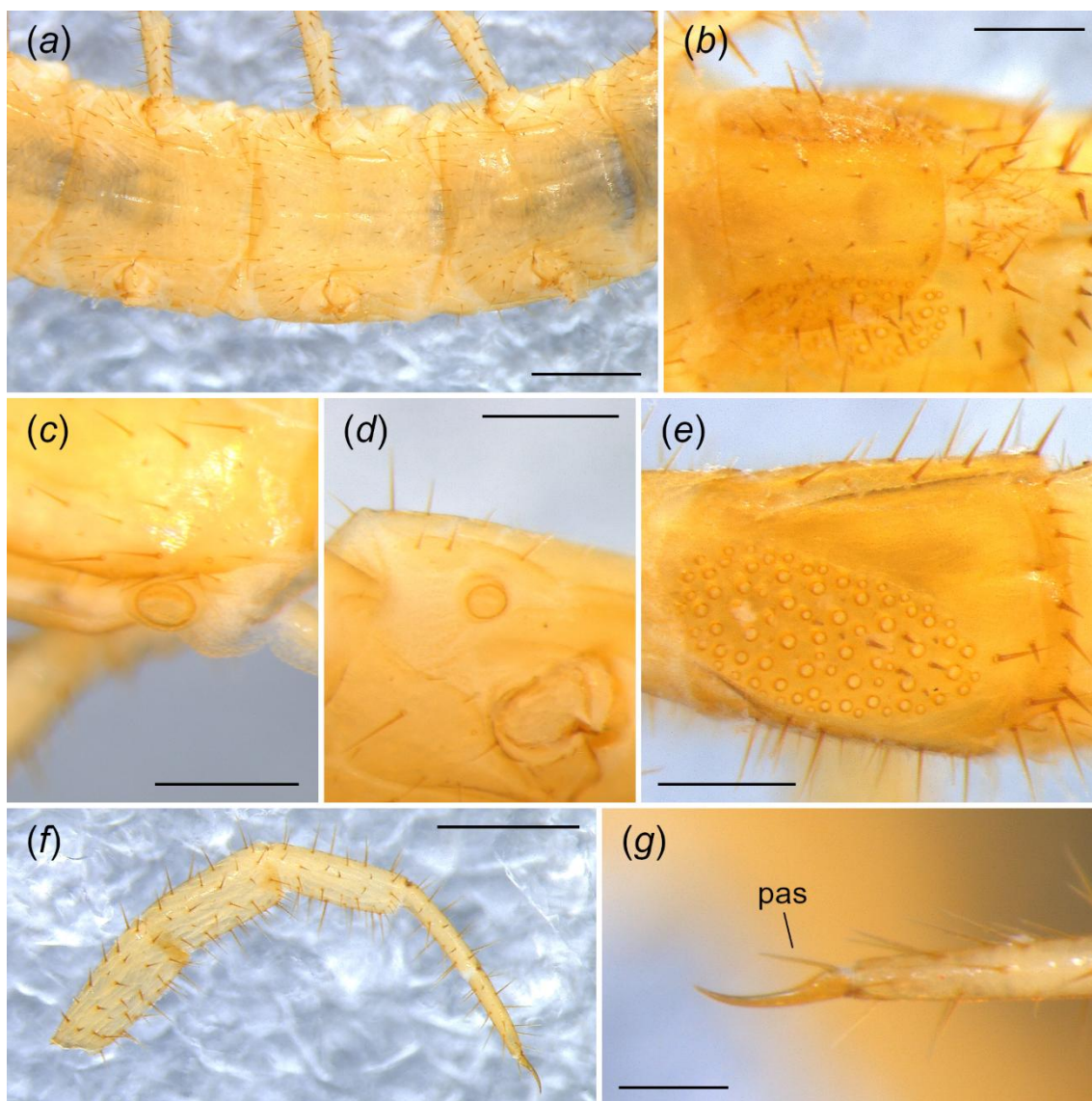
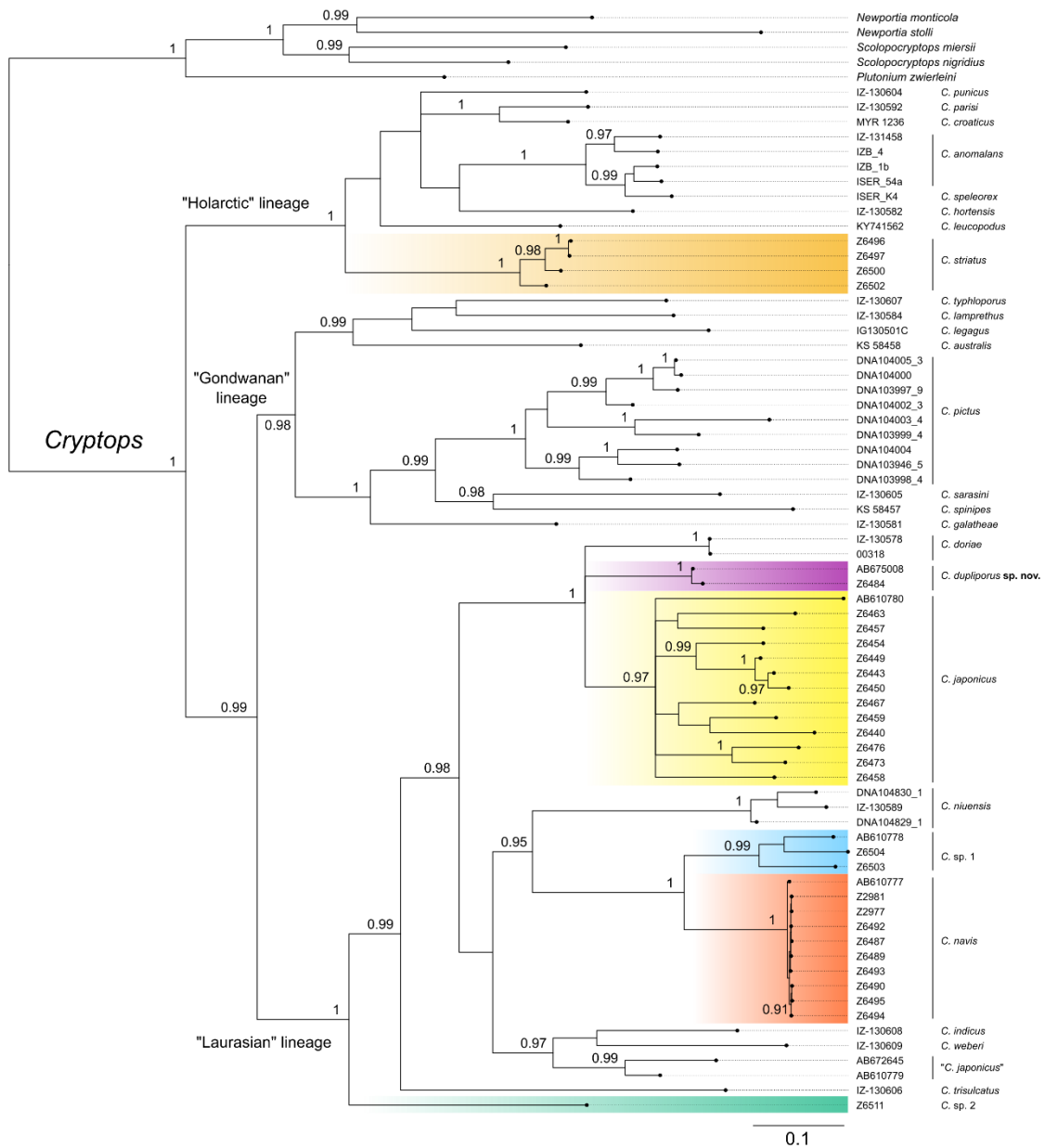
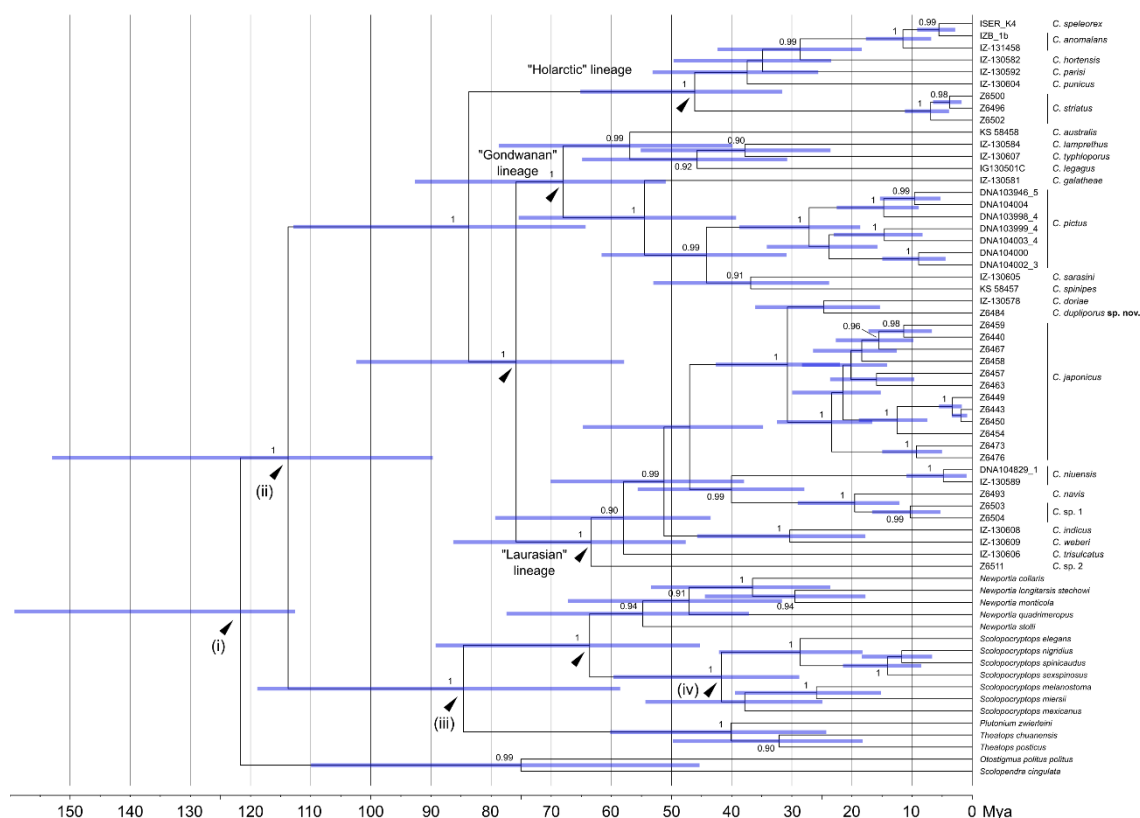


Fig. 17. *Cryptops dupliporus* sp. nov. holotype, ♀ (KUZ Z6484). **(a)** Sternites 11–13, ventral view. **(b)** Sternite of ultimate leg-bearing segment, ventral view. **(c)** Left spiracle on leg-bearing segment 3, lateral view. **(d)** Right spiracle on leg-bearing segment 8, lateral view. **(e)** Left coxopleuron, lateral view. **(f)** Left leg 20, lateral view. **(g)** Pretarsus and accessory spine of left leg 13, lateral view. Abbreviation: pas, pretarsal accessory spine. Scale bars: 0.5 mm (**a**, **f**); 0.2 mm (**b–e**); 0.1 mm (**g**).



Supplementary Fig. S1. Bayesian Inference tree for 3189 bp-aligned positions of the 18S, 28S, 16S and COI sequences of the "total dataset". Numbers on nodes indicate Bayesian posterior probabilities ≥ 0.9 . Horizontal colored bands indicate the East Asian species examined in this study.



Supplementary Fig. S2. Time-calibrated BI tree for 3189 bps of 18S, 28S, 16S and COI sequences. Numbers on nodes indicate Bayesian posterior probabilities ≥ 0.9 . Node bars represent 95% highest posterior density. (i) –(iv) on nodes denote calibration points used for the dating analysis (see Supplementary Table S2). The monophyly of the nodes denoted by triangles was fixed during the MCMC.