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Taxonomic re-appraisal of *Scolopocryptops quadristriatus* (Verhoeff, 1934) and a description of a new species from Japan and Taiwan (Chilopoda, Scolopendromorpha, Scolopocryptopidae)

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Abstract

Centipedes of the genus *Scolopocryptops* Newport, 1844 are blind species mostly described from the New World and East Asia. In this study, a Japanese species, *S. quadristriatus* (Verhoeff, 1934), which is characterised by four longitudinal keels on the tergites, is re-described, based on the likely holotype preserved in the Zoologische Staatssammlung München and specimens newly collected from near the type locality. In addition, *S. longisetosus* **sp. nov.**, a new species that bears tergal keels like *S. quadristriatus*, is described from the Ryukyu Islands in Japan and Taiwan. Although the presence of four keels on tergites is unique to these two species, phylogenetic analyses using nuclear and mitochondrial markers showed that *S. longisetosus* **sp. nov.** is not sister to *S. quadristriatus*. The obtained phylogeny indicates that the tergal longitudinal keels evolved in parallel within *Scolopocryptops* or that the presence of keels represents a plesiomorphic character of the clade containing these species.

Key Words

molecular phylogeny, nomenclature, plesiomorphic character, Ryukyu Islands, tergal keels

Introduction

Scolopocryptops Newport, 1844 is a centipede genus that mostly inhabits epigean habitats in North and South America, West Africa, East Asia and Vietnam and species have been also recorded from India, the Philippines, Indonesia, New Guinea and Fiji (Chagas-Jr et al. 2023; Le et al. 2023). The genus currently comprises 33 species and subspecies, which are classified into two groups: the Asian/North American group and the Neotropical/Afrotropical group (Chagas-Jr 2008; Edgecombe et al. 2012; Vahtera et al. 2013; Chagas-Jr et al. 2023; Le et al. 2023; Jonishi and Nakano 2023). Recent studies showed that the Asian/North American group consists of two lineages: a lineage composed of *S. elegans* (Takakuwa, 1937) and its closest relatives (hereinafter the *elegans* lineage), which is known from Far East Asia and a lineage including the rest of the Asian and North American species (hereinafter, the ex-*elegans* lineage) (Jonishi and Nakano 2022, 2023).

Scolopocryptops centipedes are characterised by a distinctive kind of collared antennal setae, the absence of eyes, 23 leg-bearing segments (except for *S. sukuyan* Chagas-Jr, Edgecombe & Minelli, 2023, which has 25 segments) and an ultimate leg prefemur with one dorso-medial and/or one ventral spinous process (Koch et al. 2010; Chagas-Jr et al. 2023; Le et al. 2023). Several Asian/North American species, for example, *S. sexspinosus* (Say, 1821) and *S. spinicaudus* Wood, 1862, are distinguished from others by the absence of complete paramedian sutures on tergites (Le et al. 2023). Amongst them, the Japanese *S. quadristriatus* (Verhoeff, 1934) bears four longitudinal keels on its tergites, which is a specific character that distinguishes this species from all other *Scolopocryptops* (Verhoeff 1934; Takakuwa 1940; Shinohara 1984; Le et al. 2023). After it was described as *Otocryptops sexspinosus quadristriatus*, based on a specimen from the vicinity of Tokyo, *S. quadristriatus* has been recorded from several localities in Honshu, the Izu Islands and Kyushu in the Japanese Archipelago (Shinohara 1949; Takashima and Shinohara 1952; Miyosi 1953; Takano 1973). Phylogenetic analyses indicated that this species belongs to the ex-*elegans* lineage (Jonishi and Nakano 2022). As summarised by Le et al. (2023), however, the taxonomic status of *S. quadristriatus* remains uncertain because only a low resolution of morphological features has been reported (Verhoeff 1934; Takakuwa 1939, 1940; Shinohara 1984).

In this study, a re-description of *S. quadristriatus*, based on the likely holotype is provided and newly-obtained specimens from near the type locality and adjacent areas were also investigated. In addition, several unidentified *Scolopocryptops* specimens obtained from the Ryukyu Islands in southern Japan and Taiwan have been studied. These individuals are morphologically similar to *S. quadristriatus*, but differ in several characters. Based on both morphological examination and phylogenetic analyses using nuclear and mitochondrial markers, these specimens are described as a new species herein.

Methods

Specimen collection and morphological observation

A specimen labelled as "*Otocryptops sexspinosus quadristriatus*" deposited at the Zoologische Staatssammlung München (ZSM A20051244), which is likely to represent the holotype of this taxon, was examined. Additional specimens of *S. quadristriatus* were collected from several localities in Tokyo and adjacent areas in eastern Honshu, Japan (Fig. 1). A total of 21 unidentified *Scolopocryptops* individuals were also collected from Okinawa, Ishigaki and Yonaguni Islands in the Ryukyu Islands and Hsinchu and Nantou Counties in Taiwan (Fig. 1). Specimens were placed in 30% ethanol for several minutes, fixed in 80% or 99% ethanol and then preserved in 75% ethanol. Ultimate leg-bearing segments of several specimens were dissected to examine genital segments.

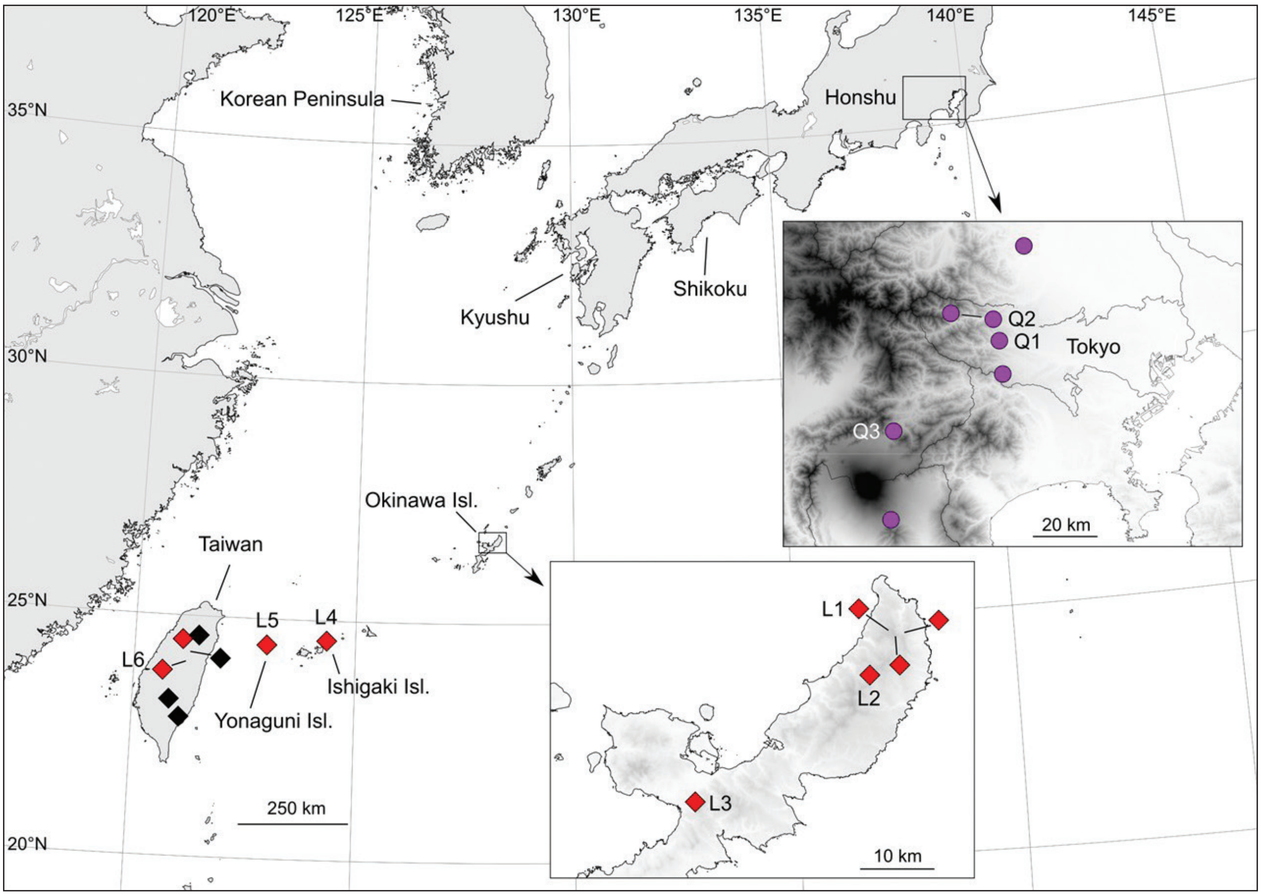

Figure 1. Collection localities of *Scolopocryptops quadristriatus* (Verhoeff, 1934) and *S. longisetosus* sp. nov. in the present study. Purple circles: *S. quadristriatus*; red diamonds: *S. longisetosus* sp. nov.; black diamonds: localities of the sequence data of Taiwanese "*S. capillipedatus*" (= *S. longisetosus* sp. nov.) obtained from INSD. Locality numbers (Q1–Q3 and L1–L6) are shown in Table 1 and Fig. 13.

All specimens were observed using a Leica M125C stereoscopic microscope with a drawing tube (Leica Microsystems, Wetzlar, Germany). The specimens were photographed using a Sony a6500 digital camera and a 65 mm macro lens and a Leica MC170 HD digital camera mounted on the Leica M125C. Images captured with the Leica MC170 were processed using Leica Application Suite v. 4.1.2. Specimens examined are deposited in the Zoological Collection of Kyoto University (KUZ).

The terminology for external features followed Bonato et al. (2010). For dissected adults and individuals with everted genital organs, genital morphology was examined following Takakuwa (1933a), Demange and Richard (1969), Iorio (2003), Siriwut et al. (2016) and Jonishi and Nakano (2022, 2023).

DNA extraction, PCR and DNA sequencing

Total DNA was extracted using a NucleoSpin Tissue kit (Macherey-Nagel, Duren, Germany). Following previous studies (e.g. Edgecombe et al. (2012, 2019)), nuclear internal transcribed spacer 2 (ITS2), 28S rRNA (28S), mitochondrial cytochrome *c* oxidase subunit 1 (COI) and 16S rRNA (16S) markers were selected for phylogenetic analyses. The primer sets used are as follows: the 5.8SF/28SRev (Murienne et al. 2011) for ITS2, 28Sa/28Sb (Whiting et al. 1997) for 28S, LCO1490/HCO2198 (Folmer et al. 1994) or the reverse primer HCOoutout (Schwendinger and Giribet 2005) for COI and 16Sar (Xiong and Kocher 1991)/16Sb (Edgecombe et al. 2002) for 16S. For ITS2 and 16S, reactions were performed using a LifeECO Thermal Cycler (Bioer Technology, Hangzhou, China); 28S and COI fragments were amplified using a GeneAmp PCR System 9700 (Thermo Fisher Scientific, Waltham, USA) and a T-100 Thermal Cycler (Bio-Rad, Hercules, USA), respectively. The PCR mixtures were heated to 94 °C for 5 min; followed by 35 cycles at 94 °C for 10 s, different annealing temperatures for each gene (50–60 °C for ITS2 and 16S, 60 °C for 28S and 50 °C for COI) for 20 s and 72 °C for 48 s for ITS2, 30 s for 28S and 16S and 42–48 s for COI; with a final extension at 72 °C for 6 min. The cycle sequencing reactions and sequencing process followed Jonishi and Nakano (2022, 2023). All sequences obtained in this study were deposited in the International Nucleotide Sequence Databases (INSD) through the DNA Data Bank of Japan (Table 1).

Molecular analyses

In addition to the 42 sequences obtained in this study, 39 sequences of Japanese and Taiwanese *Scolopocryptops* species (Jonishi and Nakano 2022, 2023) and 31 sequences of scolopocryptopid species retrieved from the INSD were included in the taxon set (Table 1).

The nuclear ITS2 sequences were aligned using MAFFT L-INS-i (Katoh and Standley 2013); the nuclear 28S and the mitochondrial 16S sequences were aligned using MAFFT Q-INS-i (Kuraku et al. 2013; Katoh et al. 2019) considering the RNA secondary structure; non-conserved regions of these genes were trimmed by Gblocks v. 0.91b (Castresana 2000). The mitochondrial COI sequences showed no indels; thus, alignment was straightforward. The first four COI positions were excluded from the analyses because this portion was missing in most of the sequences. The concatenated sequences yielded 2510 bp of aligned positions comprising 780 bp of ITS2, 536 bp of 28S, 654 bp of COI and 540 bp of 16S.

Table 1. Samples used for molecular analyses. The information on the voucher is accompanied by the collection locality and the INSD accession numbers of the DNA sequences. Locality numbers are shown in Fig. 1 and Fig.13. Acronyms: AMNH, American Museum of Natural History; KUZ; Zoological Collection of Kyoto University; MCZ, Museum of Comparative Zoology, Harvard University; and SYSU, National Sun Yat-sen University. References: 1, Jonishi and Nakano (2023); 2, Jonishi and Nakano (2022); 3, Chao et al. (unpublished); 4, Vahtera et al. (2013); 5, Vahtera et al. (2012); 6, Edgecombe et al. (2012); 7, Edgecombe and Giribet (2004); 8, Murienne et al. (2010). Sequences with an asterisk (*) were used only in the preliminary analyses.

Species	Voucher #	Locality	Locality #	INSD #				References
				ITS2	28S	COI	16S	
Asian/North American *Scolopocryptops*								
S. quadristriatus (Verhoeff, 1934)	KUZ Z4083	Hachioji, Tokyo, Japan	Q1	–	LC700508	LC700507	LC792589	This study for 16S; 2 for 28S and COI
S. quadristriatus (Verhoeff, 1934)	KUZ Z5098	Ome, Tokyo, Japan	Q2	LC792567	LC792573	LC792581	LC792590	This study
S. quadristriatus (Verhoeff, 1934)	KUZ Z5105	Minamitsuru, Yamanashi, Japan	Q3	–	LC792574	LC792582	LC792591	This study
S. longisetosus sp. nov.	KUZ Z5108	Kunigami, Okinawa Island, Japan	L1	LC792568	LC792575	LC792583	LC792592	This study
S. longisetosus sp. nov.	KUZ Z5122	Kunigami, Okinawa Island, Japan	L2	–	LC792576	LC792584	LC792593	This study
S. longisetosus sp. nov.	KUZ Z5111	Nago, Okinawa Island, Japan	L3	LC792569	LC792577	LC792585	LC792594	This study
S. longisetosus sp. nov.	KUZ Z5123	Ishigaki Island, Japan	L4	LC792570	LC792578	LC792586	LC792595	This study
S. longisetosus sp. nov.	KUZ Z5124	Yonaguni Island, Japan	L5	LC792571	LC792579	LC792587	LC792596	This study

Species	Voucher #	Locality	Locality #	INSD #				References
				ITS2	28S	COI	16S	
S. longisetosus sp. nov.	KUZ Z5127	Nantou, Ren'ai, Taiwan	L6	LC792572	LC792580	LC792588	LC792597	This study
"*S. capillipedatus* (Takakuwa, 1938)" (= *S. longisetosus* sp. nov.)	SYSU Chilo-044	Yanping, Taitung, Taiwan	–	–	–	AB617528*	–	3
"*S. capillipedatus* (Takakuwa, 1938)" (= *S. longisetosus* sp. nov.)	SYSU Chilo-056	Heping, Taichung, Taiwan	–	–	–	AB617529*	–	3
"*S. capillipedatus* (Takakuwa, 1938)" (= *S. longisetosus* sp. nov.)	SYSU Chilo-061	Datong, Yilan, Taiwan	–	–	–	AB617530*	–	3
"*S. capillipedatus* (Takakuwa, 1938)" (= *S. longisetosus* sp. nov.)	SYSU Chilo-143	Taoyuan, Kaohsiung, Taiwan	–	–	–	AB672646*	–	3
S. musashiensis Shinohara, 1984	KUZ Z4085	Ichikawa, Chiba, Japan	–	–	LC700512	LC700511	LC792598	This study for 16S; 2 for 28S and COI
S. nigridius McNeil, 1887	MCZ DNA100807	North Carolina, USA	–	–	HM453278	AY288744	AY288725	8 for 28S; 7 for COI and 16S
S. nigridius McNeil, 1887	MCZ IZ-130806	North Carolina, USA	–	–	JX422594	JX422680	JX422704	6
"*S. nipponicus*" Shinohara, 1990 sensu Edgecombe et al. (2012)	MCZ IZ-130804	Nagoya, Aichi, Japan	–	–	JX422595	JX422681	JX422705	6
S. ogawai Shinohara, 1984	KUZ Z4395	Fukuroi, Shizuoka, Japan	–	LC741599	LC741600	LC741601	–	1
S. rubiginosus L. Koch, 1878	KUZ Z4082	Enoshima, Kanagawa, Japan	–	LC741602	LC700506	LC700505	LC792599	This study for 16S; 1 for ITS2; 2 for 28S and COI
S. rubiginosus L. Koch, 1878	MCZ IZ-130823	Yuanshan, Yilan, Taiwan	–	–	–	JX422682	JX422706	6
S. sexspinosus (Say, 1821)	MCZ IZ-131450	North Carolina, USA	–	–	AY288710	AY288745	AY288726	7
S. spinicaudus Wood, 1862	AMNH IZC 00146514	California, USA	–	–	JX422596	JX422683	JX422707	6
S. elegans (Takakuwa, 1937)	KUZ Z4062	Katsurahama, Kochi, Japan	–	LC741566	LC700494	LC700493	LC792600	This study for 16S; 1 for ITS2; 2 for 28S and COI
S. elegans (Takakuwa, 1937)	KUZ Z4073	Higashimuro, Wakayama, Japan	–	LC741569	LC700500	LC700499	LC792601	This study for 16S; 1 for ITS2; 2 for 28S and COI
S. elegans (Takakuwa, 1937)	KUZ Z4373	Akiruno, Tokyo, Japan	–	LC741570	LC741571	LC741572	LC792602	This study for 16S; 1 for ITS2, 28S, and COI
S. miyosii Jonishi & Nakano, 2023	KUZ Z4375	Kirishima, Kagoshima, Japan	–	LC741573	LC741574	LC741575	LC792603	This study for 16S; 1 for ITS2, 28S, and COI
S. miyosii Jonishi & Nakano, 2023	KUZ Z4374	Saeki, Oita, Japan	–	LC741578	LC741579	LC741580	LC792604	This study for 16S; 1 for ITS2, 28S, and COI
S. miyosii Jonishi & Nakano, 2023	KUZ Z4380	Yamato-son, Amami Island, Japan	–	LC741581	LC741582	LC741583	LC792605	This study for 16S; 1 for ITS2, 28S, and COI
S. brevisulcatus Jonishi & Nakano, 2023	KUZ Z4389	Mt. Katsuu-dake, Okinawa Island, Japan	–	–	LC741587	LC741588	LC792606	This study for 16S; 1 for 28S and COI
S. brevisulcatus Jonishi & Nakano, 2023	KUZ Z4392	Mt. Fuenchiji, Okinawa Island, Japan	–	LC741589	LC741590	LC741591	LC792607	This study for 16S; 1 for ITS2, 28S, and COI
S. curtus (Takakuwa, 1939)	KUZ Z4079	Tai'an, Miaoli, Taiwan	–	LC741597	LC700502	LC700501	–	1 for ITS2; 2 for 28S and COI
S. curtus (Takakuwa, 1939)	KUZ Z4081	Iriomote Island, Okinawa, Japan	–	LC741598	LC700504	LC700503	LC792608	This study for 16S; 1 for ITS2; 2 for 28S and COI
Neotropical/Afrotropical *Scolopocryptops*								
"*S. macrodon*" (Kraepelin, 1903) sensu Chagas-Jr (2008) and Edgecombe et al. (2012)	MCZ IZ-130814	Guyana	–	–	–	JX422675	JX422699	6
S. miersii Newport, 1845	MCZ IZ-130729	Brazil	–	–	KF676364	JX422674	JX422697	6 for COI and 16S; 4 for 28S
S. miersii Newport, 1845	AMNH LP3868, IZ-130730	French Guiana	–	–	–	HQ402545	JX422698	5 for COI; 6 for 16S
Outgroup								
Newportia monticola Pocock, 1890	MCZ IZ-130777	Parque de Cahuita, Costa Rica	–	–	KF676360	KF676507	HQ402497	5 for 16S; 4 for 28S and COI

Maximum Likelihood (ML) and Bayesian Inference (BI) were applied to two separate datasets: a COI sequence dataset for preliminary analyses and a concatenated dataset of COI, 16S, ITS2 and 28S. The sequences of "*S. capillipedatus* (Takakuwa, 1938)" (see Results), of which only the COI region is available in the INSD (AB617528–AB617530, and AB672646), were used only in the preliminary analyses. The best-fit partition schemes and substitution models were identified, based on the Bayesian Information Criterion using ModelFinder (Kalyaanamoorthy et al. 2017) implemented in IQ-TREE v.1.6.12 (Nguyen et al. 2015) or PartitionFinder v.2.1.1 (Lanfear et al. 2016) with the "all" algorithm. The selected partition schemes and models are shown in Suppl. material 1. The ML phylogenetic trees were reconstructed using IQ-TREE v.1.6.12 with ultrafast bootstrapping (UFBoot; Hoang et al. (2017)) conducted with 1000 replicates. The BI trees and Bayesian posterior probabilities (BPP) were estimated using MrBayes v.3.2.7 (Ronquist et al. 2012). Two independent runs of four Markov chains were conducted for 10 million generations and the tree was sampled every 100 generations. Considering parameter estimates and assessments of convergence using Tracer v.1.7.2 (Rambaut et al. 2018), the first 2500 trees were discarded as burn-in.

Uncorrected pairwise distances for COI sequences (590–654 bp) were calculated with MEGA 11 (Tamura et al. 2021), with pairwise deletion of missing data (Suppl. material 2).

Results

Taxonomy

Order Scolopendromorpha Pocock, 1895
Family Scolopocryptopidae Pocock, 1896
Genus *Scolopocryptops* Newport, 1844

Scolopocryptops quadristriatus (Verhoeff, 1934)

Figs 2–7

Japanese name: Yosuji-akamukade

Otocryptops sexspinosus quadristriatus Verhoeff, 1934: 54; Takakuwa (1939: 699), fig. 3 (as *Octocryptops* [sic] *sexspinosus quadristriatus*); Takakuwa (1940: 73), fig. 77.

Scolopocryptops quadristriatus: Shinohara (1984: 41); Shinohara et al. (2015: 880, 906); Le et al. (2023: 437, 442).

Not *S. quadristriatus*. "*Otocryptops sexspinosus quadristriatus*": Takakuwa (1933b: 1457, 1459) (*nomen nudum*).

Type specimen. *Otocryptops s. quadristriatus* was described, based on a single specimen from the vicinity of Tokyo, without any information on the collector, collecting date or deposition of the specimen (Verhoeff 1934). Most of the Verhoeff's specimens are now kept at the Zoologische Staatssammlung München (ZSM), the Museum für Naturkunde (MfN) and the Naturhistorischen Museums Wien (NHMW) (Melzer et al. 2011). A specimen of *O. s. quadristriatus* is deposited at the ZSM, but neither MfN nor NHMW have specimens labelled as *O. s. quadristriatus* (Moritz and Fischer 1979; Schileyko and Stagl 2004). ZSM A20051244 (Fig. 2) is, thus, the only specimen of *O. s. quadristriatus* remaining within the Verhoeff's collection and is supposed to be the holotype of this nominal taxon, although the original label and collection data of this specimen are unavailable (Stefan Friedrich, personal communication). Its cephalic capsule, maxillae and left ultimate leg had been preserved in a separate vial (Fig. 2A); the body had been cut into two parts on leg-bearing segment 8 (Fig. 2B); its ultimate leg-bearing segment had been dissected. Additionally, its left legs 6, 8, 12, 14, 15, 17, 18, 20 and 22; right legs 3, 8, 12–18 and 20–22; and right ultimate leg had been lost or loosened; its left leg 16 was loosened during observation by the first author. Morphological features of the likely holotype are consistent with the original description and specimens newly obtained in this study. Thus, a description, based on both ZSM A20051244 and our specimens, is provided below.

Shinohara (1982) stated that a Japanese myriapodologist, the late Dr Yoshioki Takakuwa, sent a specimen of *O. s. quadristriatus* to Verhoeff. Given that Verhoeff also received other chilopod specimens from Takakuwa (e.g. Verhoeff (1934, 1935, 1937)), it is plausible that the likely holotype was also dispatched from Takakuwa to Verhoeff.

Material examined. ***Holotype* (?): Japan** • ♀ (approx. 33.5 mm); ZSM A20051244.

Additional material. Japan – **Tokyo** • 1, 33.9 mm (KUZ Z4083); Hachioji City, Uratakao-machi; 15 Apr 2017; Taiga Kato leg. • 1, 33.2 mm (KUZ Z5091); same data as for preceding • 1, 33.0 mm (KUZ Z5092); Hachioji City, Mt. Takao-san; 18 Nov 2017; T. Kato leg. • 1, 28.6 mm (KUZ Z5093); Hachioji City, Uratakao-machi; 35°38.69'N, 139°14.36'E; approx. 250 m alt.; 18 Oct 2021; T. Jonishi leg. • 1 ♂, 32.1 mm (KUZ Z5094) and 3, 33.1 mm (KUZ Z5095), 36.2 mm (KUZ Z5096), 27.7 mm (KUZ Z5097); same locality as for preceding; 35°38.72'N, 139°14.33'E; approx. 260 m alt.; 18 Oct 2021; T. Jonishi leg. • 1, 38.6 mm (KUZ Z5098); Ome City, Futamatao; 35°47.87'N, 139°13.56'E; approx. 230 m alt.; 19 Oct 2021; T. Jonishi leg. • 1 ♂, 38.2 mm (KUZ Z5099); Ome City, Sawai; 35°48.68'N, 139°10.91'E; approx. 350 m alt.; 19 Oct 2021; T. Jonishi leg. • 2, 33.6 mm (KUZ Z5100), 29.7 mm (KUZ Z5101) and 1 juvenile, 12.8 mm (KUZ Z5102); Akiruno City, Yokosawa; 35°44.28'N, 139°14.28'E; approx. 250 m alt.; 12 Apr 2022; Futaro Okuyama leg. • 1, 29.6 mm (KUZ Z5103); Hachioji City, Uratakao-machi; 35°38.75'N, 139°14.16'E; approx. 270 m alt.; 6 Nov 2022; T. Kato leg. – **Saitama Prefecture** • 1 ♀, 39.0 mm (KUZ Z5104); Hiki County, Hatoyama-machi; 36°0.01'N, 139°21.42'E; approx. 110 m alt.; 19 Oct 2021; T. Jonishi leg. – **Yamanashi Prefecture** • 1, 30.5 mm (KUZ Z5105); Minamitsuru County, Nishikatsura-cho; 35°30.82'N, 138°50.44'E; approx. 670 m alt.; 9 Apr 2022; Eitaro Matsushita leg. – **Shizuoka Prefecture** • 1, 30.4 mm (KUZ Z5106); Susono City, Suyama; 35°15.92'N, 138°47.95'E; approx. 910 m alt.; 2 June 2022; T. Nakano leg.

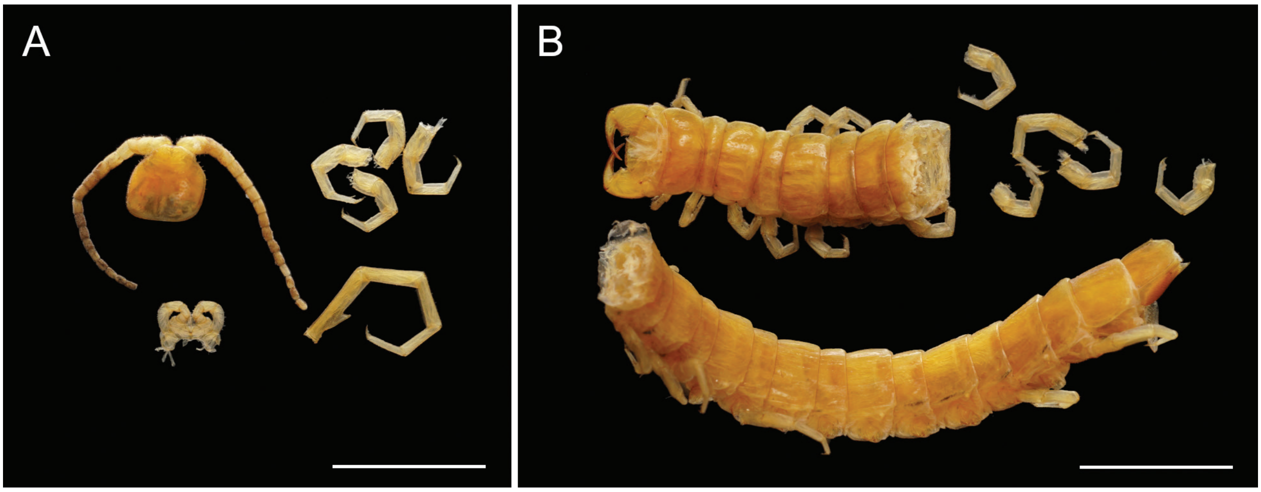

Figure 2. *Scolopocryptops quadristriatus* (Verhoeff, 1934), the likely holotype, ♀ (ZSM A20051244). **A.** Cephalic capsule, maxillae, legs and left ultimate leg; **B.** Forcipular segment, leg-bearing segments and legs. Scale bars: 5 mm.

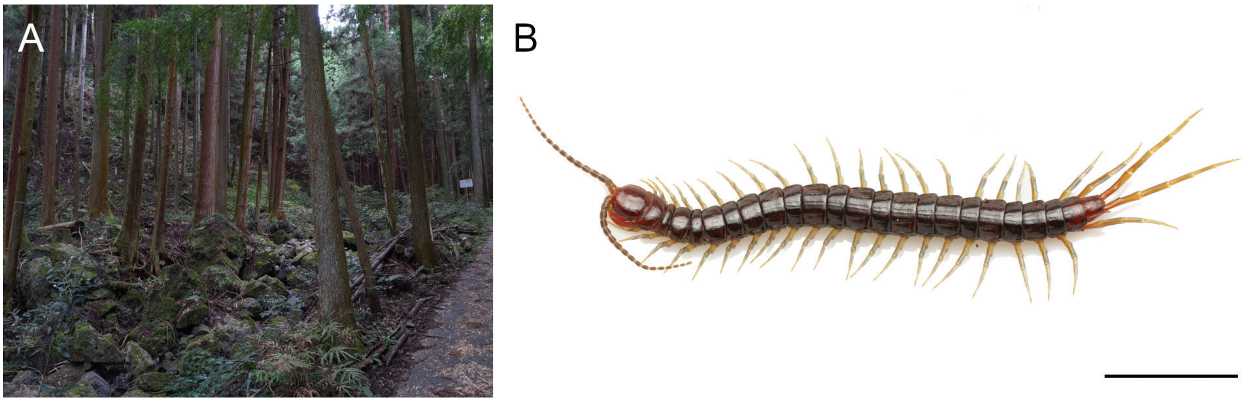

Figure 3. *Scolopocryptops quadristriatus* (Verhoeff, 1934), collected from near the type locality, ♀ (KUZ Z5104) and the habitat near the type locality. **A.** Habitat at Ome City, Tokyo; **B.** Live specimen, dorsal view. Scale bar: 10 mm.

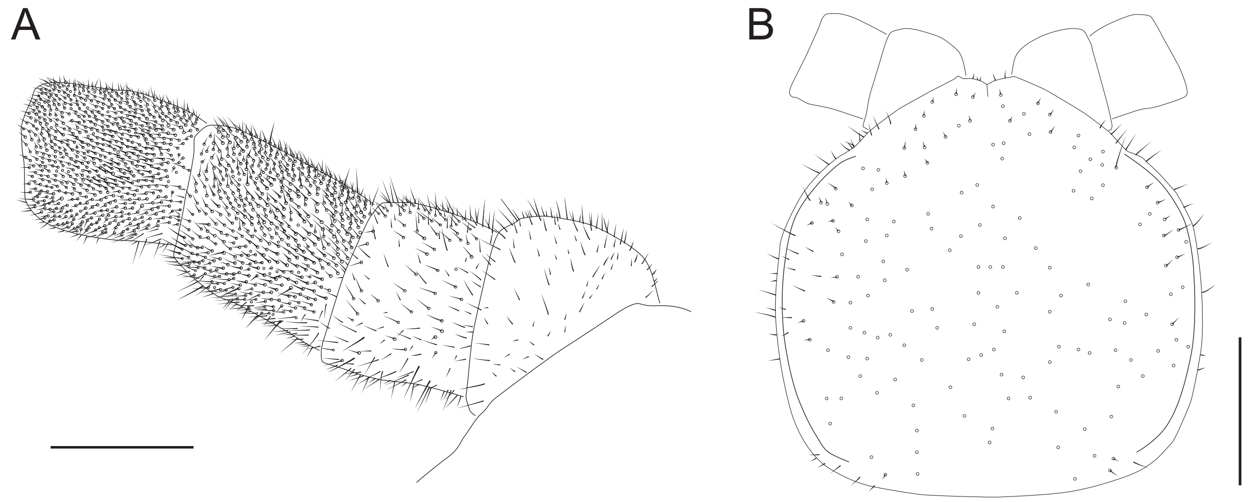

Figure 4. *Scolopocryptops quadristriatus* (Verhoeff, 1934) from near the type locality (KUZ Z5095). **A.** Basal articles of left antenna, dorsal view; **B.** Cephalic plate, dorsal view. Scale bars: 0.5 mm (**A**); 1 mm (**B**).

Diagnosis. Antenna with sparse short hairs and setae on dorsal surface of two basal articles, subsequent articles densely covered with short setae. Cephalic plate with complete lateral marginal sulci. Tergites lacking paramedian sutures, tergites 6–20 with four longitudinal keels and median depression bordered by paramedian keels.

Description [variations given in square brackets]. Body length approx. 27.7–39.0 mm in 75% ethanol.

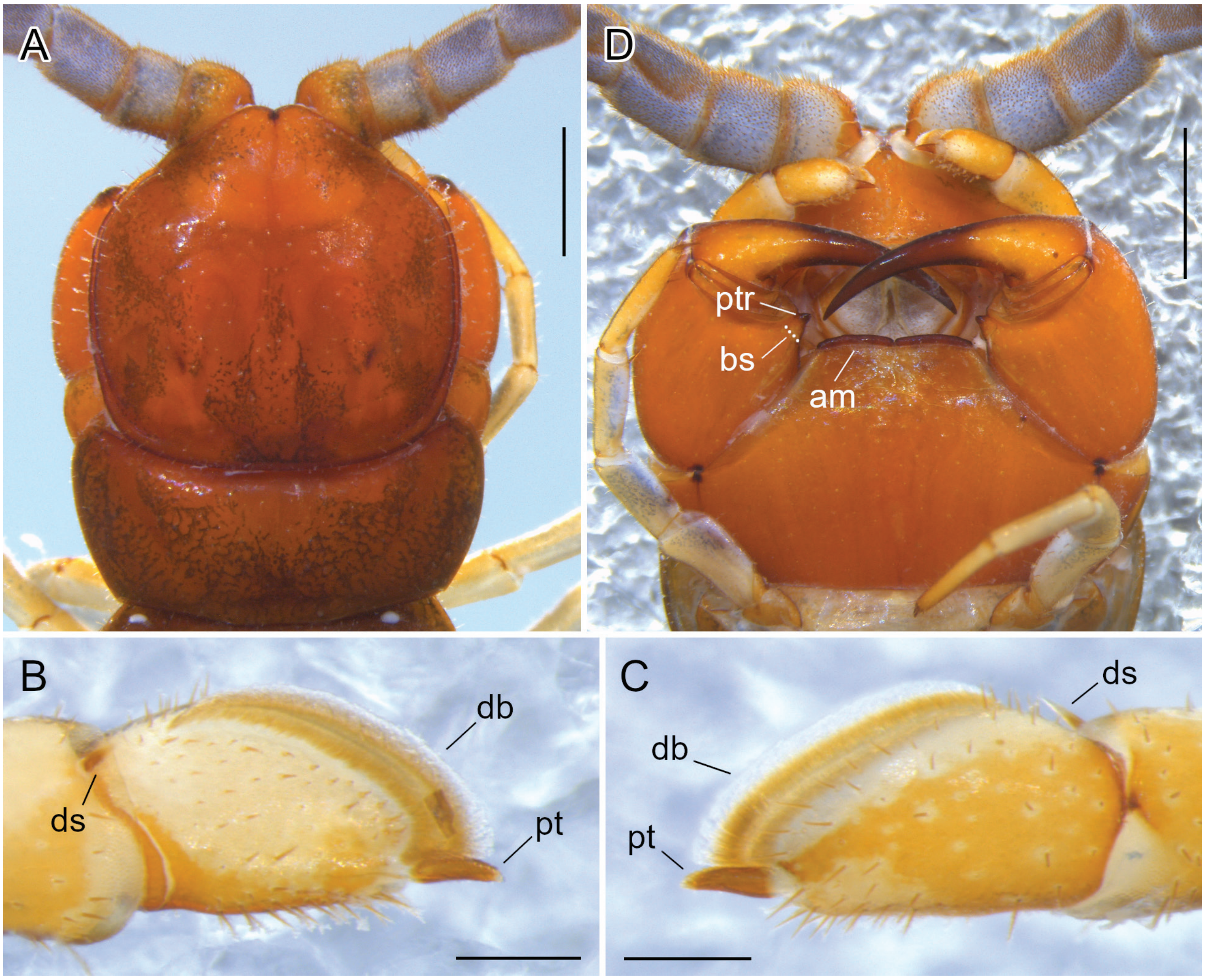

Figure 5. *Scolopocryptops quadristriatus* (Verhoeff, 1934) from near the type locality (KUZ Z5095). **A.** Cephalic plate and tergite 1, dorsal view; **B.** Distal part of article 2, article 3 and pretarsus of left second maxilla, medial view; **C.** Article 3 and pretarsus of left second maxilla, lateral view; **D.** Head, ventral view. Abbreviations: **am** — anterior margin of forcipular coxosternite; **bs** — basal suture on forcipular trochanteroprefemoral process; **db** — dorsal brush on article 3 of second maxilla; **ds** — dorsal spur on article 2 of second maxilla; **pt** — pretarsus of second maxilla; **ptr** — process of forcipular trochanteroprefemur. Scale bars: 1 mm (**A, D**); 0.2 mm (**B, C**).

Colour in life yellowish-brown with dark pigment on two basal antennal articles, purplish on subsequent articles; reddish-brown on forcipules; reddish-brown with dark pigment on anterior, lateral and posterior margins of cephalic plate, tergites 1, 22 and 23; purplish dark brown on tergites 2–21; legs and ultimate legs brownish-yellow or orange with bluish dark pigment (Fig. 3B). Colour in ethanol slightly greenish on tergites and legs (Fig. 6A).

Antennae 7.7–13.4 mm in length, approx. 0.2–0.35× as long as body, composed of 17 articles; two basal articles with sparse short hairs and setae (sensu Bonato et al. (2010)) dorsally, subsequent articles densely covered with short setae (Fig. 4A); each seta emerging from small collar. Cephalic plate as long as wide; its surface sparsely punctate with sparse minute hairs, with complete lateral margination (Figs 4B, 5A).

Second maxillae article 2 with elongated and semi-transparent [dark brown] dorsal spur distally; dorsal brush with transparent margination; pretarsus consisting of dark brown basal and semi-transparent short apical parts (Fig. 5B, C). Forcipular coxosternite and trochanteroprefemora sparsely punctate, coxosternite with median suture and transverse sutures cross median one on anterior third of coxosternite (Fig. 5D); trochanteroprefemur with small and blunt black process with basal suture (Fig. 5D); anterior margin of coxosternite strongly sclerotised and slightly convex, divided into two low lobes by median diastema (Fig. 5D).

Tergites sparsely punctate; tergite 1 with anterior transverse suture; anterior margin overlapped by cephalic plate (Figs 5A, 6A). All tergites lacking paramedian sutures; tergites 6 [5–7]–21 with longitudinal median depression bordered by paramedian keels, lateral keels present on tergites 6 [6–8]–20; median depression and keels unapparent on anterior and posterior tergites [depression and keels unapparent on all tergites in adult KUZ Z5099]

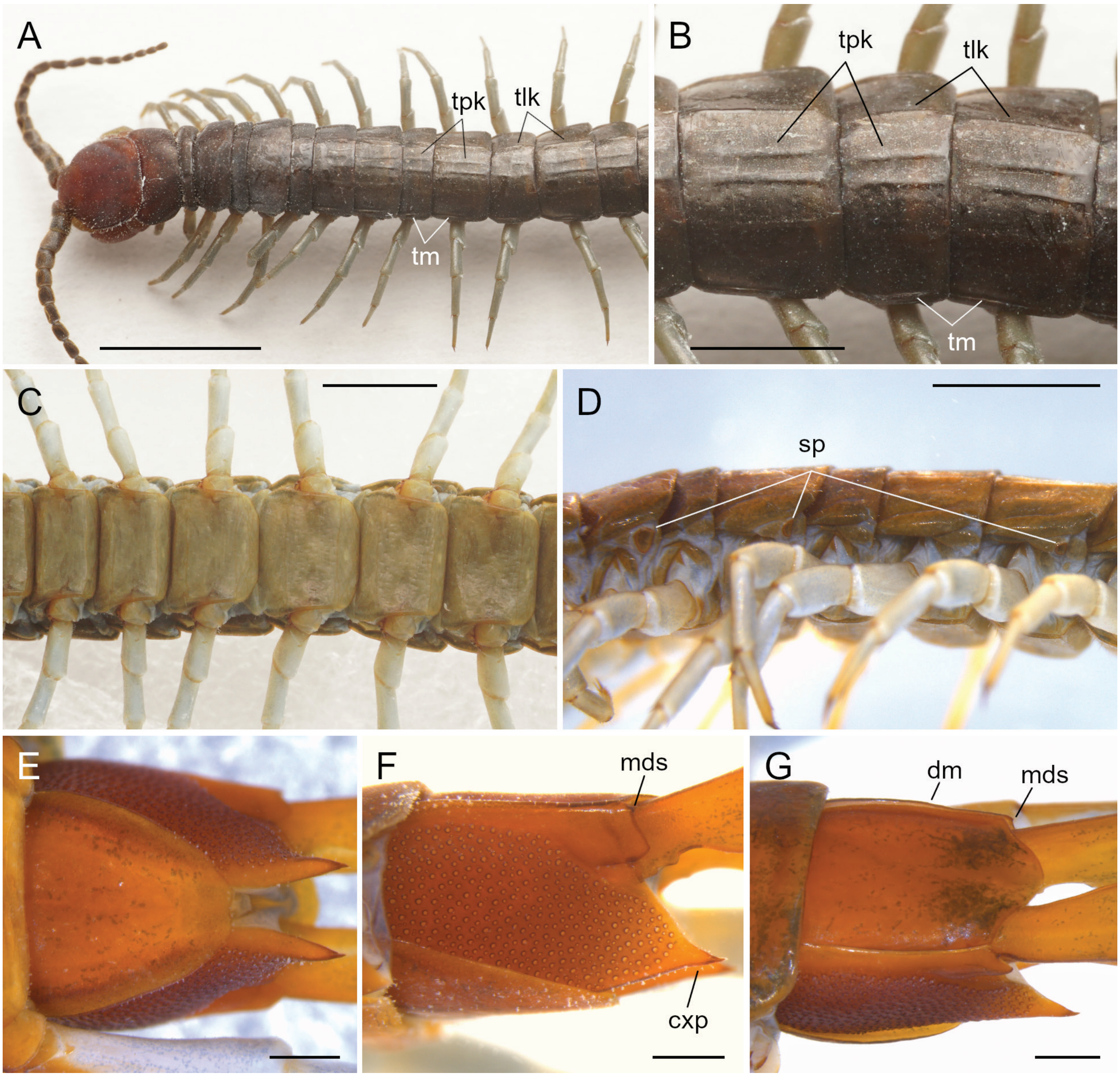

Figure 6. *Scolopocryptops quadristriatus* (Verhoeff, 1934) from near the type locality (KUZ Z5095). **A.** Cephalic plate and tergites 1–13, dorso-lateral view; **B.** Tergites 14–16, dorso-lateral view; **C.** Sternites 8–13, ventral view; **D.** Leg-bearing segments 3–8, lateral view; **E.** Sternite of ultimate leg-bearing segment and coxopleuron, ventral view; **F.** Left coxopleuron, lateral view; **G.** Tergite of ultimate leg-bearing segment, dorso-lateral view. Abbreviations: **cxp** — coxopleural process; **dm** — dorsal margin of ultimate pleuron; **mds** — minute dark spine on ultimate pleuron; **sp** — spiracle; **tlk** — tergal lateral keel; **tm** — tergal margination; **tpk** — tergal paramedian keel. Scale bars: 5 mm (**A**); 2 mm (**B–D**); 0.5 mm (**E–G**).

(Fig. 6A, B); tergites 6 [5–7]–21 [22] with complete or nearly complete lateral marginations (Fig. 6A, B); 2 or 3 short longitudinal sulci present on posterior margin of several tergites.

Sternites sparsely punctate, lacking paramedian sutures (Fig. 6C). Sides of sternite of ultimate leg-bearing segment converging posteriorly, posterior margin slightly concave [slightly convex in KUZ Z4083] (Fig. 6E).

Ovoid spiracles present on leg-bearing segments 3, 5, 8, 10, 12, 14, 16, 18, 20 and 22 (Fig. 6D).

Legs almost lacking setae [sparse minute setae present in several specimens]; tarsi of legs 1–21 undivided; legs 1–20 with lateral and ventral tibial spurs and tarsal spur, leg 21 with tibial spur and tarsal spur; leg 22 with tarsal spur only; all legs with two accessory spines.

Coxopleuron approx. 1.5–1.7× as long as sternite of ultimate leg-bearing segment (Fig. 6E, F). Dorsal margin of ultimate pleuron protruding from lateral side of tergite of ultimate leg-bearing segment, dorso-posterior margin with minute dark spine (Fig. 6F, G). Posterior and ventral margins of coxopleuron converging posteriorly, forming approx. 60–75° angle; coxopleural process short, tip of process pointed, slightly directed dorsally (Fig. 6F). Surface of coxopleuron without setae, covered with various-sized coxal pores (Fig. 6F). Pore-free area present on coxopleural process and dorso-posterior area of coxopleuron (Fig. 6F).

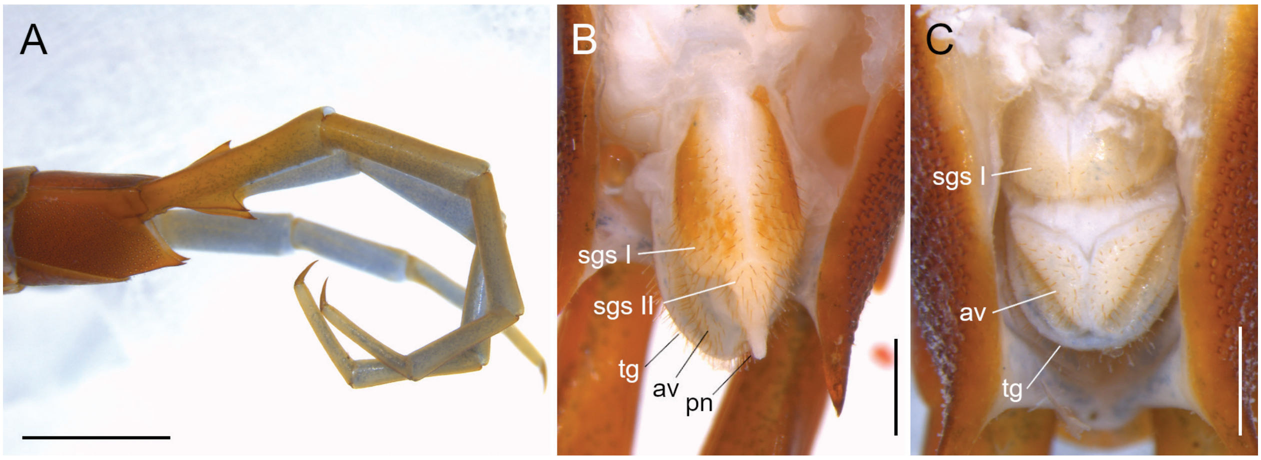

Figure 7. *Scolopocryptops quadristriatus* (Verhoeff, 1934) from near the type locality. **A.** KUZ Z5095; **B.** KUZ Z5094; **C.** KUZ Z5104. **A.** Left ultimate leg, lateral view; **B.** Male genital segments, penis and anal valves, ventral view; **C.** Female genital segment and anal valves, ventral view. Abbreviations: **av** — anal valve; **pn** — penis; **sgs I** — sternite of genital segment 1; **sgs II** — sternite of genital segment 2; **tg** — tergite of genital segment. Scale bars: 2 mm (**A**); 0.5 mm (**B, C**).

Ultimate leg 9.0–12.4 mm in length, approx. 0.3× as long as body; all articles almost lacking setae [tarsi with sparse minute setae]; prefemur with two conical and pointed spinous processes, ventral process larger than dorso-medial one; pretarsus with two accessory spines (Fig. 7A).

Genital segments occupying approx. 0.7–0.8× length of sternite of ultimate leg-bearing segment; tergite of genital segment covered with sparse minute setae (Fig. 7B, C). Sternite of genital segment 1 covered with sparse short setae, posterior margin weakly convex (Fig. 7B, C). Sternite of genital segment 2 well developed in male, covered with sparse short setae; posterior part of genital segment 2 overlapped by lamina subanalis, penis not visible in ventral view [penis visible in KUZ Z5094] (Fig. 7B); genital segment 2 not visible in female (Fig. 7C). Anal valves covered with sparse short setae (Fig. 7B, C).

Distribution. This species has been recorded from Honshu and the Izu Islands and is abundant in Tokyo and adjacent areas (Takakuwa 1939, 1940; Shinohara 1949; Takashima and Shinohara 1952; Takano 1973). Miyosi (1953) recorded *S. quadristriatus* from Nagasaki in Kyushu, but this species was not obtained during the survey conducted by the first author in Nagasaki and adjacent localities (25–27 July 2023).

Availability of "*quadristriatus*" based on Takakuwa's works. The name "*Otocryptops sexspinosus quadristriatus*", which was attributed to Verhoeff, was introduced by Takakuwa's two works (Takakuwa 1933a, b) before its formal description by Verhoeff in 1934. However, we herein decide that neither Takakuwa (1933a) nor Takakuwa (1933b) made the species-group name "*quadristriatus*" available. "*Otocryptops sexspinosus quadristriatus* Verh" first appeared in Takakuwa (1933a: 11), who intended to provide general anatomical features of *Scolopocryptops* (originally "*Otocryptops*"). Nonetheless, the detailed morphological features and figures provided in this work were unambiguously based on *S. rubiginosus* L. Koch, 1878 (referred as "*Otocryptops ruliginosus*" [sic]). Therefore, the name *quadristriatus* in the combination of *Otocryptops sexspinosus quadristriatus* in Takakuwa (1933a) did not satisfy the provision of Article 13.1 of the International Code of Zoological Nomenclature (hereinafter, Code; International Commission on Zoological Nomenclature 1999) and thus is unavailable.

In a synopsis of the Japanese centipedes, Takakuwa (1933b: 1459) provided a brief taxonomic account and morphological descriptions of the subspecies referred as "*Otocryptops sexspinosus quadristriatus* Verhoeff". However, Takakuwa considered that "*O. s. quadristriatus*" sensu Verhoeff was indistinguishable from the nominotypical subspecies "*O. s. sexspinosus*"; thus, he did not provide any description or definition that are purported to differentiate "*O. s. quadristriatus*" (see Article 13.1.1 of the Code). Therefore, we conclude that the species-group name *quadristriatus* in the combination of *Otocryptops sexspinosus quadristriatus* in Takakuwa (1933b) is also unavailable and the authorship of this nominal taxon is attributed to Verhoeff (1934), who established *O. s. quadristriatus* explicitly as a new subspecies. Moreover, according to Shinohara (1982, 1990), Takakuwa's (1933b) description of this taxon was based on specimen(s) misidentified as "*O. sexspinosus*"; *O. s. quadristriatus* sensu Takakuwa (1933b) was later described as *S. nipponicus* Shinohara, 1990 (placed in synonymy with *S. spinicaudus* by Shelley 2002).

Remarks. Verhoeff (1934) established this taxon as a subspecies of the North American *S. sexspinosus*, based on brief taxonomic accounts. He only described the absence of tergal paramedian sutures, the presence of four longitudinal keels on tergites and the colouration of head and leg-bearing segments.

Shinohara (1984) elevated *quadristriatus* to full species status, based on the following features: 1) cephalic marginal sulci reaching from postero-lateral margin of cephalic plate to antennae; 2) tergites without paramedian sutures and with four longitudinal keels; 3) arrangement of tibial and tarsal spurs on legs 19–23; and 4) a slightly slender "general form" compared with other species of the genus. It is unclear whether Shinohara compared *quadristriatus* with the North American *O. sexspinosus sexspinosus* or the Japanese "*O. sexspinosus*" (see above) and the characters of 1), 3) and 4) cannot conclusively distinguish *quadristriatus* from other species. Nonetheless, the presence of four longitudinal keels on tergites distinguishes *S. quadristriatus* from all other *Scolopocryptops* (except *S. longisetosus* sp. nov.; see below). The distinctness of *S. quadristriatus* is also supported by the molecular phylogenetic analyses (Fig. 13).

This species is absent from, but should be added to Chilobase 2.0 (Bonato et al. 2016).

Scolopocryptops longisetosus sp. nov.

https://zoobank.org/3BCC9F07-141D-4D15-8613-3CE08877C0A6

Figs 8–12

Suggested Japanese name: Kuromadara-akamukade

Scolopocryptops capillipedatus: Chao and Chang (2003: 4), fig. 17; Chao (2008: 76–80), figs 82–87; Chao and Chang (2008: 14), fig. 9.

Material examined. ***Holotype*:** Japan – Okinawa Prefecture – **Okinawa Island** • ♂, 31.4 mm (KUZ Z5107); Kunigami-son, Uka; 26°48.45'N, 128°15.97'E; approx. 300 m alt.; 4 May 2021; F. Okuyama leg. ***Paratypes*:** Japan – Okinawa Prefecture – **Okinawa Island** • 1, 24.6 mm (KUZ Z5108); Kunigami-son, Oku; 26°48.3'N, 128°17.34'E; approx. 230 m alt.; 5 May 2021; F. Okuyama leg. • 1 ♂, 30.7 mm (KUZ Z5112); Nago City, Mt. Nago-dake; 26°35.45'N, 128°0.25'E; approx. 200 m alt.; 14 June 2022; T. Jonishi leg. • 1, 29.4 mm (KUZ Z5113); same locality as for preceding; 26°35.47'N, 128°0.27'E; approx. 210 m alt.; 14 June 2022; T. Jonishi leg. • 1 ♀, 28.9 mm (KUZ Z5115); same locality as for preceding; 26°35.73'N, 128°0.19'E; approx. 190 m alt.; 14 June 2022; T. Jonishi leg. • 1 ♂, 31.1 mm (KUZ Z5117); Kunigami-son, Uka; 26°48.43'N, 128°16.04'E; approx. 330 m alt.; 15 June 2022; T. Jonishi leg. • 1 ♂, 37.2 mm (KUZ Z5119); Kunigami-son, Benoki; 26°48.06'N, 128°16.65'E; approx. 350 m alt.; 15 June 2022; T. Jonishi leg. • 1, 30.4 mm (KUZ Z5121); Kunigami-son, Yona, Mt. Fuenchiji; 26°45.15'N, 128°14.58'E; approx. 380 m alt.; 16 June 2022; T. Kato leg. • 1, 28.6 mm (KUZ Z5122); same locality as for preceding; 26°45.17'N, 128°14.58'E; approx. 380 m alt.; 16 June 2022; T. Jonishi leg.

Additional material. **Japan** – Okinawa Prefecture – **Okinawa Island** • 1 ♂, 30.2 mm (KUZ Z5109); Kunigami-son, Uka; 26°48.30'N, 128°16.11'E; approx. 320 m alt.; 4 Jan 2022; F. Okuyama leg. • 2 juveniles, approx. 10 mm (KUZ Z5110), 1 ♀, 24.4 mm (KUZ Z5111); Nago City, Mt. Nago-dake; 26°35.45'N, 128°0.25'E; approx. 200 m alt.; 14 June 2022; T. Jonishi leg. • 1, 23.4 mm (KUZ Z5114); same locality as for preceding; 26°35.47'N, 128°0.27'E; approx. 210 m alt.; 14 June 2022; T. Kato leg. • 1 ♀, 29.4 mm (KUZ Z5116); same locality as for preceding; 26°35.73'N, 128°0.19'E; approx. 190 m alt.; 14 June 2022; T. Kato leg. • 1, 24.5 mm (KUZ Z5118); Kunigami-son, Uka; 26°48.43'N, 128°16.04'E; approx. 330 m alt.; 15 June 2022; T. Jonishi leg. • 1, 27.2 mm (KUZ Z5120); Kunigami-son, Benoki; 26°48.04'N, 128°16.62'E; approx. 360 m alt.; T. Jonishi leg. – **Ishigaki Island** • 1, 19.9 mm (KUZ Z5123); Hirakubo; 24°35.01'N, 124°20.15'E; approx. 20 m alt.; 17 Dec 2021; F. Okuyama leg. – **Yonaguni Island** • 2 ♂, 27.8 mm (KUZ Z5124), 20.8 mm (KUZ Z5125); Mantabaru Forest Park; 24°27.39'N, 122°58.56'E; approx. 100 m alt.; 16 Apr 2022; Naoto Sawada leg. **Taiwan** • 1, 21.5 mm (KUZ Z5126); Hsinchu County, Wufeng Township, Shei-Pa National Park; 24°30.01'N, 121°4.61'E; 19 Mar 2019; T. Nakano leg. • 1, 22.2 mm (KUZ Z5127); Nantou County, Ren'ai Township; 24°5.1'N, 121°10.73'E; 21 Mar 2019; T. Nakano leg.

Type locality. Japan, Okinawa Prefecture, Okinawa Island, Kunigami-son, Uka (26°48.45'N, 128°15.97'E, approx. 300 m alt.).

Diagnosis. Antenna with sparse hairs and setae of various lengths dorsally on two basal articles, subsequent articles densely covered with long setae and minute setae. Cephalic plate with complete lateral marginal sulci. Tergites lacking paramedian sutures, tergites 5–20 with four longitudinal keels and median depression bordered by paramedian keels.

Description of holotype [data from other specimens given in square brackets]. Body length approx. 31.4 mm [19.9–37.2 mm] in 75% ethanol. Colour in life and in ethanol yellowish-brown with dark pigment on two basal antennal articles, purplish on subsequent articles; reddish-brown on forcipules; reddish-brown with dark pigment on lateral and posterior margins of cephalic plate, tergites 1, 22 and 23; brown with dark pigment on tergites 2–21; legs and ultimate legs brownish-yellow or orange with purplish dark pigment (Figs 8B, 10A, 11A).

Antennae 10.1 mm in length, approx. 0.3× as long as body, composed of 17 articles; dorsal surface of two basal articles with sparse hairs and setae (sensu Bonato et al. (2010)) of various lengths, subsequent articles densely covered with long setae and minute short setae [in small specimens, most setae from article 3 shorter than those of two basal articles] (Fig. 9A); setae emerging from various-sized collars. Cephalic plate as long as wide; its surface sparsely punctate with minute hairs, with complete lateral margination (Figs 9B, 10A).

Second maxillae article 2 with elongated and semi-transparent dorsal spur distally; dorsal brush with transparent margin; pretarsus consisting of dark brown basal and semi-transparent short apical parts (Fig. 10C, D). Forcipular coxosternite and trochanteroprefemur sparsely punctate, coxosternite with transverse sutures on anterior third of coxosternite; trochanteroprefemur with small and blunt black process and basal suture; anterior margin of coxosternite strongly sclerotised and slightly convex, divided into two low lobes by median diastema (Fig. 10E).

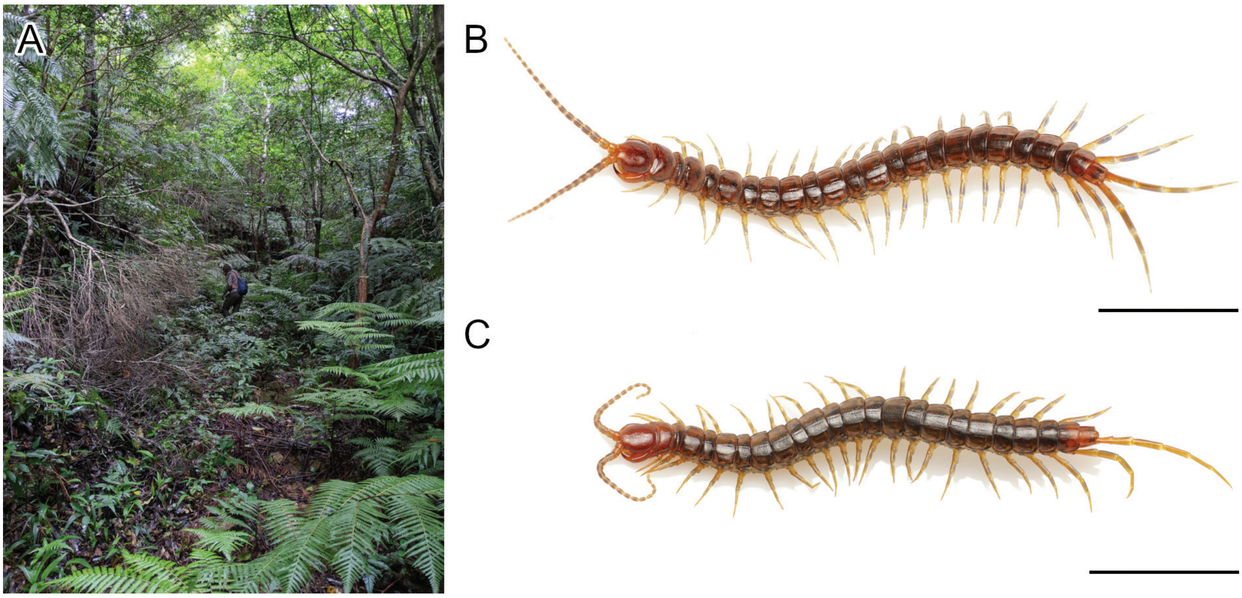

Figure 8. *Scolopocryptops longisetosus* sp. nov., paratype, ♂ (KUZ Z5119: **B**), non-type specimen from Yonaguni Island, ♂ (KUZ Z5124: **C**) and habitat near the type locality. **A.** Habitat (laurel tree forest) on Okinawa Island; **B, C.** Live specimen, dorsal view. Scale bars: 10 mm.

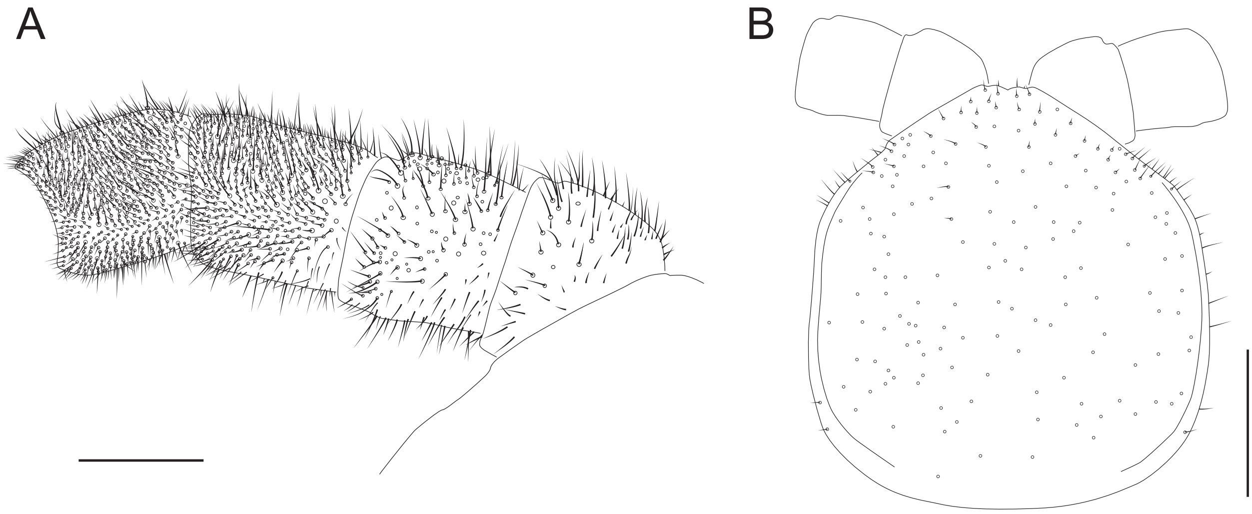

Figure 9. *Scolopocryptops longisetosus* sp. nov., holotype, ♂ (KUZ Z5107). **A.** Basal articles of left antenna, dorsal view; **B.** Cephalic plate, dorsal view. Scale bars: 0.5 mm (**A**); 1 mm (**B**).

Tergites sparsely punctate [sparse minute setae present in small individuals]; tergite 1 with anterior transverse suture, anterior margin overlapped by cephalic plate (Figs 10A, 11A). All tergites lacking paramedian sutures; tergites 5 [4]–21 [20] with longitudinal median depression bordered by paramedian keels, lateral keels present on tergites 5 [5–8]–20 [18–20]; median depression and keels unapparent on anterior and posterior tergites [depression and keels unapparent on all tergites in KUZ Z5119, Z5126 and Z5127] (Fig. 11A, B); lateral marginations complete or nearly complete on tergites 7 [5–7]–21 [22] (Fig. 11A, B); three short longitudinal sulci present on posterior margin of tergites 4, 6 [2 or 3 sulci present on tergites 3–21; absent in several specimens].

Sternites sparsely punctate, lacking paramedian sutures (Fig. 11C). Sides of sternite of ultimate leg-bearing segment converging posteriorly, posterior margin almost straight [slightly concave] (Fig. 11E).

Ovoid spiracles present on leg-bearing segments 3, 5, 8, 10, 12, 14, 16, 18, 20 and 22 (Fig. 11D).

Legs on anterior leg-bearing segments with sparse minute setae [setae denser in small individuals], posterior legs almost lacking setae [all legs setose in KUZ Z5123]; tarsi of legs 1–21 undivided; legs 1–19 with lateral and ventral tibial spurs and tarsal spur, legs 20 and 21, respectively, with tibial spur and tarsal spur; leg 22 without spurs. All legs with two accessory spines.

Coxopleuron approx. 1.8× [1.5–1.8×] as long as sternite of ultimate leg-bearing segment (Fig. 11F).

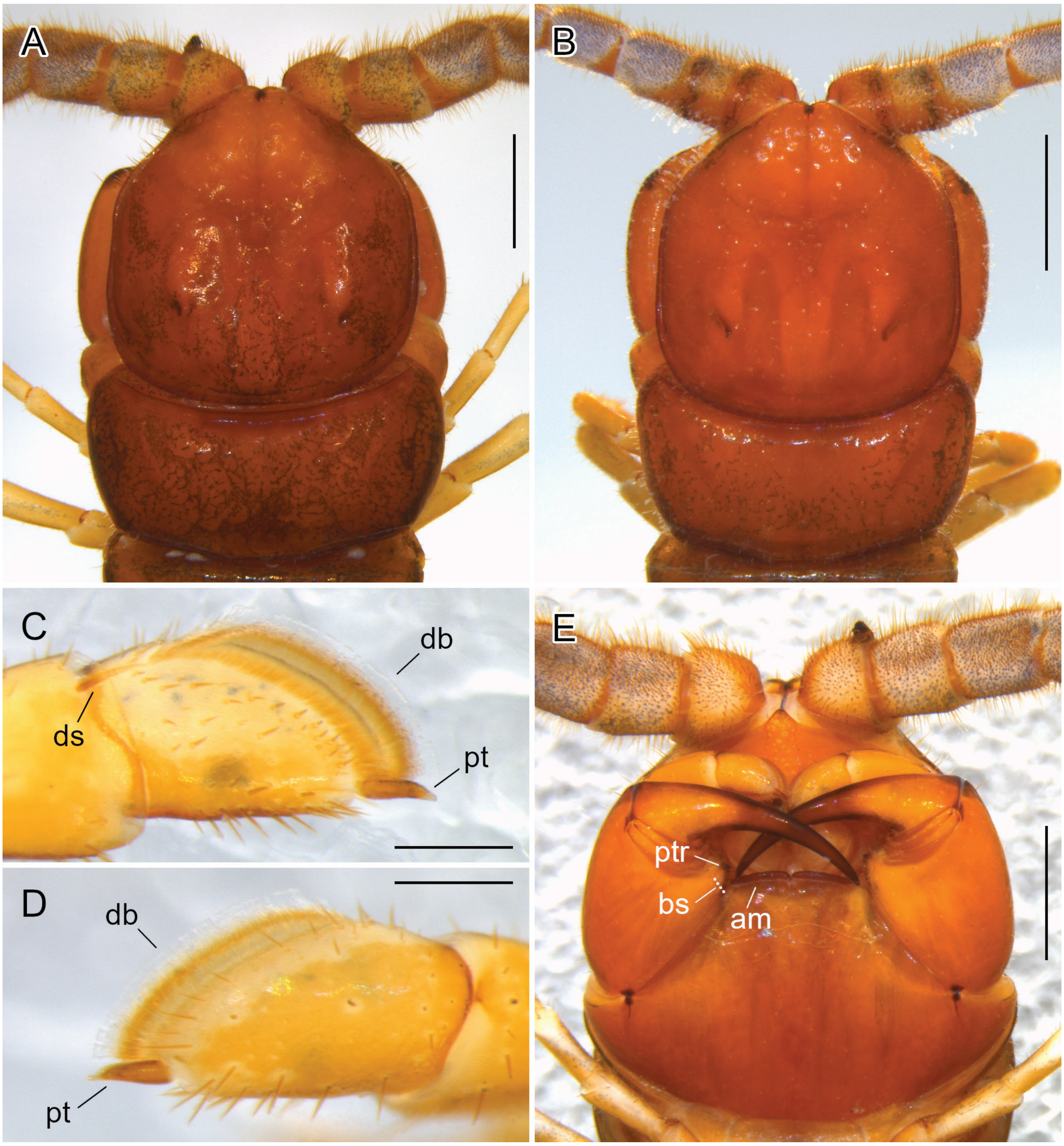

Figure 10. *Scolopocryptops longisetosus* sp. nov., holotype, ♂ (KUZ Z5107: **A, C–E**) and non-type specimen from Yonaguni Island, ♂ (KUZ Z5124: **B**). **A, B.** Cephalic plate and tergite 1, dorsal view; **C.** Distal part of article 2, article 3 and pretarsus of left second maxilla, medial view; **D.** Article 3 and pretarsus of left second maxilla, lateral view; **E.** Head, ventral view. Abbreviations: **am** — anterior margin of forcipular coxosternite; **bs** — basal suture on forcipular trochanteroprefemoral process; **db** — dorsal brush on article 3 of second maxilla; **ds** — dorsal spur on article 2 of second maxilla; **pt** — pretarsus of second maxilla; **ptr** — process of forcipular trochanteroprefemur. Scale bars: 1 mm (**A, B, E**); 0.2 mm (**C, D**).

Dorsal margin of ultimate pleuron protruding from lateral margin of tergite of ultimate leg-bearing segment, dorso-posterior margin with minute dark spine (Fig. 11F, G). Posterior and ventral margins of coxopleuron converging posteriorly, forming approx. 60° [60–65°] angle; coxopleural process short, tip of process pointed, slightly directed dorsally (Fig. 11F). Surface of coxopleuron without setae, covered with various-sized coxal pores (Fig. 11F). Pore-free area present on coxopleural process and dorso-posterior region of coxopleuron (Fig. 11F).

Ultimate leg 10.8 mm in length, approx. 0.3× [0.3–0.37×] as long as body; prefemur, femur and tibia almost lacking setae, tarsi with sparse minute setae [tarsi almost lacking setae]; prefemur with two conical and pointed spinous processes, ventral process larger than dorso-medial one; pretarsus with two accessory spines (Fig. 12A).

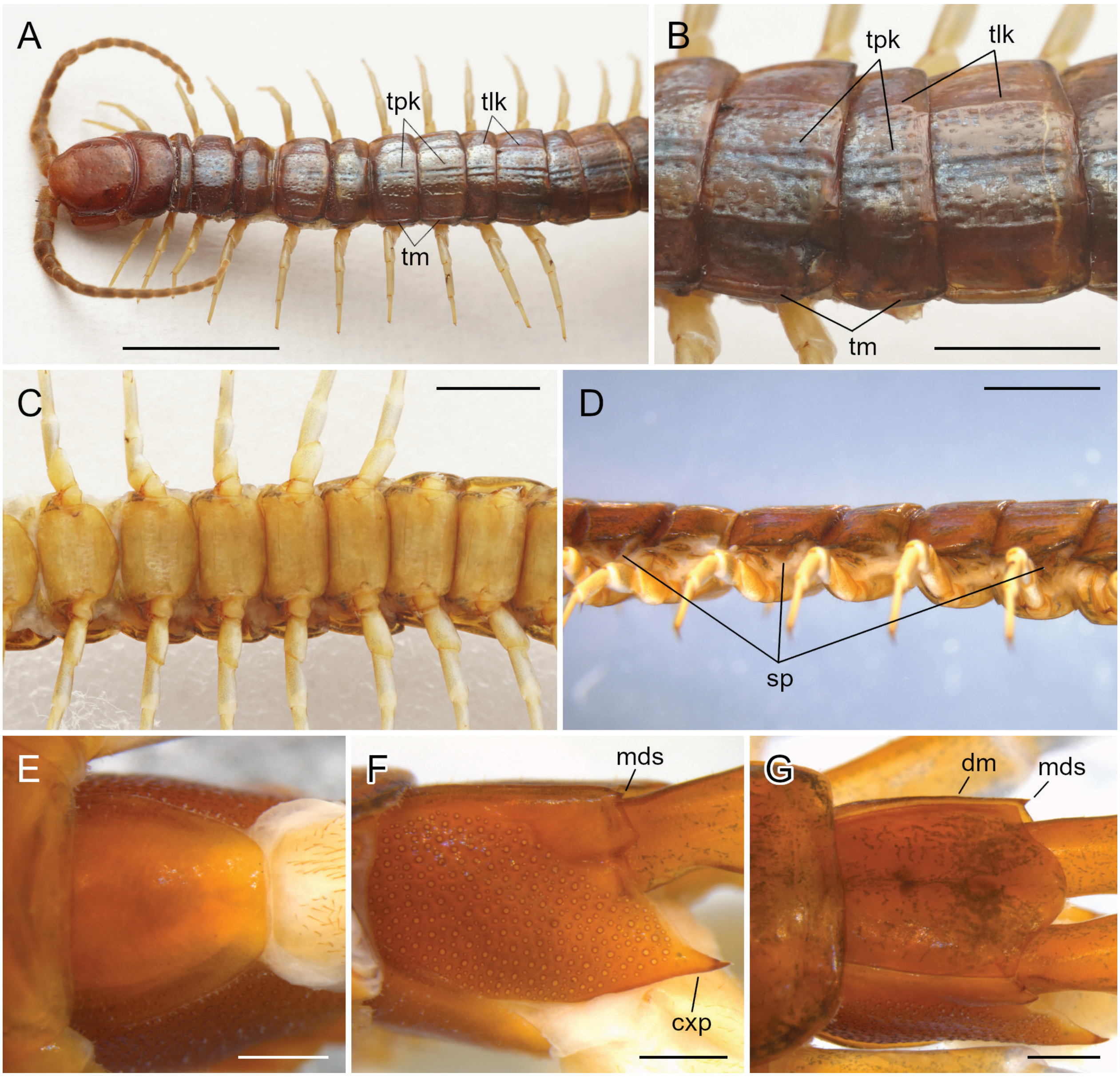

Figure 11. *Scolopocryptops longisetosus* sp. nov., holotype, ♂ (KUZ Z5107). **A.** Cephalic plate and tergites 1–12, dorso-lateral view; **B.** Tergites 10–12, dorso-lateral view; **C.** Sternites 6–12, ventral view; **D.** Leg-bearing segments 3–8, lateral view; **E.** Sternite of ultimate leg-bearing segment, ventral view; **F.** Left coxopleuron, lateral view; **G.** Tergite of ultimate leg-bearing segment, dorso-lateral view. Abbreviations: **cxp** — coxopleural process; **dm** — dorsal margin of ultimate pleuron; **mds** — minute dark spine on ultimate pleuron; **sp** — spiracle; **tlk** — tergal lateral keel; **tm** — tergal margination; **tpk** — tergal paramedian keel. Scale bars: 5 mm (**A**); 2 mm (**B–D**); 0.5 mm (**E–G**).

Genital segments occupying approx. 0.8× length of sternite of ultimate leg-bearing segment; tergite of genital segment sparsely setose (Fig. 12C, D). Sternite of genital segment 1 sparsely covered with setae, posterior margin slightly convex (Fig. 12C, D). Sternite of genital segment 2 well developed, covered with sparse setae; penis visible in ventral view; anal valves covered with sparse setae [in female, genital segment 1 as described for holotype; genital segment 2 not visible; anal valves as described for holotype] (Fig. 12C–E).

Variation. In specimens from the southern Ryukyus (Ishigaki and Yonaguni Islands; KUZ Z5123–Z5125) and Taiwan (KUZ Z5126, Z5127), dark pigment on cephalic plate absent or almost reduced (Figs 8C, 10B); ultimate leg with femur [tibia] and subsequent articles densely setose [setae relatively sparse in KUZ Z5127] (Fig. 12B).

Etymology. The specific name is derived from the Latin compound adjective, "longus" (long) and "setosus" (hairy), referring to the long antennal setae of this new species.

Distribution. This species is known from Okinawa, Ishigaki and Yonaguni Islands in the Ryukyu Islands, Japan and is also widespread in Taiwan.

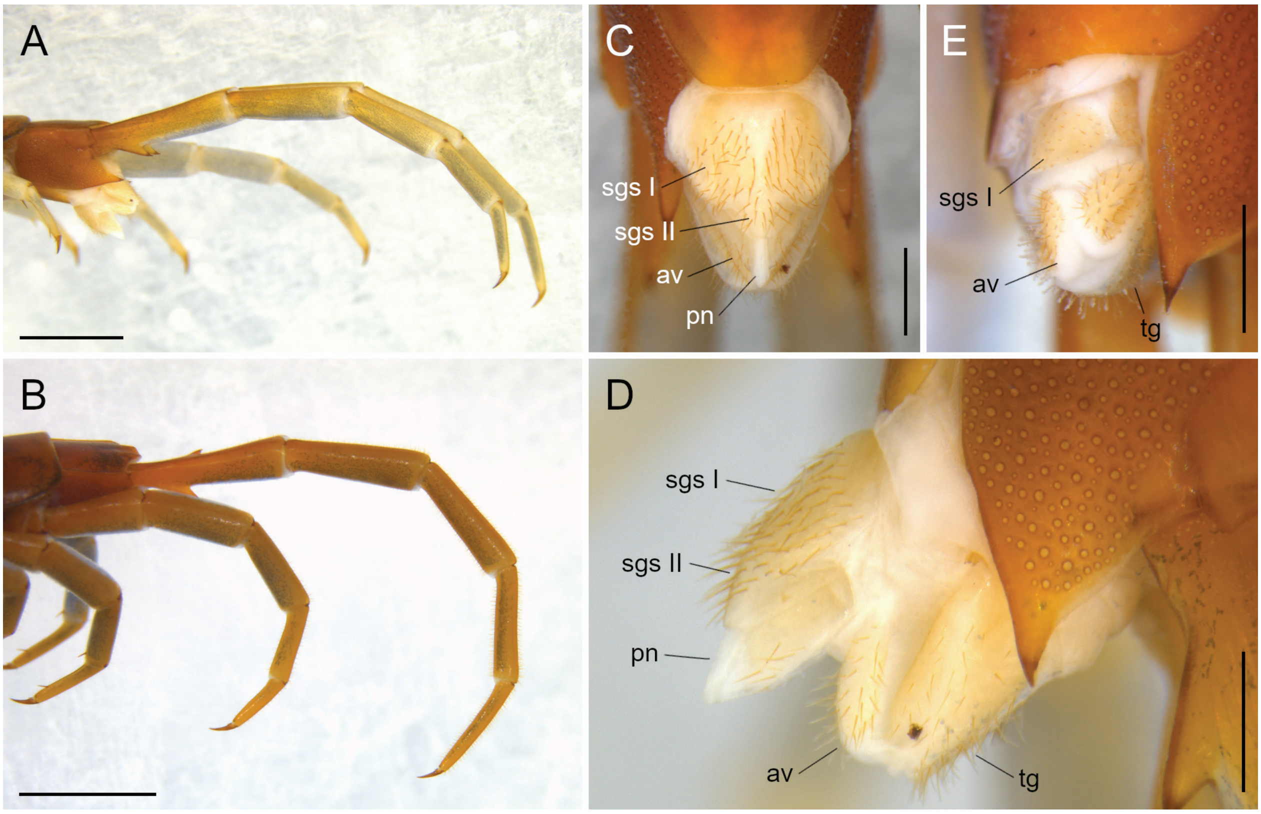

Figure 12. *Scolopocryptops longisetosus* sp. nov**.**, holotype, ♂ (KUZ Z5107: **A, C, D**); non-type specimen from Yonaguni Island, ♂ (KUZ Z5124: **B**); paratype, ♀ (KUZ Z5115: **E**). **A, B.** Left ultimate leg, lateral view; **C.** Male genital segments, penis and anal valves, ventral view; **D.** Male genital segments, penis and anal valves, lateral view; **E.** Female genital segment and anal valves, ventral view. Abbreviations: **av** — anal valve; **pn** — penis; **sgs I** — sternite of genital segment 1; **sgs II** — sternite of genital segment 2; **tg** — tergite of genital segment. Scale bars: 2 mm (**A, B**); 0.5 mm (**C–E**).

Remarks. This species resembles *S. quadristriatus*, but *S. longisetosus* sp. nov. can be distinguished by the presence of long antennal setae (vs. setae short in *S. quadristriatus*; also see the Identification key provided in the Discussion).

The phylogenetic analyses indicate that specimens of this species from Taiwan have been misidentified as *S. capillipedatus*, based on the dense setae on ultimate legs (Chao and Chang 2003, 2008; Chao 2008). However, *S. longisetosus* sp. nov. can be distinguished from *S. capillipedatus* by the presence of longitudinal keels and median depression on tergites.

Molecular phylogeny and genetic distances. The ML (ln *L* = –14816.13; not shown) and BI (mean ln *L* = –14846.27; Fig. 13) trees had almost identical topologies. In the Asian/North American group (UFBoot = 100%, BPP = 1.0), both the *elegans* lineage (UFBoot = 100%, BPP = 1.0) and the ex-*elegans* lineage (UFBoot = 98%, BPP = 1.0) were recovered as monophyletic groups. Within the latter lineage, the recovery of *S. quadristriatus* (UFBoot = 100%, BPP = 1.0) and *S. longisetosus* sp. nov. (UFBoot = 100%, BPP = 1.0) was strongly supported.

Although the interspecific relationships remained largely undetermined, the analyses showed that *S. longisetosus* sp. nov. is sister to a clade comprising three of the Japanese nominal species, *S. ogawai* Shinohara, 1984, *S. musashiensis* Shinohara, 1984 and "*S. nipponicus*" sensu Edgecombe et al. (2012) (UFBoot = 99%, BPP = 1.0) (Fig. 13).

In the preliminary analyses using the COI dataset, four sequences of "*S. capillipedatus*" from Taiwan (AB617528–AB617530, AB672646) were nested within *S. longisetosus* sp. nov. (UFBoot = 98%, BPP = 0.99; Suppl. material 3), but the relationships amongst populations were not resolved. In contrast, the concatenated analyses recovered two lineages within *S. longisetosus* sp. nov., which corresponded to the specimens from Okinawa Island (UFBoot = 100%, BPP = 1.0) and those from the southern Ryukyu Islands and Taiwan (UFBoot = 98%, BPP = 0.99). The COI pairwise distances within each lineage were 2.56–4.74% (Okinawa Island) and 4.89–9.17% (southern Ryukyus and Taiwan; including the sequences of Taiwanese "*S. capillipedatus*"). The divergence between the two lineages was 5.77–8.87% (Suppl. material 2).

Discussion

In the obtained phylogenetic trees, *S. quadristriatus* and *S. longisetosus* sp. nov. were strongly supported as monophyletic lineages. The analyses indicated that *S. longisetosus* sp. nov. comprises two lineages: Okinawa Island and the southern Ryukyus-Taiwan. These lineages differ in two external features, i.e. the presence/absence of dark pigment

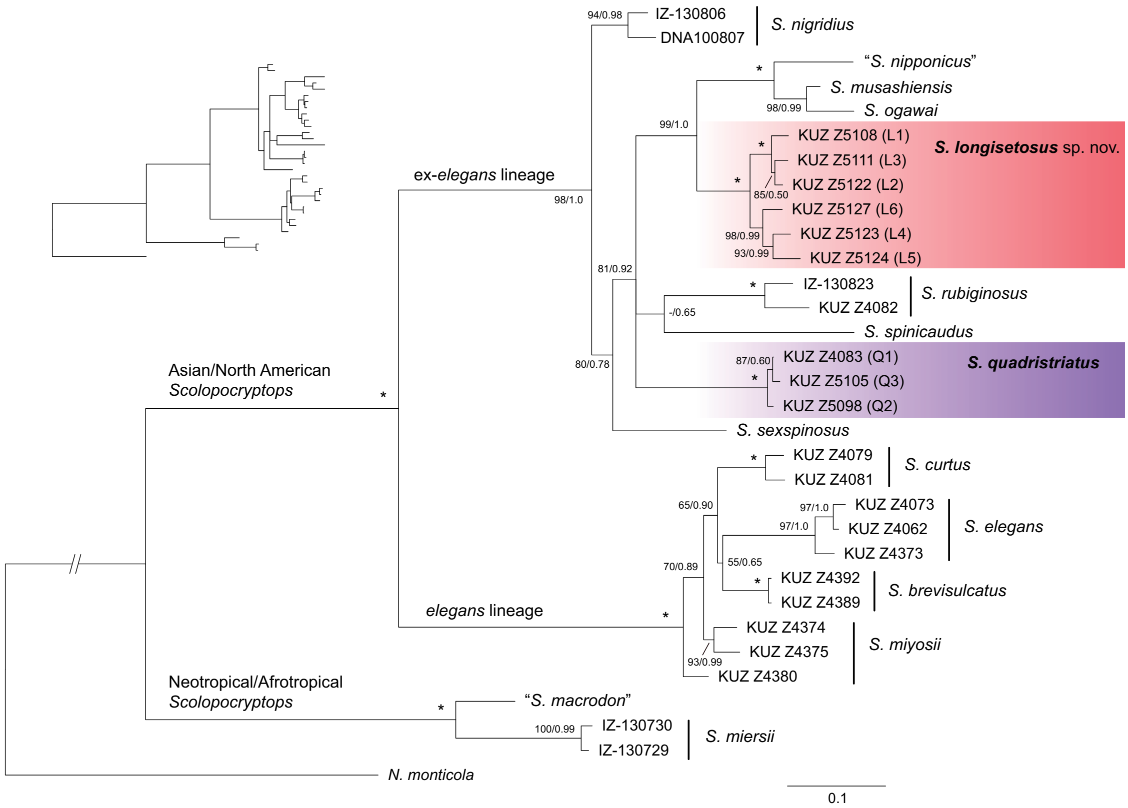

Figure 13. Bayesian Inference tree for 2510 bp-aligned positions of the ITS2, 28S, 16S and COI sequences. Real branch length is shown on the upper left. Numbers on nodes indicate ultrafast bootstrap values (UFBoot) and Bayesian posterior probabilities (BPP). An asterisk denotes the node with UFBoot = 100% and BPP = 1.0. Locality numbers (Q1–Q3 and L1–L6) are shown in Fig. 1 and Table 1.

on the cephalic plate and the density of setae on ultimate legs. However, the pigmentation is subject to intraspecific variation in this genus and other scolopendromorph taxa and the density of the ultimate leg setae is also variable within *Scolopocryptops* species (e.g. Lewis (2003); Le et al. (2023)). It should be noted that the body lengths of the specimens from the southern Ryukyus and Taiwan (19.9–27.8 mm) were generally smaller than those from Okinawa Island (23.4–37.2 mm; juveniles excluded). Nonetheless, body length difference is not considered a taxonomic character here because it may be the result of different growth rates under different habitats (as speculated on *Cryptops* species; Lewis (2007)) or simply due to sampling bias. Additionally, because the COI genetic distances between the two lineages (5.77–8.87%) fell within the intraspecific divergence of *Scolopocryptops* (Garrick et al. 2018) and is smaller than the divergence amongst the sequences from the southern Ryukyus and Taiwan (4.89–9.17%), all the specimens from the Ryukyu Islands and Taiwan are considered a single species, *S. longisetosus* sp. nov.

It is noteworthy that four COI sequences of "*S. capillipedatus*" from Taiwan belonged to *S. longisetosus* sp. nov. (Suppl. material 3). *Scolopocryptops capillipedatus*, which is characterised by the dense setae on femur and subsequent articles of ultimate legs, was originally described from South Korea and has been recorded from Japan, Taiwan and Vietnam (Takakuwa 1938; Miyosi 1971; Chao and Chang 2003, 2008; Chao 2008; Le et al. 2023). Chao (2008) provided a description of Taiwanese "*S. capillipedatus*" and noted that there were numerous long setae densely covering the femur, tibia and tarsi of the ultimate leg. However, this nominal species is clearly distinct from *S. longisetosus* sp. nov. because tergal keels are absent in *S. capillipedatus* (Takakuwa 1938, 1940). Although Chao (2008) did not mention the presence or absence of tergal keels, our specimens from Taiwan (KUZ Z5126 and Z5127) exhibited the characteristic longitudinal keels on tergites. The present result thus indicates that the records of "*S. capillipedatus*" from Taiwan were based on misidentified specimens of *S. longisetosus* sp. nov. Chao (2008) also described an unapparent median suture on tergites 1–3, which was not observed in our specimens, but described in Takakuwa's (1938) original description of *S. capillipedatus*. Morphological variability amongst Taiwanese populations needs to be examined, based on further taxon sampling.

Scolopocryptops longisetosus sp. nov. is quite similar to *S. quadristriatus* because they both have four longitudinal keels and median depression on tergites, as well as dark pigmentation on antennae and the dorsal surface of the body. Despite their phenotypic similarities, phylogenetic analyses did not support their sister relationship, but united *S. longisetosus* sp. nov. with three Japanese nominal species, *S. ogawai*, *S. musashiensis* and "*S. nipponicus*", which lack tergal keels (Fig. 13). The obtained phylogeny thus indicates that the longitudinal keels on tergites evolved in parallel within *Scolopocryptops* or that the presence of keels represents a plesiomorphic character of the clade comprising these species. Within *Scolopocryptops*, the tergal keels and median depression are unique to these two species and *S. hoanglieni* Le, Schileyko & Nguyen, 2023, which bears "'drop-like' longitudinal median depression bordered by paramedian keels" (Le et al. 2023). However, the phylogenetic implication of the tergal keels remains uncertain because the phylogenetic position of *S. hoanglieni* is undetermined (Le et al. 2023).

It is also notable that all members of the ex-*elegans* lineage, except *S. rubiginosus*, lack complete paramedian sutures on tergites (Shinohara 1984, 1990; Shelley 2002; Le et al. 2023), whereas all species of the *elegans* lineage and most of the Neotropical/Afrotropical species bear complete paramedian sutures (e.g. Chagas-Jr (2008); Chagas-Jr et al. (2023); Jonishi and Nakano (2023); Le et al. (2023)). Nonetheless, the evolutionary history of their paramedian sutures and the tergal keels remains unclear because the analyses failed to reconstruct a robust phylogeny of the ex-*elegans* lineage. Further systematic studies, for example, phylogenetic analyses using a larger taxon set including data from additional loci, need to be conducted to reveal the morphological evolution of *Scolopocryptops* species.

An identification key to *Scolopocryptops* species of East Asia

Diagnostic characters and known localities mainly follow Le et al. (2023), but were updated, based on Jonishi and Nakano (2023) and the present study.

1 Leg-bearing segment 7 with well-developed spiracles 2
– Leg-bearing segment 7 lacking spiracles 3
2 Tergite of ultimate leg-bearing segment with median suture *S. broelemanni broelemanni* Kraepelin, 1903 (eastern China)
– Tergite of ultimate leg-bearing segment lacking median suture .... *S. broelemanni esulcatus* Attems, 1938 (southern Vietnam)
3 Cephalic plate with complete lateral margination 9
– Cephalic plate lacks lateral margination or margination is much shortened 4
4 Length of the ultimate leg up to 40% of body length ..... *S. zhijiensis* Qiao, Xiao & Di, 2021 (southern China)
– Length of the ultimate leg less than 30% of body length 5
5 Coxosternite with anterior margin concave, tergites without lateral margination ..... *S. melanostoma* Newport, 1845 ("Neotropical/Afrotropical" species recorded from Lanyu Island in Taiwan and southern Vietnam) (Chao and Chang 2003; Chao 2008)
– Coxosternite with anterior margin convex or almost straight, tergites 6–21 or 20 with lateral marginations 6
6 Only basalmost antennal article with sparse minute setae or all articles densely setose; coxopleural process moderately long ..... *S. elegans* (Takakuwa, 1937) (Honshu and Shikoku in Japan)
– Several basal antennal articles with sparse minute setae; coxopleural process short 7
7 Cephalic plate lacks lateral margination; dorsal margin of ultimate pleuron not protruding from tergite of ultimate leg-bearing segment ..... *S. curtus* (Takakuwa, 1939) (southern Ryukyu Islands in Japan and Taiwan)
– Cephalic plate with short lateral margination; dorsal margin of ultimate pleuron slightly protruding from tergite of ultimate leg-bearing segment 8
8 Three or two basal antennal articles with sparse minute setae; sclerotised bands on anterior margin of coxosternite almost reaching outer part ..... *S. miyosii* Jonishi & Nakano, 2023 (Kyushu and Amami Island in Japan)
– Four basal antennal articles with sparse minute setae, sclerotised bands on anterior margin of coxosternite not reaching outer part ..... *S. brevisulcatus* Jonishi & Nakano, 2023 (Okinawa Island and adjacent islet in Japan)
9 Length of the ultimate leg more than 40% of body length; tarsus 1 and 2 of leg 22 each with well-developed spur ..... *S. longipes* Xiao, Chen & Di, 2021 (southern China)
– Length of the ultimate leg approx. 30% of body length or less; leg 22 mostly with 1 tarsal spur or lacking spur 10
10 Tergites with complete paramedian sutures ..... *S. rubiginosus* L. Koch, 1878 (China, Korea, Japan, Taiwan and Vietnam)
– Tergites without complete paramedian sutures 11
11 Tergites with median depression bordered by paramedian keels 12
– Tergites without median depression 14
12 Tergites with drop-like median depression; lateral keels absent ..... *S. hoanglieni* Le, Schileyko & Nguyen, 2023 (northern Vietnam)
– Tergites with longitudinal median depression; lateral keels present 13
13 Antennal articles covered with short setae ..... *S. quadristriatus* (Verhoeff, 1934) (Honshu in Japan)
– Antennal articles covered with long setae and short setae . *S. longisetosus* sp. nov. (Ryukyu Islands in Japan and Taiwan)
14 Two basal antennal articles sparsely setose dorsally; tibia and tarsus of ultimate leg densely setose ..... *S. capillipedatus* (Takakuwa, 1938) (Korea, Japan, and Vietnam) + *S. ogawai* Shinohara, 1984 (Japan) + *S. musashiensis* Shinohara, 1984 (Japan) (see Le et al. (2023))
– Two basal antennal articles almost lacking setae dorsally; distal articles of ultimate legs mostly not setose ..... *S. spinicaudus* Wood, 1862 (China, Korea, Japan, Taiwan, Vietnam) + "*S. nipponicus*" Shinohara, 1990 (Japan) (see Le et al. (2023))

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Supplementary material 1

Selected partitioning schemes and substitution models for the phylogenetic analyses

Authors: Taro Jonishi, Takafumi Nakano
Data type: xls

Link: https://doi.org/10.3897/zse.100.119297.suppl1

Supplementary material 2

Uncorrected pairwise distances for 654 bp of the COI sequences of *Scolopocryptops longisetosus* sp. nov.

Authors: Taro Jonishi, Takafumi Nakano
Data type: xls

Link: https://doi.org/10.3897/zse.100.119297.suppl2

Supplementary material 3

Bayesian Inference tree

Authors: Taro Jonishi, Takafumi Nakano
Data type: pdf
Explanation note: Bayesian Inference tree (mean ln L = –5113.28) for 654 bp of the COI sequences. Numbers on nodes indicate ultrafast bootstrap values and Bayesian posterior probabilities. Locality numbers (Q1–Q3 and L1–L6) are shown in Fig. 1 and Table 1.

Link: https://doi.org/10.3897/zse.100.119297.suppl3