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Taxonomic Assessment of a Threatened Large Millipede Endemic to the Southern Ryukyu Islands, Japan: a New Species of *Spirobolus* (Diplopoda: Spirobolida: Spirobolidae) from the Yaeyama Islands

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The taxonomic status of millipedes of the genus *Spirobolus* Brandt, 1833, referred to as "Yaeyama-maruyasude" from the Yaeyama Islands, Ryukyu Islands, Japan, was unresolved. We assess the taxonomic status of these Yaeyama *Spirobolus* sp. using an integrated morphological and molecular approach, and describe them as a new species, *S. akamma* sp. nov., for which partial sequences of the nuclear 28S ribosomal RNA, mitochondrial cytochrome *c* oxidase subunit I, and 16S ribosomal RNA markers are provided. This new species differs from continental China and Taiwan endemic congeners in anterior gonopod morphology (in having an elongate and subtriangular coxa, and a pentagonal mesal sternal process), posterior gonopod morphology (in having a coronoid prefemoral endite with rounded distal end, and an elongate telopodite), and in having four serrations on the cyphopod lateral flange.

Key Words: Myriapoda, Juliformia, arboreal, threatened species, SEM images.

Introduction

Millipedes of the genus *Spirobolus* Brandt, 1833 are large and indigenous to China and Taiwan (Enghoff et al. 2015). In the 19th century when this genus was treated "in much the same sense that the order Spirobolida is used today" (Keeton 1960: 5) it comprised in excess of 100 species distributed almost globally (see Sierwald and Spelda 2021). However, a 1960s review of this genus recognized only five species, the distribution of which was limited to China and Taiwan (Keeton 1960). Subsequent to Keeton's review, one species was described from southeastern China (Wang and Zhang 1993); all recognized species were endemic to East Asia. The type species of the genus, *S. bungii* Brandt, 1833, found in China, was fixed by subsequent designation (Pocock 1894). Additionally, four more species and one subspecies were described from Taiwan (Hsu 2008), but nonetheless, the master thesis (Hsu 2008) is not regarded as published within the meaning of the International Code of Zoological Nomenclature (M. J. Grygier, personal communication; also see the amended Articles 8.1 and 9.12 of the Code; International Commission on Zoological Nomenclature 1999, 2012). The five species-group names introduced by Hsu (2008), i.e., *S. formosae* "semiflavus", *S.* "panmaus", *S.* "taimalius", *S.* "redpodus" and *S.* "lienhuachihus", are thus deemed to be unavailable.

Taiwan had been considered the easternmost distribution limit of *Spirobolus* millipedes (Korsós 2004; Hsu 2008) until one taxon was reported from the Yaeyama Islands, ~240 km east of Taiwan, in the Ryukyu Islands chain of Japan (Nakamura and Korsós 2010). This Yaeyama *Spirobolus* millipede had been earlier referred to as *Polyconoceras* sp. or *Acladocricus* sp. (e.g., Omine 1962; Omine et al. 1982) and *Prospirobolus joannisi* (Brölemann, 1896) (a junior synonym of *S. bungii*; Keeton 1960) (e.g., Ikehara et al. 1974; Kikunaga et al. 1993), but was considered by Takano (1989) to be an undescribed *Spirobolus* species, the preliminary taxonomic account of which was followed by successors (Tanabe 2001; Omine 2002; Chigira and Tanaka 2004; Nakamura and Korsós 2010; Shinohara et al. 2015). Not only was this Yaeyama *Spirobolus* species considered to be undescribed, but it was also considered to be threatened, having been first listed as a "Threatened Local Population (LP)" in the Red Data Book of Okinawa Prefecture, Japan, published by the Nature Conservation Division, Department of Cultural & Environmental Affairs, Okinawa Prefectural Government (hereafter "NCD Okinawa") (NCD Okinawa 2005, 2017), and then as "Vulnerable (VU)" in the Japanese Red List since 2006 (Ministry of the Environment 2010, 2012, 2014).

The Yaeyama Islands are located at the southwesternmost area of Japanese territory, and thus they are proximally very

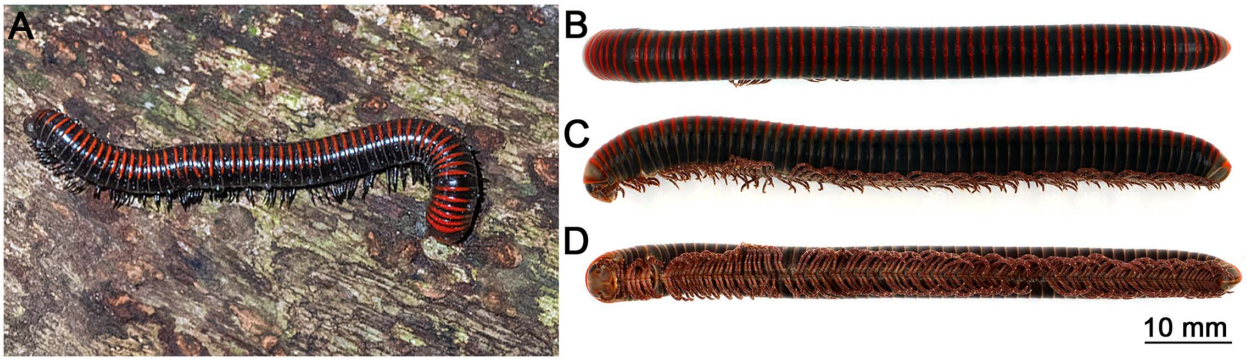

Fig. 1. *Spirobolus akamma* sp. nov., an individual from near the Mariudo Waterfall, Iriomote Island (A), and holotype male (KUZ Z4329; B–D). A, In situ habitus (photograph taken by N. Sawada); B, dorsal view; C, lateral view; D, ventral view.

close to Taiwan and China. Because close relationships between terrestrial vertebrate (see Toda et al. 2003) and invertebrate (e.g., Lai et al. 2011; Morino 2014; Sawada et al. 2021) taxa from the southern Ryukyu Islands and Taiwan, including millipedes, e.g., *Trigoniulus tertius* Takakuwa, 1940 (Takakuwa 1954; Korsós 2004; Shinohara et al. 2015), are known, we had to resolve the taxonomic status of the Yaeyama *Spirobolus* sp. to determine if it was distinct from the Chinese or Taiwanese congeners. This would enable both a more accurate assessment of its extinction risk to be made, and the identification of appropriate conservation strategies. We apply an integrated taxonomic approach involving morphology and molecular analyses of newly collected Yaeyama *Spirobolus* sp. specimens to resolve the taxonomic status of this species, which we describe as new herein. Partial DNA sequences are provided to aid future phylogenetic studies of relationships among taxa in the Yaeyama Islands, Taiwan, and in continental China.

Materials and Methods

Samples and morphological examination. *Spirobolus* millipedes (Fig. 1A) were collected from Ishigaki and Iriomote islands, the Yaeyama Islands in the southern Ryukyu Islands, Japan, in 2019 and 2022. Specimens were fixed and preserved in ~80% ethanol. In the laboratory, the legs of some specimens were removed to extract DNA.

Specimen examination, dissection, and drawing were performed using a stereoscopic microscope with a drawing tube (Leica M125C). Images were captured using a Leica MC170 HD digital camera mounted on the Leica M125C and prepared using Leica Application Suite v. 4.12 software. The antenna, mandible, and posterior gonopod of two specimens were dehydrated through a graded ethanol series, and dried using hexamethyldisilazane (Nation 1983). Samples were then sputter-coated with gold (JEOL Ltd., JFC-1200 Fine Coater) and observed by scanning electron microscopy (JEOL Ltd., JSM-5800LV).

Specimens examined in this study have been deposited in the Zoological Collection of Kyoto University (KUZ).

PCR, DNA sequencing and analyses. One nuclear and two mitochondrial markers [28S rRNA, cytochrome *c* oxidase subunit I (COI), and 16S rRNA] were obtained from three paratypes: two from Ishigaki Island, and one from Iriomote Island. Methods for genomic DNA extraction, polymerase chain reactions, and cycle sequencing reactions are as described by Kato et al. (2022). Seven newly obtained sequences have been deposited in the International Nucleotide Sequence Databases (INSD) through the DNA Data Bank of Japan.

Pairwise comparison of uncorrected *p*-distances for COI sequences of the new species (658 bp) and two congeners were calculated using MEGAX (Kumar et al. 2018), with pairwise deletion of missing data. COI sequences of *S. bungii* (658 bp, obtained from the complete mitochondrial genome sequence; INSD accession number MT767838) and *Spirobolus* sp. (583 bp; INSD accession number OP104941) were included in the analyses.

Taxonomy

Family **Spirobolidae** Bollman, 1893
Genus ***Spirobolus*** Brandt, 1833
Spirobolus akamma sp. nov.
[Japanese name: Yaeyama-maruyasude]
(Figs 1–8)

Polyconoceras sp.: Omine 1962: 1, 6 (list; as *Polyconoxcerus* [sic] sp.); Omine 1965a: 48, fig. 7 (as *Polyconoceros* [sic] sp.).

Polyconoceras callosus (Karsch, 1881): Omine 1965b: table 1 (list; as *Polyconcerus* [sic] *callosuesp* [sic]).

Spirobolus joannisi Brölemann, 1896: Ikehara et al. 1974: table 1 (list; as *Spirobolus joannisu* [sic]).

Prospirobolus joannise [sic]: Ikehara and Shimojana 1975: 125, one text-fig.; Kikunaga et al. 1993: 91 (list); Yokotsuka 2002: 242, one text-fig.; Yokotsuka 2004: 242, one text-fig.; Yokotsuka 2011: 242, one text-fig.

Acladocricus sp.: Omine et al. 1982: 119, 121, photo 5.

Spirobolus sp.: Takano 1989: 4, fig. 1; Murakami 1993: 98 (list); Tanabe 2001: frontispiece 5; Omine 2002: 157, 161, table 5; Chigira and Tanaka 2004: 16 (list), photo 18; Tanabe in NCD Okinawa 2005: 306; Takano in Ministry of the Environment 2010: 5; Nakamura and Korsós 2010:

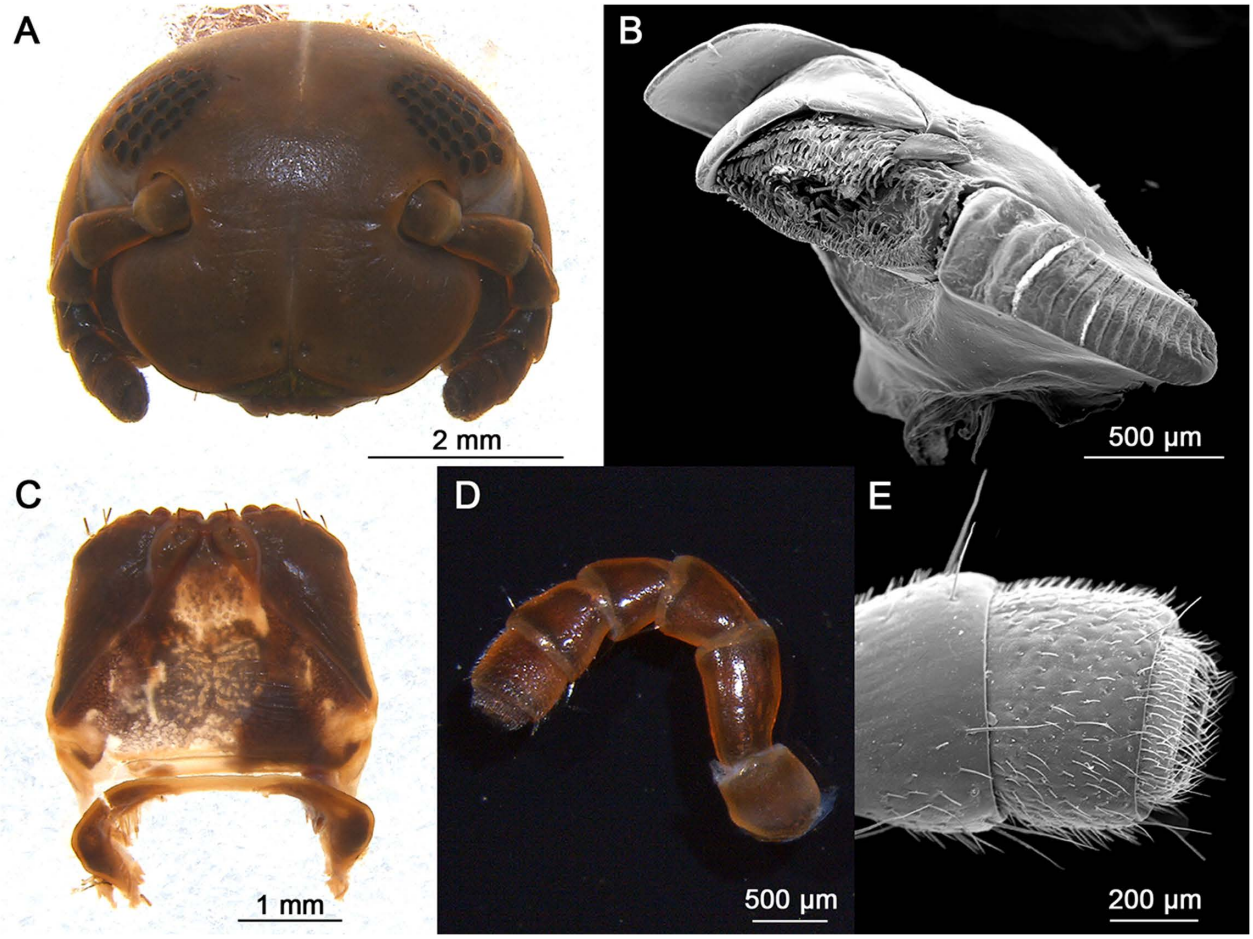

Fig. 2. *Spirobolus akamma* sp. nov., paratype male (KUZ Z4328; A, C), paratype female (KUZ Z4332; B), and holotype male (KUZ Z4329; D, E). A, Head, frontal view; B, right mandible, mesal view; C, gnathochilarium, ventral view; D, right antenna, sub-mesal view; E, antennomeres V–VII of left antenna, sub-mesal view.

79, 81 (list); Takano in Ministry of the Environment 2014: frontispiece 2, 56; Shinohara et al. 2015: 981, one photo; Nakamura in NCD Okinawa 2017: 36, one photo, 419; Horii 2020: 122, one text-fig.

Diagnosis. The new species is characterized by the following combination of characteristics: coxa of anterior gonopods long and subtriangular; mesal sternal process of anterior gonopods pentagonal; prefemoral endite of posterior gonopods coronoid, distal end rounded, with mesal margin lacking notch; telopodite of posterior gonopods more than 2× longer than prefemoral endite; lateral flange of cyphopods with 4 serrations.

Material examined. *Holotype*. KUZ Z4329 (Fig. 1B–D), male, Mt. Omotodake (24.41671°N, 124.19145°E), Ishigaki Island, Yaeyama Islands, Ryukyu Islands, Japan, 13 October 2020, col. Naoto Sawada (NS).

Paratypes. Four specimens from Ishigaki Island: KUZ Z4328, male, near the type locality (24.41608°N, 124.19150°E), 3 June 2019, col. Yuta Fujimori; KUZ Z4331–Z4333, three females, same data as for holotype. Six specimens from Iriomote Island, Yaeyama Islands, Japan: KUZ Z4330, female, Mt. Tedo (24.37084°N, 123.82051°E), 21 October 2020, col. Minoru Anzai; KUZ Z4334, Z4335, Z4338, three males, and KUZ Z4336, female, near Mariudo Waterfall (24.36030°N, 123.80045°E), 21 April 2022, col. NS; KUZ Z4337, female, near Yutsun Waterfall (24.36721°N, 123.88435°E), 20 April 2022, col. NS.

Description. Adult males: 63.1–74.7 mm long, vertical diameter of largest body ring 5.9–6.3 mm; body with 55–57 podous rings + telson. Adult females: 75.5–92.2 mm long, vertical diameter of largest body ring 6.48–7.52 mm; body with 55–59 podous rings + telson.

Head. Head capsule (Fig. 2A) smooth, area below antennal sockets with wrinkles. Occipital furrow reaching level of lower edge of antennal sockets. Incisura lateralis open. Labrum with 2 or 3 teeth, 5–8 supralabral setae, and 16–28 labral setae. Eye diameter ~0.75× greater than interocular space; with 7 or 8 vertical rows of ommatidia, 5 or 6 horizontal rows, and with 31–39 ommatidia per eye forming suboval cluster. Antennae (Fig. 2D, E) short, reaching to posterior margin of collum, when stretched back accommodated in shallow furrow composed of horizontal segment in head capsule and vertical segment in mandibular cardo and stipes. Antennomere lengths II > I > III > V > VI > IV > VII; antennomere I and II glabrous, III with some ventral setae, IV sparsely setose, V, VI and VII densely setose, and V and VI with sensilla basiconica bacilliformia latero-apically

(Fig. 3A, B); with 4 apical sensilla. Mandibular stipes broad at base, apically gradually narrowed; subanterior margin of stipes mucronate. Gnathal lobe (Fig. 2B) external tooth with 2 large and prominent cusps; inner tooth with 4 cusps; lateral tooth thin; 8 pectinate lamellae; molar plate with 15 transverse furrows. Gnathochilarium (Fig. 2C) typically spirobolidan; each stipes with 3 apical setae; each lamella lingualis with 2 setae, one behind the other; basal part of mentum transversely wrinkled; basal part of stipes longitudinally wrinkled.

Collum. Surface smooth, with marginal furrow along lateral part of anterior margin; lateral lobes narrowly rounded, not extending as far ventrad as ventral margin of body ring 2 (Fig. 4A).

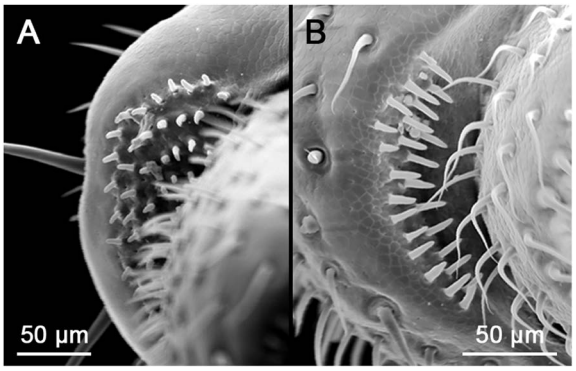

Fig. 3. *Spirobolus akamma* sp. nov., paratype female (KUZ Z4332). A, Antennomere V of left antenna, latero-apical view, showing sensilla basiconica bacilliformia; B, antennomere VI of left antenna, latero-apical view, showing sensilla basiconica bacilliformia.

Body rings. Surface very smooth, parallel-sided in dorsal view (Fig. 1B, C). Prozona smooth. 'Tergo-pleural' suture visible on pro- and mesozona; mesozona ventrally with fine oblique striae, dorsally punctate; metazoa ventrally with fine longitudinal striae. 'Pleural' parts of rings with fine oblique striae. Sterna transversely striate. Pleurotergal tips of body ring 2 (Fig. 4B) gaping ventrally, not connected to sternite; inner outline of pleurotergal tips of female body ring 2 viewed anteriorly nearly straight (upper part slightly convex, lower part concave slightly), with apex of pleural flange subpointed; pleurotergal tips of male body ring 7 fused ventrally. Ozopores present from body ring 6, situated in mesozona, ~1/4 pore diameter in front of metazoa (Fig. 4A).

Telson. Entirely smooth; preanal ring tapering, not exceeding anal valves (Fig. 4C). Anal valves impressed submarginally; margins slightly protruding, liplike. Subanal scale broadly triangular (Fig. 4D).

Legs. Midbody leg length 76% of body diameter in holotype male (leg-pair 15), 76% of body diameter in paratype female (KUZ Z4332: leg-pair 15). Prefemur basally constricted, femur longer than other podomeres (Fig. 4H). Postgenital legs unmodified, with few ventral setae (e.g., 0-1, 0, 0-1, 0, 0-1, 1-2; leg-pairs 10, 15 and 20). Adhesive pads absent. Claw slender, ~1/3× longer than tarsus. First and second legs (Fig. 4E, F) modified, coxae fused to sternites and greatly elongated. Coxae of male legs 3–7 with short rounded processes (Fig. 4G).

Anterior gonopods. Mesal sternal process (mp) pentagonal, not reaching as far as coxal tip (Fig. 5A, B). Coxa (co) long, subtriangular, apically gradually narrowed, rounded, with pronounced projection beyond sternal process (Fig. 5A, B). Telopodite (tea) apically far overreaching coxa (Fig. 5C, D); apex of telopodite hooklike, bending laterally (Fig.

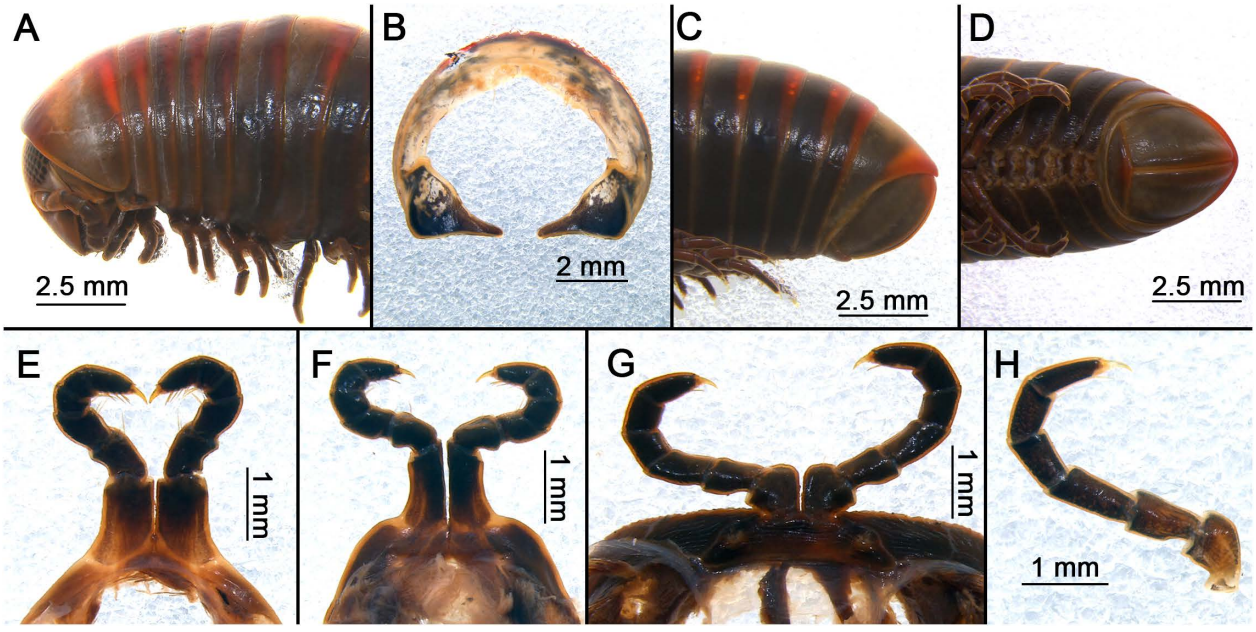

Fig. 4. *Spirobolus akamma* sp. nov., paratype male (KUZ Z4328; A, E–G), paratype female (KUZ Z4332; B), and holotype male (KUZ Z4329; C, D, H). A, Head, collum and body rings 2–7, lateral view; B, body ring 2, anterior view; C, caudal end with porous rings + telson, lateral view (terminal four leg pairs removed); D, telson, ventral view (terminal four leg pairs removed); E, 1st leg pair, anterior view; F, 2nd leg pair, posterior view; G, 3rd leg pair, anterior view; H, left leg of 15th leg pair, anterior view.

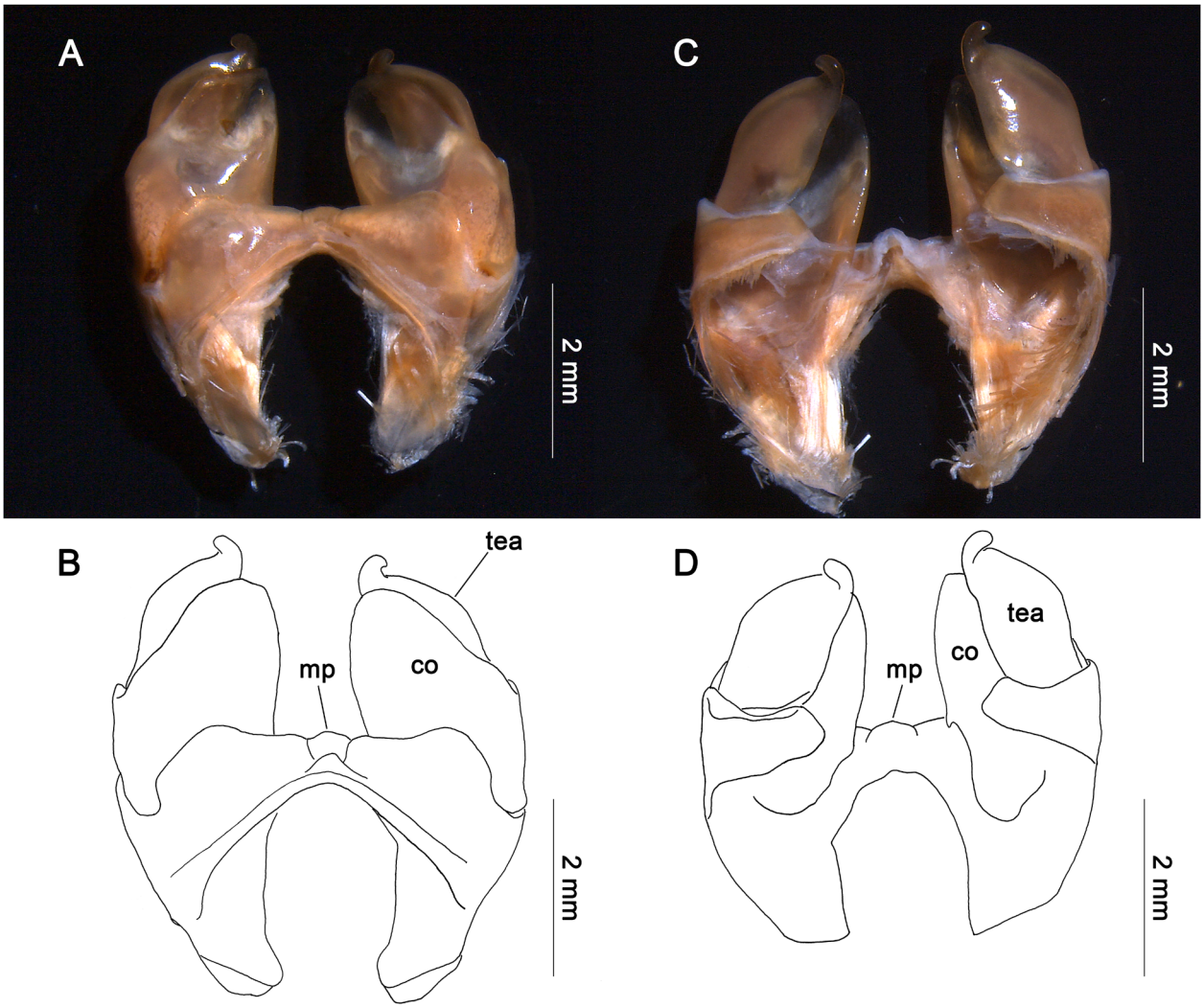

Fig. 5. *Spirobolus akamma* sp. nov., holotype male (KUZ Z4329), anterior gonopods. A, B, Anterior view; C, D, posterior view. Abbreviations: co, coxa of anterior gonopod; mp, mesal sternal process; tea, telopodite of anterior gonopod.

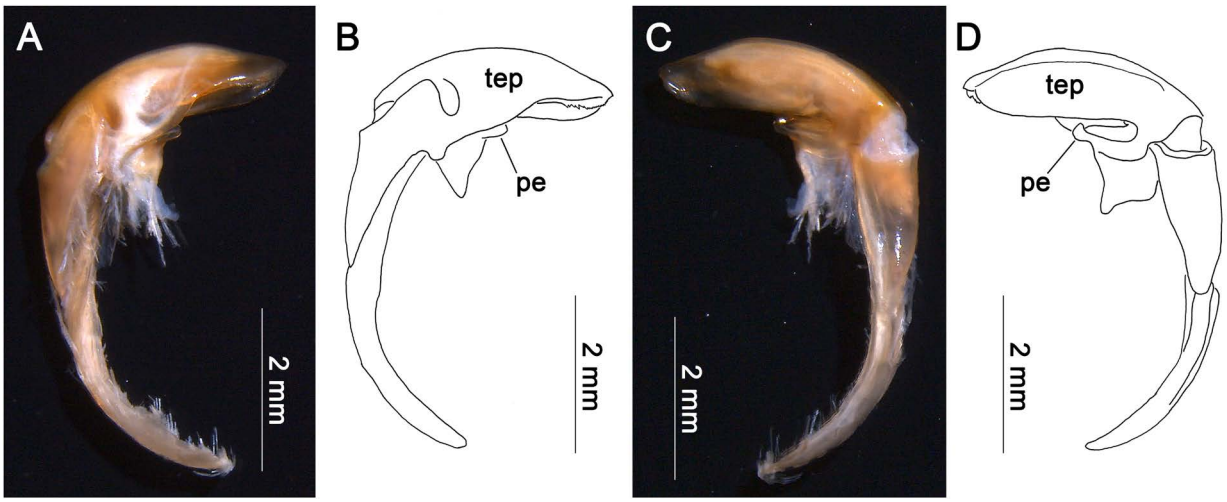

Fig. 6. *Spirobolus akamma* sp. nov., holotype male (KUZ Z4329), left posterior gonopod. A, B, Anterior view; C, D, posterior view. Abbreviations: pe, prefemoral endite; tep, telopodite of posterior gonopod.

5A–D).

Posterior gonopods. Telopodite (tep) slender, more than 2× longer than prefemoral endite (pe) (Fig. 6A–D); inner side of apex slightly concave, with or without tiny serrations (Figs 6B, 7); outer side of apex slightly swollen; outer margin of telopodite with longitudinal groove (Fig. 6D); prefemoral endite coronoid, with rounded distal end (Fig. 6D).

Cyphopods. Cyphopods broad distally (Fig. 8A, C); distal-lobe cephalic face without longitudinal groove (Fig. 8A). Lateral flange (lf) narrow, with 4 serrations; 1st serration as large as 2nd at midpoint of flange; 4th serration at proximal end of flange smallest (Fig. 8C). Valves (av and pv) prominent, of equal size (Fig. 8B).

Coloration. In life, both anterior and posterior margins of collum and dorsoposterior margin of body rings 2 to preanal ring reddish, with remainder of body rings blackish (Fig. 1A). Reddish color faded in ethanol.

Etymology. The specific name *akamma* is derived from the Yaeyama folk tale "赤馬" (Akamma means "red horse" and is the name of the horse beloved by the protagonist), and thus is treated as indeclinable.

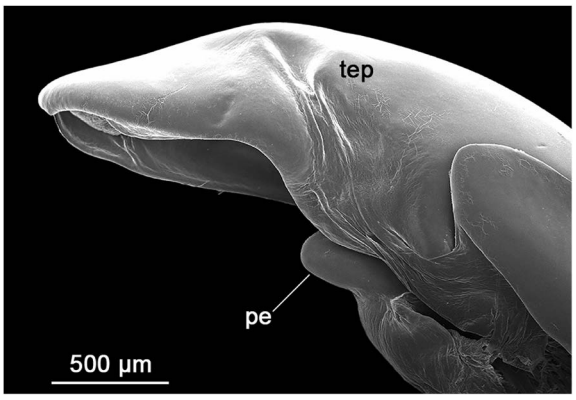

Fig. 7. *Spirobolus akamma* sp. nov., holotype male (KUZ Z4329), apical part of right posterior gonopod, anterior view. Abbreviations: pe, prefemoral endite; tep, telopodite of posterior gonopod.

DNA sequences and genetic distances. In total, seven sequences were obtained: paratype male (KUZ Z4328) from Ishigaki Island, three sequences, 28S (531 bp; INSD accession number LC727543), COI (658 bp; LC727547) and 16S (431 bp; LC727545); paratype female (KUZ Z4332) from Ishigaki, one sequence, COI (658 bp; LC727549); and paratype female (KUZ Z4330) from Iriomote Island, three sequences, 28S (531 bp; LC727544), COI (658 bp; LC727548) and 16S (431 bp; LC727546).

The paratype male 28S sequence from Ishigaki and paratype female 28S sequence from Iriomote were identical; their 16S sequences revealed 4/431 (0.9%) base pairs to be polymorphic.

The COI uncorrected *p*-distance between *S. akamma* sp. nov. and *S. bungii* was 12.8–13.4%, with the distance between *S. akamma* sp. nov. and *Spirobolus* sp. 11.7–12.7%. The COI divergence between *S. bungii* and *Spirobolus* sp. was 4.1%. Additionally, the COI genetic distance of our *S. akamma* sp. nov. specimens was 0.2–0.9%. The low genetic divergence corroborates the taxonomic conclusion that *Spirobolus* populations on Ishigaki and Iriomote islands are conspecific.

Distribution and habitat. *Spirobolus akamma* sp. nov. occurs on Ishigaki and Iriomote islands in Yaeyama Islands; this species has been also recorded from Kohama Island, a small islet located between Ishigaki and Iriomote islands (Chigira and Tanaka 2004). This species has been reported from terrestrial and arboreal habitats (Ikehara and Shimojana 1975; Yokotsuka 2002; Shinohara et al. 2015), and most of our specimens were also collected from arboreal habitats.

Remarks. The new species clearly belongs to the genus *Spirobolus* because it possesses the following diagnostic generic characteristics (Keeton 1960; Hsu 2008): boat-shaped posterior gonopods; a short prefemoral endite of the posterior gonopods, being neither subrectangular nor as long as the telopodite of the posterior gonopods; and with thick cyphopods, with teeth on the lateral flange. A BLAST search (Altschul et al. 1990) of partial COI sequences of *S. akamma* sp. nov. (LC727547–LC727549)

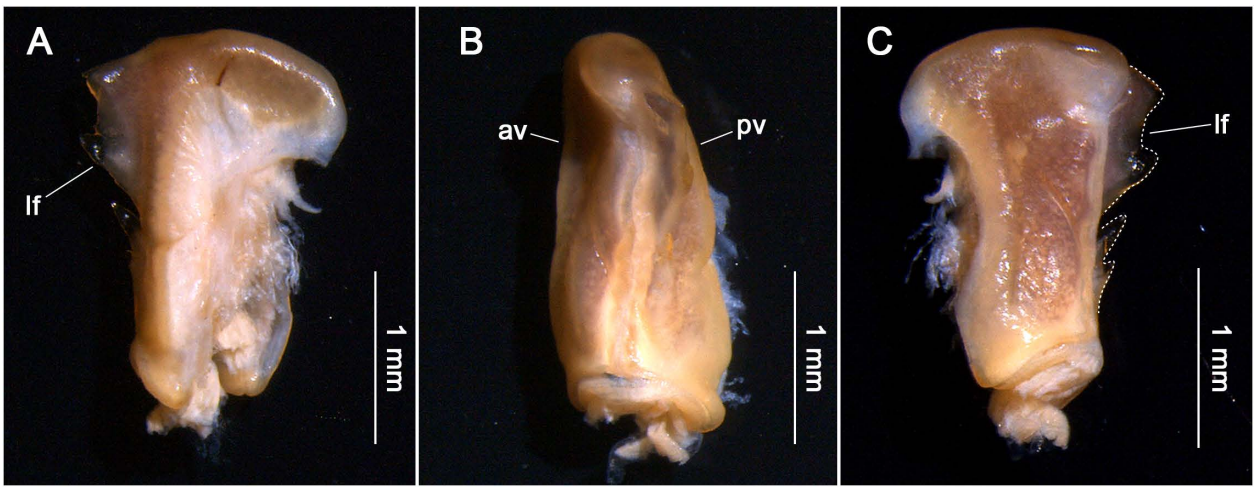

Fig. 8. *Spirobolus akamma* sp. nov., paratype female (KUZ Z4332), left cyphopod. A, Anterior view; B, lateral view; C, posterior view, dashed lines indicate the lateral margins of serrations. Abbreviations: av, anterior valve; lf, lateral flange; pv, posterior valve.

based on BLASTN 2.13.0+ (Zhang et al. 2000) at the NCBI website (https://blast.ncbi.nlm.nih.gov/) revealed them to be mostly identical (87.1–87.7%; with 98% query coverage) to the sequence from the complete mitogenome of *S. bungii* (NC_056899 = MT767838). BLAST results preliminarily corroborated our conclusion that *S. akamma* sp. nov. is a member of *Spirobolus*.

Spirobolus akamma sp. nov. may be most morphologically similar to *S.* "lienhuachihus", from Lienhuachih, central Taiwan, but it differs in possessing a pentagonal mesal sternal process of the anterior gonopods, and a lateral flange on the cyphopods with 4 serrations [*S.* "lienhuachihus" has a concave mesal sternal process of the anterior gonopods, and cyphopods with a lateral flange with 5–7 serrations (Hsu 2008)].

Although the new species shares most characteristics of the posterior gonopods with *S. grahami* Keeton, 1960, which is endemic to Sichuan and Guizhou in southwest China, the former is distinguishable from the latter by having the telopodite of the posterior gonopods more than 2× longer than the prefemoral endite of the posterior gonopods [in *S. grahami*, the telopodite is less than 2× the length of the prefemoral endite (Keeton 1960)]. While *S. akamma* sp. nov. and *S. walkeri* Pocock, 1895 share general features of the cyphopods, the new species differs from it in the number of serrations of lateral flange of cyphopods (4 in *S. akamma* sp. nov. vs. 3 in *S. walkeri*; Keeton 1960). The distribution of *S. f.* "semiflavus" includes the northeastern part of Taiwan, and is thus most geographically close to *S. akamma* sp. nov. (Hsu 2008). However, *S. f.* "semiflavus" is unequivocally distinguishable from *S. akamma* sp. nov. by gonopodal and cyphopodal features.

The morphological features of *S. akamma* sp. nov. coincide with the Takano's (1989) description of *Spirobolus* sp. from Yaeyama Islands. In anterior gonopod morphology, *S. akamma* sp. nov. is also similar to "*Polyconoceras* sp." from the Yaeyama Islands as described by Omine (1965a). We posit that these previously reported "Yaeyama-maruyasude" are conspecific with *S. akamma* sp. nov.

Acknowledgments

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